Reproductive ecology of *Lepidium sisymbrioides* ssp. *matau*

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Summary

Lepidium sisymbrioides ssp. *matau* is known only from a single locality, where there is a main population of less than 200 plants and a few outlying and scattered individuals. This study was undertaken to determine the taxon's reproductive ecology, in particular to ascertain if there are intrinsic reproductive constraints to recruitment.

Seed production and viability, seedling establishment and growth, and general population dynamics, were studied in the field and in cultivation. The results showed that although there was a bias towards males in the wild and cultivated populations, most wild females flowered in every year of the study period (1992–1995) and produced large numbers of viable seeds, with no evidence of pre-dispersal seed predation. Seedlings established readily in cultivation, and most flowered by their third year. The few losses of mature plants in the wild were almost offset by recruitment of seedlings. Almost all plant losses were clearly the result of burial following soil movement. Removal of sheep grazing appears to have no effect on plant reproductive performance, either directly (herbivory was insignificant on both protected and unprotected *Lepidium* plants) or indirectly (*Lepidium* recruitment was no better in grazed than in ungrazed pasture). Changes in vegetation cover between years appeared to have no effect on *Lepidium* recruitment.

Studies of other plant species of semi-arid environments have shown that post-dispersal seed predation may significantly limit recruitment. The frequency, timing and volume of rainfall are also likely to be major determinants of successful establishment of *Lepidium sisymbrioides* ssp. *matau* seedlings in this semi-arid environment, not least because competing species also take advantage of rainfall events.

Competition for nutrients and soil moisture from other plant species is unlikely to be significant in limiting survival of established plants as *Lepidium sisymbrioides* ssp. *matau* is the only rosette-forming, very deep-rooted, perennial herb in the local native flora, and there are no naturalised plants of similar form in its habitat. However, the availability of suitably deep gravel substrates for development of its root system may constrain establishment and survival, and the clumping of plants in the wild may reflect this.

1. Introduction

Lepidium sisymbrioides ssp. *matau* and its close relatives *L. s.* ssp. *kawarau* and *L. s.* ssp. *sisymbrioides* are small herbaceous perennial plants restricted to dry habitats in eastern South Island. They are the only known dioecious members of the large cosmopolitan cress family, the Brassicaceae. All three are of restricted distribution, and the Threatened Plant List of the New Zealand

Botanical Society (Cameron *et al*. 1995) lists the status of *L. s.* ssp. *matau* as critical.

Herbarium specimens at the Landcare Research New Zealand Ltd herbarium at Lincoln show that *Lepidium sisymbrioides* ssp. *matau* was recorded from five sites in the Maniototo basin and near Alexandra in Central Otago last century. Recently it has only been located as one small population and a few scattered individuals, totalling fewer than 200 plants, confined to gravelly hillslopes and terrace faces at Galloway in the lower Manuherikia valley. Part of the population grows in a fenced area of grassland 10–30 cm tall that is protected from sheep grazing, and part in adjacent sheep-grazed grassland with a sward height of <10 cm.

Lepidium sisymbrioides ssp. *matau* was thought to be restricted to salty soils, and its rarity was attributed to the substantial decline in area of these in Central Otago. However, recent research (Allen & McIntosh 1993) has shown that, although salty soils occur at the Galloway locality, the plants avoid them and grow only on adjacent non-salty topsoils.

There is an abundance of apparently suitable habitat adjacent to existing plants and surrounding the known population of *L. s.* ssp. *matau*. It is probable that more plants exist than have been recorded: *L. s.* ssp. *matau* is almost invisible when not flowering because its grey-brown leaves are easily hidden amongst other vegetation and against the similar-coloured soil.

Nevertheless, it is evident that there are constraints on the ability of *L. s.* ssp. *matau* to occupy all the available habitat. These could include extrinsic factors, such as competition from other plant species, and intrinsic factors, such as low seed viablility. This study examines the taxon's reproductive ecology, in particular to ascertain if there are reproductive constraints to recruitment, as part of a wider examination of the ecology of all three subspecies of *Lepidium sisymbrioides*. The objectives were:

- to determine seed production,
- to determine seed viablility,
- to assess the effects of soil type, competition, and sheep grazing on germination and establishment.

2. Methods

The study was undertaken at the locality of the main population of *Lepidium sisymbrioides* ssp. *matau* on Galloway Station, near Alexandra, where most plants are established within a fenced area protected by a Conservation Covenant (Allen & McIntosh 1995), and at the Landcare Research premises in Dunedin.

Seeds were collected by removing up to half the fruits produced by any individual plant in December 1992, 1994 and 1995. Viability of the 1992 seeds was tested in December 1992–January 1993 by sowing 20 seeds on moist filter paper in each of 10 petri dishes and recording emergence of cotyledons. Seeds

from the 1992 collection were also stored in a sealed plastic bottle until October 1994, then the procedure was repeated with 90 seeds sown in a single dish. Seeds from the 1994 collection were stored similarly, then sown in November 1995 in five petri dishes. Seeds from the 1995 collection were sown in 10 petri dishes in February 1996.

Establishment was tested by sowing five seeds in each of eight pots containing topsoil (0–10 cm depth) from the Galloway site, and repeating this with soil from four other sites with populations of a *Lepidium sisymbrioides* subspecies, in January 1993. The pots were kept in a greenhouse and regularly watered, and germination and growth of plants were recorded.

Population sex ratios were determined by annual census of the wild population and from the sex of cultivated plants.

Recruitment in the wild was recorded on three transects, one in each of the two distinct groups of plants in the fenced (ungrazed by sheep) protected area and one in the adjacent unfenced (grazed) group. On these, plants were mapped in 28 (ungrazed area) and 40 (grazed area) 0.5 x 0.5 m quadrats subdivided into a 0.1 m grid, in 1993 (ungrazed area only), 1994 and 1995, and their sex and number of rosettes and inflorescences were recorded.

Ground cover was recorded by point intercept on the transects of the ungrazed area in 1993, 1994 and 1995.

3. Results

3.1 SEX RATIO

Table 1 shows the number of male and female plants flowering at the Galloway site in 1992, 1993, 1994 and 1995. Female flowering plants numbered between 58% and 85% of males in each year. Although the sex ratio favours males, this is not unusual (Lloyd & Webb 1977), and may facilitate pollination.

TABLE 1. NUMBER OF MALE AND FEMALE PLANTS FLOWERING AT GALLOWAY IN 1992, 1993, 1994 AND 1995. a = UNGRAZED AREA, b = GRAZED AREA; n = TOTAL NUMBER OF PLANTS RECORDED, INCLUDING THOSE THAT WERE NOT FLOWERING.

YEAR	1992a	1993a	1994a	1994b	1995a	1995b
male	24	43	50	21	60	33
female	14	30	38	22	33	23
n	38	76	97	57	102	70

3.2 FLOWERING AND SEED PRODUCTION

Of the 134 plants that successfully established in pots, four males and two females (4.5% of all plants) flowered in 1993. Of the 98 that survived until

December 1994, 19 males and five females (24.5%) flowered, and in November 1995 28 males and 27 females (67.9%) flowered of the 81 survivors.

Wild plants would be expected to reach sexual maturity later than those grown under more favourable greenhouse conditions, so it is likely that few seedlings established in the wild would flower in their first and second years (see 3.5 below).

In the wild there is evidently no shortage of pollinators, as all female plants which flowered also produced seeds. There was no difference in flowering success between plants protected from sheep grazing and those exposed to it; only one plant had inflorescence damage that could be attributed to herbivory.

Annual records 1992–1995 showed a range of 1–8 inflorescences (= panicles) per plant each year, although the mean varied from 1.5 to 3.4 with year (Table 2). There was an average of five (range 3–7) racemes per panicle. A count of fruits (= silicles) on 12 randomly selected racemes gave an average of 36 (range 21–61) silicles per raceme, each containing two seeds.

TABLE 2. MEAN NUMBER OF INFLORESCENCES PER FEMALE PLANT IN *LEPIDIUM SISYMBRIOIDES* SSP. *MATAU* IN 1992, 1993, 1994 AND 1995. n = THE NUMBER OF FEMALE PLANTS RECORDED FLOWERING AT THE GALLOWAY SITE IN EACH YEAR.

YEAR	1992	1993	1994	1995
mean	3.4	2.4	2.0	1.5
range	1–8	1–7	1–7	1–4
n	14	30	60	56

Thus an 'average' flowering female plant of *Lepidium sisymbrioides* ssp. *matau* produces *c.* 800 seeds.

3.3 SEED VIABILITY

Germination of the seeds collected in 1992 was first recorded 18 days after sowing in December 1992 and ceased after 38 days (Fig. 1). Mean germination was 10% (range 5–20%), a low rate probably resulting from fungal infection of the seeds. Germination rate of the same seed collection in the pots of soil was higher (see below), and in 1994 a rate of 41% was achieved in the single *in vitro* sowing from these seeds.

Seeds collected in 1994 had a germination rate of 23% (range 17–36%) a year later in the November 1995 sowing. Seeds collected in late 1995 had a mean germination rate of 26.5% (range 22.2–78.9%) in the February 1996 sowing, with germination spread from 13 to 58 days after sowing (Fig. 2).

3.4 ESTABLISHMENT

Germination and rosette diameter growth results for pot-grown plants are given in Table 3.

FIGURE 1. GERMINATION OF *LEPIDIUM SISYMBRIOIDES* SSP. *MATAU* SEEDS COLLECTED AND SOWN IN DECEMBER 1992.

FIGURE 2. GERMINATION OF *LEPIDIUM SISYMBRIOIDES* SSP. *MATAU* SEEDS COLLECTED IN DECEMBER 1995 AND SOWN IN FEBRUARY 1996.

Germination and establishment success of wild-collected seeds in cultivation thus demonstrates that viablilty is adequate, even after a year's dry storage, and should not limit recruitment.

TABLE 3. PERCENTAGE GERMINATION AND MEAN ROSETTE DIAMETER OF *LEPIDIUM SISYMBRIOIDES* SSP. *MATAU* PLANTS GROWN IN SOILS FROM FIVE LOCALITIES, 10 MONTHS AFTER SOWING.

SOIL LOCALITY	PERCENTAGE GERMINATION	MEAN DIAMETER (mm)
Patearoa	80.0	61.4
Falls Dam	92.5	41.7
Galloway	55.0	80.8
Slapjack Creek	50.0	46.2
Pisa Flat	57.5	76.2

3.5 RECRUITMENT IN THE WILD

The results of the complete census of the fenced and unfenced populations are given in Table 4.

The increases implied by the results shown in Table 4 do not represent recruitment, but rather the discovery of mature plants that had been overlooked in earlier surveys because they had not been flowering.

TABLE 4. NUMBER OF *LEPIDIUM SISYMBRIOIDES* SSP. *MATAU* PLANTS RECORDED IN FENCED AND UNFENCED AREAS, 1992–1995, GALLOWAY.

	FENCED				UNFENCED	
YEAR	1992	1993	1994	1995	1994	1995
male	24	44	54	60	25	36
female	14	31	40	39	26	29
unknown	0	1	3	3	6	5
total	38	76	97	102	57	70

Percentage ground cover on the ungrazed transects is given in Figure 3. Although there was a decline in bare ground (gravel, sand, silt) and a corresponding increase in litter on the east transect, and a decline in moss on the west transect, there were no other consistent trends. Considerable annual variation in cover occurred, especially in the dominant exotic annual species *Trifolium arvense* (both transects), and the exotic perennials *Lolium perenne* (east transect) and *Rumex acetosella* (west transect). The dominant native grass, an unidentified *Rytidosperma* species (possibly *R. buchananii* or *R. maculatum*), showed relatively little variation in cover on both transects.

Of the 26 *Lepidium sisymbrioides* ssp. *matau* plants (15 male, 11 female) recorded in the recruitment quadrats inside the ungrazed area in November 1993, one male had disappeared by November 1994, but another male plant had established, along with one female and one of unknown sex. By November

FIGURE 3. GROUND COVER OF GRAVEL, SAND, SILT, DUNG, LITTER, MOSS, LICHEN AND PLANT SPECIES ON TWO TRANSECTS (EAST AND WEST) IN THE FENCED AREA *OF LEPIDIUM SISYMBRIOIDES* SSP. *MATAU* HABITAT, GALLOWAY. SPECIES NAME ABBREVIATIONS ARE THE FIRST THREE LETTERS OF THEIR GENERIC AND SPECIFIC EPITHETS. RESULTS FOR 1993 ARE SHOWN BY OPEN COLUMNS, 1994 BY DARK HATCHED COLUMNS, AND 1995 BY LIGHT HATCHED COLUMNS.

1995, two further male and four female plants had disappeared, but three new plants of unknown sex (not flowering) had been recruited. Except in one case, the loss of plants was due to burial by soil and gravel originating from rabbit burrowing and some natural erosion. The cause of the loss of the other plant was not evident. The six recruited plants occupied habitat apparently indistinguishable from their surroundings.

The unfenced population first recorded in recruitment quadrats in November 1994 consisted of seven male and fourteen female plants, and eight of unknown sex. By November 1995, there had been a loss of one plant of each sex, and a gain of two plants of unknown sex. Again, the cause of loss was not evident.

Recruitment of seedlings has been almost sufficient to replace plants lost through mortality over the course of this study. However, recruitment recorded in November 1995 may represent seedlings established as a result of the exceptionally high rainfall of December 1993 to March 1994, and may thus be optimal rather than average. These seedlings may have been too small to be detected in November 1994, after less than a season's growth.

FIGURE 4. ALEXANDRA MEAN RAINFALL 1945–1990 AND RAINFALL 1992–1995, IN THE MONTHS AUGUST–NOVEMBER, DECEMBER–MARCH, AND THE YEAR AUGUST–AUGUST.

4. Discussion and conclusions

Flowering and germination data indicate that reproduction of *Lepidium sisymbrioides* ssp. *matau* is not constrained in the wild by seed production or viability. Factors limiting the recruitment of *L. s.* ssp. *matau* in the wild thus operate after the production of viable seed. They could include seed and seedling predation, inadequate dispersal, competition, or environmental limits to establishment such as habitat availability and rainfall.

Apart from the observation that no seed predation was evident before the seeds were released from silicles, determination of seed predation was beyond the scope of the present study. However, some general principles apply. Seed predation can limit recruitment in arid and semi-arid plant communities, especially where the vegetation is open (Abramsky 1983, Reichmann 1979, Louda 1982, Risch & Carroll 1986). Pathogens, post-dispersal seed predators, parasites and herbivores (mainly invertebrates) may concentrate their activites where resources are common, so more distant seeds and seedlings may survive better than those close to the parent (Willson 1992). *Lepidium sisymbrioides* ssp. *matau* plants at Galloway occur mainly in three groups which are

separated by distances considerably exceeding the extent of each group. Although the seeds are small and light, the rarity of plants between the groups on apparently suitable habitat suggests that dispersal distances are usually not greater than a few metres. Thus post-dispersal seed and seedling mortality from the agencies listed by Willson (1992) and Crawley (1992) may be significant.

Lepidium sisymbrioides ssp. *matau* seeds are relatively long-lived in dry storage, *in vitro* germination takes place over at least two months, and a small proportion of seeds germinated weeks or months after the majority in the pot experiments. It is possible that soil-stored seeds provide *L. s.* ssp. *matau* with the ability to stagger germination and thus take advantage of rare favourable environmental conditions, especially rainfall events, and to avoid catastrophic losses when conditions are adverse. Invertebrate predation of soil-stored seeds could thus significantly reduce the establishment of seedlings (Crawley 1992).

Climate, and particularly rainfall, is likely to be a major factor limiting reproductive success of *Lepidium sisymbrioides* ssp. *matau*. The area has a semi-arid climate (Hubbard & Wilson 1988), with annual rainfall as little as 300 mm/yr and a water deficit of ca. 140 mm/yr, mainly in summer and autumn. In this environment, suitable reproductive conditions for *L. s.* ssp. *matau* will only occur when certain sequences of climate events allow germination and establishment in the face of predation and competition from other plant species (event-driven change; Walker 1993). The timing, volume and frequency of rainfall are critical (Westoby 1980), especially as other species will also take advantage of the rainfall event. Nevertheless, although rainfall after seed production in summer (December–March) 1993–94 was exceptionally high, it did not result in a flush of seedling establishment of the magnitude that might be expected if increased rainfall volume and frequency were the major determinants of recruitment.

No clear relationship between *Lepidium sisymbrioides* ssp. *matau* recruitment and competition from other plants is evident from the cover data. The annual variation in cover values of some dominant plant species, both annual and perennial, in the absence of grazing agrees with the results of a study of vegetation change on adjacent Galloway and nearby Earnscleugh Stations (Allen *et al.* 1995), and is typical of vegetation in a semi-arid climate. The lack of differences in flowering, seed production, and seedling establishment between groups of *L. sisymbrioides* ssp. *matau* plants growing in grazed (short) and ungrazed (tall) vegetation supports the conclusion that competition is not the major limitation on recruitment at this site.

Within the groups of *Lepidium sisymbrioides* ssp. *matau* plants, sibling competition, especially for soil moisture, may be significant. Nevertheless, given that all the seedlings recorded were within these groups, rather than distant from them, this seems unlikely. The extremely deep rooting habit of *Lepidium sisymbrioides* (McIndoe 1932) suggests that root competition between mature plants and other herbaceous species is unlikely to be important. Its life-form (perennial rosette-forming deep-rooted herb) is unique in the local native flora, and allows *L. s.* ssp. *matau* to co-exist with perennial and annual grasses and forbs of very different habit by utilising different growth opportunities (Westoby 1980). Although some exotic species present in the general area, such as lucerne (*Medicago sativa*), are superficially similar in

habit (perennial herb with deep root system), none of these appear to occupy the same habitat, and thus they do not compete for the same resources.

In order to exploit the advantage of a deep root system, *Lepidium sisymbrioides* ssp. *matau* plants must establish on a substrate which allows the roots to develop. McIndoe (1932) considered that *Lepidium sisymbrioides* distribution would be limited by the presence of deep (>2 m) gravel soils which would allow its taproot to penetrate to and exploit deeply-stored soil moisture which is not available to competing plants. Gravels overlie deeply weathered schist at the study site (McIntosh *et al.* 1989). The depth of gravel is unknown because no soil pit has been excavated and the substrate is not suitable for auger determination of gravel depth. It is possible that variations in gravel depth are responsible for the patchy distribution of *L. s.* ssp. *matau*.

Plant cover may affect the availability of soil water for *Lepidium sisymbrioides* ssp. *matau*. In grazed semi-arid grasslands, when the cover of relatively short-rooted grasses is high, most rainfall is absorbed by these and little penetrates to the depth of tree roots (Walker *et al.* 1981), which are analogous to those of *L. s.* ssp. *matau*. When grass cover is reduced, although infiltration may also decline because of the development of soil crusting, a greater proportion of rainfall penetrates to the depth where it is exploited by deep roots. However, no loss of mature plants in the fenced area could be attributed to the increased cover of herbaceous species that has resulted from the removal of sheep grazing, and there was no evident difference in recruitment between this and the sheep grazed area. It may require a particularly dry year to show any effects of cover on water availability.

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