White butterfly (*Pieris rapae*) and the white rust *Albugo candida* on Cook's scurvy grass (*Lepidium oleraceum*)

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Abstract: Once widespread, Cook's scurvy grass (or nau, *Lepidium oleraceum*) is now confined to a few offshore populations. Classed as nationally endangered by the New Zealand Department of Conservation, populations of Cook's scurvy grass are threatened by a number of factors, including introduced herbivorous insect species such as the white butterfly (*Pieris rapae*) and white rust infection caused by the oomycete *Albugo candida*. In this paper, we investigate the occurrence of white butterfly on Cook's scurvy grass and possible interactions with the white rust infection on the northernmost of the Matariki Islands in the Firth of Thames, New Zealand. We found that larger host plants were more likely to be infested with white butterfly. The occurrence of white butterfly eggs and larvae also decreased as levels of white rust increased. Twenty-eight percent of the white butterfly larvae collected and reared in the laboratory were parasitised by the braconid wasp species *Cotesia rubecula*. We also reared a hyperparasitoid belonging to the super-family Chalcidoidea from one of the parasitoid cocoons. Further studies on the trophic interactions between Cook's scurvy grass, *Albugo candida* and white butterfly and its parasitoids could improve the understanding of the threats posed by plant pathogens and insect herbivores to populations of Cook's scurvy grass, which in turn may lead to new management strategies for conservation.

Keywords: Matariki islands; oviposition; parasitoids; trophic interactions

Introduction

Although found in considerable abundance when the first Europeans arrived in New Zealand (Cooper & Cambie 1991), Cook's scurvy grass, *Lepidium oleraceum* Sparrm. ex G.Forst. (Capparales: Brassicaceae), also known as coastal cress or nau, is now restricted to a few coastal and offshore populations. It is classed as 'nationally endangered' by the Department of Conservation, New Zealand (Hitchmough et al. 2007), with several factors implicated in its decline. These factors include a decrease in quantity and quality of suitable habitat, browsing from domestic stock or possums, extinction of local populations through natural disasters or over-collecting by humans, competition with invasive plant species, and herbivory by Brassicaceae crop pests (Esler 1975; Norton et al. 1997). In addition, Cook's scurvy grass is susceptible to white rust, a disease among Brassicaceae, caused by common pathogens like the oomycete *Albugo candida* (Armstrong 2007).

One herbivore that uses Cook's scurvy grass as a host plant for its offspring is the 'small white' or white butterfly, *Pieris rapae* L. (Lepidoptera: Pieridae). The white butterfly was accidentally introduced to New Zealand in 1929/30, and rapidly extended its distribution all over New Zealand in the following 5–8 years (Muggeridge 1942). Female white butterflies lay their eggs mainly on plants of the family Brassicaceae, which offers a wide range of abundant host plants. Besides chemical measures, exotic parasitoid wasp species have been introduced to mitigate the impact of the white butterfly on Brassicaceae crops in New Zealand (Cameron & Walker 2002). An abundance of different hosts, coupled with behaviour known as the 'egg spreading syndrome'

(Root & Kareiva 1984), may have helped to establish white butterfly populations in New Zealand. Female white butterflies usually lay only one egg at a time and their directional flight pattern when searching for oviposition sites tends to result in proportionately higher egg numbers on isolated host plants compared with host plants growing in denser stands (Cromartie 1975). Root and Kareiva (1986) argue that by distributing eggs over several well-separated host plants the chance of at least some offspring surviving predation and patch extinction events is increased. The pattern of egg distribution observed for the white butterfly contrasts with some other insect species that tend to concentrate their eggs on plants growing in dense groups (Tahvanainen & Root 1972; Root 1973).

Insect herbivores are typically guided by visual and volatile cues when searching for suitable host plants (Bernays & Chapman 1994). Leaf colour and size of a host plant have been shown to be important factors in the detection process for white butterfly females (reviewed in Hern et al. 1996). In particular, the colour green, a common cue among herbivorous insects (Hern et al. 1996), seems to attract ovipositing white butterfly females (Traynier 1979). In one study, greener, well-fertilised plants were more likely to be approached by ovipositing white butterfly females than were unfertilised plants of a darker shade (Myers 1985). White butterflies also responded to total leaf area by preferentially laying eggs on plants with larger leaves (Jones 1977a; Ives 1978). It is likely that white butterflies use leaf colour and size as signals to gauge the quality of a host plant for their offspring.

Our aim was to identify factors that affect the occurrence of white butterfly eggs and larvae on Cook's scurvy grass. In particular, we examined how infection of Cook's scurvy grass

plants by *Albugo candida* may affect the presence or absence of white butterflies on plants in the study area. Infection by white rust, as the name suggests, often becomes visible because of white pustules emerging from the leaf surface that are created by the sporangia of *Albugo candida*. The white pustules may lead to a change in leaf colour and could affect host plant selection by ovipositing white butterfly females. In addition, we tested whether the size of the host plant, as well as the number of other host plants in the immediate neighbourhood, influenced the presence or absence of white butterfly life stages on the specific focal plant.

Methods

One of the remaining populations of Cook's scurvy grass is found on the northern island of the Matariki Islands group in the Firth of Thames, New Zealand (36°51.6' S, 175°24.3'E; Fig. 1). The island is privately owned by Ngāti Maru and the iwi supports the monitoring and protection of this important plant population. The island's proximity to the mainland (c. 250 m) allows for colonisation by winged insects like the white butterfly. Our survey, on the eastern part of the island where Cook's scurvy grass occurs, took place in March 2006. We examined all available (51) plants for the presence of white butterfly eggs and larvae. All white butterfly larvae encountered, as well as a number of parasitoid cocoons, were collected and placed into rearing tubes. We followed the development of both larvae and parasitoid cocoons in the laboratory at 21ºC and 70% humidity. White butterfly larvae were reared on a diet of daily fresh cabbage leaves (*Brassica oleracea* var. 'summer-cross'). Parasitoids that emerged from larvae or cocoons were identified as far as possible to species level. Parallel to our survey for the presence of white butterfly, the Department of Conservation monitored the plant population. From their monitoring, we incorporated data on the height and width of plants, and on the proportion of the plant's leaf area infected by the oomycete *Albugo candida*. The product of plant height and width was used as a measure of host plant size.
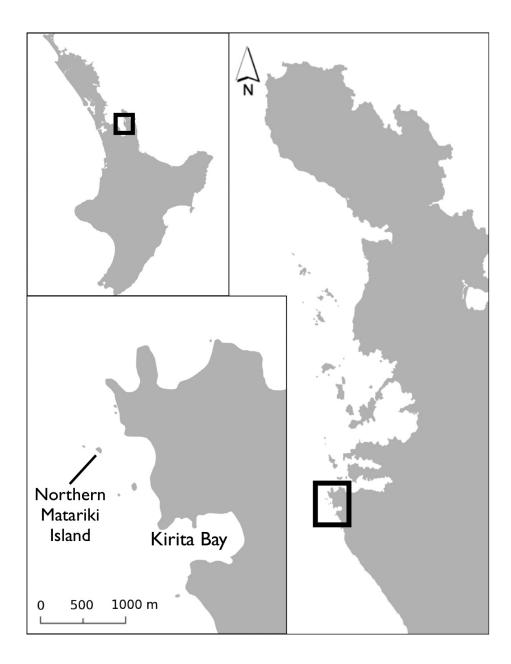

Figure 1. Location of Matariki Islands in Firth of Thames (see North Island inset) and outline of Matariki Island group; survey conducted on eastern part of Northern Matariki Island; land outline shown as high-tide water mark.

We analysed occurrence of white butterfly based on the presence or absence of eggs and larvae combined. As with eggs, the presence of larvae can be used as an indication of an oviposition event since larvae rarely leave a host plant unless the foliage available on a host plant becomes scarce (Harcourt 1961; Jones 1977b).
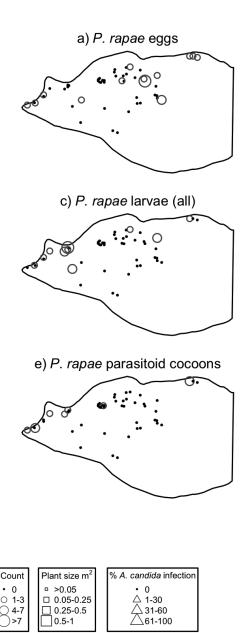
Generalised linear models were used to investigate which factors might influence the occurrence of white butterfly on Cook's scurvy grass. Host plant size, the proportion of leaf-area infection by *Albugo candida*, number of host plants within 1-m radius from focal plant (fine-scale plant density), and number of host plants within a radius of 1–6 m from focal plant (coarse-scale plant density) were the independent variables. An interaction term between plant size and infection by *Albugo candida* was also included in the full model because of a positive association between host plant size and the presence/absence of *Albugo candida* infection (GLM (logit): $\beta = 1.361$, $z = 2.006$, df = 49, $P = 0.045$).

We simplified the full model based on the sample-size-corrected Akaike Information Criterion (AIC$_c$; Akaike 1974;

Burnham & Anderson 2002) using stepwise backward deletion of model terms. All statistical models were fitted in R v. 2.9.0 using logistic regression (GLM method with binomial error distribution; Ihaka & Gentleman 1996; R Development Core Team 2009).

Owing to low sample sizes we were not able to analyse occurrence patterns of parasitoid wasps among white butterfly larvae and Cook's scurvy grass plants.

Results

A total of 51 Cook's scurvy grass plants (plant size and location shown in Fig. 2b) were examined for white butterfly eggs, larvae and parasitoid cocoons. White butterfly was present on 19 plants, represented by 28 eggs, 36 larvae, and one pupa (Fig. 2a, c). Ten out of the 36 white butterfly larvae were parasitised by the braconid wasp *Cotesia rubecula*, an introduced biocontrol agent (Fig. 2d). We also counted 14 parasitoid cocoons present on plants, of which we collected
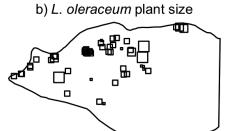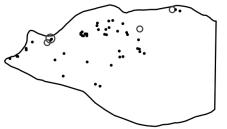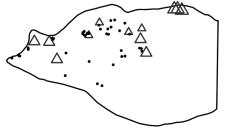

Figure 2. Distributions of (a) white butterfly (*Pieris rapae*) eggs, (b) Cook's scurvy grass (*Lepidium oleraceum*) plant sizes, (c) white butterfly larvae, (d) parasitised larvae, (e) parasitoid cocoons, as well as (f) the proportion of *Albugo candida* infection among the examined plants; symbol size relates to value range.

five (Fig. 2e). All except one of the cocoons were found on plants where white butterfly was also recorded. Of the five cocoons collected, four hatched. Three of these cocoons were identified as *Cotesia rubecula*, with an unidentified hyperparasitoid (super-family Chalcidoidea) emerging from the fourth. Thirteen of the 51 Cook's scurvy grass plants that were examined showed signs of infection by the oomycete *Albugo candida*. Of the infected plants, the percentage of leaf-area visibly affected by white rust ranged from 5% to 90% with a median of 50% (Fig. 2f).

The statistical model with the lowest AIC_c included two main effects, plant size and proportion of infection by *Albugo candida*, and their interaction (4.676 ΔAIC_c to full model; 34.7% deviance explained by final model). The results from this final model showed two main patterns. First, white butterfly eggs and larvae were more likely to be present on larger Cook's scurvy grass plants (GLM (logit): $\beta = 8.194$; $z = 2.171$; $df = 47$; $P = 0.030$). Secondly, the negative interaction term between plant size and proportion of white rust infection (GLM (logit): $\beta = -54.390$; $z = -1.930$; $df = 47$; $P = 0.054$) indicates that the increasing level of *Albugo candida* infection typically found on large plants may reduce the positive effect of host plant size on occurrence of white butterfly and could make it less likely for the butterfly to be found on large plants when they show a high degree of infection by *Albugo candida* (Fig. 3). While the model gives a reasonable fit for the effect of plant size in situations with low *Albugo candida* infection (Fig. 3a), the predictions when there are high levels of the white rust infection are less robust due to the low number of plants with >10% infection and especially the absence of small plants (<0.1 m^2) with high infection rate (Fig. 3b). After allowing for the interaction term, the degree of infection by *Albugo candida* was of marginal significance in the final model as a main effect (GLM (logit): $\beta = 25.896$; $z = 1.821$; $df = 47$; $P = 0.069$). The density of surrounding plants (at both fine and coarse scales) did not appear to influence the occurrence of the white butterfly, as their model terms were dropped during stepwise reduction of the full model.

Discussion

Our study identified the size of host plant as an important factor influencing the occurrence of white butterfly eggs and larvae on Cook's scurvy grass. Similarly, Ives (1978) showed that bigger plants were more readily accepted by female butterflies for oviposition than were smaller plants. The white rust *Albugo candida*, however, was also more prevalent on larger Cook's scurvy grass plants. These two factors interacted in their influence on the white butterfly such that large plants that were heavily infected by the fungus tended not to host as many eggs or larvae of the white butterfly. Larger plants are expected to be older, in which case the infection may have had more time to spread to different parts of the plant.

It seems likely that infection by *Albugo candida*, especially when a large proportion of the plant's leaf area is affected, may deter female white butterflies from ovipositing. A possible mechanism could be the change in foliage coloration caused by the reduction in chlorophyl content in plant tissue infected by *Albugo candida* (Tang et al. 1996). Indirect three-way interactions between host plant, pathogen and herbivore are not uncommon (Hatcher 1995), and previous studies have shown that plant quality is likely to be an important factor in the detection and acceptance of host plants by white butterfly females. Langan et al. (2001) and Chen et al. (2004) showed that plants with higher physiological activity and better nutrient levels were more likely to receive eggs by female butterflies of the genus *Pieris*. The 'appropriate/inappropriate landings theory' formulated by Finch and Collier (2000) identifies a three-link chain for selection of host plants: plant volatile stimuli – visual stimuli – non-volatile plant chemicals. Final acceptance of a potential host plant is based on success in all three evaluation steps. Those host plants that are in a better physiological and morphological state could therefore be more attractive in all three steps than plants that are suffering from, for example, nutrient deficiency or water shortage.

The acceptability of a potential host plant can also be affected by the occurrence of conspecific herbivores already
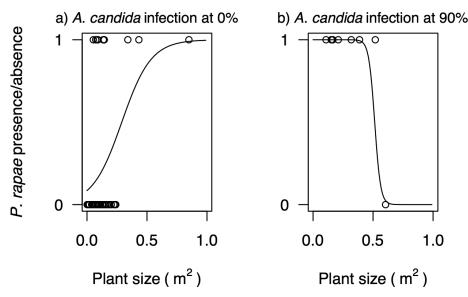

Figure 3. Sigmoidal lines are a graphical representation of the logistic regression model predicting probability of white butterfly (*Pieris rapae*) occurrence based on size of host plant assuming (a) 0% and (b) 90% infection of host plant by *Albugo candida*. Open circles show the presence/absence data of white butterfly on Cook's scurvy grass (*Lepidium oleraceum*) plants with either (a) ≤10% infection by *Albugo candida*, ($n = 42$) or (b) >10% infection by *A. candida* ($n = 9$).

present in the form of previously laid eggs or larvae. Although we were not able to test for this effect, previous research by Sato et al. (1999) has shown that white butterfly females avoid potential host plants with higher loads of conspecifics, thus potentially reducing intraspecific competition for food resources and risk of parasitism. This avoidance behaviour could also reduce the risk of newly laid eggs being eaten by older conspecific larvae (Gilbert 1984).

We did not detect patterns relating the occurrence of white butterfly to the neighbourhood density of host plants. However, observations by other researchers examining the number of white butterfly eggs per plant in settings of different plant density showed that host plants that grew in more isolated stands received a comparatively higher number of eggs per plant than aggregated plants (Jones 1977a; Root & Kareiva 1984; Yamamura 1999). While these experiments mainly dealt with colonisation processes on empty host plant patches, the number of eggs and larvae in our survey could be influenced by ongoing population processes in an occupied host plant patch, which might form different patterns over time than those expected during the initial phases of a colonisation-type experiment. One of the factors that might influence white butterfly population dynamics is predators and parasitoid wasps (e.g. Van Driesche 2008). Our survey provides evidence of further trophic levels affecting the white butterfly population in the form of the parasitoid wasp *Cotesia rubecula* and its hyperparasitoid. Hyperparasitism of *Cotesia rubecula* has previously been recorded by Cameron and Walker (2002) in an agricultural context in New Zealand, so the presence of a hyperparasitoid on the Matariki Islands (c. 250 m offshore from mainland) is not surprising. Aerial colonisation is known for a number of invertebrate species in aquatic and terrestrial environments (Cáceres & Soluk 2002; Srygley & Dudley 2008). Modes of wind-borne dispersal can range from active utilisation of wind speed and direction as shown for migrating *Pseudoophonus griseus* (Coleoptera: Carabidae) beetles (Feng et al. 2007), to more passive dispersal as seen for the cabbage aphid *Brevicoryne brassicae* (Bukovinszky et al. 2005). Body size is likely to play an important role in how wind affects insect movement and dispersal. The small body size of the hyperparasitoid of *Cotesia rubecula* may suggest that accidental dispersal brought it to the island.

Another interesting aspect for the management of introduced pests like the white butterfly is the role of parasitoid wasps and insect predators in regulating populations of herbivorous insects on small islands. Higher trophic levels are often thought to be less persistent (and possibly more likely to cause population crashes of their hosts) in small isolated populations (Price et al. 1980; Kruess & Tscharntke 2000). We do not know to what extent the populations of white butterfly, *Cotesia rubella* or the hyperparasitoid are supplemented by colonisations from the mainland and whether their population dynamics are influenced primarily by local or regional effects. For many species of conservation concern, island habitats represent a refuge from enemies, yet this relative isolation may mean that the web of trophic interactions surrounding them is simplified, potentially less stable, and more vulnerable to the sudden local loss or addition of key species that affect trophic cascades (Holt & Loreau 2001; Lozan et al. 2008).

The impact of insect herbivores like the white butterfly and plant pathogens like *Albugo candida* on plant fitness and survival in Cook's scurvy grass is unknown to us. However, *Capsella bursa-pastoris* (shepherd's purse) plants infected by plant pathogens such as *Albugo candida* were shown to have lower survival and reproduction rates than uninfected plants (Alexander & Burdon 1984). It is not unreasonable to expect a similar effect on fitness and reproduction for Cook's scurvy grass plants infected by *Albugo candida*. Thus, infection by *Albugo candida* and the added herbivory pressure through white butterfly larvae may lay a heavy burden on fitness and reproduction of Cook's scurvy grass plants as well as on recruitment of new seedlings.

Conclusion

Our study demonstrates the existence of trophic interactions involving Cook's scurvy grass and the white butterfly, potentially modified by interactions with fungi and parasitoid wasps. However, further research is needed to investigate the implications of these interactions for conservation of Cook's scurvy grass. As with many threatened species our sample sizes are small, but comparisons between different populations of Cook's scurvy grass could help to further identify important patterns among the different trophic levels found in this study system. Since introduced insect herbivores and their natural enemies are not confined only to Cook's scurvy grass, investigations could be extended to gain a more complete picture of the effects that introduced insect herbivores and plant pathogens may have on native plant populations.

Acknowledgements

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