New Zealand Journal of Botany, 1989, Vol. 27: 401–414
0028–825X89/2703–0401–$2.50/0

Reproductive and vegetative biology of *Cirsium vulgare* (Savi) Ten. (Compositae: Cynareae)

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Abstract Achenes of *Cirsium vulgare* germinated at constant temperatures between 7°C and 32°C. Fresh achenes had a higher optimum temperature of germination (23.5°C) than older achenes which had been stored for 10 months (20°C). Fresh achenes also germinated more slowly and had a lower maximum level of germination. Achenes that were buried in the soil showed a decrease in viability over time. At depths of 2 cm achenes either germinated or were destroyed. At greater depths the achenes showed an exponential decay rate in viability with time. The slope of this exponential curve decreased with increasing depth of burial. Germination in the field was synchronous with rainfall pattern over the summer, although subsequent germination may occur if achenes are brought to the surface. Young seedlings were not damaged by frosts of –2°C. After germination a major root system developed rapidly, whilst a rosette more slowly formed above ground. Rosettes increased in diameter until the winter when growth ceased, although horizontal growth was reinitiated if the rosette became damaged. In late winter or early spring vertical growth is initiated, leading to the formation of a bushy plant with subsequent flowering and production of achenes. *C. vulgare* flowers throughout the spring and summer with the maximum number of plants flowering in the late spring or early summer. Each capitulum holds approximately 200 achenes and a large plant may produce in excess of 50,000 fertile achenes. Apart from fertile achenes, "shrunken" and "hollow" achenes are also produced by non-pollination and self-pollination respectively. After the capitulum has matured the achenes are wind dispersed. However, despite the presence of a pappus the majority of achenes fall within a circle of radius 1.5 times the height of the parent plant. In conjunction with the production of non-viable achenes through self-fertilisation, this is expected to result in marginal spread of this species from existing infestations.

Keywords *Cirsium vulgare*; weeds; seed biology; vegetative growth; reproductive biology; wind dispersal; biological control

INTRODUCTION

Cirsium vulgare (bull or spear thistle, known as Scotch thistle in New Zealand) is a biennial herb, typically 50–150 cm in height, that occurs throughout New Zealand in disturbed habitats and pasture. This thistle was introduced from Europe in the latter half of last century, probably as a contaminant of grass or cereal seeds. Two chromosome races have been recorded from Europe (Tutin et al. 1976) with $2n$ = 68 and 102 respectively. Local populations sampled by Michaux (1984) had a diploid chromosome number of 68.

Cirsium vulgare reproduces entirely through achenes, henceforth referred to as seeds. Disc florets are contained within a capitulum, which itself is composed of numerous simple bracts that have long, sharp apical spines. The seeds are held upon a receptacle and are surrounded by setae which develop from the receptacle surface (Fig. 1A). The pappus is attached to the achene along a disc-like structure.

The stamens are situated near the base of the tubular corolla (Figs. 1B and 1D). There are five stamens from which free filaments emerge, eventually fusing to form an anther tube. The style enters the anther tube at the base. When the floret has matured the style breaks through the end of the anther tube carrying with it pollen that has adhered to it (Fig. 1C). The pollen is stored in the anther tube.

Received 23 May 1988; accepted 31 January 1989

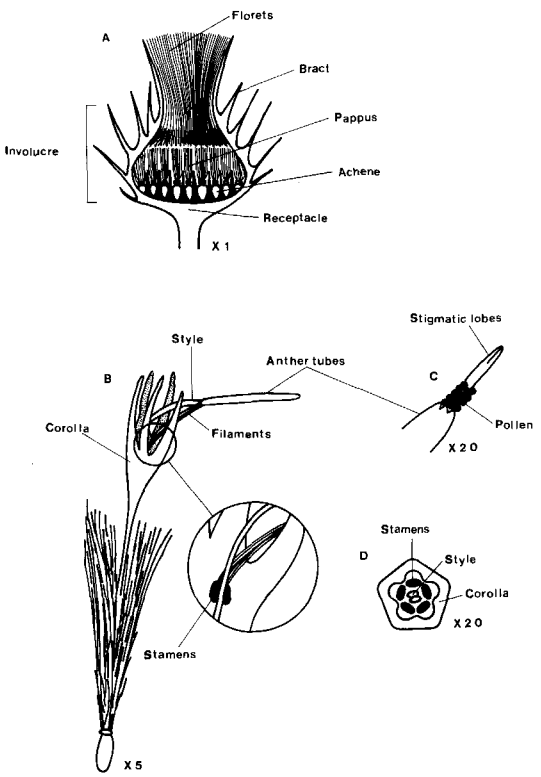

Fig. 1 **A** transverse section through a capitulum. **B** a single floret with detail of stamen positions. **C** detail of stigmatic lobe and adhered pollen. **D** transverse section through a corolla.

Mechanical stimulation, such as produced by pollinating insects, causes the style to extend further. This extension continues until the style is straight. Following this the stigmatic lobes open and the stigma is ready to receive pollen. Florets do not mature synchronously, the outer florets maturing first and the innermost last. This is probably a reflection of the order in which the florets develop, presumably a reflection of the phyllotaxis of flower development.

The number of flower heads on a plant is correlated to its overall size, as measured by the plant's maximum diameter as a rosette ($y = 4.4x - 152$; $r^2 = 0.81$; y = flower numbers; x = maximum rosette diameter [cm]). The flower heads are either single or in groups of three, situated at the apex of the numerous branches of the inflorescence (terminal flower heads), or growing at the apex of lateral stems (lateral flower heads). The corolla is a light purple colour and the filament tube somewhat darker. Individual flower heads last for only a few days before the floral tissue wilts, the involucre bracts then turn brown and open out (the time taken depending on the humidity) exposing the pappus to the air. The innermost seeds are dispersed first as the receptacle arches upwards due to the opening of the bracts (Small 1918). The pappus attached to them then becomes subject to air movement. A single plant may remain in a flowering state anywhere from one to six weeks depending on the number of flowers on it. Pollinators include the honey bee (*Apis mellifera*), bumble bees (*Bombus* spp.), and hoverflies (Diptera: Syrphidae), although various adult Lepidoptera, Thysanoptera, and Hymenoptera (*Leioproctus* spp.) may also act as pollinators.

This study was carried out as part of an investigation into the feasibility of controlling *C. vulgare* through an integrated approach involving such factors as pasture management and the introduction of biological control agents. In order to implement such an approach considerable detail of the biology of the target weed has to be known. The overwhelming preponderance of papers in the literature concern biochemical responses of weed species. In comparison there are few that focus on general biology – an indication of the type of data required when herbicidal control is the desired option. Traditionally this type of control has been the only option, yet for a variety of reasons other control strategies are now being explored and in some cases implemented. Because these alternative methods require a knowledge of why the weed is a problem before a solution can be found to control it, details of many aspects of the weed's biology need to be known. It is this information for *C. vulgare* that is reported in this paper.

SAMPLE SITES AND MATERIALS

Two study sites were used at Kaukapakapa which is 40 km north-west of Auckland (36°35'S 174°25'E). Kaukapakapa is situated in a broad river valley. The soil is predominantly a heavy clay loam, although some restricted areas of alluvial silt are also found. The climate is typical of much of Northland, with annual rainfall in excess of 1000 mm and a mean temperature of 16°C. The winters are wet and the valley soils are frequently saturated. In summer these soils are subject to extensive drying causing retardation of pasture growth and the development

of deep cracks, particularly so on the clay soils. Despite this area's proximity to the Kaipara harbour, heavy frosts are experienced during the winter as cold air flows into the valley where it is retained by the surrounding hills.

Study site A was a 30 × 30 m plot on pasture which gently sloped towards the north-east. This site was unfenced to allow both sheep and cattle to graze, and was selected because it had a high density of Scotch thistles growing on it (0.23 m^{-2}). Study site B was a 6 × 6 m plot of bare soil on which a number of thistle seedlings had established naturally, and to which a further 27 were transplanted (total number of plants = 64).

METHODS

Flowering phenology

A total of 275 plants were growing at sites A and B. Every two weeks the numbers of flowering plants at these two sites were noted. A plant was recorded as flowering from the time the first flower head opened until the last flower head died.

Effect of different pollination treatments on seed production

Three plants were chosen from a group of a dozen plants that were growing along a fence line adjacent to site B during early March of 1982. All of the plants were flowering and numerous bees were present, ensuring that adequate cross-pollination would occur. Six terminal buds on each plant were chosen and treated with a household insecticide spray to kill any small insects, such as thrips, which may have been present and acted as pollinators. Four of these buds on each plant were then enclosed in a wire frame over which white muslin was stretched and tied securely at the base. When the buds flowered two of the enclosed flowers per plant were self-pollinated by hand using a soft paint-brush. This was repeated daily until the flower died. The other four buds per plant, two of which were covered in muslin, received no treatments. Thus, a total of six buds were cross-pollinated by the usual pollinators of this species, six buds were selfed, and six buds remained unpollinated.

The mature seed heads were removed and left to dry for a week. The heads were then opened in the manner described below and the number of shrunken and normal seeds recorded. The normal seeds were then germinated in an incubator at 20°C and 12 hours of light. The remaining ungerminated seeds were dissected and the number of empty seeds recorded.

Seed production and fertility

Seeds were collected by removing all unopened but mature seed heads (i.e., floral tissue had withered) from every thistle growing in a 2.5 ha paddock adjacent to site B (n = 26 plants). A random sample of 30 seed heads was then drawn from this collection. Each head was cut transversely about 1 cm above the base of the receptacle and the seeds removed. The seed head was then dissected and any remaining seeds removed. Two seed forms were found, "normal" and "shrunken". The mean number of seeds of all types was 211 ± 21 seeds per flower head.

The shrunken seeds were discarded and the normal seeds from the 30 seed heads were mixed. Eight samples of 50 seeds were then randomly selected. These were put to germinate in an incubator at 20°C and 12 h light. Any ungerminated seeds remaining 48 hours after the last germination were dissected. A number of hollow seeds were found and their numbers were recorded. The small number of filled seeds that did not germinate were not recorded. Data concerning the production of these different seed types were subsequenty obtained from a sample of six seed heads collected from site A throughout the year.

Dispersal of seeds

An experiment was designed to investigate the efficiency of wind in dispersing *C. vulgare* seeds from a single plant. This plant was 1 m high and produced 89 flower heads which yielded 18,800 seeds based on an estimate of 211 seeds per seed head. All thistles surrounding this plant were removed prior to the start of the experiment. A hinged circular seed trap, partitioned into a central area with four equal areas surrounding it (area = 0.06 m^2), was fitted around the base of the plant. Sixteen seed traps, 10 cm deep, were constructed from plastic tubs. These tubs, of equal area to the partitions in the basal seed trap, were arranged in four lines running north, south, east, and west. They were placed at distances (measured from the centre of the traps) of 0.33 m, 0.67 m, 1.0 m, and 1.5 m from the stem of the plant. These traps, half filled with water, were buried so that the top of the trap was level with the soil surface. These traps were visited daily and the number of seeds in each recorded before removal.

Longevity of seeds in the soil

It is known that many seeds, particularly those with a hard testa, can remain viable in the soil for many years (Harrington 1972). Popay et al. (1987) have

demonstrated this for seeds of nodding thistle (*Carduus nutans*). Casual observation of the effects of soil disturbance, with the subsequent proliferation of thistle seedlings, suggested that *C. vulgare* seeds remain viable when incorporated into the soil seed bank. An experiment was designed to try and quantify aspects of this phenomenon.

Forty-five replicates of 100 seeds were withdrawn at random from a bulk seed sample collected previously. These replicates were placed in forty-five open plastic petri dishes to allow for microbial and predator action. Fifteen of these dishes were buried at each of three depths. These depths were 2 cm, 10 cm, and 20 cm, which corresponded approximately to the top, middle, and bottom of the topsoil. The petri dishes were not drilled to provide drainage. However, it is unlikely that the moisture content of the soil in the petri dishes was different from the surrounding soil because capillary action should ensure even distribution of moisture. Free water would collect in the bases of the petri dishes only when the surrounding soil was itself saturated.

At intervals of three, six, and twelve months after placement, five dishes from each depth were recovered. Seeds were sieved from the soil and the viability of the seed estimated using trizolium tetrachloride. This colourless, water soluble compound is reduced to a red form by living tissue (Colbry et al. 1961). Prior laboratory testing showed no significant differences in viability estimates between germination trials and those obtained through staining. These results are detailed in Michaux (1984) together with a discussion on the difficulties associated with this technique.

Temperature requirements for germination

Nine replicates of three 9 cm diameter petri dishes (27 dishes in total), lined with Whatman filter paper and containing 100 seeds, were placed at different positions along a thermogradient plate. The lowest temperature attained by the thermogradient plate was 7°C. The temperature across the centre of each petri dish was calculated from a temperature-distance graph obtained from steady state readings of thermometers placed along its length. Full details of the temperatures at which individual petri dishes were kept are given in Michaux (1984), but ranged from 9°C to 40°C. Seeds were arranged individually along the equator of the petri dish, with approximately equal numbers either side of this line. Seeds were defined as having germinated when radicle length reached 1 mm, germinated seeds being counted and removed every 24 hours. The filter paper was kept moist with distilled water throughout the experiment.

Two separate experiments were sequentially run on the thermogradient plate, one using old seed the other fresh, in order to see if there were any differences in germination characteristics. Old seed had been collected 10 months prior to the start of the experiment, sun dried on newsprint, and stored on a laboratory shelf in cork-stoppered glass vials. Fresh seed had been collected from plants growing in the two study sites the day prior to the start of the experiment (February, 1983). Data for old seeds were collected over 7 days (no germination on day 1) and the experiment terminated when the fastest germinating dishes had reached maximum germination percentages, i.e., when no further germination occurred. Data for the new seeds were collected over 12 days (no germination on day 1, and no data collected on day 9). This experiment was terminated after 12 days because the equipment was required for undergraduate teaching courses.

Periodicity of seedling emergence

The method described is similar to that used by Roberts & Chancellor (1979). Seeds were collected during the peak flowering period in December from plants growing in the two study areas. Two wooden boxes, each measuring 50 × 25 × 12 cm, were filled to within 3 cm of the top with sterilised peaty loam. Two batches of 1000 seeds were drawn at random from the bulk collection, and each mixed with sufficient soil to fill the boxes. The two boxes were placed in the open above ground level, and covered with mesh. One of the boxes was watered whenever the soil showed signs of drying out, the other received no additional watering other than rainfall. At the end of each month seedlings were counted and removed, and the soil was stirred to a depth of 3 cm to bring fresh seeds to the surface.

Vegetative growth

Following germination, the young seedling rapidly grows a number of main roots that allow the plant to become established quickly. This initial establishment is followed by rosette growth before vertical growth is initiated. Growth rates were investigated by tagging all plants within randomly chosen quadrats at each study site ($n = 20$ plants at site A, $n = 21$ plants at site B), and measuring the diameter or height (whichever was appropriate) at two weekly intervals.

RESULTS

Flowering phenology

The results of flowering phenology are summarised in Fig. 2. For this sample of 275 plants, flowering lasted from the middle of October to the middle of March, a period of five months, with a peak in the second half of December. Although the peak period of flowering of this sample is representative, the range of flowering time is probably affected by the sample size. All 275 plants flowered, the individual duration of flowering varying with the size of the plant. Large plants with several hundred buds can be expected to be in flower for six weeks. Subsequent to flowering all the plants died.

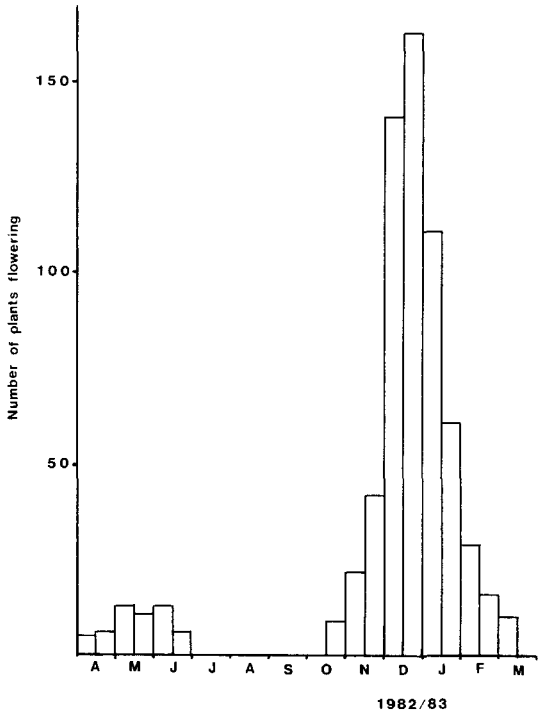

Fig. 2 Flowering phenology based on a sample of 275 *C. vulgare* plants at sites A and B. Counts recorded fortnightly from April 1982 through to March 1983.

Effect of different pollination treatments on seed production

The results from the effect of different pollination treatments on the production of different seed types are given in Table 1. An ANOVA performed on the raw data showed a significant interaction term between pollination treatment and seed type (F ratio = 90.8, $P>F = 0.000$, d.f. = 4).

The data indicate that non-pollination results in shrunken seeds and self-pollination in hollow seeds. The hollow seeds present in the seed heads that were non-pollinated resulted from self-pollination caused by the build up of pollen within the wire and muslin covers that surrounded the flower head. The high level of shrunken seeds in the self-pollinated seed heads is a reflection of the inefficiency of the self-pollinating technique. The levels of self- and non-pollination in the control are consistent with other results (see Table 2).

Table 1 Effects of different pollination treatments on the proportions of different seed-types of *C. vulgare* produced. All numbers are mean percentages with 95% confidence intervals.

	non-pollination	self-pollination	cross-pollination
shrunken	85±8	31±27	3±3
hollow	13±6	63±28	5±3
viable	1±4	6±8	92±6

Seed production and fertility

The data from this study are presented in Table 2. The important conclusion from these data is that

Table 2 Seasonal variation in fertility of samples of *C. vulgare* seeds from January 1982 until January 1983. All figures are means with 95% confidence intervals. ND = no data.

Month	No. of capitula examined	No. seeds per capitulum	% shrunken	% hollow	% viable
January	30	211±21	4±2	11±5	86±5
May	6	207±40	22±9	75±3	5±3
June	6	236±50	96±9	ND	0
November	6	345±103	6±3	53±7	41±6
December	6	282±118	2±1	15±7	81±6
January	6	340±51	3±4	3±3	95±3

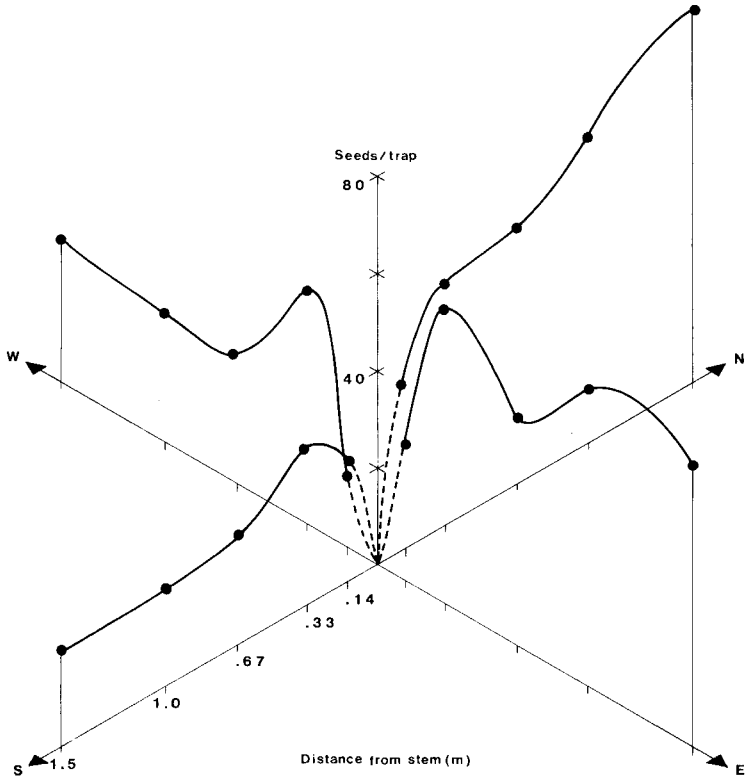

Fig. 3 Dispersal of seeds from a single plant 1.0 m high, based on trap counts at the distances from the stem indicated. Prevailing wind from the south-west.

fertility (i.e., realised fecundity) varies with time. During the main flowering period (i.e., December – January) the majority of seeds produced by a single plant are viable and fertility is at a maximum. A small number of shrunken and hollow seeds are produced during this period because of low levels of non-pollination and self-pollination respectively. As the season progresses, two factors come into play which cause a decrease in fertility. The first of these is a decrease in the density of flowering plants as the flowering season ends, resulting in an increase in self-pollination, and a corresponding increase in the number of hollow seeds produced.

The second factor is the decrease in number of pollinators, mainly *Apis mellifera* and *Bombus* spp., resulting in non-pollination and the production of shrunken seeds. The results from this study suggest that low densities of flowering plants resulted in a decrease in fertility prior to falling pollinator numbers. At the beginning of the flowering season there is a rapid increase in fertility as the density of flowering plants increases. Because pollinators are already active prior to the start of the flowering season, a low level of non-fertilisation was recorded during November and December.

Dispersal of seeds

The results for the numbers of seeds trapped at given distances from the plant are summarised in Fig. 3. This diagram shows that more seeds are dispersed in the downwind direction (between north and east) beyond 0.33 m from the plant, i.e., beyond a third of the plant height.

The numbers per trap were then converted into density measures, which were used to calculate the number of seeds falling within the areas sampled by those traps. The totals for each area were then summed and this figure expressed as a percentage of the estimated number of seeds produced by the plant. These results are presented in Table 3. Of the estimated 18 800 seeds produced by the plant, 17 200 (91%) are calculated to have fallen in a circle with a diameter of 1.5 times the plant height.

Longevity of seeds in the soil

The results of this experiment are given in Table 4. Decrease in seed viability is clearly affected by both length and depth of burial, and, as demonstrated by the two-way ANOVA, by an interaction effect between the two. The best fit exponential decay

curves for the results of burial at 20 cm and 10 cm are given in Fig. 4. Seeds buried just below the surface either germinate or are destroyed through insect or microbial activity. Very few can be expected to remain viable (as estimated by TTC staining). Those buried at greater depths show an exponential decay in viability, with some indication that this rate of decay decreases with depth. Numbers of viable *C. vulgare* seeds in the soil seed bank are maintained through a combination of annual importation of fresh seed and induced dormancy in a proportion of older seed, that proportion being related to both age and depth of burial.

Temperature requirements for germination

The results are summarised in Fig. 5 and 6. In Fig. 5 the mean germination percentage, rounded to the nearest whole number, was plotted against temperature. This was repeated for each day that the experiment ran, resulting in six separate "curves" for old seeds (Fig. 5A) and ten for fresh seeds (Fig. 5B). Following the analysis suggested by Thompson (1970) the graphs were then simplified to aid comparison. This was achieved by calculating the maximum and minimum temperatures at which 50% of the maximum observed germination occurred, for each day that this level was reached. This is done by reading these temperatures from the graphs in Fig. 5 where the 50% germination line cuts the curves.

Table 3 Analysis of seed dispersal data. Plant height = 1m. Estimated number of seeds = 18800 (89 capitula × 211 seeds/capitulum). Estimated % of seeds falling within 1.5 × plant radius = 91.5%.

Sector radius	Area (m^2)	Density (m^{-2})	No. of seeds in sector
0–0.18m.	0.06	720	40
0.18–0.33m.	0.28	2080	580
0.33–0.67m.	1.07	2720	730
		2220	590
		2100	560
		2910	780
0.67–1.00m.	1.73	3080	1330
		1210	520
		1500	650
		3110	1350
1.00–1.50m.	3.93	3390	3330
		1130	1120
		1860	1830
		3950	3880
Total seed			17200

These temperatures are plotted against time in Fig. 6. The best fit quadratics through these points are also given in Fig. 6. The two curves summarise germination characteristics including the maximum, minimum, and optimum temperatures for germination (Thompson 1970). The optimum temperature for germination is at the turning point of each parabola, which for old seeds is 20°C and for fresh seeds is 23.5°C. The maximum and minimum temperatures of germination for both types of seeds have extrapolated values of approximately 32°C and 7°C, respectively. The two types of seeds also differ in rate of germination and maximum observed germination percentage. Fresh seeds have both slower rates, and lower percentage germination than old seeds.

Periodicity of seedling emergence

The seedling counts are summarised in Fig. 7. The results show that most seeds germinate as soon as sufficient moisture is present. The phenology of seedling emergence is thus synchronised with rainfall. The majority of seeds are dispersed between November and March which, under normal rainfall patterns in this area, produces two thistle crops – one derived from early germinating seeds, the other from early autumn germination following increased rainfall in March or April. Finally, the young seedlings which were present during frosts, when minimum air teperatures of –2°C. were recorded, appeared to be unharmed.

Vegetative growth

The results of vegetative growth are summarised in Fig. 8. The plants at site A were already well established when the study started in April (mean diameter 54±11 cm), but continued to grow until the

Table 4 Results and analysis of burial and recovery data for *Cirsium vulgare* seeds. Raw data is for number of seeds stained with trizolium tetrachloride (maximum possible = 100).

	Depth of Burial		
	2cm.	10cm.	20cm.
Retrieval Time			
3 months	1,0,0,0,0	30,14,13,7,6	44,33,28,22,21
6 months	3,1,1,0,0	16,15,10,9,6	27,19,19,17,6
12 months	2,1,0,0,0	20,8,7,6,3	12,12,9,6,3

	d.f.	Anova s.s.	F-value	P>F
depth	2	2443.2	34.82	.0001
time	2	564.4	8.04	.0013
depth*time	4	635.0	4.52	.0046

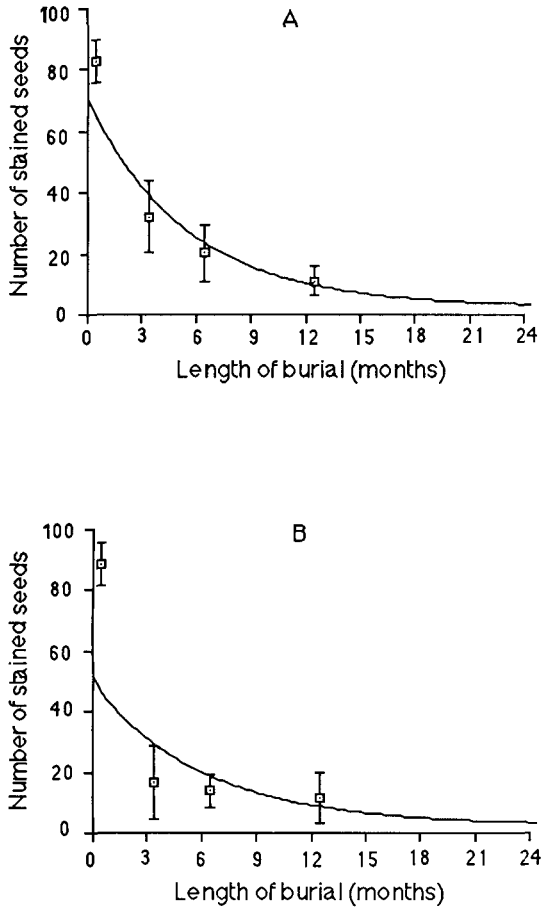

Fig. 4 Decrease in numbers of seeds stained with trizolium tetrachloride as a function of time. **A**: Decay curve for seeds buried to 20 cm depth. **B**: Decay curve for seeds buried to 10 cm depth. Error bars are 95% confidence intervals. Best fit exponential curve generated and drawn by computer. A $y = 62.3 \times 10^{-0.078x}$ $r^2 = 0.94$
B $y = 43.7 \times 10^{-0.071x}$ $r^2 = 0.64$.

middle of May. During early July the plot was subjected to heavy density grazing by cattle which resulted in considerable damage to the rosettes. This damage stimulated regrowth with the result that by late September the mean rosette diameter had returned to predamage levels. From the middle of August vertical growth was initiated resulting in a period when plants increased both in diameter and height, but by early October lateral growth had ceased and all growth was concentrated in height increase.

The results from site B are similar. Rosette growth continued for slightly longer than for the larger rosettes at site A which, together with the

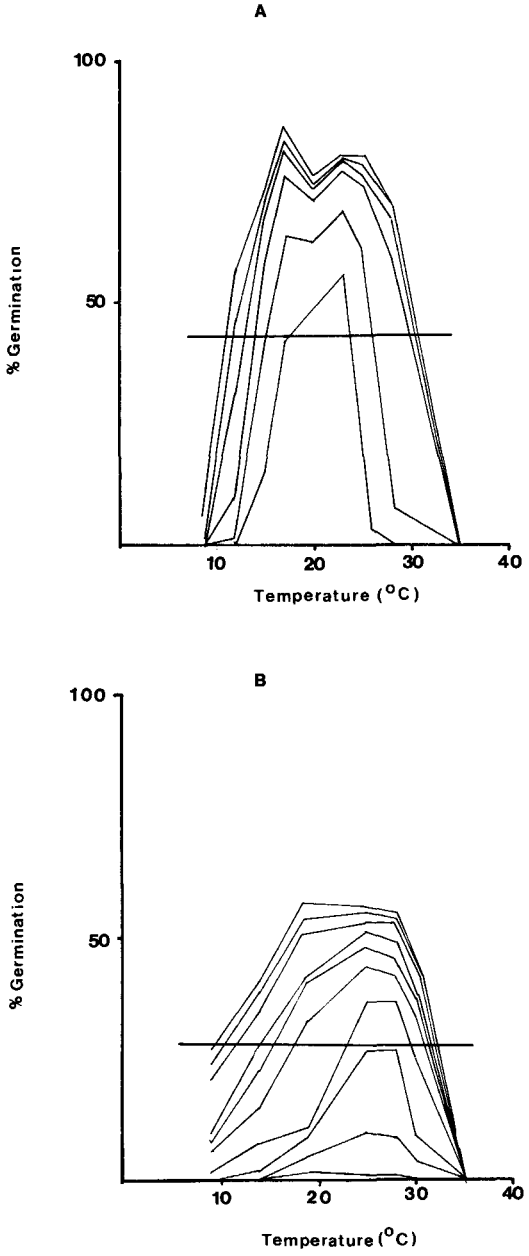

Fig. 5 Germination characteristics of old (**A**) and fresh seeds (**B**). Horizontal bar represents 50% of the maximum observed germination in each case. Each line represents the results for one day.

effects of damage in stimulating regrowth, suggests that lateral growth is inhibited by some internal feedback mechanism rather than by environmental cues such as temperature or photoperiod. Vertical

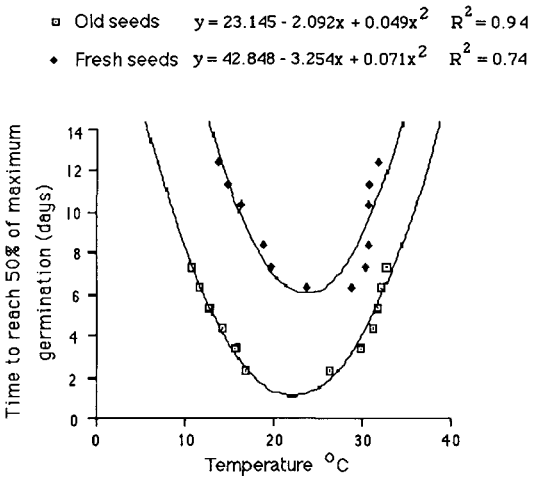

Fig. 6 Summary graph of the germination characteristics of old and fresh seeds. Best fit parabolas generated and drawn by computer.

growth was synchronous in both areas which suggests that lengthening days may have cued this response. The mean maximum height of plants in the two areas was not significantly different ($P>0.2$) despite the mean maximum diameters being significantly different ($P<0.0001$).

DISCUSSION

The peak flowering period for the sample of plants studied was in the second half of December, with a range between October and March. However, it is usually possible to find some *Cirsium vulgare* plants flowering at most times of the year. It is probable that plants flowering in late autumn originate from seeds dispersed early in the main flowering period, or from seeds that have been brought to the surface from the seed bank during the winter or early spring. It is normal for thistles to live for eight to nine months in the rosette stage. However, with the accelerated growth expected during the spring and early summer, and again in the early autumn after rain, it is likely that these plants could complete their development within a single season, behaving as annuals.

Local populations of this species appear to be largely self-infertile. This phenomenon was also reported by Sempala-Ntege (1969) for English populations that he sampled, but appears to be at variance with results reported for Dutch populations by van Leeuwen (1981). Van Leeuwen concluded that "absence of cross-pollination resulted in reduced

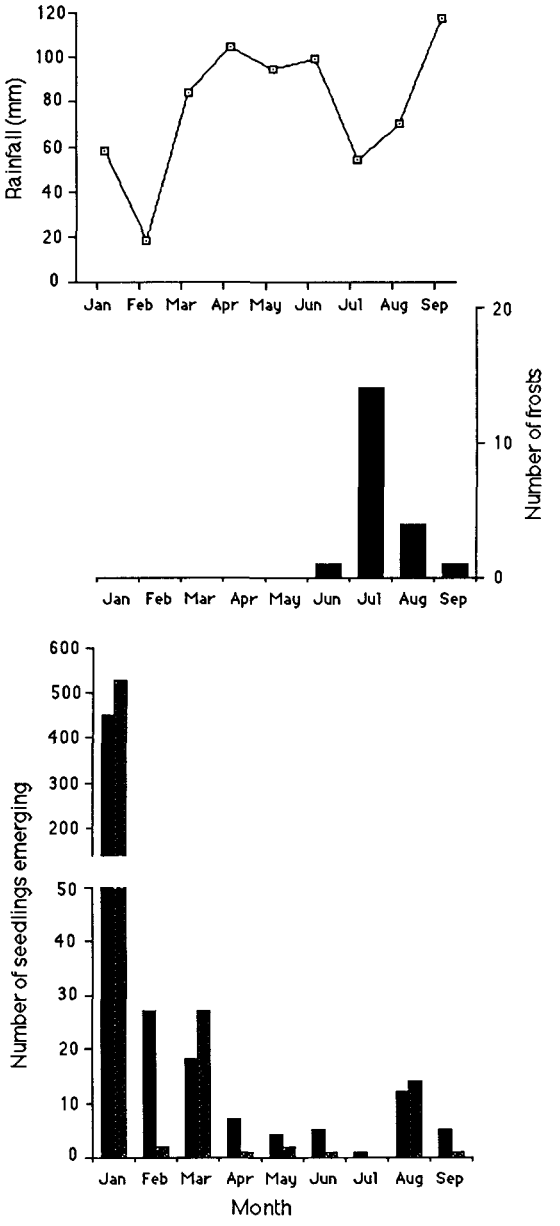

Fig. 7 Upper: Details of local rainfall pattern and number of frosts for January through to October 1982. Lower: Seedling emergence pattern in two seed boxes kept outside over the same period. Solid shading watered, cross hatched unwatered.

achene production ....", but lack of quantitative data concerning the magnitude of this reduction makes a comparison of results difficult. From his description it would appear that a similar phenomenon operates in Holland, but at much reduced level.

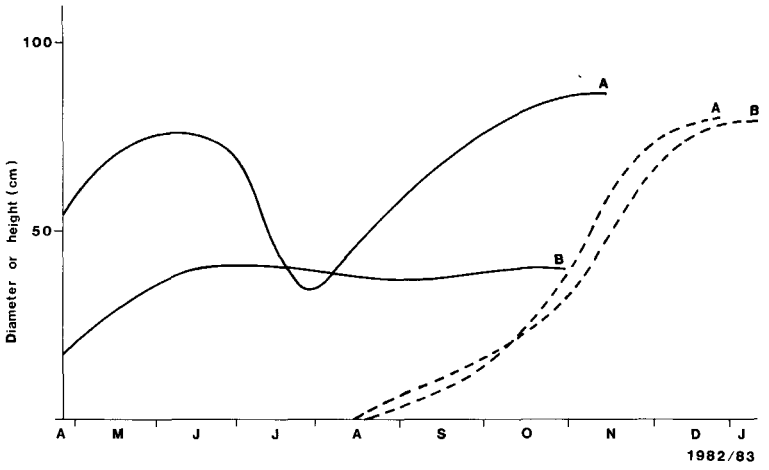

Fig. 8 Lateral (solid line) and vertical growth (broken line) based on measurements taken from 41 *C. vulgare* plants from April 1982 through to January 1983 at sites A and B.

The bases of plant self-infertility have been discussed by Heslop-Harrison (1978), who notes that a sporophytic self-incompatibility system is developed principally in the Cruciferae and the Compositae. In this system incompatible pollen grains are inhibited from developing while still on the stigma, either before or shortly after the pollen tube has emerged. The genetic basis for this is believed to be a single sterility locus with a variable number of alleles existing at the locus. In the sporophytic system, pollen carries the parental (diploid) genotype and any shared sterility allele between pollen and stigma results in incompatibility.

If such a system operates in *C. vulgare* then the situation must be more complex than outlined above because, independent of the number of alleles at the sterility locus, self-pollination should always result in an absence of viable seeds. Details of the incompatibility system of this species may explain the differences already noted between the results reported by Sempala-Ntege (1969) and this paper with those of van Leeuwen (1981).

Although *C. vulgare* requires cross-pollination to set fertile seed – a somewhat surprising result from this study considering the opportunist nature of the weed – this is achieved by the majority of plants flowering over a restricted time period when pollinators are active. Only those plants that flower in the main flowering period, or where plants are growing in sufficient density, will contribute substantially to the following generation.

Seeds of this species have an attached pappus allowing for wind dispersal. However, the results of this study suggest that this is an inefficient dispersal mechanism for the majority of seed. It is estimated that only 9% of the seed was dispersed beyond 1.5 m from the plant used in this experiment. This estimate seemed low, particularly when viewed against the results indicated in Fig. 3. Two reasons account for this probable underestimation of the percentage of dispersed seeds. Firstly, seeds with a pappus tended to swirl around the ground surface, therefore the seed traps effectively sampled an area greater than the area of the trap. This could have been minimised by laying out additional seed traps, or by not burying the seed traps. Secondly, because seeds could not escape once trapped, there was no further possibility of subsequent, longer distance dispersal. It is difficult to see how one might overcome this problem.

As an additional check on the validity of this estimated dispersal figure, data from the field trials were collected. An estimate of the number of seeds that had fallen in one of the original 3× 3 m quadrats of site A was calculated. A corner quadrat was chosen in which three plants had matured, producing 194 000 seeds (918 flowers × 211 seeds). The number of small seedlings growing in this quadrat was estimated to be 4 800 which, from survival probabilities (Michaux 1984), were produced by 113 000 seeds. Assuming no seeds had been lost to the seed bank and that no importation of seed occurred (or they were equal) it was calculated that 58% of the seeds produced had fallen within that quadrat.

A final piece of field evidence is presented in Fig. 9 which summarises the analysis of thistle distribution in study area A. The observed results were obtained from the distribution of thistles in the original 100 3 × 3 m quadrats that site A was divided into. The expected values were generated using the Poisson distribution and a χ^2 goodness of fit test performed (Kershaw 1964). The observed distribution is highly clumped. Such a distribution

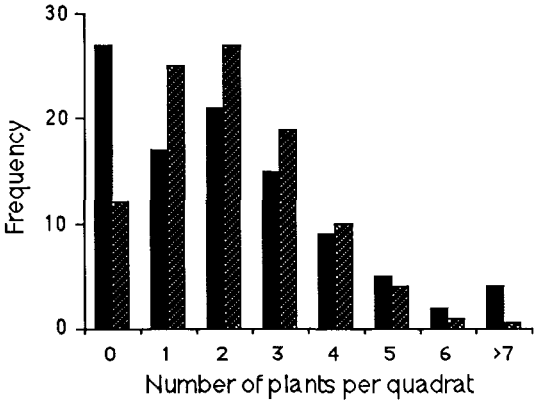

Fig. 9 Histogram showing observed (full) and expected (cross-hatched) distribution of numbers of thistle rosettes per 3 × 3 m. quadrat. Observed data based on the original 100 3 × 3 m quadrats that site A was divided into. Expected numbers generated using a Poisson distribution with mean (number of plants/quadrat) of 2.11. $\chi^2 = 48.4$, $P < 0.001$, 6 d.f.).

can be explained in a number of ways, but the most parsimonious explanation is that it is a reflection of the distribution of the preceding generation. This clumped distribution is consistent with limited dispersal.

Sheldon & Burrows (1973) investigated the relative efficiency of Compositae "dispersal units" (pappus and seed) of a number of species in aiding wind dispersal under a given set of conditions. They concluded that a number of factors affect dispersal distance. Some of these relate to the structure of the dispersal unit, the most important of which is the complexity of the pappus unit. Those composites with complicated pappus structures such as pappus hairs (like *C. vulgare*) have lower terminal velocities and higher aerodynamic drag coefficients, and hence remain airborne longer.

A number of external factors were also considered to have important effects on dispersal efficiency. Sheldon & Burrows (1973) concluded that the occurrence of a convective current has greater effect than the strength of horizontal air movement which, in any case, may detach pappus from seed if it is too strong. The effect of relative humidity on the opening and closing of the involucre bracts, on the force with which the seeds are held in the receptacle, and on the opening of the pappus is described in Dandeno (1905) and Small (1918). The height from which a seed disperses also affects its dispersal distance, as do details of the surrounding terrain. The main conclusion of their work is that primary projectory distances are generally in the order of a few metres. It should be stressed that seeds have the potential for further dispersal, provided that they remain attached to the pappus. However, it would seem that the pappus is not a very efficient means of dispersal, even under "ideal" conditions.

Experimental and field observations of other studies tend to confirm these conclusions. Poole & Cairns (1940) investigated the dispersal of ragwort seeds (*Senecio jacobaea*) from a large infestation. They calculated that 60% of the seeds were deposited within the infestation and that most of the rest remained in the capitula. Approximately 0.5% became windborne with approximately 80% of these being deposited within 37 m. They conclude that only a total of 0.1% of seeds would have been transported further than 37 m, predominantly in the downwind direction.

These results appear general; wind dispersal is not an efficient means of seed dispersal in the sense that the great majority of seeds fall in the immediate vicinity of the parent plant (Augspurger 1986; Augsperger & Franson 1987; Forcella & Woods 1986; Sharpe & Fields 1982). In comparison with seed dispersal distances reported by Werner (1975) for seeds of *Dipsacus sylvestris* Huds., which have no wind dispersal structures, it is apparent that for the majority of seeds the dispersal distance is similar whether wind dispersal structures are present or not. Differences are apparent, however, in extreme dispersal distance which are a feature of wind dispersed seeds. As Augspurger (1986) notes "the relative importance of mean and extreme dispersal distances is unknown".

Long distance dispersal of only a small percentage of *C. vulgare* seeds, combined with its self-incompatibility and high mortality rates for very young seedlings (Michaux 1984), suggests that successful long distance dispersal in this species would be a rare event and that spread of infestations is marginal. That is, infestations will increase in size each year, but that this spread will be moderate. What will happen is that the density of plants within the infestation will increase each year. Data reported in Michaux (1984) sugests that this increase will be in the order of a factor of 9 per year on pasture and considerably higher on bare ground. Seeds are certainly not spread uniformly over a wide area, as has been assumed by authors such as Auld et al. (1979) when modelling control strategies for fecund annuals and biennials. The rapid spread of this

species throughout New Zealand following its introduction is therefore likely to have been aided by humans. Seeds were possibly moved from district to district with stock and plant products such as grass and cereal seed or hay.

After seeds are dispersed from the mature plant the majority lie on or just below the ground surface, with the remainder becoming incorporated into the soil seed bank. The number of C. *vulgare* seeds within the soil seed bank will decline until fresh seeds are added to the seed bank the following season. However, based on the results of this study, a proportion of seeds from earlier years will remain viable for longer than a year, and thus one can expect a steady buildup of *C. vulgare* seeds in the soil seed bank. At any one time the seeds in the soil seed bank will therefore be of mixed age classes. The proportions of different age classes should be in the form of an exponential series. This ability of *C. vulgare* seed to remain dormant if buried to sufficient depth is not, as discussed previously, an uncommon phenomenon. Its importance with respect to the control of this and other weeds is in minimising pasture damage during the wet winter months. Over-stocking during the winter will result in pasture damage and, by bringing viable seed to the surface, increase the level of thistle infestation the following season.

Seeds on the surface are exposed to light. Although it has not been established by this study, light is probably responsible for the differences noted in the germination characteristics of old and fresh seed. That is, light alters conditions within seeds to enhance germination rate, lower optimum germination temperatures, and increase maximum germination percentages.

It has been established that germination percentages of *C. vulgare* seeds are affected by different light treatments (Grime et al. 1981). These authors used three light treatments, full light, shade (2.4% of full light intensity), and dark. The germination percentages recorded were 71%, 75%, and 19%, respectively. This last figure is significantly diferent from the full light figure ($P< 0.01$). Their results show that germination of seeds of this species is inhibited by the absence of light. Williams (1966) reported that an increase in germination percentage was obtained when fresh *C. vulgare* seeds were treated with thiourea, a compound known to overcome the light requirement for germination in some species. It is quite probable that the differences in germination results reported by Roberts & Chancellor (1979) for *Cirsium vulgare* seeds in the UK, and the results reported in this paper, are due to this phenomenon. It is possible that winter temperatures in the UK were too low for germination during the experiment conducted by Roberts & Chancellor, but as these workers failed to stir the soil in the wet winter months, and thus failed to bring fresh seed to the surface, germination would not be expected.

Light can inhibit or stimulate germination through the alteration of an equilibrium that exists between two different forms of phytochrome (PR and PFR) within seed (Borthwick et al. 1952). PFR is active and promotes germination. The equilibrium is shifted towards this form by the absorbtion of red light (l = 630–660nm), and away from this form to the inactive PR by absorption of far-red light (l = 730nm). Futhermore, PFR can be destroyed in the dark by enzymic action, PFR killer, or chemical degradation (Black 1969; Furuya 1968; Briggs & Rice 1972; Kendrick & Frankland 1976).

It would appear that there is insufficient PFR in fresh C. *vulgare* seeds, and that the differences in germination characteristics of fresh seeds already described are a result of the phytochrome equilibrium producing excess PR. The inhibition of germination of buried seeds can be understood in terms of reversion of PFR to PR and/or the destruction of PFR in the dark. It is probable that inhibition of germination would also occur when seeds lie under an unbroken grass cover, because the light reaching the seeds would be enriched with far-red wavelengths (Vezina & Boulter, 1966), causing conversion of PFR to PR. If this last conclusion is correct, then the most important cause of thistle infestation is inadequate sward cover on pastures in the late summer and early autumn when the majority of seed dispersal occurs. Manipulation of grazing regimes during this period has the potential to be included in an integrated approach to thistle control.

This study suggests that when adequate rain falls massive germination of ripened seeds occurs, a conclusion also reached by Forcella & Wood (1986) for this species in Australia. Because seeds tend to germinate where pasture cover is minimal or absent, the young seedlings have limited competition for space from useful pasture species. As they grow the development of a rosette kills surrounding grasses. Once plants have become established it is not possible to control them through grazing manipulation, as damage to established rosettes is compensated for by stimulating regrowth and is, in any case, undesirable because of the probability of initiating a fresh infestation from seeds in the soil seed bank. Removing plants manually should be done after vertical growth has been completed and food reserves have been

maximally depleted but before seed has set. The timing of this will vary from year to year but, on the basis of the results of this study, can be expected in October and November.

C. vulgare is a weed that requires repeated effort on the part of the pastoral farmer if it is to be maintained at low infestation levels. The data reported here, together with an analysis of its associated fauna reported elsewhere (Michaux 1989), make it clear why this is so. Intrinsic factors of the weed's biology, in particular those related to its reproductive capabilities and seed germination characteristics, interact with extrinsic factors to produce high population growth potentials. The most important of these extrinsic factors are the presence of a non-damaging, largely incidental fauna, and the suitability of much of our pastoral land as thistle habitat. There is little that can be done to alter intrinsic factors, these are simply biological characteristics of the weed, but considerable scope exists for the manipulation of the extrinsic factors to ensure that potential population growth is not realised. Introduction of biological control agents and manipulation of pastoral habitats should alter the plant-environment dynamics sufficiently to disadvantage *C. vulgare*.

ACKNOWLEDGMENTS

This work was carried out in partial fullfillment for the degree of MPhil. at the University of Auckland. My thanks to Professor E. C. Young and Dr J. Ogden for discussion and comments on the manuscript. K. Richards drew figures 1, 2, 3, 5, and 8. T. Belsen constructed the seed trap. L. Michaux typed the manuscript. Alan Jordan allowed me to use his land (site A) and maintained his good humour throughout. Comments by the editor and an anonymous referee to earlier manuscripts are gratefully acknowledged.

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