Evaluating the Impact of *Rhinocyllus conicus* on *Carduus nutans* in New Zealand

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*Rhinocyllus conicus* (nodding thistle receptacle weevil) has reduced densities of *Carduus* species in North America, but has had little apparent effect on *Carduus nutans ssp. nutans* (nodding thistle) in New Zealand since its introduction in 1972. Research since 1984 at sites at Argyll (Hawkes Bay, North Island) and Feready (Canterbury, South Island) measured the impact of *Rhinocyllus*. Seed losses to *Rhinocyllus* at Argyll stabilized at around 40-50% within three years of the release of *Rhinocyllus*, while in Canterbury *Rhinocyllus* destroyed less than 9% of seeds. Losses of seed to *Rhinocyllus* mainly occurred early in the flowering season (November and December), but surviving seed was still set at least a month before germination in the field. There were only small differences in germinability (89-94%) of seed collected at different dates through the 1988-89 season at Feready. Survival from germination to flowering was density-dependent at Argyll in 1984 and 1985. The measured density-dependence would ameliorate a 40% decrease in seedling densities to about a 13% reduction in flowering plant density, which would probably be scarcely detectable. Therefore *Rhinocyllus* is providing little control of *C. nutans* in New Zealand, despite destroying as much seed as it does in North America. Recent introductions of two more insects in New Zealand may provide better control.

**Introduction**

*Carduus nutans* L. (Asteraceae), nodding thistle, is a Eurasian plant which is now naturalized in North and South America, Australia and New Zealand. However, the genus *Carduus* is taxonomically difficult. The Australian and New Zealand populations are predominantly or completely *C. nutans ssp. nutans* (Webb et al. 1988, Popay and Medd 1990). While the North American material is sometimes described as *C. nutans* in the broad sense, the commonest species there is *C. thistlei* (McCarty and Lamp 1982, Popay and Medd 1990).

In North America and Australasia *Carduus* species have become economically important weeds of pasture and rangelands. Biological control was attempted in Canada with the release in 1968 of *Rhinocyllus conicus* (Froelich) (Coleoptera: Curculionidae), the nodding thistle receptacle weevil, collected in France (Harris 1984, Jessep 1989). The larvae of *Rhinocyllus* feed in the receptacle of the inflorescence, and so prevent seeds from forming. Each larva destroys about 28 seeds (Popay et al. 1984, Kelly et al. 1990).

*Rhinocyllus* has been very effective in Saskatchewan in Canada, where by 1980 thistle densities were markedly reduced (Harris 1984). The insect was also liberated in the USA and has been credited with reducing thistle populations in Virginia by 95% within 6 yrs (Kok and Surles 1975, Surles and Kok 1978).

Releases of *Rhinocyllus* from the Canadian populations were made in both New Zealand and Australia. In New Zealand the insect was imported in 1972, and is now established throughout the range of *C. nutans* (Jessep 1989). The effect of *Rhinocyllus* on seed production has been recorded at several sites in New Zealand. At Argyll in Hawkes Bay,
reductions in seed output caused by *Rhinocyllus* reached a peak of 49% only 4 yrs after the insect was released in that area (Kelly et al. 1990), and seem to have settled down to around 40% losses (Kelly and Wood 1991). Further south, in Canterbury, <9% of seed was lost over 3 sites and 2 yrs, apparently because of worse synchrony between the insect and plant life cycle and lower densities of *Rhinocyllus* (Kelly and Wood 1991).

However, despite the losses at Argyll of 40% of the seed crop since 1983-4, the thistle seems to be as common there now as it ever was (Kelly and McCallum 1990, Kelly and Wood 1991). There certainly has not been the kind of dramatic decrease recorded in Saskatchewan and Virginia. If large reductions in the seed crop do not lead to corresponding decreases in flowering plant density, density-dependent mortality later in the life cycle may be compensating for the reduced density of seeds. Therefore it is necessary to examine the fates of seeds and consider the whole life cycle of *C. nutans*. In an earlier paper we found no evidence for density-dependent mortality in the survival of seed sown at different densities, but suggested that survival of seedlings through the rosette stage may well be density-dependent (Kelly and McCallum 1990).

As well as the average levels of seed lost over the whole season, several other factors need to be considered in assessing the effect of *Rhinocyllus*. The pattern of seed loss within each season is relatively predictable. Early in summer (November and December in New Zealand), high *Rhinocyllus* densities ensure that almost 100% of seeds are destroyed; during the peak of flowering in January, the losses fall to 30% or less because the increase in inflorescence density combines with a decrease in the number of insect larvae/unit area; and at the end of the season (February-April) losses may again exceed 50% because very few flowers are set at this time. This pattern is found in both New Zealand (Popay et al. 1984, Kelly et al. 1990, Kelly and McCallum 1990, Kelly and Wood 1991) and North America (Rees 1977, Surles and Kok 1978). Therefore, as well as reducing the total number of seeds set, *Rhinocyllus* delays the timing of seed set. If earlier-ripened seeds were able to germinate sooner, had higher viability, or differed in other ways from later-ripened seed, then *Rhinocyllus* might have an effect beyond the simple mean levels of seed loss.

Therefore the aims of this paper were: (1) to see if the predominantly early-season losses of seed caused by *Rhinocyllus* had any effect on the germination time or mean viability of surviving seeds; and (2) to quantify any possible density-dependence at the seeding and rosette stages, and determine if this was strong enough to compensate for observed levels of seed loss.

**Methods and Materials**

**Sites**

The work reported here comes from two sites in the North Island and one in the South Island. All had naturally occurring *C. nutans* populations in permanent pasture dominated by ryegrass (*Lolium perenne* L.; Poaceae) and clovers (*Trifolium* spp.; Fabaceae). The main North Island site was at Argyll (39°54'S, 176°34'E), 13 km N of Waipukurau in central Hawkes Bay. The area is normally warm and dry over summer, so that the perennial grasses often die back, exposing bare ground. The study site was the same paddock used for other work on thistle biology (Popay et al. 1984, Kelly 1988, Harrington 1989, Kelly et al. 1990). A second North Island site was established at Midland (40°14'S, 175°43'E), 18 km northeast of Palmerston North in the Manawatu. This area is on the west of the main mountain ranges and has slightly cooler and wetter summers than Hawkes Bay; as a consequence, *C. nutans* is not such a serious weed there (Kelly and McCallum 1990). The South Island site was at Fereday (43°49'S, 172°10'E; the F, site of Kelly and Wood 1991), 50 km southwest of Christchurch. The Canterbury plains at Fereday have similar summer temperatures to Hawkes Bay but get less summer rainfall, so also tend to show drought effects on the pasture grasses.

More details of the sites and their climates are given in Kelly and McCallum (1990).

**Demography in the Field**

Germination, rosette survival and seed set were recorded in permanent plots at Argyll and
Midland. At each site 5 transects, 0.5 x 10 m, were established in July-August 1984. All thistle seedlings emerging in these transects were mapped to 1 mm every 6 wks and their fates recorded. At Argyll new germination after April 1985 was recorded in only 2 transects, and recording of new seedlings ceased completely in April 1986, but all plants recorded as seedlings were followed until they died (the last survived until June 1987). At Midland new germination was recorded in all 5 transects only till June 1985 and thence in 3 of the 5 until February 1987. For more details see Kelly (1988). The number of inflorescences on flowering C. nutans plants within the transects was recorded at each census, so the number of inflorescences ripening between censuses could be determined. The estimated mean number of seeds/inflorescence at each date was calculated from the diameter and the number of Rhinocyllus larvae in each inflorescence in samples collected through the flowering season, following the methods of Popay et al. (1984) and Kelly et al. (1990).

To test for density-dependence at the rosette stage, each 0.5 x 0.5 m quadrat of the transects at Argyll was treated as a sampling unit. The number of new C. nutans seedlings emerging in each quadrat over the whole calendar year was recorded, as was the number of those seedlings which eventually managed to set seed. Plants took up to 3 seasons to flower (Kelly and McCallum 1990). Linear and quadratic regressions were used to search for relationships between seedling density and the percentage of seedlings which set seed. Older rosettes already present in the quadrats were not considered in this analysis. In 1984, 1,266 seedlings were recorded in the 80 quadrats which had at least 1 C. nutans seedling. In 1985, 4,201 seedlings were found in 36 quadrats.

The mean seed weight and seed germinability was determined through the course of the 1988-9 season at Fereday in Canterbury. Inflorescences were collected on four dates from December 1988 to March 1989, and ripe, well-filled seeds were extracted. Samples of 20 seeds were weighed fresh and then groups of 50 seeds were placed on filter paper in Petri dishes 16 d after collection and watered with distilled water. The dishes were placed in growth cabinets at temperatures between 25/15 and 15/5 °C with 12 hr illumination. Since there was little difference between temperature regimes in the final percentage germination after at least 31 d (McCallum 1989) pooled results are given here based on 60-80 replicates/collection date for seed weight and 36-48 for germinability.

Results and Discussion

Timing of Seed Set and Germination

Germination at all sites was overwhelmingly in autumn, as has been shown before (Popay and Kelly 1986, Popay et al. 1987, Kelly and McCallum 1990). The exact timing of germination depends on when the first major rainfall occurs after the end of summer. Two extremes are shown in Fig. 1, where in 1985 germination was relatively early at Argyll (February-March) and relatively late at Midland (May-June). In both cases, germination was well after seed set was completed; seed set is shown for Argyll in 1984-85. Because very little seed escapes damage by Rhinocyllus before mid-December seed set was delayed, as well as reduced in density. However there is rarely much germination before late February in any year (Popay and Kelly 1986) and early germinating seedlings suffer high mortality (Kelly and McCallum 1990) due to desiccation. Therefore it seems that the altered timing of seed set is of little consequence. Even the later seeds which escape Rhinocyllus are set well before germination occurs in the field.

Seed Germinability Through the Season

The weights and viability of seeds from Fereday 1 varied significantly through the 1988-9 season (Table 1), but not by much. In that season 92% of seeds were set in inflorescences which had no Rhinocyllus larvae present (Kelly et al. 1990), so the pattern is not modified by any possible effects of larval feeding. The germinability of seeds was uniformly high (>88%), so there was no evidence that the early seeds (which are disproportionately affected by Rhinocyllus when it is at high densities) were of higher quality than
those set later in the season. Those set at the peak of flowering in January had very high germinability. The overall levels of germinability agree with data for *C. nutans* ssp. *nutans* in Australasia (Popay and Medd 1990) and for related *Carduus* taxa in North America (Surles and Kok 1978, McCarty and Lamp 1982, Harris 1984).

![Graph showing cumulative germination percentages over time]

**Figure 1.** The relative timing of seed set for *Carduus nutans* at Argyll in 1984-5, and germination in the field in 1985 at Argyll and Midland. Seed set is shown both for the actual case of *Rhinocyllus* present (+R), and the hypothetical timing that would have resulted if *Rhinocyllus* had not been present (-R).

**Table 1.** Mean weight and germinability (on filter paper 16 d after collection) of *Carduus nutans* seeds collected through the 1988-9 season at Fereday 1, Canterbury. Means with the same superscript are not significantly different according to Duncan's multiple range test.

<table>
<thead>
<tr>
<th>Collection Date</th>
<th>Mean Weight (mg)</th>
<th>Germinability (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>22.xii.88</td>
<td>2.41^c</td>
<td>88.9^b</td>
</tr>
<tr>
<td>6.i.89</td>
<td>3.05^a</td>
<td>94.0^a</td>
</tr>
<tr>
<td>7.i.89</td>
<td>2.96^a</td>
<td>89.6^b</td>
</tr>
<tr>
<td>8.iii.89</td>
<td>2.73^b</td>
<td>93.1^a</td>
</tr>
</tbody>
</table>

*Density-Dependent Rosette Survival*

*C. nutans* seedling densities shown for Argyll in 1984 were lower and survival to flowering higher than in 1985, because the late start to recording in 1984 meant that some early seedling losses would have been missed. In both years there was a significant relationship between seedling density and the probability of flowering (Fig. 2). Curiously, in both years a quadratic regression gave the best fit. We interpret the low survival at high densities as indicating density-dependent survival, as would be expected from seedlings germinating at up to 334 in 0.25 m$^2$ (>1300 m$^{-2}$). The low survival at low densities may reflect the fact that some quadrats, perhaps those with longer grass cover, were much less suitable for *C. nutans*. Either the failure of *C. nutans* to set seed there in the past reduced the seed supply, since *C. nutans* seeds are not well dispersed (Kelly et al. 1988), or the longer turf suppressed germination (Phung and Popay 1981). In either case few seedlings germinate, producing low seedling densities, and they also have almost no chance of surviving to flower.

Since rosette survival is density-dependent, we need to consider what the effect would be of an overall reduction in seed density of say 40%, as observed at Argyll since 1983. We must assume that there is no density-dependent effect on seed predation rates by birds (cf. McCallum and Kelly 1990). Germination is density-independent as shown by Kelly and McCallum (1990). If seedling densities are therefore also reduced by 40%, clearly at high densities survival will increase as density is reduced. If the observed low survival at low densities is due to these quadrats being in unfavourable patches, then when medium density (favourable) quadrats have their density reduced, they would not be expected to show lower survival; rather survival should increase in line with the underlying relaxation of density-dependent mortality. To estimate this effect, we excluded the low-density quadrats from the analysis (<20 seedlings/quadrat in 1984 and <100 in 1985) and fitted a linear regression to the remaining data to estimate the density-dependent effect (giving y = 11.8–0.146x and y = 3.16–0.0105x, respectively). Then, for each initial density, the estimated percent survival to flowering was calculated both before and after a 40% reduction in density. The magnitude of the increase in survival depends on the initial
Figure 2. Survival of *Carduus nutans* seedlings at Argyll from germination to flowering (%) in relation to initial density (seedlings emerging per 50 x 50 cm quadrat in that calendar year) in 1984 and 1985. (a) 1984, n = 80 quadrats, \( y = -0.633 + 0.466x - 0.00659x^2 \), \( R^2 = 0.174 \), \( P < 0.001 \); (b) 1985, \( n = 36 \), \( y = 0.0191x - 6.26 \times 10^{-4}x^2 \), \( R^2 = 0.447 \), \( P < 0.01 \).

density (Fig. 3). At high densities, where survival was initially very low (e.g. 0.1%), a decrease in density which increased survival to 1% would provide a 10-fold increase in flowering plants, whereas at lower densities survival was already relatively high and survival may increase by only a factor of 1.10 or less, as shown in Fig. 3. For relaxed density-dependence to compensate for 40% seed losses, an overall increase in survival of 67% is needed (100/60). The overall mean increase in survival depends on the exact frequency distribution of seedling densities, but at the median densities observed in 1984 and 1985, the increases in survival would have been 30.4 and 44.9% respectively. This would have produced reductions in flowering plant density of 22 and 13% respectively, after starting with 40% fewer seedlings. Since the late start of

Figure 3. The increase in survival to flowering as a function of initial seedling density, if seedling densities were reduced by 40%, for *Carduus nutans* at Argyll. The estimated survival at the lower density is divided by the original survival to give the change as a ratio; a linear relationship between density and survival is assumed (see text). Actual median seedling densities for each year, and the 67% increase in survival needed to fully compensate for a 40% reduction in seedling density, are shown.

censuses in 1984 meant that some early (density-dependent?) mortality was not recorded, those data may underestimate the strength of the density-dependent effect, so the 1985 data may be the better estimate of the overall impact of *Rhinocyllus conicus* on *C. nutans*. Given the wide year-to-year fluctuations in thistle numbers as a result of climatic variability, a reduction in density of 10-15% might not be evident to the casual observer, or easy to prove statistically, and would certainly not be regarded as successful biological control.

Of course, since *C. nutans* has a large seed bank which may persist for more than 13 yrs under pasture (Popay *et al.* 1987), it is possible
that it would take some years before any reduction in thistle density caused by reduced seed production would become evident. The soil seed bank might have to be depleted before numbers of flowering plants were reduced. However, Kok and Surles (1975) showed that thistle densities in Virginia decreased within 6 yrs of the introduction of *Rhinocyllus*. In any case, the analysis above suggests that the number of flowering plants at Argyll will not change very much, because density-dependent mortality is compensating for the reduced seed output there.

**Regulation of Thistle Populations in New Zealand and North America**

Sheppard *et al.* (1990) pointed out that the success of non-predated thistle seeds depends on 3 major factors: climate, availability of microsites for germination, and seed longevity. The interaction of those factors with changes in seed crop size determines the number of flowering plants. To those three factors we must add density-dependent rosette mortality (which was not found at their very dry, open site in France but may often be important in climatically more favourable sites in Australasia and North America), and competition between rosettes and pasture perennials. It should also be remembered that the microsite limitation shown by Sheppard *et al.* (1990) is a very rigid form of density-dependent establishment.

This leads to the question of why *Rhinocyllus* has been demonstrably so effective at reducing thistle densities in Saskatchewan and Virginia while it seems to be ineffective in New Zealand. The first possibility to consider is the taxonomic differences mentioned above; the majority of North American plants referred to as *C. nutans* in a broad sense are *C. thoermeri*, while in New Zealand we have almost exclusively *C. nutans* ssp. *nutans*. *Rhinocyllus* seems to have races, each of which is specialized on a particular host species of thistle (Harris 1984), so perhaps the New Zealand insects (which were imported from Canada) are less well adapted to *C. nutans* ssp. *nutans* than to *C. thoermeri*. This may account for the very low losses of seed in Canterbury (Kelly and Wood 1991). However, this explanation is unconvincing for the Argyll site.

Seed losses at this site have been 40-50% since 1983, which is similar to the levels of loss reported for North American sites where biological control has been effective. Harris (1984) estimated total seed losses in Saskatchewan to be only about 50%, using a figure of 25 seeds destroyed/larva (cf. 27-29 in New Zealand: Popay *et al.* 1984, Kelly *et al.* 1990). Surles and Kok (1976) reported losses of 35 and 36% in 2 consecutive yrs which preceded a 95% drop in thistle density. While McCarty and Lamp (1982) reported a 78% reduction in seed output, this figure was based on comparisons of infested and uninfested sites and so may be unreliable due to site differences. Therefore, the reported seed losses at successful North American sites (35-50%) are no higher than seen at Argyll, which gives little support to the idea that the race of *Rhinocyllus* in New Zealand is poorly adapted to local thistle populations.

Therefore the explanation for the differences between North America and New Zealand might lie in interactions between the suite of factors listed above. In favourable sites, density-dependent factors may largely compensate for seed losses. However, sometimes positive feedback loops are triggered which amplify the small reductions in density into large decreases. For example, on flat prairies in Saskatchewan, rosette survival over winter is higher where snow collects to provide insulation. High densities of dead thistle flowering stalks help to trap snow. If flowering density decreases, less snow may be trapped, and rosette survival over winter may suddenly decrease, further reducing flowering density the next year (Harris 1984). In another example, when dense flowering thistles die off, the bare ground exposed provides a suitable site for the next crop of seedlings to germinate. If flowering density is reduced a little, perennial grasses may be able to persist among the flowering thistles, and these may then expand before germination and progressively reduce the available space for seedlings (Harris 1984). The latter example may account for the reduced thistle density in Virginia. These non-linear responses are harder to predict than the linear effects of density-dependence, and unfortunately they do not seem to be operating in New Zealand.
However, this is not to say that *Rhinocyllus* is of no value in New Zealand. By reducing the seed output at Argyll by 40% it must be reducing dispersal, making containment of populations easier. *Rhinocyllus* may also set the stage for another agent (in combination with *Rhinocyllus*) to provide effective biological control. Since this study was begun in 1984, 2 more insects have been released on *C. nutans* in New Zealand: *Trichosirocalus horridus* (Panzier) (Coleoptera: Curculionidae), the crown root weevil (Jessep 1989) and another seed feeding gall fly (Jessep, C.T., personal communication, 1991). We can only hope that 1 of these new insects is the straw that breaks the camel's back.

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**References**


