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Pre-dispersal Seed Predation by Tephritidae Is Common among Species of Australian Alpine Asteraceae

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Abstract

This study examined levels of predation (% flower heads with insects and/or damage) and number of Tephritidae (seed-fly) in flower heads of 29 species of Australian alpine Asteraceae. Pre-dispersal seed predation was common among the Asteraceae, with all but four species with some flower heads containing Tephritidae. Levels of predation within species were also high, with most flower heads damaged in just under half of the species, and >90% of flower heads damaged in five species. Three species had flower heads containing *Tephritis bushi* (Diptera: Tephritidae, sp. nov.) while 23 species had flower heads containing *Tephritis poenia* (Diptera: Tephritidae (Walter)). Among species levels of all predation and number of Tephritidae per flower head were positively correlated with the diameter of the flower head, but not the color or type of flower head. The expected positive association between pre-dispersal seed predation and altitude and the negative association between predation and flowering time were uncommon among populations of 10 species tested. These results indicate that pre-dispersal seed predation is likely to be an important factor in the reproductive ecology of alpine Asteraceae, with species with larger diameter flower heads having higher levels of predation and more Tephritidae per flower head.

Introduction

The reproductive success of alpine plants can be constrained by the limited time for plant growth, floral and fruit development, and limited diversity and abundance of pollinators (Inouye and Pyke, 1988; Molau et al., 1989; Pickering, 1997; Körner, 2003). In addition to these factors, the reproductive success of alpine plants can be affected by pre-dispersal seed predation. In contrast to the extensive literature on other aspects of alpine reproductive ecology, there is limited research on pre-dispersal seed predation. Information on pre-dispersal seed predation is available in New Zealand for 21 species of Asteraceae (Spence, 1990) and two genera of Poaceae (*Chionochloa* sp., Kelly et al., 1992; *Festuca novae-zelandiae*, Lord and Kelly, 1999), in Switzerland on *Geum reptans* (Weppler and Stocklin, 2006), in Sweden on *Bartsia alpina* (Molau et al., 1989), in the Rocky Mountains on *Polemonium viscosum* (Galen, 1990) and in Sweden and the French Alps on *Trollius europaeus* (Hemborg and Despres, 1999). There appears to be no research on pre-dispersal seed predation in other alpine floras including those in Australia, Africa, South America, and much of Asia.

Studies of alpine and other species have found that floral traits such as size, color, type, and timing of flowering can affect levels of pre-dispersal seed (Louda, 1983; Molau et al., 1989; Spence, 1990; Kelly et al., 1992; Briese, 2000; Crawley, 2000; Cariveau et al., 2004; Honek and Martinkova, 2005). For example, species with larger floral displays (diameter of flower/flower head) have been found to have higher levels of pre-dispersal seed predation than those with smaller floral displays (Louda, 1983; Fenner et al., 2002). The effect of the size of floral display on levels of predation and amount of damage to flowers or flowering heads has also been found within species (Molau et al., 1989; Briese, 2000; Fenner et al., 2002; Cariveau et al., 2004).

A common pattern with pre-dispersal seed predation is variation in the levels of predation among populations of the same species, and among species in the same location (Louda, 1983; Spence, 1990; Lord and Kelly, 1999; Fenner and Lee, 2001; Fenner et al., 2002; Scheidel et al., 2003). Some of this variation is likely to be due to such as size of floral displays and phenology of flowering and of the predators (Briese, 2000). In some cases variation in pre-dispersal seed predation levels among populations of the same species of plant are correlated with climate, altitudinal gradients, or both (Louda, 1983; Kelly et al., 1992; Lord and Kelly, 1999; Scheidel et al., 2003). Increasing altitude can result in higher levels of pre-dispersal seed predation (*Celmisia lyallii* and *Celmisia spectabilis*, Spence, 1990; *Arnica montana*, Scheidel et al., 2003). However, in other species it has been found to have no effect on pre-dispersal seed predation (*Centaurea pseudophrygia*, Scheidel et al., 2003) or even result in decreasing levels of pre-dispersal seed predation (*Chionochloa*, Kelly et al., 1992; *Festuca novae-zelandiae*, Lord and Kelly, 1999).

For Asteraceae where flower heads (capitula) often contain the larvae of insects, including Tephritidae that feed entirely within the flower head, pre-dispersal seed predation may affect reproductive success (Edwards et al., 1996; Briese, 2000; Pilson, 2000; Fenner et al., 2002; Honek and Martinkova, 2005). Although Asteraceae are important components of alpine floras in many regions of the world (Costin et al., 2000; Körner, 2003), there appears to be only one published study of pre-dispersal seed predation for alpine Asteraceae (Spence, 1990). In this study, 9 out of 21 species of Asteraceae examined were host to a single species of Tephritidae. In the largest alpine region in Australia, Asteraceae accounts for 24% of the native angiosperm flora (48 native Asteraceae species, three weed species from Europe) (Costin et al., 2000). However, there is no publicly available research on pre-dispersal seed predation in this or any other alpine areas in Australia.
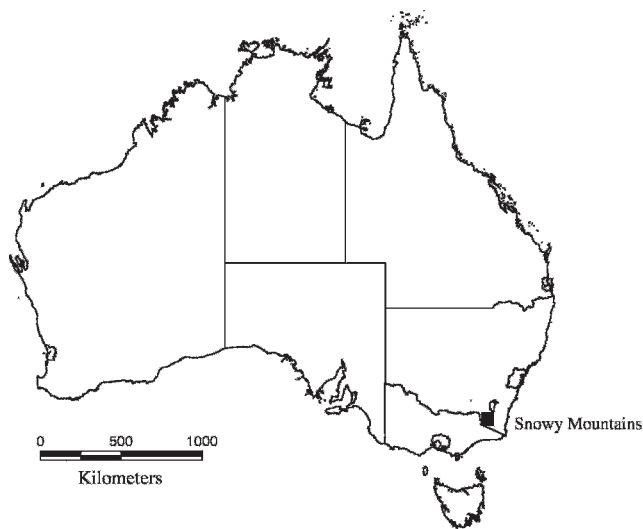
FIGURE 1. Location of the Snowy Mountains (36°27′S, 148°16′E) in Australia where 29 species of alpine Asteraceae were sampled.

To examine the role of pre-dispersal seed predation in these Australian alpine Asteraceae, flower heads of 27 native and 2 weed species were examined to determine (1) if pre-dispersal seed predation is common in Australian alpine Asteraceae; (2) what predators are present and if they are specialists or generalists; (3) if the floral display (diameter, color, and type of flowering head) affected levels of pre-dispersal seed predation; and (4) if altitude and timing of flowering effected levels of pre-dispersal seed predation among populations of 10 of the species.

Materials and Methods

STUDY SITE

The Kosciuszko alpine zone in the Snowy Mountains in southeastern Australia is the largest contiguous alpine area in Australia (Fig. 1). The alpine area extends from the climatic treeline at approximately 1850 m to the top of Australia's highest mountain, Mt. Kosciuszko, at 2228 m covering an area of approximately 100 km^2 (Costin et al., 2000). Low growing shrubs, grasses, and forbs characterize the alpine zone and occur in a number of different communities depending on the biotic and abiotic characteristics of a site.

SAMPLING METHODS

To obtain information about pre-dispersal seed predation across as wide a range of species of alpine Asteraceae as possible, levels of predation (proportion of flower heads with damage, and proportion with Tephritidae) and types of Tephritidae were measured for populations of 27 native and 2 weed species of Asteraceae within the Kosciuszko alpine area. This was done by sampling one randomly selected flowering head per plant from each of 10 randomly selected plants from different populations (clusters of plants separated by at least 100 m from other populations of the same species) of each species. Sampling occurred between the 9 January and 11 February 1998, with each population sampled once (Table 1). The sample size of 10 flower heads per population was a compromise. Sampling more flower heads per population would have provided a more accurate measure of pre-dispersal seed predation levels. However, this was not undertaken as destructive

sampling had to be minimized as some species had high conservation value (rare or endemic), small population sizes, and/ or produced few flower heads per plant. Therefore a minimum sampling size for populations was established to allow consistence in effort among species, while minimizing damage to plants. For 10 of the more common species of Asteraceae, 10 or more populations could be sampled. As a result it was possible, for these species, to examine variation among populations in pre-dispersal seed predation, including due to factors such as the altitude of the population and time of sampling.

Flower heads were removed, bagged, and then kept in cold storage until they were examined under a dissecting microscope for evidence of damage and insects. Evidence of predation (holes in florets, seed, receptacle, etc.), and the number and type of any insects present was recorded. To confirm the identity of any Tephritidae larvae and puparia found in flowers, flower heads were stored in open containers until the adult flies emerged. The Tephritidae were collected, frozen and later identified by Dr. Richard Drew at Griffith University.

To examine the effect of differences in floral traits among species, information on the size, color, and type of flower heads was obtained from floras. The diameter of flower heads of each species was estimated from the taxonomic descriptions in the *New South Wales Flora Online* accessed online on PlantNet (2007), except for *Rhodanthe anthemoides* (not in PlantNet), which is from Costin et al. (2000). Where a range of diameters were given, the midpoint was used. The color of the flower head (color of ligules and disk florets) and type of flowering head (radiate, ligulate, discoid, or discoid with papery brackets) for each species was determined from the *Kosciuszko Alpine Flora* (Costin et al., 2000).

DATA ANALYSES

Three measures of pre-dispersal predation were calculated at the population level for each species: (1) the level of all types of pre-dispersal seed predation (proportion of the 10 flower heads sampled with damage, arcsine square root transformed in the analyses), (2) the level of pre-dispersal seed predation by Tephritidae (proportion of the 10 flower heads with Tephritidae arcsine square root transformed in the analyses), and (3) the average number of Tephritidae per flower head (average of the 10 heads sampled per population, natural log $(x + 1)$ in the analyses). To determine if there were significant differences in pre-dispersal seed predation among species, one-way ANOVA were performed in SPSS 14.0 on the level of all pre-dispersal seed predation, or in the level of predation by Tephritidae, with species as the independent variable. To determine if there were differences in the number of Tephritidae in flowering heads within and among populations, and among species, individual flower head data were analyzed using a nested one-way ANOVA in SPSS 14.0. The dependent variable was the number of Tephritidae per flower head, with populations nested within species.

To determine the effect among species of floral traits on pre-dispersal seed predation, species level estimates of pre-dispersal seed predation were calculated by pooling data from all populations of a species. Then the effect of the size of flower heads on pre-dispersal seed predation among species was determined by correlating the diameter of the flower head (in mm) of species (natural log transformation) against the species level estimates of all pre-dispersal seed predation, Tephritidae predation, and the number of Tephritidae per flower head. To reduce the potential impact of phylogenetic affinities on the results, the correlations were repeated on a subset of the data with only one species (randomly chosen) included for each genera.

TABLE 1

Characteristics of 29 species of Australian alpine Asteraceae and levels of pre-dispersal seed predation. Number of replicates is the total number of flowering heads sampled for that species, and the number of populations sampled (usually one flower head per plant from ten plants per population [random flower head, random plant]). Predation is the percentage flowering heads that have any type of predation (any damage/presence of predators), two species of Tephritidae (*Tephritis bushi* and *Tephritis poenia*), any Tephritidae, thrips, aphids, or caterpillars. The mean number of Tephritidae larvae and puparia per flower head is also given.

| Species | Flowering head | | | Number replicates | | Percentage predation | | | | | | | Mean per flower head |
	Color	Type	Diameter (mm)	All flower heads	Pop.	All	T. bushi	T. poenia	Seed fly	Thrips	Aphids	Caterpillars	Seed fly
Olearia algida	White/Yellow	Radiate	9.5	30	3	0%	0%	0%	0%	0%	0.00	0%	0.00
Parantennaria uniceps	White	Discoid	5	30	3	0%	0%	0%	0%	0%	0.00	0%	0.00
*Achillea millefolium**	White	Radiate	5	30	3	0%	0%	0%	0%	3%	0.00	4%	0.00
*Hypochaeris radicata**	Yellow	Ligulate	10	99	10	15%	0%	0%	0%	0%	0.00	0%	0.00
Erigeron paludicola	Reddish brown	Radiate	13.5	100	10	17%	0%	3%	8%	0%	0.00	0%	0.74
Euchiton fordianus	White/Yellow	Discoid	3	30	3	17%	0%	0%	17%	10%	0.00	0%	0.20
Brachyscome scapigera	White/Yellow	Radiate	12	30	3	20%	0%	3%	3%	10%	0.00	3%	0.20
Ewartia nubigena	White/brown	Discoid/ paper	6.5	29	3	21%	0%	7%	17%	4%	0.00	3%	0.24
Senecio gunnii	Yellow	Discoid	3	30	3	23%	0%	13%	23%	0%	0.00	0%	0.60
Erigeron setosus+	White/Yellow	Radiate	8.5	100	10	25%	0%	4%	25%	0%	0.00	0%	1.74
Brachyscome stolonifera+	White/Yellow	Radiate	12	79	8	26%	0%	15%	16%	0%	0.00	0%	0.28
Euchiton argentifolius	Reddish brown	Discoid	3.25	30	3	27%	0%	10%	20%	0%	0.00	0%	0.53
Microseris lanceolata	Yellow	Ligulate	17.5	99	100	34%	0%	13%	14%	0%	0.00	0%	0.79
Brachyscome sp. aff. tadgellii	White/Yellow	Radiate	20	100	10	42%	10%	31%	38%	0%	0.00	0%	0.84
Senecio pinnatifolius var. pleiocephalus	Yellow	Radiate	5	100	10	49%	0%	26%	34%	0%	0.00	0%	0.80
Senecio pectinatus	Yellow	Radiate	25	10	1	50%	0%	30%	30%	0%	0.40	10%	0.50
Brachyscome spathulata	Violet/Yellow	Radiate	15	40	4	58%	0%	53%	53%	0%	0.00	0%	2.79
Craspedia maxgrayi	Yellow	Discoid	35	100	10	64%	0%	60%	66%	0%	0.00	0%	4.19
Olearia phlogopappa var. subrepanda	White/Yellow	Radiate	20.5	30	3	66%	43%	13%	57%	0%	0.00	3%	0.60
Brachyscome nivalis	White/Yellow	Radiate	40	100	10	70%	0%	60%	70%	5%	0.00	0%	1.45
Celmisia costiniana	White/Yellow	Radiate	40	108	10	78%	51%	11%	58%	0%	0.00	0%	4.78
Craspedia lamicola	Yellow	Discoid	25	100	10	79%	0%	72%	75%	0%	0.00	0%	6.83
Podolepis robusta	Yellow	Ligulate	25	10	1	80%	0%	0%	70%	70%	0.00	20%	1.90
Craspedia costiniana+	Yellow	Discoid	25	20	2	85%	0%	85%	85%	15%	0.00	5%	10.80
Craspedia jamesii	Orange	Discoid	25	20	2	90%	0%	75%	80%	10%	0.00	10%	5.00
Leptorhynchos squamatus	Yellow	Discoid	11.5	20	2	90%	0%	90%	90%	0%	0.00	0%	4.05
Rhodanthe anthemoides	White/Yellow	Discoid/paper	25	30	3	93%	0%	87%	90%	20%	0.00	7%	4.23
Craspedia alba	Cream	Discoid	12.5	20	2	95%	0%	95%	95%	10%	0.00	5%	6.10
Helichrysum scorpioides	Yellow	Discoid/ paper	25	20	2	95%	0%	95%	95%	20%	0.00	5%	13.00

Pop. = Population. Further details of sampling methods in text.

+ Endemic to Kosciuszko alpine area.

* Weed from Europe.

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To determine if there were differences among species in pre-dispersal seed predation with color and type of flower head, one-way ANOVAs were performed on the species level measures of all predation, Tephritidae predation, and the number of Tephritidae per flower head.

To examine variation in pre-dispersal seed predation within and among species, population level data were analyzed for the 10 Asteraceae species with 10 or more populations. First, one-way ANCOVAs were performed on the level of all predation per population, Tephritidae predation per population, and the number of Tephritidae predators per flower head per population, with species as the independent variable and the altitude of the population as the covariate. To test within species for changes in pre-dispersal seed predation with altitude (range ~1700 to 2100 m), or with Julian date among populations, Pearson's correlation coefficients were calculated separately for each species between the dependent variables (altitude or Julian date) and the level of all predation, Tephritidae predation, and the average number of Tephritidae predators per flower head per population.

Results

HOW COMMON IS PRE-DISPERSAL SEED PREDATION?

Based on the results from 1544 plants, pre-dispersal seed predation is common in most Australian alpine Asteraceae. Ninety percent of the species sampled had pre-dispersal seed predation, with larvae of Tephritidae the most common predator (Table 1). There was considerable variation in pre-dispersal seed predation among the 29 species in the level of predation, and in the number of Tephritidae per flower head (Table 1). There were significant differences in the level of all pre-dispersal seed predation (one-way ANOVA, d.f. = 28, F = 529.893, P < 0.001) and predation by Tephritidae (one-way ANOVA, d.f. = 28, F = 409.354, P < 0.001). For the number of Tephritidae per head, both species (nested one-way ANOVA, d.f. = 28, F = 7.497, P < 0.001), and populations (nested in species, d.f. = 117, F = 7.814, P < 0.001) were significant.

Only three species of alpine Asteraceae had no damage to flowering heads (the natives *Olearia algida* and *Parantennaria uniceps* and the weed *Achillea millefolium*). For the weed *Hypochaeris radicata* flower heads contained no larvae or puparia of Tephritidae, but there was evidence of previous damage by caterpillars and other insects in 15% of flower heads. Five species of native Asteraceae had very high levels of pre-dispersal seed predation with more than 90% of flower heads containing Tephritidae (*Craspedia jamesii*, *Leptorhynchos squamatus*, *Rhodanthe anthemoides*, *Craspedia alba*, and *Leucochrysum albicans* subsp. *alpinum*). The average number of Tephritidae (larvae and puparia) found in a flower head varied from none to 10.8 in *Craspedia costiniana*. However, the maximum number of Tephritidae per flower head was much higher with a maximum of 62 in *Craspedia lamicola*, 49 in *Erigeron setosus*, 42 in *Brachyscome* sp. aff. *tadgellii*, and 37 in *Microseris lancolata* and *Craspedia maxgrayi*.

WHAT ARE THE PRE-DISPERSAL SEED PREDATORS?

Four morphologically distinct types of larvae were found in the alpine Asteraceae flowering heads. The two most common were identified as *Tephritis bushi* (Diptera: Tephritidae, sp. nov.) and *Tephritis poenia* (Diptera: Tephritidae (Walter)) from emergent adults. *Tephritis bushi* larvae were only found in *Celmisia costiniana* (51% of flower heads), *Brachyscome* sp. aff. *tadgellii* (10%), and *Oleria phylogopappa* (43%). *Tephritis poenia* was oligophagous, occurring in 23 of the 29 species of Asteraceae examined. *Podolepis*

TABLE 2

Pearson correlations (r) between the diameter of the flower head and level of predation and number of predators per species for 29 species of alpine Asteraceae.

Variable		All species	One species per genera
	N	29	16
All predation	r	0.676	0.717
	P	**<0.001**	**0.002**
Predation by Tephritidae	r	0.623	0.661
	P	**<0.001**	**0.005**
Mean # of Tephritidae	r	0.482	0.606
	P	**0.008**	**0.013**

P-values for 2-tailed tests. Numbers in bold are significant at P = 0.05 level.

robusta did not contain larvae from these two species, but 70% of its flower heads contained other unidentified larvae.

The same Asteraceae species could have both species of Tephritidae, but rarely in the same flower head. Individual *Oleria phylogopappa* flower heads either had one or at the most two larvae from one or other species of Tephritidae but not both. For *Celmisia costiniana* only four flower heads out of the 63 flower heads with Tephritidae contained both species of Tephritidae. However, they tended to have many Tephritidae per flower head and as a result many of the *Celmisia costiniana* flower heads had most or even all florets and developing seed damaged. For *Brachyscome* sp. aff. *tadgellii*, only 5 out of the 36 flower heads with Tephritidae contained both species.

Occasionally other insects were found in flower heads such as caterpillars, thrips, and aphids (Table 1). Sometimes caterpillars had damaged flower heads by eating florets bracts and the receptacle; however, this was uncommon.

DID THE FLORAL DISPLAY AFFECT LEVELS OF PRE-DISPERSAL SEED PREDATION AND NUMBER OF PREDATORS?

There was considerable variation in the size of flowering heads among species, with values ranging from 3 to 40 mm. The level of all pre-dispersal seed predation was positively correlated with the diameter of the flower head, with species with larger flower heads having higher levels of all predation, of predation by Tephritidae as well as having more Tephritidae per flower head (Table 2, Fig. 2). These significant correlations occurred for all 29 species, and when only one species per genus was examined (Table 2).

The type and color of flower heads varied among the alpine Asteraceae. The most common colors were white with yellow centers (10 species) and just yellow (10 species). The most common type of flowering head was radiate (both tubular and ligulate florets) closely followed by discoid (10, only tubular florets). Flowering head color and types were not consistently correlated with the level of predation or the average number of Tephritidae per flower head (Table 3). When all species were compared, there was a significant relationship between levels of all predation and color of the flower head, but the relationship was not significant when data for just one species per genus was analyzed.

HOW VARIABLE WAS PRE-DISPERSAL SEED PREDATION AMONG POPULATIONS OF DIFFERENT SPECIES OF ASTERACEAE AND WHY?

For the 10 species of Asteraceae for which it was possible to sample flowering heads from 10 or more populations (Figs. 3 and
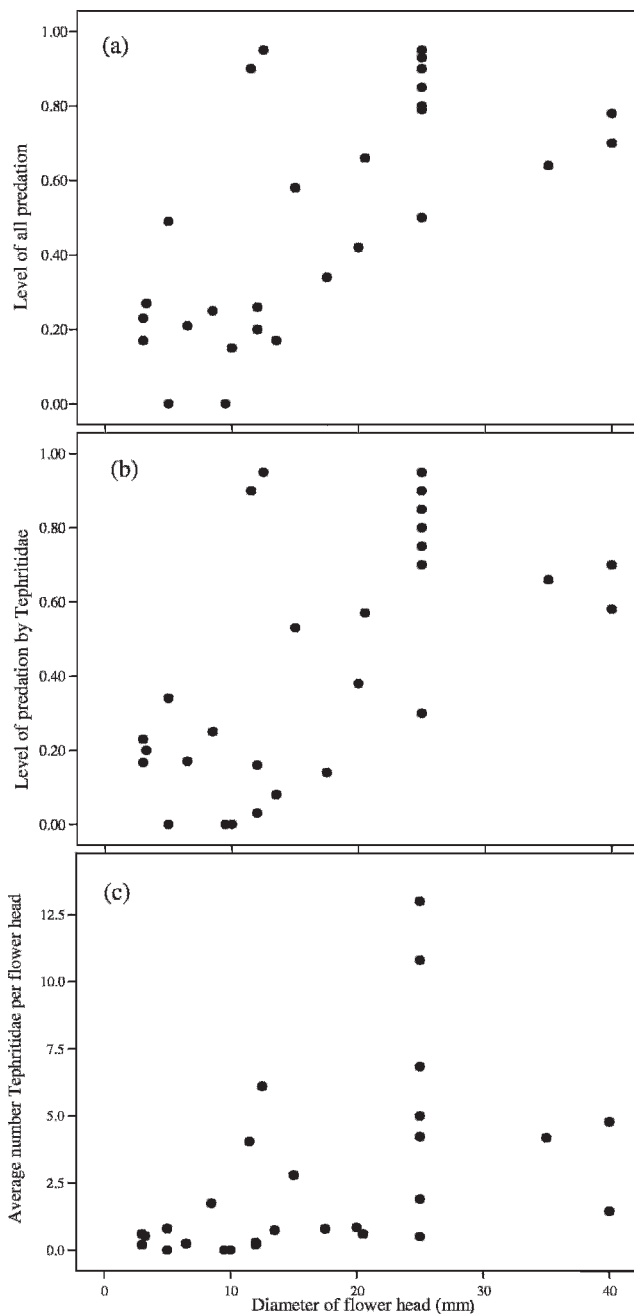
FIGURE 2. Relationship between the diameter of flower heads and **(a)** the level of all predation (proportion of flower heads damaged), **(b)** the level with Tephritidae (proportion with larvae or puparium), and **(c)** the mean number of Tephritidae per flower head for 29 species of Australian alpine Asteraceae.

4), significant differences were found among species in predation (levels of all predation, $F = 8.793$, $P < 0.001$; levels of Tephritidae predation, $F = 11.549$, $P < 0.001$; and average number of Tephritidae per flower head, $F = 9.818$, $P < 0.001$). There was also considerable variation in the levels of pre-dispersal seed predation and in the number of Tephritidae per flower head among populations within species of Asteraceae.

Levels of predation and the number of Tephritidae were not affected by the altitude of populations. Altitude was not a significant covariate in the ANCOVA (all predation, $F = 0.781$, $P = 0.379$; predation by Tephritidae, $F = 0.277$, $P = 0.600$; average number of Tephritidae per flower head, $F = 0.148$, $P = 0.701$). When predation values were correlated with altitude for each

Asteraceae species separately, the only significant correlation was for *Craspedia lamicola* (Table 4, Fig. 3). In this species the average number of Tephritidae per flower head increased from 0.9 per head at 1730 m a.s.l. to 14.2 at 2100 m (Fig. 3).

Levels of predation and the number of Tephritidae were also not affected by the date on which a population was sampled, with each population sampled once. Julian date was not a significant covariate in the ANCOVA (all predation, $F = 2.577$, $P = 0.112$; predation by Tephritidae, $F = 1.038$, $P = 0.311$; average number of Tephritidae per flower head, $F = 2.162$, $P = 0.145$). When predation values were correlated with Julian date of sampling among populations of each species separately, the only significant correlations were for *Craspedia maxgrayi* and *Erigeron pappocromus* (Table 4, Fig. 4). For both species there was a decrease in predation during the sampling period, although there was considerable variation (Fig. 4).

Discussion

PRE-DISPERSAL SEED PREDATION BY TEPHRITIDAE IS COMMON IN AUSTRALIAN ALPINE ASTERACEAE

All but 4 of the 29 species experienced pre-dispersal seed predation by Tephritidae and for 14 species more than 50% of flower heads were infested. Two species of Tephritidae were identified, the generalist *Tephritis poenia* and the more specialized *Tephritis bushi*. The Asteraceae were sampled just past the peak of flowering and start of seed maturation in the Kosciuszko alpine area (Inouye and Pyke, 1988; Pickering, 1997). At this time plants that rely on pollinators are competing to attract Diptera and Hymenoptera which are the most common pollinators in the region (Inouye and Pyke, 1988; Stock and Pickering, 2002). In addition to attracting pollinators, the large showy flower heads on many of the Asteraceae were also attracting pre-dispersal seed predators including Tephritidae.

A previous study of pollinators of Australian alpine flowers recorded two unidentified species of *Tephritis* visiting flowering heads of *Craspedia* (species not specified but included orange and yellow flower heads), *Leucochrysum albicans* subsp. *alpinum*, *Helichrysum scorpioides*, *Hypochaeris radicata*, and *Leptorhynchos squamatus* (Inouye and Pyke, 1988). In a study of host specificity of Tephritidae in Australia (Edwards et al., 1996), *Tephritis poenia* emerged from the flowers of the alpine Asteraceae species *Helichrysum scorpioides*, *Leucochrysum albicans* subsp. *alpinum*, *Helichrysum rutidolepis*, *Craspedia* sp., and *Leptorhynchos squamatus*, as well as a lower altitude population of *Leptorhynchos tenuiflorus*, *Ammobium alatum*, and *Leucanthemum vulgare* supporting its status as a generalist predator of Asteraceae.

Although the effect of Tephritidae on seed production by the alpine Asteraceae was not examined, the large numbers of Tephritidae and high levels of predation in flower heads of several species of Asteraceae could dramatically reduce seed production. For species such as *Celmisia costinina*, very little viable seed can be harvested from flower heads in most seasons (personal observation). It is unlikely that the alpine Asteraceae could compensate for seed loss by producing more flowers in the same season as they are likely to initiate flower buds the previous autumn, and many (but not *Celmisia costinina*) produce relatively few flower heads per plant (personal observation). High levels of seed loss due to fly predation have been found in the native alpine grasses of *Chionochloa* in New Zealand (Kelly et al., 1992).

Tephritidae predation of flowering heads appears to be common in at least one other alpine flora, with flowering heads of 10 out of the 21 species of Asteraceae tested in New Zealand containing at least one species of seed fly, *Trypanea longipennis*

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TABLE 3

Results of one-way ANOVA examining the effect of flower head color and type on mean predation per species for 29 species of alpine Asteraceae.

	All species						One species per genera			
	Flower head color			Flower head type			Flower head color		Flower head type	
Variable	d.f.	F	P	d.f.	F	P	F	P	F	P
Level of all predation+	3	3.849	**0.022**	3	1.182	0.336	3.230	0.061	0.970	0.439
Level of predation by Tephritidae+	3	2.535	0.080	3	2.026	0.136	1.809	0.199	1.257	0.333
Mean # of Tephritidae per flower head*	3	1.775	0.178	3	2.258	0.106	1.670	0.229	0.927	0.458

Number in bold is significant at $P = 0.05$ level.

+ Arcsine square root transformed.
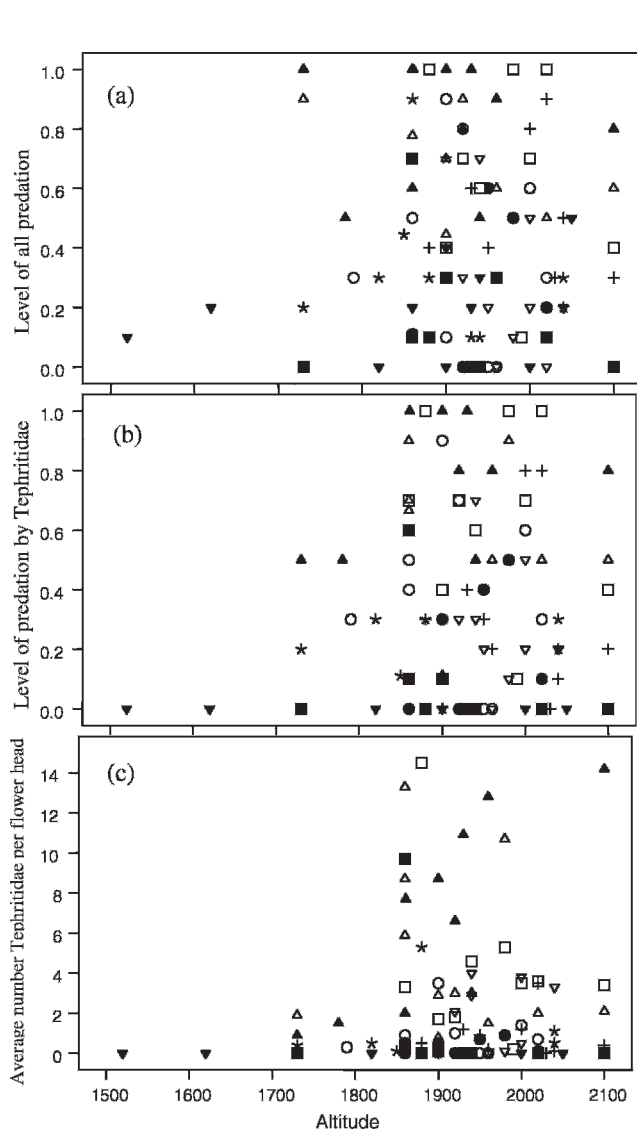
* Natural log transformed.

FIGURE 3. Relationships between altitude (m a.s.l.) and (a) the level of all predation (proportion of flower heads damaged), (b) the level with Tephritidae (proportion with larvae or puparium), and (c) the mean number of Tephritidae per flower head for each of 10 species of Australian alpine Asteraceae. Clear circle = *Brachyscome* sp. aff *tadgelli*, dark circle = *B. stolonifera*, clear up triangle = *Craspedia costiniana*, dark up triangle = *C. lamicola*, clear square = *C. maxgrayi*, dark square = *Erigeron paludicola*, clear down triangle = *E. setosus*, dark down triangle = *Hypochaeris radicata*, star = *Microseris lancolata*, and plus = *Senecio pinnatifolius*.
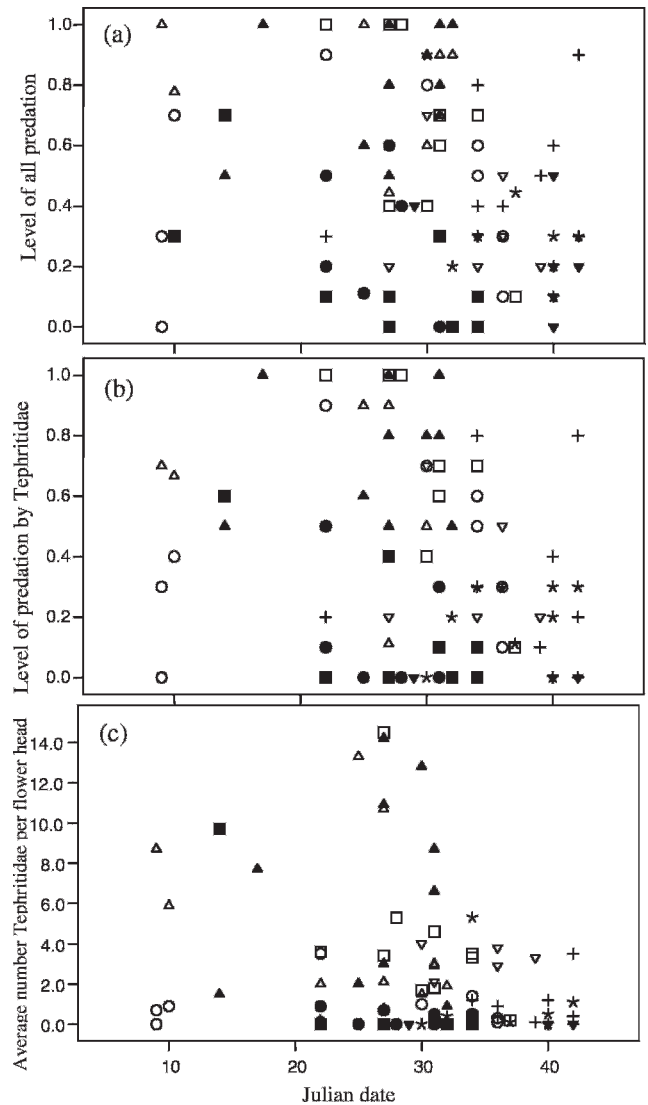

FIGURE 4. Relationships between Julian date (number of days from 1 January) and (a) the level of all predation (proportion of flower heads damaged), (b) the level with Tephritidae (proportion with larvae or puparium), and (c) the mean number of Tephritidae per flower head for each of 10 species of Australian alpine Asteraceae. Clear circle = *Brachyscome* sp. aff. *tadgelli*, dark circle = *B. stolonifera*, clear up triangle = *Craspedia costiniana*, dark up triangle = *C. lamicola*, clear square = *C. maxgrayi*, dark square = *Erigeron paludicola*, clear down triangle = *E. setosus*, dark down triangle = *Hypochaeris radicata*, star = *Microseris lancolata*, and plus = *Senecio pinnatifolius*.

TABLE 4

Pearson correlations (r) between altitude and Julian date sampled and rates of predation and number of predators per population for 10 species of alpine Asteraceae.

Variable		B. sp. aff tadgellii	B. stolonifera	C. costiniana	C. maxgrayi	C. lamicola	E. paludicola	E. setosus	H. radicata	M. lancolata	S. pinnatifoliuius
N (# of populations)		10	8	11	10	10	10	10	10	10	10
Altitude											
Level of all predation+	r	−0.214	0.401	−0.393	−0.150	−0.123	−0.139	−0.325	0.133	−0.192	0.071
	P	0.554	0.324	0.232	0.679	0.734	0.701	0.359	0.713	0.595	0.845
Level of predation by Tephritidae+	r	−0.164	−0.004	−0.026	−0.150	0.281	−0.271	−0.325		−0.020	−0.144
	P	0.651	0.993	0.941	0.679	0.432	0.481	0.359		0.955	0.691
Mean # of Tephritidae per flower head*	r	0.049	−0.048	−0.162	−0.195	**0.808**	−0.223	−0.146		0.067	−0.047
	P	0.893	0.910	0.634	0.589	**0.005**	0.565	0.687		0.854	0.898
Julian date											
Level of all predation+	r	0.101	−0.306	−0.238	**−0.687**	0.307	**−0.653**	−0.328	0.101	−0.560	0.250
	P	0.781	0.461	0.482	**0.028**	0.388	**0.041**	0.355	0.781	0.092	0.486
Level of predation by Tephritidae+	r	0.201	−0.277	−0.215	**−0.687**	0.023	−0.568	−0.328		0.474	−0.047
	P	0.577	0.507	0.526	**0.028**	0.950	0.111	0.355		0.167	0.897
Mean # of Tephritidae per flower head*	r	−0.046	−0.216	−0.462	−0.551	0.219	**−0.739**	0.070		0.124	0.247
	P	0.900	0.608	0.152	0.099	0.544	**0.023**	0.847		0.732	0.492

P-values for 2-tailed tests. Numbers in bold are significant at $P = 0.05$ level.
+ Arcsine square root transformed.
* Natural log transformed.

(Spence, 1990). The levels of predation recorded for the flower heads of Australian alpine Asteraceae, however, were often higher than those for New Zealand alpine species. In New Zealand, the highest levels of predation of flower heads were only 60% in a population of *Celmisia lyallii*. In contrast, in the Australia alpine Asteraceae 12 species had higher levels of pre-dispersal seed predation, including *Celmisia costinina*. Also the number of larvae and puparia per flower head were higher for many of the Australian species than for New Zealand species. Therefore, Tephritidae may be even more important predators of flower heads for alpine Asteraceae in Australia than in New Zealand.

Hypochaeris radicata and *Achillea millefolium* are common alpine weeds (Johnston and Pickering, 2001; Pickering and Hill, 2007). In the Australian Alps, no Tephritidae larvae or puparia were found in any of the flower heads of *Hypochaeris radicata*, and *Achillea millefolium* sampled. Similarly, there was no predation on flower heads of either species in New Zealand, and only low levels of predation of *Hypochaeris radicata* in Britain where both species are native (Fenner and Lee, 2001). It appears that these two species may not experience high levels of pre-dispersal seed predation wherever they grow, rather than specifically benefit from reduced predation of flower heads when they grow outside their natural range.

FLORAL TRAITS AND PREDATION

The Australian alpine Asteraceae results confirm those of previous studies that have found a relationship between the size of floral displays as measured by the diameter of flower heads and pre-dispersal seed predation (Fenner et al., 2002). It also extends what has been found in some previous studies (Fenner et al., 2002), by establishing that the pattern applies to many alpine species, to a large range of flower heads sizes, and to the number of Tephritidae per flower head as well as to the level of predation.

Additional research on the Australian alpine Asteraceae could test if the diameter of the flower head is positively correlated with levels of predation within species, as has been found for species in other geographical locations (Molau et al., 1989; Fenner et al., 2002). This could be done either by measuring natural variation in the size of flower heads and levels of pre-dispersal seed predation, or by manipulating the size of floral displays (removing petals etc) to test if the level of predation of flower heads, and/or the number of predators per flower head were affected.

Two other aspects of floral display were examined: color and type of flowering head. However, although flower color affects visitation levels of pollinators, and Australian alpine insects show clear preferences for white and yellow over orange, red, and purple colors in experiments (Pickering and Stock, 2004), there was no consistent effect of the color of flowering heads on pre-dispersal seed predation. This may be due to the limited range of colors among the Australian alpine Asteraceae. Flower colors in Australian and New Zealand alpine floras are predominantly white and yellow, with few of the darker colors (reds, blues, and purples) associated with other alpine floras where bees are common pollinators (Primack, 1978; Pickering and Stock, 2004). Comparing predation levels among Asteraceae in other regions with greater color variation should therefore be undertaken to further examine if flower color could affect levels of pre-dispersal seed predation.

VARIATION IN PRE-DISPERSAL SEED PREDATION WITHIN SPECIES OF ASTERACEAE

There was considerable within-species variation in pre-dispersal seed predation and number of predators among

populations of the Australian alpine Asteraceae. Similar variation among populations of the same species of Asteraceae has been found in other studies including in Greece (Briese, 2000), Germany (Scheidel et al., 2003), England (Fenner and Lee, 2001), Czech Republic (Honek and Martinkova, 2005), and New Zealand (Spence, 1990; Fenner and Lee, 2001). It has been suggested that among population variation may be due to climatic or altitudinal gradients (Scheidel et al., 2003). Decreasing pre-dispersal seed predation with increasing altitude (1000 to 1600 m) was found in native alpine grasses of *Chionochoa* in New Zealand (Kelly et al., 1992). Some lower elevation populations of the alpine Asteraceae *Celmisia lyallii* and *Celmisia spectabilis* in New Zealand had higher rates of pre-dispersal seed predation, but not all (Spence, 1990).

The Australian alpine Asteraceae were not sampled over a very large altitudinal range with nearly all populations in the alpine zone. However, for *Craspedia lamicola* there was an increase in the number of Tephritidae per flower head with increasing attitude but no changes in the percentage of flower heads with predators. Additional sampling including populations from a greater altitudinal range would provide a more robust test of any relationship.

There were some differences in pre-dispersal seed predation levels with date of sampling of a population for *Craspedia maxgrayi* and *Erigeron paludicola*. Again, sampling flower heads at different times in the flowering season within and among populations of the same species would provide a better test of any relationship between timing of flowering and pre-dispersal seed predation.

Conclusions

Tephritidae predation is common in most Australian alpine Asteraceae. The level of predation and the number of Tephritidae per flower head was related to the diameter of the flower head, but not color or type of flower head among species of Asteraceae. These high levels of pre-dispersal seed predation are likely to adversely affect seed set in some of the species. The current results indicate that Tephritidae predation may be an important factor affecting reproduction in species of alpine Asteraceae.

Acknowledgments

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