A STUDY OF THE FACTORS INFLUENCING THE EMERGENCE AND ESTABLISHMENT OF RAGWORT (*Senecio jacobaea* L.) SEEDLINGS IN PASTURES

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Abstract

This study was designed to help understand the factors determining the emergence and establishment of ragwort seedlings in pastures. To achieve this it was necessary to determine (a) whether the germination of seeds was affected by the presence of light; (b) the influence of herbage cover on the emergence of seedlings; (c) the seasonality of seedling emergence; (d) the impact of treading on the emergence of seedlings and (e) the behaviour of seedlings in a real farm situation.

In the first experiment, soil containing ragwort seeds was collected from a dairy pasture and subjected to constant light or dark conditions in growth chambers. Seeds subjected to light produced significantly more seedlings (55.6% seedling emergence) than those left in darkness (13.8% seedling emergence). It was concluded that germination is positively affected by light. Apparently, seeds which germinated in the dark were those originally close to the soil surface.

In the second experiment, a hill country pasture near Woodville was either denuded of herbage cover or left intact once every month. For one year, ragwort seedlings were counted to provide information on the seasonality of seedling emergence. Seedling emergence was constantly higher on bare soil than under the pasture canopy, except in summer when no germination was observed for lack of moisture. Peaks of seedling emergence occurred in September (bare soil and intact pasture) and in June (bare soil). Seedling emergence (bare soil) was high even at low temperatures in winter. Seed germination was strongly checked by either the lack of moisture over summer or the presence of herbage cover at any time of the year.

The third experiment was carried out at the same site. A number of defoliation treatments were imposed involving combinations of the presence and absence of herbage cover, treading and grazing. Any form of disturbance to pasture caused a significant increase in seedling emergence. The greatest emergence was found where soil had been denuded of herbage cover, whether trodden or untrodden. Treading generally stimulated germination through damage to the vegetation cover, and some increase in emergence also resulted from soil movement by hooves. Seedling emergence was minimal where pasture was undisturbed.

The fourth experiment was carried out on a commercial dairy farm near Palmerston North over a 12 month period. Without interfering with the normal management system, several pasture attributes were monitored every week at three different sites within the farm to help explain the emergence and mortality of ragwort seedlings. Seedlings were counted every week in permanent quadrats and mapped every fortnight. Seedling emergence and survival varied greatly both between sites and throughout the year. The major determinant of seedling emergence was found to be the proportion of bare soil. Bare soil was largely caused by treading in wet months and by drought during summer/early autumn. No emergence was observed over summer when soil moisture levels were low. Depending on the site, peak emergence occurred in June, August and November. The major causes of seedling mortality were water stress, earthworm casts, treading damage and competition from neighbouring plants. Although autumn emergence was small compared to the emergence observed in winter and in spring, it is apparently the most important period of emergence during the year, since seedlings which emerge in winter and in spring are prone to die over summer from water stress. Ragwort seedlings survived longer periods when the sward height was between 2 and 7 cm (approx.) and when herbage mass was between 500 and 2000 kg DM ha^{-1}.

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Table of Contents

List of Tables

List of Figures

List of Plates

Introduction

Amongst the many plants currently regarded as pasture weeds, ragwort (*Senecio jacobaea* L.) occupies a special position determined by its capacity to overcome a broad range of adverse conditions such as those imposed by climate, herbivores and humans. The potential to grow vigorously, the ability to reproduce itself vegetatively, the capacity to regrow after some physical or chemical damage, the massive production of seeds with different morphology and mechanisms for dispersal, the ability of seeds to remain dormant in the soil for several years, and the production of defensive toxins are just some examples of the extraordinary adaptations which help this species to succeed in a competitive environment prone to moderate levels of disturbance (Poole and Cairns 1940; Harper 1958; Thompson and Makepeace 1983; McEvoy 1984a).

Because ragwort is predominantly a non-perennial (frequently biennial) monocarpic species (Poole and Cairns 1940; Schmidl 1972; Thompson 1985), preventing its establishment in the first place appears to be the most appropriate control strategy, though when plants have become established, avoiding seeding is an important point too.

The recommended way to prevent its establishment is by "developing and maintaining a dense, vigorous and uniform sward" as pointed out by Popay (1980), a practice emphasised in the majority of works addressing the ragwort problem (*eg* Cameron 1935; Poole and Cairns 1940; Harper 1958; Schmidl 1972; Phung and Popay 1981; Rahman *et al.* 1993).

Considering the consistency of the findings of such studies, there is little doubt that the presence of a dense pasture cover has a strong negative effect on the number of ragwort seedlings. However the understanding of how this process operates is still very incomplete. One reason for that is the difficulty of identifying and monitoring young seedlings in the field (Forbes 1977). It is also difficult to isolate the factors influencing seeds and seedlings, particularly in field studies.

Consequently, there is a lack of information on the germination of ragwort seeds naturally occurring in the soil seed bank and the subsequent fate of seedlings affected by changes in herbage mass, soil moisture, intensity of treading by grazing animals, and the existence of patches of bare soil that are expected to occur in a pasture throughout the year. If factors such as these could be clearly associated with the success or failure of seedlings becoming established, we would not only gain an insight into the causes of the establishment of the weed, but we could also design pasture management practices intended to discourage germination or possibly even to eliminate seedlings.

Such knowledge is as important to grazing management decisions (*eg* by showing a minimum pasture cover necessary to keep seedlings in check) as it would be to a chemical control programme (*eg* by indicating the time of the year when the largest number of seedlings will be present, a stage known to be the most susceptible to herbicides).

Nevertheless the increasing costs of herbicide application, the current trend towards the reduction in the use of pesticides, the lack of solid information on the economics of controlling pasture weeds and the relative difficulty of controlling adult plants compared to seedlings, indicate that the recommendation for preventing the establishment of the weed is the best alternative that farmers can use to avoid the ragwort problem.

The first scientific reports of attempts to understand the ragwort problem in this country date back many decades (Cameron 1935; Poole and Cairns 1940) and a range of control methods, from herbicides to insects, have been tried since then. Under the New Zealand Noxious Plants Act, ragwort must be kept in check. Despite this, it was recently voted as the most important weed on New Zealand dairy farms (Bourdôt *et al.* 1994). Perhaps a deeper understanding of the reasons for the occurrence of the species may help us to control it more efficiently.

1.1. Objectives

The main objective of this study was to understand the factors influencing the emergence and the establishment of ragwort seedlings in pastures so that recommendations could be formulated which would help to keep the species under control. To achieve that it was necessary to determine the following:

(i) The influence of light on the germination of seeds obtained from the soil seed bank.

(ii) The seasonality of seedling emergence, *ie* how seeds respond to fluctuations of soil moisture and temperature conditions over the year and how herbage cover can influence germination.

(iii) The impact of treading on the emergence of seedlings, *ie* whether treading increases subsequent seed germination.

(iv) How all of these factors would interact in a real farm situation.

1.2. An outline of the experimental programme

Four experiments were conducted and are described in Chapters 3, 4, 5, and 6. The first experiment (January to March 1994) investigated the effects of light flux on germination of ragwort seeds collected from a dairy farm soil seed bank. Germination took place under the controlled conditions of growth chambers.

The second experiment (August 1993 to July 1994) monitored the periodicity of seedling emergence on denuded or intact plots protected from grazing animals on a hill country pasture.

The third experiment (August 1993 to January 1994) attempted to study the effects of treading on seedling emergence and was carried out on the same site as the second experiment.

The final experiment (July 1993 to August 1994) monitored several pasture attributes with the purpose of relating them to the number of seedlings found at different times of the year. It was carried out on a commercial dairy farm under normal management practices.

CHAPTER TWO

Literature Review of *Senecio jacobaea* L.

2.1. Introduction

This review covers the most important aspects of the biology and control of ragwort (*Senecio jacobaea* L.). However, a little more attention is given to its germination, emergence in the field and subsequent fate of the seedlings, because of the special importance that such knowledge will have in this study.

The work by Poole and Cairns (1940) deserves special attention. Although it was published 55 years ago and is now outdated in terms of plant physiology, herbicides, and experimental procedures, it is still an important reference for anyone wishing to understand this remarkable plant. This is indicated by the number of times it has been cited in the literature on ragwort.

2.2. Morphology

Senecio jacobaea L., mostly known as ragwort but also as common ragwort in Britain (*eg* Watt 1987a) or tansy ragwort in the USA (*eg* Bedell *et al.* 1981), is a member of the large Asteraceae family, and is just one of the many species in the genus *Senecio* L. Four different varieties of ragwort were described in Britain (Harper and Wood 1957), namely *discoideus* L., *abrotanoides* Murr., *stenoglossus* Brenan, and *condensata* Dr. These authors also described several hybrids between *Senecio jacobaea* L. and *S. aquaticus*, *S. squalidus*, *S. erucifolius*, *S. cineraria*, and *S. alpinus*, but no mention of these different varieties and hybrids is found from any other country.

2.2.1. ***Seedlings*** Ragwort seedling cotyledons are described by Poole and Cairns (1940) as thick, short stalked, ovate or slightly obovate, with a broad, flattened or shallowly stalked tip.

The first true leaf appearing a month after germination with only a few further leaves developing in the winter months. Cameron (1935) observed the initial smooth margins of the first leaves soon take on the indented outline characteristic of mature ragwort. As stated by Poole and Cairns (1940), if the plant is undisturbed, a single crown is formed from the top portion of the first root, while the initial tap root is gradually replaced by a horizontally-growing, ramified root system.

2.2.2. *Rosettes* Successive leaves become increasingly pinnatifid with or without cottony hairs on the undersides (Harper and Wood 1957), which is usually paler than the upper surface. Vigorous rosette plants may achieve more than 40 cm in diameter (Poole and Cairns 1940).

2.2.3. *Flowering plants* Undamaged plants produce a single stem, branching above the middle to give a flat-topped, more or less dense compound corymb (Poole and Cairns 1940), and during this period most rosette leaves are lost (Harper and Wood 1957). When conditions are very favourable, stems can reach a height of 1.5 metres or more (Poole and Cairns 1940). The inflorescence produces from 70 to 2,500 capitula per plant, while the number of "seeds" (botanically known as achenes) per capitulum remains fairly constant from area to area, usually around 70. The total number of seeds produced per plant will then vary from about 5,000 to 175,000 (Cameron 1935).

Two distinct groups of florets (the flower unit containing one "seed") in each capitulum can be identified: (a) disk florets, found in the inner part of the capitulum, produce seeds (one each) with a number of small hairs (pappus). These are lighter than the seeds produced in the (b) ray florets (also one per floret); these seeds are hairless and usually bigger than disk seeds (Poole and Cairns 1940; Harper and Wood 1957; McEvoy 1984a).

2.3. Origin, distribution and habitat

Native to Europe, western Asia and northernmost African regions, ragwort has become established in USA, Canada, Argentina, New Zealand and Australia (Schmidl 1972a). Its first record in New Zealand is apparently in 1874, when it was found growing near Dunedin (Thompson 1922).

In Europe, ragwort is mostly found on waste land, pastoral land of poor quality, roadsides, sand-dunes (Cameron 1935), in some woodlands, in overgrazed grassland, and particularly on disturbed ground, especially associated with high rabbit populations (Harper and Wood 1957). It is generally absent when the water table is high or the soil is maintained near field capacity, where it is often replaced by *Senecio aquaticus* (Harper and Wood 1957). Harper and Wood (1957) claim that a decrease in sheep production in Britain during the 1940s resulted in an increase in ragwort populations (see also Section 2.6.5).

In New Zealand ragwort grows in similar habitats to those reported for Europe, but particularly dense populations are more common on medium to light soil types, where rainfall exceeds 890 mm per annum and where sheep are not present, typically on dairy farms (Poole and Cairns 1940).

The geographical distribution of ragwort in New Zealand was first reported by Poole and Cairns (1940) and was later updated by Radcliffe (1969). This latter report showed that the species was spread all over the North Island, with larger populations in Northland, Coromandel, East Cape, Hawkes Bay, Taranaki, Wairarapa, and the yellow brown pumice soils of the central North Island. While the former report mentions only dairy farms, the latter showed the populations to be increasing in hill country areas as well. South Island was not included in the latter reference, but the former points Southland as a region of major occurrence. This sort of data is very rare (Bourdôt *et al.* 1994), and apparently the current, exact regions occupied by ragwort are not known. The most recent account of the ragwort spread is given by Webb *et al.* (1988), who claim that the species is widespread throughout the North, the South, the Kermadec and the Chatham Islands. Other sources of information (*eg* Regional Council reports, farm news, personal observations, etc) indicate that, in New Zealand, the species occurs wherever the factors mentioned in the previous paragraph are present, combined with those described in Sections 2.4.

No New Zealand records exist for the soil pH range in which ragwort can occur, but Harper and Wood (1957) state that in the UK ragwort can be found in soils with pH readings from 3.95 to 8.2.

2.4. Phenology

As with any other plant species, the environment and its seasonal variations play an important role in determining the different phases of a ragwort population. However, as we shall see in this section and also in Section 2.6, human activities can considerably affect its life cycle, either favouring or discouraging its establishment and persistence.

2.4.1. ***Dormancy and germination*** Ragwort seeds are able to remain viable in the soil for a considerable period of time. Harper (1958) and Anon. (1977) report dormancy periods of up to 8 and 6 years respectively. Thompson and Makepeace (1983) showed that in contrasting clay and silt loam soils, viable seeds were present after 6 years of burial. The time taken for seed viability to be reduced to 1% was estimated to be at least 4-5 years in the 0-2 cm surface layer and 10-16 years below 4 cm soil depth.

Poole and Cairns (1940) demonstrated that seed germination can occur even when seeds are fully immersed in water. This varied from 32% to 70%, compared to 76% germination under more optimal laboratory conditions, and was performed with a wide range of water sources (rivers, lakes, rain, drains, etc).

According to van der Meijden and van der Waals-Kooi (1979), freshly shed seeds have no innate dormancy, *ie* they are able to germinate immediately after shedding, when they reach their maximal potential for germination. In fact they state that seeds can even germinate when still attached to the capitulum. This agrees with earlier observations by Poole and Cairns (1940) who obtained 50% to 86% germination in freshly harvested sound seed. However, while the latter observed that viability was lost rather rapidly during storage (76%, 68%, and 21% germination in the first, second, and third year of storage, respectively), the former did not find any significant decrease in germination over a period of three years.

Some delay in germination can occur after exposure to very low relative humidity, as demonstrated by van der Meijden and van der Waals-Kooi (1979) after submitting seeds to 40% relative humidity ("drought shock") and temperatures varying from -20°C ("cold shock") to 35°C for 2 or 6 days. Delay was longest in seeds subjected to a drought shock at 25-35°C. Such delay was interpreted as an induced dormancy, which only lasted from 1.4 to 14.4 days.

In Australia, Schmidl (1972a) obtained 85% germination for seeds collected in summer and 60% for those collected in autumn from late-flowering plants at alternating temperatures of 30/25°C for 12 h light/12 h dark, respectively. Unfortunately this report had minimal information on the methods and materials used, *eg* light conditions, seed source and previous storage conditions, existence of other treatments, etc.

On the other hand, more detailed information is given by van der Meijden and van der Waals-Kooi (1979) who found, over a range of temperature and moisture regimes, maximum germination (92.5%) at 15°C and 29% soil moisture content. Although ragwort germinated within a broad range of temperatures, a clear check occurred above 30°C and below 5°C. Germination was also greatly reduced when soil moisture was lower than 3.6%. Note that the substratum used was very sandy, otherwise this limiting moisture content would certainly be much higher. As a general trend, at any given temperature, an increase in soil moisture increased germination, so the optimum temperature for germination also changed with the soil moisture regime. Seeds which had experienced low moisture conditions (1.8 and 3.6%) and high temperature (30°C) were appreciably reduced in germination potential, even after transfer to a more favourable regime. Germination was said to be higher at alternating day/light temperatures, but no convincing evidence was presented (*ie* plotted data resulted in two very similar curves for which no measure of variability was provided). From the same experiments they found an almost complete inhibition of germination[1] when seeds were covered by a sand layer thicker than 4 mm in laboratory tests (0% germination when depth ≥ 8 mm), with maximum germination (near 80%) from seeds covered by a sand layer of 1 mm. A lower germination (just above 20%) was obtained from seeds laid on the sand surface. This was thought to be due to a lack of moisture, since when these seeds were covered by a thin sand layer further germination occurred. However, in 1940, Poole and Cairns had not observed such difference between surface-laid seeds and those covered with a thin soil layer, except in the speed of germination, as surface seeds had their germination retarded. The lower germination obtained by van der Meijden and van der Waals-Kooi (1979) from seeds covered by a layer thicker than 4 mm was attributed to the absence of light at such depths and from this they concluded that light is

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[1] They probably assessed emergence rather than germination properly, but this was not clear. As pointed out by Harper (1977), the word "germination" should be used when it refers to a laboratory test where seeds with an emerged radicle are counted. In the soil, as this cannot be observed, emerging seedlings are counted and expressed as a percentage of the total seeds initially present. This will represent all seeds that germinated (in the laboratory sense) minus those that died in the pre-emergence stage.

required for germination.

However, Maguire and Overland (1959) had obtained 6% and 36% germination in complete dark conditions at constant temperature of 20°C and alternating temperatures of 20-30°C, respectively. No germination was obtained in the dark when the temperature was kept constant at 15°C. On the other hand, 76% germination was obtained in alternating light (duration not specified) at 15°C, while at 20-30°C germination was only 26%. Seeds had been stored for one year (no details about storage conditions are given) and were germinated on moist paper in Petri dishes. Unfortunately details about methods and materials were insufficient and no information was given about the variability in the data.

Working with several plant species Phung and Popay (1981) demonstrated that vegetation height can affect ragwort germination (at least partly) by altering the light spectral composition (see Chapter 3 for a more detailed discussion on radiant energy). Red/far-red ratio was measured in three treatments, *viz* bare ground (vegetation removed using paraquat), short pasture (kept at 2-3 cm high), and long pasture (kept at 6-7 cm high) all placed in a glasshouse, where germination was assessed by the emergence of seedlings counted regularly up to 35 days from sowing. Red/far-red ratios measured 26.9, 1.9 and 0.5 in bare ground, short pasture and long pasture, respectively. As a result, ragwort germination was 30.8% in bare ground, 14.4% in short pasture and 15.2% in long pasture ($LSD_{0.05}$ = 9.6%). Although there was no significant difference between short and long pasture for this species, germination in these two treatments clearly contrasted with that from bare ground.

2.4.2. *Seed recruitment and seedling establishment* Ragwort is portrayed as being restricted to colonizing open patches created by disturbances that are generally unpredictable in space and time (Cameron 1935; Poole and Cairns 1940; van der Meijden and van der Waals-Kooi 1979). As pointed out by McEvoy (1984a), this generalization has potentially profound consequences for the reproductive biology, population structure, evolution, distribution, abundance, and control of such a species.

Cameron (1935) carried out a field trial in Britain to determine the effect of above ground vegetation on the emergence of ragwort seedlings which comprised six different treatments (limited information was given): (a) long grass; (b) long grass cut short, resulting in small areas of bare soil, to represent an overgrazed pasture; (c) short, continuous turf, regarded as a well-managed pasture under continuous grazing; (d) hard, compacted soil; (e) "ordinary tilth", seeds uncovered; and (f) "ordinary tilth", seeds covered. Each plot (0.30 m^2) was sown with 100 ragwort seeds (32,800 m^{-2}), which had given 80% germination in the laboratory (treatments were not replicated). On examination one to two months later, the following seedling numbers were found per square metre: (a) nil; (b) 656; (c) nil; (d) 6,562; (e) 17,388; and (f) 18,044. According to the author, this confirmed previous anecdotal observations that ragwort did not become established where the plant community was "unbroken". This experiment could be criticized based on the current knowledge of statistics and on the importance of having animals in treatments intending to represent some animal effect on the environment. However, it was the first one studying the relationship between pasture attributes and ragwort seedling numbers.

Later, Poole and Cairns (1940) carried out some experiments at Ruakura (New Zealand) attempting to determine how these seedlings become established. They sowed 100 ragwort seeds in several plots (0.91 m^2 each) permanently set in a cattle-grazed pasture, counting seedlings and sowing again every month for a period of one year. The aim was to count all seedlings at the cotyledon stage, but some were missed. It was found that emergence occurred throughout the whole year. On average, 4.1% of the sown seeds produced visible seedlings, but the number of seedlings that actually survived this early phase was said to be much smaller (no survival figures were shown). However two peaks of emergence were observed over the year: one in spring, boosted mainly by the winter-sown seeds which had not germinated, and the other in autumn, chiefly comprised by the autumn-sown seeds (the way in which these results were presented made such interpretation very difficult). In these two peak seasons, cotyledons appeared in the first month after sowing, while during less favourable times, such as dry summer conditions or cold, wet winter months, the seeds remained two or three months in the soil before producing visible seedlings. According to the authors, nearly all seedlings were still quite small during the subsequent summer.

In a second experiment, a similar procedure was used but plots were established in two different pastures, *ie* one pasture grazed by sheep and the other by cattle. Different treatments were assigned to those pastures, *viz* "continuous grazing, spelling during winter, the sowing of extra white clover and browntop seed to increase the density of the pasture, extra top dressing, etc". No more information about these treatments was given, neither about measurements nor time involved (apparently one year). No difference was found between either of these treatments and the explanation was that emergence had taken place soon after sowing and before the treatments had time to exert an effect on the pastures. The only difference in seedling emergence noticed was between the sheep and the cattle-grazed pastures, 1.9 and 7.2%, respectively. This was found to correspond (no actual correlation was worked out) to the average pasture densities at the time of germination, as well as to the amount of bare ground over the same period.

Following a similar approach, they monitored the emergence of ragwort seedlings arising from seeds sown monthly in cultivated plots, *ie* "well-worked nursery soil" (Fig. 2.1). The greatest germination took place in late winter and early spring. A positive correlation between emergence and soil moisture was stated as being important to explain the results, though no attempts were made to actually demonstrate such a correlation. However, under those conditions with no herbage cover nor animals present, soil moisture probably did have a major influence on the results.

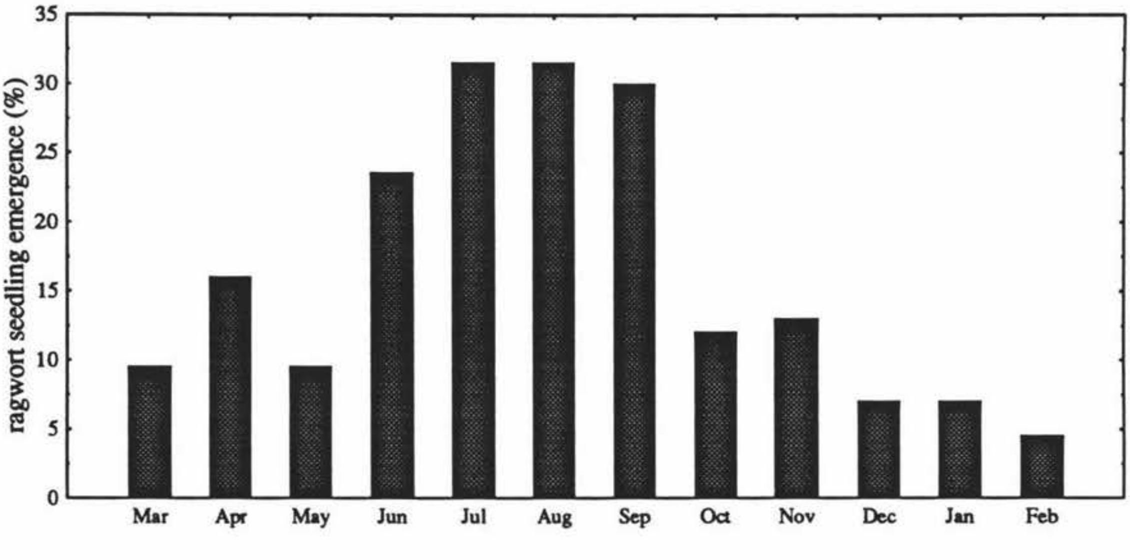

Figure 2.1. Emergence of ragwort seedlings obtained by Poole and Cairns (1940) by sowing cultivated plots at monthly intervals from March 1937 to February 1938 at Ruakura (New Zealand).

We should bear in mind that under natural conditions there would be a limited period when seeds would be shed (see Section 2.4.6.) while in the three experiments above seeds were deposited in the soil every month.

A similar experiment is also reported by van der Meijden and van der Waals-Kooi (1979) who established 25 plots (0.3 x 0.6 m each) in a sand dune area in the Netherlands, removing all the above ground vegetation (method not stated) from one half of each plot both before and during the period of the experiment, leaving the other half untouched. Three different habitat types were recognized in the area (*viz* an open woodland; a grassy area of dense vegetation with occasional small shrubs; and an open vegetation with mosses, lichens, occasional herbs, grasses and patches of bare sand) where plots were located. Three thousand ragwort seeds were sown (once only) in each plot and emerging seedlings were initially counted once a week, but less frequently when they became established. The fate of such seedlings was not monitored. Differences in seedling numbers between two successive counts were considered the net result of emergence and mortality. The results showed greatest emergence when the temperature was between 10-15°C and soil moisture content greater than 10%. However this relationship between emergence and gravimetric soil water content cannot be simply extrapolated to other environments because the actual available water (expressed as the soil water potential) will vary considerably with changes in soil texture, structure, layering, depth, organic matter, and stones (McLaren and Cameron 1990). Nevertheless, curves produced by Rundel and Jarrell (1989) show that 10% gravimetric water content is approximately equivalent to a soil water content of zero and -0.1 MPa, for a sand and a sandy loam soil, respectively. Thus for these soils, 10% water content is approximately the point where water availability becomes maximum.

Working in Oregon, USA, McEvoy (1984b) discovered another important strategy by which ragwort can improve its establishment. He marked several adult plants and determined how seedling densities change with increasing distance from each adult by following the emergence of seedlings within 400 5 x 5 cm squares in 1 x 1 m quadrats, up to 50 cm from the centre of the parent plant. This distance was considered sufficient to test whether the neighbourhood of an adult within the perimeter of the rosette opening is habitable by offspring or possibly even more suitable than more distant areas. It is important to mention that the experimental area had not been grazed for 11 years prior to the commencement of this four-year trial, was never ploughed, and had not been burned in many years. Ragwort was found to reduce its dependence on "exogenous disturbances" by creating local small-scale patches. He asserted that the horizontally-flattened rosette overtops and kills the surrounding vegetation by competition and possibly allelopathy as well. Seedling densities were found to be higher in rosette openings than in the vegetation immediately surrounding the opening, though it was not determined how much of this difference could be due to different seed densities in the soil. Such colonization of rosette openings was interpreted as a phenomenon which permits the species to persist locally despite the presence of intense competition by perennials and the absence of major disturbances. However, sites created by the death of the parent plants were said to be insufficient to sustain ragwort more than a few generations, since each loss of an opening, for whatever cause, would mean a decline in ragwort numbers. According to the author, these findings illustrate how ragwort achieves a balance between dispersal and competitive abilities unique to its evolutionary role.

2.4.3. ***Rosette development*** From the literature on ragwort it is not clear when a seedling becomes a rosette, but usually a plant bearing more than 4 or 5 fully-expanded true leaves would then be called a rosette. Poole and Cairns (1940) claim that plants can remain as small seedlings for several months without any apparent growth or growing very slowly. Thus plants may vary in age considerably when they become rosettes.

An important characteristic of the rosette stage is the capacity of ragwort to then become a multiple-crowned plant if it suffers some damage. According to Poole and Cairns (1940) the formation of the crown begins at an early stage, when the top is about 7 cm in diameter, and commences from a thickening of the top portion of the first root.

2.4.4. ***Vegetative multiplication*** A detailed study by Poole and Cairns (1940) showed that the ragwort root system is a vigorous vegetative propagator. It was initially thought that a root segment could generate a new plant if it had a portion of the crown attached to it. Their studies demonstrated that root cuttings, with or without a portion of the crown attached, can be induced in a glasshouse to form buds and send forth shoots in about a month. Also if the crown is cut off plants growing in the field and the roots are left *in situ*, there is vigorous regrowth from the roots. According to the authors, some important conditions must be satisfied for a cut or injured root to produce a shoot: (a) the cut surface must heal over; (b) the root should be young with ample food reserves; (c) a vascular cambium should be present; and (d) the cell walls of the dividing tissue (pericycle) should be irrigated with food solution.

Harper (1958) stated that if a plant is damaged in successive years, a very stout crown resembling that of lucerne may developed from which as many as 22 stems may grow. These may eventually become divided into separate single-stemmed plants by rotting of the crown. He asserts that the roots of rosettes form buds more readily than those of flowering plants.

According to Poole and Cairns (1940) even roots from seedlings at the cotyledon stage may produce shoots. Harper (1958) also states that the regeneration from root buds may occur when a plant dies naturally after flowering.

2.4.5. ***Flowering and life history strategy*** Essentially, a ragwort plant will behave as a biennial unless damaged by stock, implements, chemicals or human activities (*eg* by pulling). If such damage is intensive and/or frequent (*eg* by trampling and grazing), a minority of plants would show a biennial cycle, with most plants taking more than two years to flower. Conversely, if growing conditions are exceptionally favourable some few plants may flower in the first year (*ie* behave as annuals) (Poole and Cairns 1940; Harper 1958).

It has been demonstrated, at least for a sand-dune environment in the Netherlands, that the induction to flowering is dependent upon the attainment of a certain rosette size, with essentially no difference in this relationship between plants in their first and later years. Some individuals produced more seeds when flowering was delayed, but no consistent pattern was found to permit a generalization (van der Meijden and van der Waals-Kooi 1979).

In Britain, flowering starts about mid-June (early summer) and continues up to November (late autumn) (Cameron 1935). In New Zealand, ragwort flowers from November to April, occasionally continuing until July (Webb *et al.* 1988).

Although the plant is expected to die after flowering, Poole and Cairns (1940), Schmidl (1972a) and Forbes (1977) observed that 33%, 28%, and 44% respectively of their flowering plants regenerated after flowering. This regeneration appears more likely when plants have suffered earlier damage. Thompson (1985) found over three years, that between 1% and 25% of flowering plants regrew while four plants flowered three times.

2.4.6. ***Seed production and dispersal*** As mentioned earlier (Section 2.2.3), ragwort plants can produce a considerable number of seeds, most of which are viable. In Waikato (probably as in most North Island regions), seed shedding starts in late December, with its main fall in March and April (Poole and Cairns 1940).

It was initially thought (*eg* Cameron 1935) that these ripe seeds, because of the presence of a pappus, would be carried away for long distances. However, Poole and Cairns (1940) demonstrated through a field experiment that nearly 40% of the seed is retained in the flower head and of the remaining 60%, the majority will fall within a few metres of the parent plant. Even when considering the dispersal in the prevailing wind direction, 73.4% of seeds fell within the first 4.5 m; 18.6% from 9-18 m (98.8% within the first 18 m); and 1.1% from 18-36 m (99.9% within the first 36 m). Harper (1958) states that this limited wind dispersal is partially due to the pappus detaching from the seed soon after their release from the capitulum. Moreover, in humid weather the pappus hairs become matted together in the capitulum (sometimes by fungal mycelium) and literally all the seeds may then fall to the ground around the parent. Though Poole and Cairns' (1940) findings showed that wind is not responsible for long-distant dispersal of ragwort seeds, a short-distant displacement probably increases the chances of establishment.

Wardle (1987) asserts that no study has yet investigated the influence of strong winds on the long-distance dispersal of ragwort seeds, and points out that such winds, even if occasional, could still be highly important. He speculates about a case where isolated ragwort plants may have been derived from seed blown by strong north-west winds, possibly many kilometres away. However, such cases could also be explained by plants establishing from a soil seed bank years after the last flowering plant was seen in the area, as discussed by Popay and Thompson (1981).

Poole and Cairns (1940) noticed that the weight of the seed decreased with increasing distance from the source, particularly beyond 1.83 m. Seeds which were deposited 36 m from the source were on average 35% lighter than those deposited near the source. Yet germination decreased only 5% in seeds deposited at 36 m when compared to those deposited closer to the source.

From a study done by McEvoy (1984a) in the USA, seeds from disc florets were lighter than those from ray florets. The former were also more structurally adapted for dispersal, having a pappus (generally associated with anemochory, *ie* wind dispersal) and also trichomes (possibly for epizoochory, *ie* dispersal on the outside of animals), while those from ray florets possessed none of these structures. Moreover, the capitula produced 4.46 times as many disc seeds as ray seeds. This heteromorphism has also been discussed by Green (1937), Poole and Cairns (1940) and Harper (1958).

Considering the importance of the morphological aspects of ragwort seeds to the success of the weed, it would be interesting to know whether there is more than one variety of ragwort (Section

2.2) in New Zealand. If that was the case, there might be different potential for dispersal between different varieties (*eg* one could have longer and more persistent pappus). This could determine a need for further studies on ragwort dispersal by the wind.

There certainly has to be another form of dispersal to account for the widespread occurrence of the species, or even a combination of many forms, which is more likely. Man has been pointed as the most important agent in this spread (Harper 1958). Bloxham (1954) argued that ragwort was mainly spread by mowing plants in full flower and allowing them to lie without being collected and burnt, and also by allowing plants to flower in a hay crop, thus spreading seeds throughout the farm or even to other farms when hay is sold. He also mentioned "cheap grass seed mixtures" as possible means of ragwort dispersal. Reports by the Department of Agricultural Seed Testing Station in the 1930s showed that only 0.18% of seed samples contained ragwort seeds (Poole and Cairns 1940), and in the 1960s it had been reduced to 0.04% (Radcliffe 1969). However, these reports do not disprove Bloxham's (1954) claim because they only account for the trade of inspected seeds.

Harper (1958) stated that the early spread of ragwort in New Zealand was along railway lines, "suitable channels of disturbed ground". He also pointed to other possible means of dispersal besides the wind, such as seeds becoming attached to the hooves and coats of cattle and other stock, or being ingested by sheep and passing through the digestive tract undamaged, though trials to test the validity of these claims have yet to be conducted. However, Guthrie-Smith (1953), reporting the spread of weeds in a New Zealand sheep station (Tutira), claimed that horses were largely responsible for ragwort dissemination. He found ragwort seedlings to be common on horse droppings and concluded that they were originated from ingested seeds, probably shed seeds that were swallowed with the herbage.

Poole and Cairns (1940) checked the possibility that birds would be spreading ragwort seeds, but found no dispersal, at least through droppings. They also noted that seedlings were often found along stream beds, suggesting a possible spread of seed by water. However Bloxham (1954) reported farmers pulling flowering or seeding ragwort and dumping it into nearby creeks or leaving the pulled heads in heaps on the creek banks. He stated that ragwort seeds could, then, be carried downstream by flood waters and that detecting the farmer responsible for the spread by noxious weed inspectors was a difficult task.

2.4.7. ***Studies on population dynamics*** Forbes (1977) studied the population flux and mortality of a ragwort infestation in Aberdeen, Scotland. He mapped (method not specified) ragwort plants in several life stages within permanent quadrats laid out on a pasture. However, seedlings with one or two permanent leaves were seldom recorded and seedlings at the cotyledon stage were never identified. For this reason the author acknowledged that the "seedling category was considerably under-recorded". Also, some seedlings may have originated from regenerating root or crown fragments, but this could not be determined for the same reason explained above. His aim was to construct a model of population flux and mortality of a hypothetical ragwort population in which the proportions of plants following the various life-paths were constant from year to year. It was stressed that data should be used with care as results were obtained from only one year of observations. The hypothetical model run for a 7-year period showed that 57% of all emerging plants die as seedlings, but it was observed that, because of the under-recording of the seedling category, this figure was an underestimate. The model also revealed that a large proportion of plants die as rosettes, most of which never reach the flowering stage. According to the model, 29% of plants die as single rosettes and 6% die as multiple rosettes. The remaining 8% (of all emerging plants) die immediately after flowering.

Thompson (1985) also studied the dynamics of ragwort populations. Three different dairy pastures were selected near Hamilton (New Zealand), each one on a different soil type. Permanent quadrats were laid out and the location and diameter of all ragwort plants was recorded (method not specified). The fate of these plants and also of new plants that subsequently appeared were assessed in October, February and April of each year. Compared to Forbes's (1977) studies in Scotland, Thompson's (1985) trial had the positive aspect of being run for three years. However, the seedling category seems to have been poorly estimated as they were only assessed twice a year (September and December). Even three assessments per year (*ie* once every four months) would seem insufficient to detect emergence and death of plants. In fact even one assessment every three months, as used by Forbes (1977), would hardly seem appropriate: three months could be enough time for a seed to produce a seedling, become a rosette and for some reason die without ever being noticed. The author observed that most seedlings emerged soon after seedfall (April and May), but this was apparently not considered in the construction of the life paths. As with Forbes (1977), Thompson failed to differentiate seedlings that were regrowths from those originated from seeds. Despite these limitations, the author found that soil type, climate and site contour had only minor effects on the behaviour and growth of ragwort plants. A similar proportion of plants changing from one growth-stage category to another was found in the two studies.

2.5. Significance as a weed

Following a survey conducted by Bourdôt *et al.* (1994) of North and South Island dairy farmers, ragwort was listed by 77% of the respondents (137 farmers and 10 consultants) as a problem weed in dairy farms. It was the weed listed most often, easily outranking Californian thistle (*Cirsium arvense*) which was the second placed species, listed by 47% of respondents. Ragwort was also considered by the dairy farmers as being more important than any other weed in terms of its research requirements.

2.5.1. ***Toxicity*** According to Mayer (1990) ragwort is the most common and important cause of livestock poisoning by plants in Britain. The toxicity problem is associated with the occurrence of numerous pyrrolizidine alkaloids that constitute 0.2-0.4% of the plant dry weight. The alkaloids include jacobine, jacodine, jaconine, jacoline, senecionine, and seneciphylline (Field and Daly 1990). These alkaloids are thought to be metabolised in the liver to toxic pyrrole derivatives which inhibit hepatocyte mitosis (Mayer 1990).

Ragwort is poisonous to cattle, horses, and occasionally to sheep, either if eaten fresh, in hay or in silage (Harper 1958). Some authors suggest that the ingestion of *Senecio* spp. is linked to dietary deficiencies of phosphorus, cobalt or copper (Mendez *et al.* 1987). Table 1.1 shows the sensitivity of various animal species to ragwort.

The disease caused by ragwort ingestion is known variously as Pictou disease (Canada), Sirasyke (Norway), "walking disease" (Nebraska), and Winton disease (New Zealand) (Harper 1958). According to Connor (1977) it was the New Zealand Department of Agriculture Ruakura Experimental Station which established for the first time in 1902 the relationship between certain hepatic disorders of animals and the genus *Senecio*.

Mayer (1990) described the symptoms[2] as follows: (a) horses - abdominal pain, diarrhoea, constipation, tenesmus, hepatic encephalopathy, incoordination, yawning, head pressing, apparent blindness, collapse, coma and death; (b) cattle - abdominal pain, diarrhoea or constipation, tenesmus (rectal prolapse possible), weight loss, inappetence, nervous signs less marked than in horses; (c) sheep - weight loss, depression, increased sensitivity to copper toxicity reported in Australia.

Table 1.1. Comparative sensitivity of various animal species to dietary *Senecio jacobaea* (Cheeke 1994).

Species	Chronic Lethal Dose of ragwort (% body weight)
gerbil	3640
Japanese quail	2450
Guinea pig	525
hamster	340
sheep	**300**
goat	**125**
rabbit	115
rat	20
horse	**7**
cow	**4**

Cattle and horses will generally not feed on ragwort unless they are forced to do so, but sheep become fond of it specially in the rosette stage (Cameron 1935). Meeklah (1983) claimed that sheep have an enzyme which can detoxify jacobine, thus are about 10 times less susceptible than cattle (Table 1.1 indicates there is actually a 75-fold difference) but points out that toxicity is a function of dosage, so if sheep are forced to eat enough then they will eventually die. Also the metabolic balance of cobalt and copper is upset, so they may be more susceptible to copper

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[2] I have personally witnessed a case of an acute intoxication (in human) caused by the inadvertent ingestion of <u>one</u> capitulum of a related species (*Senecio brasiliensis*) which, as with any *Senecio* species, also contains pyrrolizidine alkaloids (Odrizola *et al.* 1994). The apparent symptoms were a generalized swelling, particularly of the sebaceous, sweat, thyroid, parathyroid, and mammary glands accompanied with pain, difficulty in moving as well as some skin eruptions and jaundice.

poisoning if their ragwort damaged livers have to cope with copper later.

The exact mechanism of the greater tolerance to ragwort observed in sheep is currently unknown. Both liver and rumen microbe detoxification pathways have been pointed out as possible explanations. However, Cheeke (1994) argues that gut microbes are not heritable, while liver enzymes are. He points out that sheep are able to detoxify the alkaloids even when brought from ragwort-free areas to highly infested country and that this is evidence against the microbe detoxification theory, as microbes need a period of adaptation to a new diet. Also that toxin-degrading microbes are not sustained in the rumen if there is not a continuous presence of the toxin. He proposes a linkage between a hepatic detoxification capability and feeding behaviour, as an evolutionary strategy allowing animals to exploit food resources containing toxins.

According to Anon. (1975) the greatest danger of ragwort poisoning exists in contaminated silage. It does not lose any of its toxicity and cattle are unable to select the plants in this form (*ie* cannot avoid eating it). The alkaloids may diffuse through the entire mass of silage, so discarding a layer does not remove the danger. Also, ragwort is said to be more palatable to animals in the form of silage or hay (Popay and Thompson 1981) as well as in the field when cut, pulled out or sprayed (Anon. 1975).

Ragwort poisoning is generally a chronic hepatotoxicity resulting from recurrent sublethal doses of alkaloids (Connor 1977). Once an animal has consumed the fatal dose of ragwort there is no known antidote and little seems to be known of sublethal poisoning, but according to Anon. (1975) it may be a common cause of poor performance and loss of condition in both cattle and sheep. Anon. (1975) also states that in New Zealand, lambs reared in ragwort rich areas do not fatten when brought on to clean pastures. Similarly, Connor (1977) reported that cows taken to country free from ragwort died from having previously grazed it on infested areas.

The problem of intoxication can be serious sometimes. Cameron (1935) reported cases of several deaths of cattle and horses. In one case a farmer was said to have lost 47 dairy cows in a period of a few months. There seems to be a lack of official records concerning such deaths, which would facilitate considerably the assessment of the problem in New Zealand. However, this problem seemed to be greater in the past when nobody new what caused Winton disease and, thus, nothing was done to avoid ragwort ingestion (Connor 1977). With the advent of modern herbicides and management practices to avoid overexposure to ragwort, fewer problems seem to occur.

2.5.2. ***Herbage production and utilization*** It is generally assumed that competition between ragwort and pasture plants results in losses of herbage production (*eg* Cameron 1935; Poole and Cairns 1940; Harper 1958; Popay and Thompson 1981; McEvoy 1984b). Thompson and Popay (1981) argue that, because ragwort is disliked by cattle, pasture growing close to a ragwort plant or under its leaves is avoided. A ragwort infestation would then cause pasture to be underutilized. However the hypothesis of a negative relationship between ragwort density (or ground cover) and herbage production and/or utilization has never actually been tested.

Allen and Meeklah (1972) have found for nodding thistle that one 30-cm (diameter) plant per m^2 prevents grazing on 10% of the pasture area. This sort of information is extremely scarce for any pasture weed and non-existent for ragwort.

2.5.3. ***Contamination of honey and milk*** Roots and flowers are the ragwort parts which contain the highest concentrations of pyrrolizidine alkaloids (Dickinson and King 1978). Bull *et al.* (1968) detected such alkaloids in honey which was produced by bees that had fed on ragwort flowers.

Dickinson (1976) and Dickinson and King (1978) studied the performance of dairy cows and dairy goats that were fed on ragwort plants, assessing the milk of these intoxicated animals and the health of the offspring that fed on this milk as well. Ragwort was more detrimental to cows than to goats, as they presented body weight losses and reduced milk flow, while does did not. Pyrrolizidine alkaloids were shown to pass into milk of both species. The alkaloid found in milk samples obtained from cows was jacoline while both jacoline and jaconine were confirmed in samples obtained from goats. Calves and kids that ingested this milk demonstrated no lesions typical of pyrrolizidine alkaloid toxicity and appeared to remain healthy during the experimental period. From this evidence, the potential danger to human beings drinking milk from either goats or cows was considered only slight. However, it was stressed that a number of questions remained unanswered, such as the carcinogenicity of these pyrrolizidine alkaloids. Certainly knowing the susceptibility of humans to these alkaloids would be an important point as well.

2.5.4. ***Allelopathy*** Ahmed and Wardle (1994) have investigated the potential for ragwort to exert an allelopathic effect on desirable pasture species. They assessed the percentage of seedling emergence, speed of emergence, shoot dry weight, and root dry weight of different pasture species (perennial ryegrass, lucerne, red, white, and subterranean clovers) following exposure to aqueous leachate, soil leachate, tissue extract, and decomposing tissue from ragwort. They found ragwort to have the potential to inhibit seed germination, seedling emergence and growth of those species. Tissues of flowering plants were considerably more inhibitory than those from rosettes. Decomposing tissue from above ground material was the most inhibitory. Red clover appeared to be the most susceptible and ryegrass the least. It was argued that the inhibition of germination, emergence and growth of other species might be a strategy developed by ragwort to favour the subsequent establishment of the seedlings of its own species. They concluded that a high presence of perennial ryegrass is likely to increase the tolerance of pasture to allelopathic effects of ragwort.

2.6. Control

It has been frequently asserted that an invasion of a grassland by ragwort may be prevented or restricted by maintaining an actively growing continuous sward (Cameron 1935; Poole and Cairns 1940; Harper 1958; Schmidl 1972a; Anon. 1975; Popay and Thompson 1981; Phung and Popay 1981) even where seeds are abundant (Harper 1958). Invasion often results from a combination of environmental and management factors (Forbes 1974). Abundance of the weed is usually an indication of a gross mismanagement in the past (*eg* overgrazing, low fertility, etc) and it is rare that the elimination of the weed will by itself create good pasture (Harper 1958). Thus control requires an appreciation of the reasons for its presence and persistence (Allen and Meeklah 1972). The spread of ragwort and its persistence on agricultural land suggest that containment is a more reasonable objective than eradication (Field and Daly 1990).

2.6.1. ***Economics*** In a grazing system, if it is assumed that the greatest net economic returns are attained from swards formed solely by pasture species, then any invader, regardless of its action, that ultimately reduces net returns from the sward is an undesirable plant, *ie* a weed. The importance of the invader, in this case ragwort, can thus be determined by the loss of net returns which is a function of its abundance, forage value (perhaps in a way positive for sheep but certainly negative for cattle), ability to depress production and/or utilization of desired species and any direct effects on animals that might cause losses in quantity or value of their product. Once this is determined it can be used as a basis for management decisions by comparing the costs of controlling the invader with anticipated losses (Medd *et al.* 1987).

However, by reviewing the literature available on the economics of controlling pasture weeds, an enormous lack of knowledge on this subject becomes evident. The main determinant of this problem is the complexity of a grazing system (Doyle and Elliott 1983; Auld *et al.* 1987; Medd *et al.* 1987). The information needed to calculate the losses caused by the presence of a pasture weed, for instance, is simply not available.

Ormrod (1966) illustrates the complexity of the problem by saying that although it is vital that any control measure results in an increase in herbage production, grass is only one input to a livestock enterprise, with another important input being the skill of the farmer as stockman. Many variables can influence whether an increase in herbage production will result in an increase in profit.

No control measure can be justified on a farm scale if it is not economically viable. However, ragwort is a rather special case, as the New Zealand Noxious Plant Act dictates the control of ragwort within 20 m of farm boundaries, independently of economic issues.

2.6.2. Chemical control Several herbicides have been tried on ragwort with varying degrees of success. As with most weed species, ragwort is more difficult to kill at the later stages of its life cycle when higher rates of herbicides are required (Wardle 1987).

One of the greatest problems encountered in herbicide use for ragwort control is that those which are more efficient (*eg* the phenoxyacetics 2,4-D and MCPA) are generally more dangerous to legumes. As stated by Meeklah (1983), herbicides may affect animal production through a reduction in clover quantity more than if the weed was left alone. According to Popay and Thompson (1981), of the available herbicides which can be used to control ragwort, only 2,4-DB is harmless to clovers, but has little effect on larger rosettes, being only useful for control of seedlings and small root regrowths, particularly in new pastures. Even so, most farmers seem to prefer the use of phenoxyacetics as they give them more flexibility in the timing of application.

Following applications of 2,4-D, Martin *et al.* (1986) stated that rate and time of herbicide application, ragwort plant size and its stage of growth all influence the level of control. They showed that later timing can sometimes be permitted by using higher rates, but stressed the importance of considering the information provided by Thompson and Saunders (1984) who had demonstrated, also in a ragwort control trial, that damage to pasture, especially to clovers, becomes more severe as the herbicide rate is increased.

Meeklah (1983) found MCPA to be effective from 1.4 to 2.5 kg active ingredient (ai) ha^{-1}, but was more easily affected by bad weather in comparison with 2,4-D ester which is only affected by heavy rain. Forbes (1974) found MCPA at 1.4 kg ai ha^{-1} effective in preventing flowering if it was applied at the rosette stage and that 2,4-D ester at 1.68 kg ai ha^{-1} gives better control of both flowering and first year plants than MCPA at 2.24 kg ai ha^{-1}. Forbes (1982) found autumn application of 2,4-D or MCPA to have several advantages over spring application but stressed that it was more damaging to clovers. Amongst six clover-safe herbicides he found that only asulam gave better than 90% control and that none was as effective as 2,4-D or MCPA.

The application of 2,4-D increases the water-soluble carbohydrate content of ragwort for more than 14 days after application (Irvine *et. al* 1977). While there is no actual evidence that this increases its palatability to cattle, it was recommended to keep stock out for three weeks.

Coles (1967) found that treatments containing picloram either alone as a granular formulation or in combination with 2,4-D as spray treatments were more effective than 2,4-D on its own. As a disadvantage, picloram can persist in the soil for up to 12 months and is very damaging to clovers (Hance and Holly 1990). To reduce such damage, plants can be spot treated by applying picloram in pellets over the top of the plants (when possible) and/or on the soil surface near the plant. Pellets should not be used on heavy soils, as this will decrease the amount being absorbed by plants, nor during cold winter or dry summer periods (Walton and Walton 1993).

The effectiveness of glyphosate and 2,4-D/picloram were compared by Makepeace and Thompson (1982) using a rope wick applicator. Best results were achieved with 2,4-D/picloram 100/25 g l^{-1} (1:1 dilution of product with water) at the bolting stage and with glyphosate 120 g l^{-1} (1:2 dilution) at the flowering stage. Thompson (1983) treated ragwort with glyphosate (Roundup 1:2 in water, 2,4-D/picloram (Tordon 50-D 1:1), and 2,4-D/dicamba (Dicambone 75D 1:1) applied with a rope wick applicator in a double pass in opposite directions at bolting, flowering and at bolting repeated at flowering. At the bolting stage, glyphosate was less effective than the other two treatments. Glyphosate was more effective as a repeat treatment applied to recovering plants flowering in late January. Glyphosate was also more effective in reducing the percentage of viable seeds, although the mixtures used also worked well when compared to untreated plots.

Clopyralid is also effective against ragwort. Although the herbicide is potentially damaging to pasture, if applied as a spot spray at the late rosette stage it can prevent seed production and give high rates of mortality at the low rate of 0.3 g ai l^{-1} (Friend 1987).

Martin *et al.* (1988) investigated the efficiency of triberunon, a non-hormone broadleaf herbicide, for ragwort control at several plant stages, but found it to be very poor when compared to control levels achieved by picloram combined with 2,4-D.

As pointed out by Meeklah (1983), herbicide is recommended for short term control and without any follow-up treatment the effect is likely to last no more than two years. In the third year it may be necessary to spray again (Anon. 1975).

Rahman *et al.* (1990) and Rahman *et al.* (1993) reported an experiment involving the use of glyphosate and 2,4-D combined or not with the application of N, P, and K, which were assessed over a period of three years. A pasture was sprayed with 2.2 kg ai ha^{-1} of 2,4-D butyl ester and with 2.2 kg ai ha^{-1} of glyphosate, direct drilled with perennial ryegrass and white clover, and fertilized afterwards by broadcasting N (urea, both nil and 50 kg ha^{-1}), P (superphosphate at nil and 60 kg ha^{-1}), and K (muriate of potash at nil and 50 kg ha^{-1}), all carried out in spring. While K fertilizer exerted no detectable effects, N and P enhanced pasture production throughout the whole experimental period, which appeared to coincide with inhibition of ragwort population numbers. No interactions were observed between fertilizer addition and initial herbicide treatment, indicating, as suggested by the authors, that in the longer term the influence of soil fertility on ragwort establishment is largely independent of the herbicide used during the resowing phase. Respraying with 2,4-D in the second year initially reduced ragwort numbers but in a few months had more ragwort than the non-resprayed plots. This was found to be caused by a suppression of clover biomass exerted by 2,4-D.

2.6.3. *Biological control* Many insect species have been reported to feed on ragwort in New Zealand during some stage of their life (Cottier 1931; Cameron 1935), most of them native. Of these, very few have shown potential to reduce ragwort populations (Cameron 1935), except the magpie moth (*Nyctemera annulata*) whose larvae can cause extensive damage under certain limited conditions. However their effectiveness is reduced by high levels of parasitism (Syrett 1992).

Between 1929 and 1932 cinnabar moth (*Tyria jacobaeae*) was introduced to New Zealand (Syrett 1983) for biological control of ragwort following promising results obtained in Europe (Cameron 1935). It was originally released throughout the whole country (Syrett *et al.* 1991; Syrett 1992), but establishment was very limited and the actual reason is unknown. Possible reasons were adverse climatic conditions or parasitism (Syrett 1983). A recent survey found that the moth is now common in southern North Island from Wellington to Pahiatua (Syrett 1992).

It is the larval stage of cinnabar moth which feeds on flowers and leaves of ragwort, often leaving only a bare stem (Syrett *n.d.*). However, Harper (1958) points out that damaged plants usually regenerate and may flower and set seed in the same year.

Crawley and Nachapong (1985) found that seeds produced by plants that had regrown after cinnabar moth defoliation are much lighter (0.26 mg dry weight) than seeds from primary capitula (0.41 mg) and that their germination was also reduced, though marginally (from 86.4% for primary seeds to 78.8% for regrowth seeds). In the field, both kind of seeds produced equal numbers of seedlings when sown in cultivated soil. In dense vegetation none produced seedlings. However, in cut grass (offering reduced but substantial competition), seeds from primary shoots produced as many seedlings as they did in cultivated soil but smaller seeds from regrowth shoots produced virtually no seedlings under these conditions. Thus, while the smaller regrowth seeds are equally viable, they produce less competitive seedlings than those from primary shoots.

The ragwort seedfly (*Pegohylemyia jacobaeae*) was first released in New Zealand in 1936 (Kelsey 1955; Syrett 1983) and is now widely established (Syrett *et al.* 1984; Syrett *et al.* 1991; Syrett 1992). The larvae consume immature seeds and part of the receptacle (Syrett 1992), but as with the cinnabar moth, it has not caused significant damage to ragwort, mainly due to poor establishment (Syrett *et al.* 1984).

Another insect species which was also introduced (1981) and is thought to have its place as a control agent is the ragwort flea beetle (*Longitarsus jacobaeae*) (Syrett 1983). Their larvae feed on the crown of rosette plants during winter, extending damage to roots and leaf petioles. They were also released throughout the whole country and have established so well that redistribution from the original site is now being carried out (Syrett 1992).

Further information on biological control of ragwort has been presented by Schmidl (1972b); Harris (1973); Harris *et al.* (1975); Harris *et al.* (1976a); Harris *et al.* (1976b); and in Islam and Crawley (1983). For a recent, detailed ecological study on the biological control of ragwort see McEvoy *et al.* (1993).

2.6.4. *Mechanical control* According to Harper (1958), cutting prolongs the life of the plant by stimulating a strong regrowth from crown and roots, regardless of the height of cutting. The more completely the plants are left alone the more strictly biennial is the life cycle. Thus cutting is not recommended except where the field is to be ploughed the following spring, in which case seeding can be avoided and the more vigorous plants which result from cutting would be destroyed (Anon. 1975). If flowering stems are cut, they should be gathered up and burned or dumped away from stock.

Pulling is regarded as inefficient and too laborious, being not recommended except for very small or light infestations when it would be uneconomic to deal with them in any other way (Anon. 1975). Harper (1958) states that plants are difficult to pull out as rosettes but are easier in the flowering stage. Meeklah (1983) states that pulling during flowering may or may not produce new plants, depending on how far advanced the plant is into flowering.

2.6.5. *Control by sheep* Although grazing animals when used for controlling pasture weeds can be regarded as biological control agents (Popay and Field 1992), some distinction should be made as there is much more scope from management of grazing animals (*eg* reproduction, grazing pressure, grazing duration, etc) than with organisms such as insects, fungi, bacteria, etc.

Poole and Cairns (1940) observed that sheep may even demonstrate a preference for ragwort once they have acquired a taste for it.

Anon. (1975) and Popay and Thompson (1981) stated that sheep may greatly weaken plants by grazing on them in early spring. For clearing existing infestations, Anon. (1975) recommends sheep grazing in early spring for light to medium infestations only, because of the poisoning risk with heavy infestations.

Control by sheep results from keeping the plants from seeding (Bedell *et. al*, 1981). However this is seldom a means of eliminating the weed. According to Harper (1958), some plants are killed by sheep grazing but most plants which are prevented from flowering persist as very small rosettes giving a superficial impression of elimination. However Sharrow and Masher (1982) stated that sheep grazing will not induce multi-stemmed crowns and that most plants eventually die without having set seed.

Old ewes eat ragwort down to the crown whereas younger sheep eat only the leaves (Cameron 1935). Moreover, younger sheep are claimed to be more susceptible to poisoning.

According to Harper (1958), grazing only with cattle leads to an increase in ragwort establishment and a change from cattle to sheep or the introduction of some sheep into the system usually reduces the population.

In a grazing trial, Amor *et al.* (1983) noted a large variation in ragwort populations subjected to different grazing regimes. Ragwort was more abundant on ungrazed sites and scarcer on sites grazed by sheep, except during summer when cattle grazing treatments had higher ragwort population. Sheep grazing either prevented or considerably reduced flowering.

Betteridge *et al.* (1994) worked with ewe hoggets set stocked and mob stocked at 1.5 and 3 stock units (su) ha^{-1} to control ragwort on a bull-beef farm. A cattle-only treatment (10.5 su ha^{-1}) was included as a control. Seventy two percent of ragwort plants in the set stocked (3 su ha^{-1}) treatment died within 12 months without setting seed, while the same percentage died after setting seed in the cattle treatment. Set stocking resulted in higher ragwort mortality than mob stocking while 3 su ha^{-1} resulted in higher mortality than 1.5 su ha^{-1}. Mob stocking reduced flowering but increased multi-stem development. A combination of cattle and 3 sheep su ha^{-1} in a set-stocked system was shown to give good control of ragwort and to give good returns from the animal products.

2.6.6. ***Pasture management*** According to Harper (1958), a good strategy for controlling ragwort populations is by ploughing, cultivating and then growing densely competitive pastures. However, Cameron (1935) claimed that serious infestations could also be eliminated simply by maintaining soil at a high phosphate status and by controlled grazing. Harper (1958) argued that the ragwort root system runs below the mass of grass roots, thus top-dressings of fertilizer would give preferential stimulation to the herbage plants (probably more applicable to phosphorus, as it is less mobile in the soil). Ploughing is only recommended (Anon. 1975) where the sward has seriously deteriorated. In many circumstances, however, it may be economically or physically impossible.

The experiment by Rahman *et al.* (1990; 1993) mentioned in Section 2.6.2 is the most recent indication of the importance of fertilizers to complement herbicide application.

Bedell *et al.* (1981) summarized the following pasture management practices to keep ragwort plants from establishing and also to achieve high pasture productivity: (a) use high-yielding pasture species and cultivars; (b) fertilize according to soil needs; (c) graze after new pasture plants are firmly established; (d) maintain a dense stand; (e) graze uniformly by subdividing the paddocks and moving stock in a planned sequence to avoid overgrazing; (f) avoid grazing during irrigation (soil disturbance). For long-term ragwort control it is also important to keep plants from flowering and setting seed (Bedell *et al.* 1981).

Importance of Light to the Germination of Ragwort Seeds

3.1. Introduction

To interpret the results of the field experiments (Experiments 2, 3, and 4) conducted in this project (described in Chapters 3, 4, and 5 respectively), it was necessary to confirm that ragwort seed germination is light-dependent as claimed by van der Meijden and van der Waals-Kooi (1979). The following factors suggested that confirmation of this claim was necessary:

(i) Maguire and Overland (1959) reported 6% to 36% germination in complete darkness, obtained when temperature was kept constant at 20°C or alternated 20/30°C respectively. No germination occurred when, in the same dark conditions, temperature was kept constant at 15°C. Unfortunately, details about origin and storage conditions of the seeds were minimal. Also the authors did not report any variability in their data.

(ii) The work by van der Meijden and van der Waals-Kooi (1979) did not conclusively show the influence of light on ragwort seed germination. They had seeds covered by sand layers of variable thickness which produced less germination at greater depths. Light was thus thought to be the limiting factor, as its intensity would be reduced with increasing depth.

(iii) These experiments, as with the vast majority of seed germination tests, used seeds collected from seed-heads. There is no reason why we should assume that the seeds we were interested in, *ie* those in the soil seed bank of pastures, would have the same light requirement as those from seed-heads (see Section 3.5.1). This uncertainty alone would have been enough to justify the experiment.

Phung and Popay (1981) demonstrated that ragwort seeds (collected directly from heads) have their germination affected (as assessed by seedling emergence) by different pasture heights. Seeds sown on bare plots produced more seedlings than those under a pasture canopy. The red/far-red light ratio (R:FR), as expected, was found to be higher on the bare ground surface and was thought to explain the results. However, as the authors acknowledged, fluctuations of temperature could be another factor explaining the differences in germination. Bare ground fully exposed to the sun would be heated up more than partly shaded soil. Fluctuation in temperature has been shown to stimulate seed germination of several species (*eg* Thompson *et al.* 1977). However, the studies by Maguire and Overland (1959), Schmidl (1972a), and van der Meijden and van der Waals-Kooi (1979) give only an indication that alternating temperature favours the germination of ragwort seeds, as none of them was actually designed to determine this.

3.2. Objectives

To study this issue fully a complex set of experiments would be necessary, with combinations of different temperatures, light, moisture, relative humidity, seed sources, etc.

Instead, a simple experiment was planned to answer the following questions:

(i) Can ragwort seeds, when drawn from a soil seed bank, respond positively to light flux in terms of germination?

(ii) How would germination in the light compare with germination in the dark? Can these seeds germinate in conditions of absolute darkness?

3.3. Methods and materials

3.3.1. ***Soil sampling*** On 15 January 1994 soil samples containing ragwort seeds were collected from a dairy farm 6 kilometres from Palmerston North where a field experiment (described in Chapter 5) had been initiated. This was carried out during the night to avoid any contact of seeds with light. The moon phase was "new moon" and no artificial illumination was used.

Furthermore, the soil was extremely dry (11% moisture content[1], ±SE 1.4%), which makes any accidental light reaction less probable (see Section 3.5.1, viii) as seeds would be very dry as well.

Samples were obtained using a 2.6-cm-diameter corer taken at an average depth of 0-2 cm (minimum of 0-1.5 cm and maximum of 0-2.5 cm). Soil was transported in a bag which had been prepared with four layers of brown paper to provide a light proof container (measurements carried out with the LI-1000 Li-Cor light meter showed there was no light penetrating the bag). Approximately 5 kg of soil was taken.

3.3.2. ***Sample handling and treatment set up*** The bag was kept at room temperature until the next night, when the soil was then processed in a darkroom at Massey University on 16 January 1994 under a fluorescent light (only one tube) covered with two layers of green cellophane filter. The soil was thoroughly homogenized by hand mixing and sieved through a 2-mm mesh to remove coarse objects like roots, stolons, etc. Its high sand content and its dryness allowed good homogenization and sieving.

Sixty plastic pots were filled with pure sand up to 1 cm from the top. Forty of them received 60 g (approx. 70 cm^3) of the homogenized soil, resulting in a layer of approximately 4 to 5 mm on top of the sand. All pots were covered against light and taken to two growth chambers. Lights outside the darkroom were turned off and pots transported under the light of a 6-volt torch which had also been covered with green cellophane filter (three layers).

Two growth chambers had been set up both at 20°C and 80% relative humidity. One of the chambers remained with its white fluorescent lights turned on during the whole experimental period, which constituted "the light treatment". Average irradiance in this chamber was 570 (±SE 6.5) $\mu mol\ s^{-1}\ m^{-2}$ and a red/far-red light ratio of 1.3 (±SE 0.03). Lights in the other chamber were kept off during the same period, which was called "the dark treatment". This was the only difference between the two treatments.

Each growth chamber had 20 pots of the dairy farm soil. These pots were placed into metal

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[1] Obtained by the gravimetric method.

trays to absorb water from underneath. Another 20 pots, containing sand only, were placed in the same way into the illuminated chamber. Etiolated seedlings, found in the dark chamber, were transplanted to these sand pots to acquire the minimum characteristics needed for identification, since the soil contained seeds of other species as well. The dark chamber was sealed and a warning sign was displayed to make sure it would not be opened inadvertently.

3.3.3. *Seedling counts* Trays in both chambers were refilled periodically with water. Every time the dark chamber had to be opened, room lights were turned off and the safe torch was used.

At weekly intervals, emerged seedlings in the light treatment were mapped and followed through until they could be identified with certainty. After being identified, they were cut at ground level and removed. Seedlings found in the dark chamber were transplanted to the sand pots in the light chamber, mapped and had their transplanting date recorded as well. Their identification and removal followed the same procedure as for the seedlings in the light treatment.

When the rate of emergence decreased the soil layer in each pot from both treatments was stirred thoroughly to expose seeds near the bottom of the layer to surface conditions.

The treatments continued until seedling emergence ceased for at least a week, at which time pots from both treatments were taken to a glasshouse for two reasons: (i) to encourage germination of the dark treatment seeds to allow calculation of percentage emergence (see Section 3.4) for each treatment; and (ii) to determine whether further emergence in the light treatment pots would occur in the glasshouse.

3.4. Results

Because germination could not be assessed directly, emergence of ragwort seedlings was used to determine germination behaviour. This was obtained in the following way:

$$E\ (\%) = (E_{chamber} / E_{total}) \times 100 \qquad \text{Eq. 2.1}$$

where E (%) is the percentage of ragwort seedling emergence; $E_{chamber}$ is the number of ragwort seedlings obtained in the chamber; E_{total} is the total ragwort seedling emergence, *ie* $E_{chamber}$ plus the number of ragwort seedlings which emerged in the glasshouse.

Emergence in the first week differed little between treatments, with 10.9% and 11.6% for light and dark treatments respectively (Fig. 3.1 a). During the third week, emergence had decreased to only 5.4% (light) and 0.5% (dark), so the soil was stirred (as described earlier). This disturbance caused a significant increase in seedling emergence of the light treatment (36.3%), but no further emergence was observed following this disturbance in the dark treatment. The light treatment still produced some seedlings 2 weeks after the disturbance (2.4%), but no more seedlings emerged after 5 weeks of exposure to light.

T tests were performed to compare these weekly germinations shown in Fig. 3.1 (a). Treatment means in count 1 had equal variances allowing the use of a straight *t* test. However, from counts 2, 3, 4, and 5 the variances of light and dark treatments were unequal so the Satterthwaite equation for calculating the degrees of freedom was used. Weekly emergences were only significantly different[2] immediately following the disturbance ($P < 0.001$), *ie* during the fourth week.

Fig. 3.1 (b) shows the accumulated emergence over the five weeks of study in the chambers. The final accumulated emergence (Week 5) in the light treatment was 55.6%, significantly higher ($P < 0.0001$, from a *t* test for equal variances) than the final accumulated emergence in the dark treatment, which reached 13.8%.

Two weeks after no emergence in the chambers, pots were taken to a glasshouse (6 March 1994) and soil was stirred again. They remained there until 23 March 1994, when seedlings were finally counted.

The glasshouse seedling emergence in pots coming from the light treatment accounted for 44.4%

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[2] (a) The alternative hypothesis H_1 to the null hypothesis H_0: $\mu_{light} = \mu_{dark}$ used in all *t* tests performed in this experiment was $\mu_{light} \neq \mu_{dark}$, which is a two-tailed *t* test therefore more conservative than the one-tailed $\mu_{light} > \mu_{dark}$. It was chosen to allow the possibility that light could even inhibit germination (known to occur in some species, *eg* Salisbury and Ross 1992).

(b) All statistical analyses reported in this study (including oncoming chapters) were based on an acceptable type I error rate of 5%, *ie* $\alpha = 0.05$.

of its total emergence, whereas in the dark treatment pots glasshouse emergence accounted for 86.2% of the total emergence.

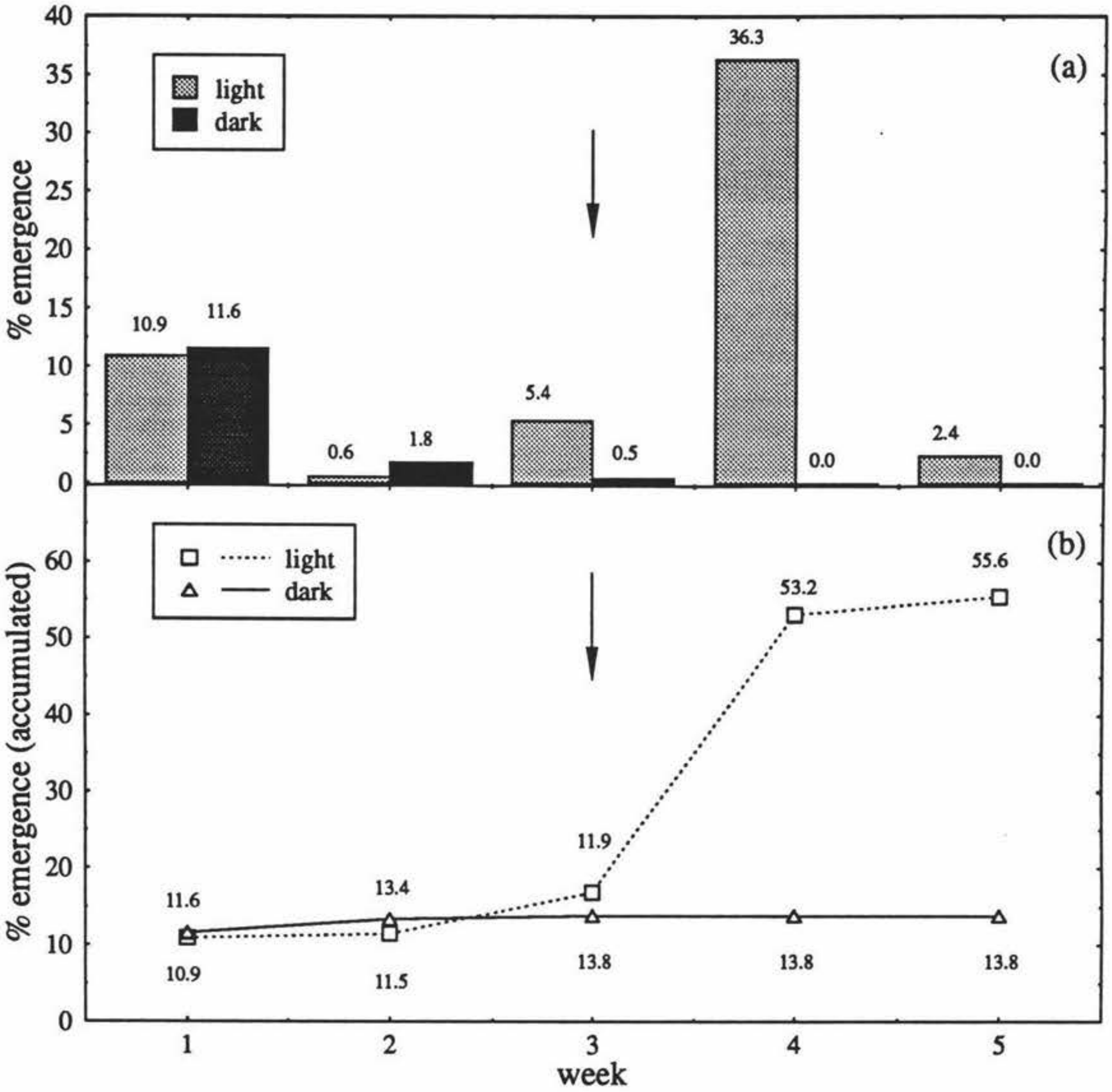

Figure 3.1. Emergence of ragwort seedlings from soil kept constantly in either conditions of light or dark at 20°C in growth chambers. (a) Weekly emergence. (b) Accumulated emergence. Arrows indicate when the soil was stirred.

To test whether the soil had been well homogenized so that a similar number of seeds were able to produce a visible seedling under the conditions imposed for either treatment, the means of treatment E_{total}, as described in Equation 2.1, were tested for location through a straight *t* test.

No significant difference was found between light (9.05 ±SE 0.96 seedlings per pot) and dark (8.2 ±SE 0.63 seedlings per pot) treatment E_{total} values. Had it not been so, the comparison of treatment means would still be meaningful, as we used percentage emergence rather than the absolute number of emerged seedlings.

3.5. Discussion

The significant difference between the final accumulated emergence in the light and the dark treatments clearly indicates that ragwort seeds used in this experiment were responsive to light. Nevertheless, 13.8% of the viable seeds in the dark treatment produced visible seedlings. A ragwort seed bank may contain thousands of seeds per m^2 (see Chapter 4). Even if just a few hundred of them were in the first 4-5 mm (as considered in this experiment), an emergence of 13.8% without the need for light is still a considerable number of seedlings. Supposedly these seeds could germinate without the need for any disturbance of the surrounding environment.

3.5.1. ***Some important points about phytochrome*** To assist in the interpretation of the emergence figures obtained in this experiment some aspects concerning the role of phytochrome in the germination of seeds should be considered (Borthwick *et al.* 1954; Borthwick 1972; Bradbeer 1988; Salisbury and Ross 1992):

(i) All plant organs, including seeds, contain phytochrome (P).

(ii) There are two types of P: type 1 and type 2. The type found in seeds is type 2. It is more stable than type 1 and, unlike type 1, it does not disappear in darkness by destruction and reversion.

(iii) P (either type 1 or 2) can exist as P_r or P_{fr} forms. P_r is the blue, inactive form of the pigment and is the form in which P is synthesized. It absorbs red light thus being transformed into P_{fr}, the olive green, active form which absorbs far-red light.

(iv) The actual physiological action of P_{fr} is still controversial, but its participation as a trigger of the germination of seeds is almost universally accepted. The minimum amount of P_{fr} needed for the activation of seeds is apparently unknown, but it seems that a seed has to have a minimum level of ϕ to germinate, ϕ being the amount of P_{fr} divided by the total P (total $P = P_{fr} + P_r$).

(v) Both P forms are interconvertible. The ratio of red to far-red light (R:FR) determines which form is more abundantly formed. Even very low irradiances with red and far-red light are adequate to establish a photoequilibrium between P_r and P_{fr} (the relative amount of total P in the form of P_{fr}) because both absorb these wavelengths very effectively.

(vi) In seed germination, for instance, responses caused by red light are nullified by an immediate exposure to far-red light and vice versa.

(vii) The sunlight R:FR is about 1.1 to 1.2. P_r absorbs red light more effectively than P_{fr} absorbs far-red light. Consequently P_r is converted more effectively to P_{fr} than P_{fr} into P_r. For this reason the sunlight acts primarily as a red source that forms more P_{fr} than P_r.

(viii) Photodormancy (seeds that require light for germination are said to be photodormant) is broken by light only when seeds are partially or fully imbibed. Only then is P_r sufficiently hydrated to be transformed to P_{fr}.

(ix) In seeds that survive many years in the soil, P_r is stable and only awaits the proper combination of moisture, light, and temperature to become P_{fr} and induce germination.

(x) Some seeds (*eg* Grand Rapids lettuce) when imbibed, exposed to light to form P_{fr}, and then immediately dehydrated, will germinate in darkness upon remoistening for up to a year, which shows that P_{fr}, like P_r, is stable in dry seeds for long periods.

As Salisbury and Ross (1992) state, an implication of a stable P_r and P_{fr} is that whether a seed requires light to germinate depends on how much P_{fr} was produced in it during ripening on the mother plant. However, based on the points outlined above, the light requirement apparently depends on how much P_{fr} is produced at any imbibed state until dehydration, be it in the mother plant or in the soil seed bank.

It is important to bear in mind that none of the studies summarized above involved the use of ragwort seeds. Although it is likely that most of those points are applicable to ragwort, we should still consider the possibility that other mechanisms may also be involved.

3.5.2. Germination in dark Maternal conditions experienced by seeds during their development can be important in determining whether they will require light to germinate (Cresswell and

Grime 1981; Fenner 1991; Orozco-Segovia *et al.* 1993). Because the seeds used in this experiment had been in the soil seed bank for at least one year, where they would have been subjected to very different and variable conditions of light, moisture and temperature, this factor becomes irrelevant. If they had been fully covered by the pasture canopy, a thick soil layer or litter right after shedding, their maternal conditions would theoretically be relevant. However this is very unlikely and they would have been subjected to the influence of temperature (Section 3.5.4), so maternal conditions will not be considered as a possible explanation for the results obtained in this experiment.

Whatever the reason for seeds germinating in the dark, the difference in emergence between the light and the dark treatments presumably resulted from conditions during the soil seed bank phase. Seeds closer to the soil surface would have received a higher R:FR thus containing a higher ϕ (see Section 3.5.1, iv) than those deeper in the soil more thoroughly covered by the canopy or its litter. Therefore 13.8% (the percentage emergence obtained in the dark treatment) could be a percentage of seeds in our samples exposed to higher R:FR. Their P_{fr} would be at a ϕ level capable of triggering off germination, *ie* they did not need further $P_r \rightarrow P_{fr}$ photoconversion. Their germination would have been prevented in the field only by lack of moisture. This proportion of seeds cannot be directly extrapolated to other pastures as it will certainly depend on particular cover and moisture conditions.

As mentioned earlier, type-2 P does not undergo dark reversion or destruction, at least for one year (Salisbury and Ross 1992). Therefore, as far as P_{fr} is concerned, seeds in the dark treatment would have conditions to germinate for longer than 3 weeks (as observed in this experiment). Apparently, emergence stopped when all seeds containing a minimum ϕ had germinated.

The green light torch used in the dark chamber could be considered a possible reason for the results. Salisbury and Ross (1992) state that green safe lights have to provide low irradiance and advise that it should be tested before being used, while Grime and Jarvis (1975) and Blom (1978) implied that some species are more sensitive to green light than others. However, evidence suggests the torch was a safe light source. Firstly, a large proportion of the seedlings occurred in the first count when the chamber had not even been opened. Secondly, emergence steadily decreased after that. If the green light was stimulating germination there should have been some reaction after the disturbance (as observed in the light treatment).

Another possibility is that the darkroom green light caused germination. However, seeds were dry when exposed to the darkroom green light, so the $P_r \rightarrow P_{fr}$ photoconversion could not happen (Section 3.5.1, viii). Bradbeer (1988) mentioned that "air dry seeds can show a response to light", but the statement was not substantiated and he was apparently referring to white light (or any light containing red wavelength) rather than green light.

3.5.3. ***Germination in light*** As disturbance did not stimulate any emergence in the dark treatment, the post-disturbance emergence in the light treatment can be entirely attributed to light. If dark treatment seeds had reacted to disturbance, other factors might be have been involved, *eg* better aeration.

The 55.6% of seeds which emerged in the light treatment would consist of approx. 13.8% which came from the field with a minimum ϕ plus approx. 41.7% which had their ϕ augmented by exposure to the red photons of the chamber white light. This $P_r \rightarrow P_{fr}$ photoconversion became only apparent between the second and the third week, when more seedlings started to appear in the light treatment than in the dark treatment.

Wesson and Wareing (1969) demonstrated the role of light in the germination of natural populations of buried weed seeds following a disturbance of the soil when it was still usual to attribute it to high levels of carbon dioxide in deeper soil layers, even though the involvement of phytochrome was still unknown to them. They dug pits in the field to depths of 5, 15 and 30 cm, covered some pits with glass (light treatment), some with asbestos (dark treatment) and others were left opened (also a light treatment). They obtained large emergence figures (counted on the bottom of the pits) in the glass covered pits, less emergence in the open pits (maybe by the drying of the upper soil layer) and no emergence whatsoever in the pits covered by asbestos. The reason given was the presence of light in those treatments. If that was so, it would be related to the ϕ level discussion presented above. The absence of germination in the dark pits means that either seeds had previously received far-red light and remained with low ϕ levels or P_{fr} had been degraded during the time, certainly many years, that seeds had been there (Bradbeer 1988). However differences in temperature regimes between those treatments have apparently not been considered, though Thompson *et al.* (1977) have shown this to be important.

3.5.4. ***Germination in the glasshouse*** The large proportion of seedlings emerging in pots coming from the light treatment during the glasshouse phase was unexpected. As the main objective was stimulating germination in the dark treatment pots, glasshouse temperature and light conditions were not monitored during the experimental period. However, the glasshouse light conditions were assessed in March 1995 and showed that R:FR was 1.5 (±SE 0.01) on a cloudy day and 1.8 (±SE 0.09) on a sunny day. These values are just slightly higher than the R:FR found in the growth chamber (1.3), and therefore do not seem to account for the large emergence observed in the glasshouse. Glasshouse irradiance varied from 106 (±SE 2.9) µmol s^{-1} m^{-2} to 1197 (±SE 42.5) µmol s^{-1} m^{-2} for cloudy and sunny days respectively. As we saw in Section 3.5.1, the photoconversion of P is a low fluence process which seems to rule out the possibility that a higher irradiance in the glasshouse would have been more favourable to germination than the irradiance in the growth chamber.

There could also have been a partial inhibition of germination caused by the constant, hence rather artificial, light conditions in the light treatment chamber contrasting with a normal day/night cycle in the glasshouse.

However, the most likely cause was probably the difference in temperature conditions in the glasshouse. In the growth chambers seeds were at a constant 20°C, but in the glasshouse this would have varied greatly. The nearby AgResearch Grasslands meteorological station recorded the following variation in air temperature during the time pots were in the glasshouse (6 to 23 March): minimum 4.6°C, minimum (mean) 9.5°C, maximum 25.4°C, maximum (mean) 20.4°C. Because the glasshouse was not set to maintain any given temperature its pattern of variation was probably comparable to the station, perhaps achieving higher temperatures during the day. The glasshouse range of temperature was probably around 10°C, which would be very different from the constant 20°C in the growth chambers.

There is evidence (Maguire and Overland 1959; Schmidl 1972a; van der Meijden and van der Waals-Kooi 1979) that ragwort seeds germinate better when kept at alternating temperatures. However these experiments were all conducted with seeds directly from seed-heads and none conclusively showed alternating temperatures were the actual trigger. Nevertheless, investigations (*eg* Thompson *et al.* 1977) with many other species (including seeds from soil) show that alternating temperatures can even substitute for light as a trigger for germination of light sensitive seeds.

3.6. Summary

The main points discussed in this chapter can be summarized as follows:

(i) Ragwort seed germination collected from the soil seed bank was enhanced by the presence of light, resulting in 55.6% emergence.

(ii) These seeds can germinate in complete darkness, provided they have a minimum amount (ϕ) of P_{fr}. In this experiment, 13.8% of the seeds were in this condition. Those seeds had not germinated in the field probably due to a lack of adequate moisture. This percentage would presumably vary in other situations depending on the particular cover and moisture conditions present.

(iii) Seeds containing the minimum ϕ level are probably those closer to the surface which receive higher R:FR.

(iv) Exposure to light is apparently the only explanation for the post-disturbance germination observed in the light treatment.

(v) $P_r \rightarrow P_{fr}$ photoconversion only became evident (as assessed by seedling emergence) after two weeks of constant light exposure.

(vi) Alternating temperatures presumably improved ragwort germination, though this experiment was not designed to investigate this factor.

Implications of these findings will be discussed in more detail in subsequent chapters, as this knowledge helps with the interpretation of the field trial results.

Seasonality of Ragwort Seedling Emergence in the Field

4.1. Introduction

An important part of a well-planned weed control programme is knowing the time of the year when seeds germinate, particularly for species like ragwort, which largely depend on seeds for the establishment and regeneration of their populations (Popay 1987). Such knowledge can be used to create an environment that will discourage seed germination during that period, thus preventing the establishment of the seedlings. However, if for some reason seedling emergence cannot be prevented, the same knowledge can help determine the best time of the year to spray pastures so that ragwort is treated at the seedling stage, when it is more susceptible to herbicides.

In Section 2.4.2 we outlined the experiments carried out by Poole and Cairns (1940) who studied the influence of above ground vegetation on the emergence of ragwort seedlings as well as the periodicity of this emergence. However, the behaviour of seeds naturally occurring in the soil may be different from that of the monthly-sown seeds used by them. Seeds lying in the soil seed bank are expected to experience changes in their phytochrome form determined by the red/far-red light ratio (Chapter 3), thus making field germination a rather more complex process. Furthermore, according to the natural ragwort life cycle, there would be a single, large input of seeds into the soil each year (usually in March and April), rather than a frequent and regular deposit of seeds throughout the year (Section 2.4.6).

4.2. Objectives

The primary aim of this experiment was to determine the seasonality of ragwort seedling emergence based on seeds that had been naturally deposited in the soil seed bank. Another aim was to establish whether the pattern of seedling emergence could be affected by different herbage cover conditions.

4.3. Methods and materials

A hill country pasture dominated by browntop (*Agrostis capillaris*) on the bull beef unit of the AgResearch Ballantrae Hill Country Research Station near Woodville was selected for this trial. The site was chosen for two major reasons: (a) ragwort is becoming an important weed in the area, apparently as a consequence of an increase in the cattle:sheep ratio in recent years (K. Betteridge, pers. comm.), and (b) the local soil seed bank was known to contain ragwort seeds.

During the period of study there were no mature ragwort plants in the experimental area. The last seed rain had occurred at least one year earlier.

Two treatments were imposed within an area of approximately 900 m^2, each treatment consisting of 5 randomly-distributed replicates (0.4 x 0.4 m plots). In the first treatment, pasture was sprayed with a 4.8 g $litre^{-1}$ solution of glyphosate (Roundup) then clipped to ground level 1 week later, leaving the soil completely denuded of herbage cover (Plate 4.1). The herbicide was used to prevent pasture from regrowing for at least 1 month after clipping, when seedlings were counted. The second treatment consisted of an intact pasture. In this treatment, small ragwort seedlings present during treatment imposition were cut and removed without disturbance to pasture. Both treatments were enclosed by cages to prevent access by livestock (Plate 4.2).

Small plots were used because it was difficult to obtain a completely-denuded soil (*ie* to clip pasture to ground level) over larger areas, especially once every month. Moreover, counting seedlings at the cotyledon stage in such a dense pasture was a time-demanding procedure, especially if similar seedlings of other species were present.

In order to obtain information about the annual fluctuation in soil moisture, a total of 10 soil cores (one from around each plot) was taken every week (0-15 cm deep). Cages (1 x 0.5 m) were bigger than the plots (0.4 x 0.4 m), thus allowing half of the caged area to be used for soil collection. In the bare soil treatment, the second half of the caged area was also sprayed and

Plate 4.1. Pasture clipped at ground level 1 week after spraying with glyphosate.

Plate 4.2. Clipped plots caged to prevent access by livestock. See an example of the intact pasture on the top right corner of the plate.

clipped so that possible differences in soil moisture between covered and uncovered soil could be detected. Soil temperature (10 cm deep) and rainfall data were obtained from a nearby (approx. 500 m) meteorological station.

Treatments were applied afresh every month following the same method from August 1993 to July 1994. Because the distribution of ragwort seeds in the soil was unknown, choosing where to establish a new set of plots was considered an unbiased procedure. Plots were laid out wherever the surface was relatively even to facilitate clipping and free from clumps of rushes (*Juncus* sp.).

Within the experimental area, pasture cover (visually estimated) varied from 1000 kg DM ha^{-1} to 3000 kg DM ha^{-1} over the year. The paddock was never overgrazed nor heavily trampled at any time. The area was intermittently grazed by bulls (only once by ewes) at an approximate stocking rate of 95 stock units ha^{-1} following the normal grazing management of the farm.

4.4. Results

Variances of the treatments were not homogeneous. As no transformation was able to homogenize them, the nonparametric Wilcoxon two-sample test (Wilcoxon 1945) was used to analyze monthly treatment means (performed by the SAS "NPAR1WAY" procedure). Also, Steel and Torrie (1981) claimed that nonparametric procedures are more efficient than the parametric ones in detecting real differences when n (sample size) ≤ 10 (note that $n = 10$ in this experiment).

Ragwort seedling emergence was consistently higher on bare soil for most of the year (Fig. 4.1). February and March were the only months when differences between treatments were not significant (Table 4.1). In March, there was virtually no emergence in either of the treatments. Under intact pasture, seedling emergence was on average only 8.5% of that from bare ground. However, if we do not include the months when emergence on bare soil was also low (*ie* from January to April), this figure is reduced to only 2.7%. Plate 4.3 gives an example of seedling emergence recorded on bare soil.

Each treatment produced a different pattern of seedling emergence over the year, though both treatments showed similar trends from August to October and from November to March (Fig. 4.1). Emergence on bare soil reached two peaks during the year, one in early spring (September) and the other in early winter (June). However, under intact pasture, seedling emergence had a marked increase in September only (though not significant as shown in Table 4.1). In the same treatment, emergence was remarkably constant (5 seedlings m^{-2}) from May to July, nearly the same seedling number observed in August of the previous year.

Table 4.1. Seasonality of ragwort seedling emergence from bare and pasture-covered soil.

Month	Number of Seedlings m^{-2}		
(1993-94)	Bare Ground	Intact Pasture	$P > Z$[1]
August	446.0 a[2]	6.2[3]	**
September	600.0 a	21.8	*
October	466.0 a	5.0	**
November	264.0 ab	12.5	**
December	169.0 b	11.2	**
January	50.0 b	2.5	*
February	3.7 c	2.5	ns
March	0.0 c	0.0	ns
April	58.8 b	0.0	*
May	237.5 b	5.0	**
June	642.5 a	5.0	**
July	511.3 a	5.0	**

[1] Wilcoxon Two-Sample Test for testing location of "bare ground" and "intact pasture". ** = $P < 0.01$, * = $P < 0.05$, ns = not significant (*ie* $P > 0.05$).

[2] Means sharing the same letter are not significantly different (*ie* $P > 0.05$) according to the Wilcoxon Two-Sample Test.

[3] No significant difference was found throughout the year.

In the covered ground treatment, seedlings were only found in small gaps in the canopy. On bare soil, seedlings developed much faster than the ones competing with pasture, producing thicker, greener and larger leaves. Although the fate of these seedling was not closely followed, it was noticed that only seedlings growing on bare ground were able to reach the rosette stage,

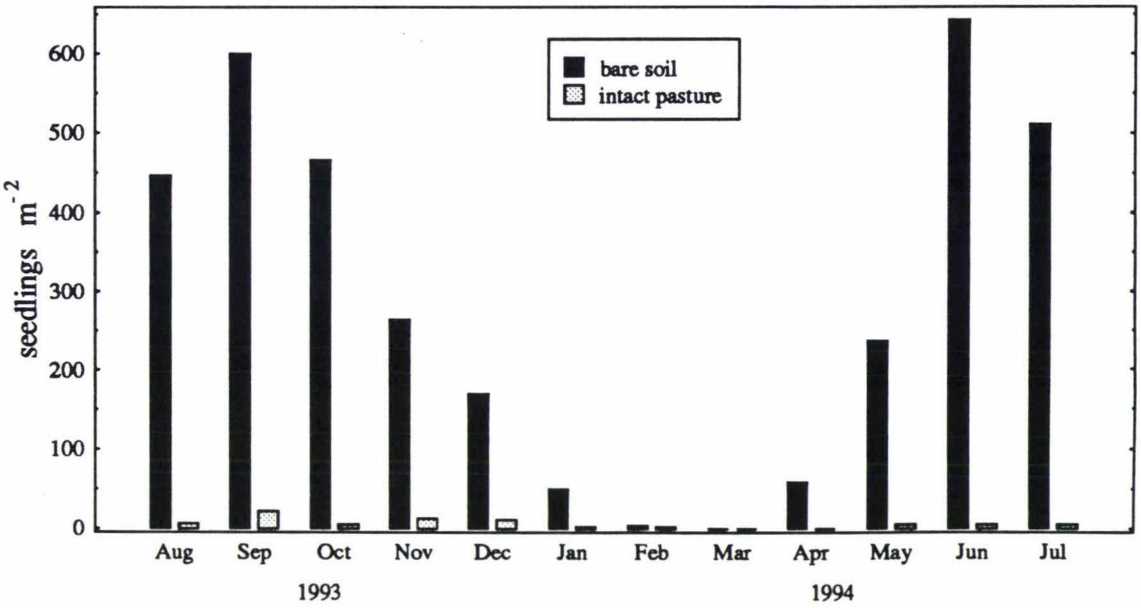

Figure 4.1. Ragwort seedling emergence on bare soil and under intact pasture cover (see significance tests on Table 4.1).

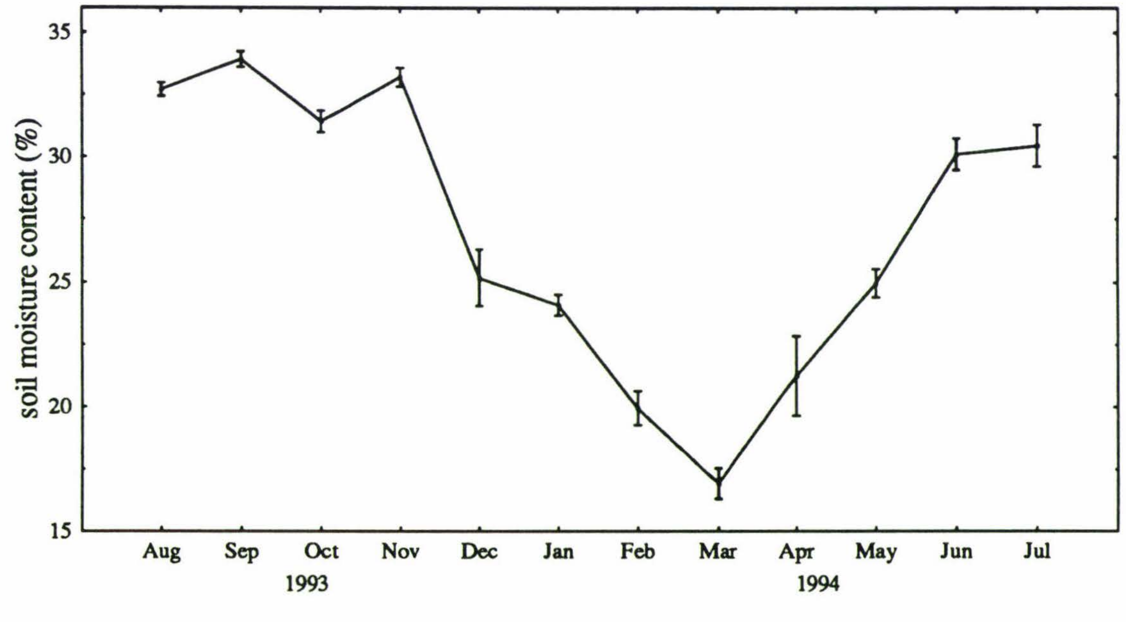

Figure 4.2. Gravimetric soil moisture content (± SE) of samples collected every week (August 1993 to July 1994) from bare soil and intact pasture. The curve represents the average soil moisture of both treatments.

at least during the period of study. Even several months after plots had been sprayed and clipped, their position could be identified by the large number of ragwort plants, contrasting with the rest of the area where there was no ragwort present (Plate 4.4).

Soil moisture was very similar for covered and uncovered ground. The average values are presented in Fig. 4.2. Rainfall and soil temperature are shown in Figs. 4.3 and 4.4, respectively.

4.5. Discussion

Based on the evidence produced by the first experiment (Chapter 3), the higher seedling emergence observed in this trial on uncovered plots may be interpreted as the result of a direct effect of light upon the seeds. As demonstrated by Phung and Popay (1981), the red/far-red light ratio is much higher on a bare surface than underneath the pasture canopy. This higher proportion of red light promotes the conversion of phytochrome within seeds from the inactive (P_r) to the active form (P_{fr}), thus stimulating seed germination (see Section 3.5.1).

However, light spectral composition may not be the only factor determining these results. Thompson *et al.* (1977) showed that fluctuations in soil temperature recorded on bare soil can stimulate the germination of seeds of several species (ragwort was not studied) and even substitute for the light requirement. As soil temperature was not monitored locally and separately for each treatment, this hypothesis could not be tested in this trial. Though seedlings recorded in pasture-covered plots were always seen in gaps, the size of these gaps was very small (1.5-2 cm in diameter). Presumably, temperature in such gaps would not be different from that in the immediately adjacent zone.

Seedling emergence on bare ground (Fig. 4.1) seems closely associated with the fluctuations recorded in soil moisture over the year (Fig. 4.2). Besides the overall similarity, note that the lowest seedling emergence coincides exactly with the lowest soil moisture content (March). As shown in Table 4.2, these two variables are highly correlated (r = 0.86). According to our judgement criteria, 74% of the variation in seedling emergence is accounted for by soil moisture (Table 4.2).

Plate 4.3. Ragwort seedlings 3 weeks after clipping (June 1994) at an approximate density of 700 seedlings m^{-2}.

Plate 4.4. Ragwort seedlings and rosettes in January 1994, 4 months after clipping.

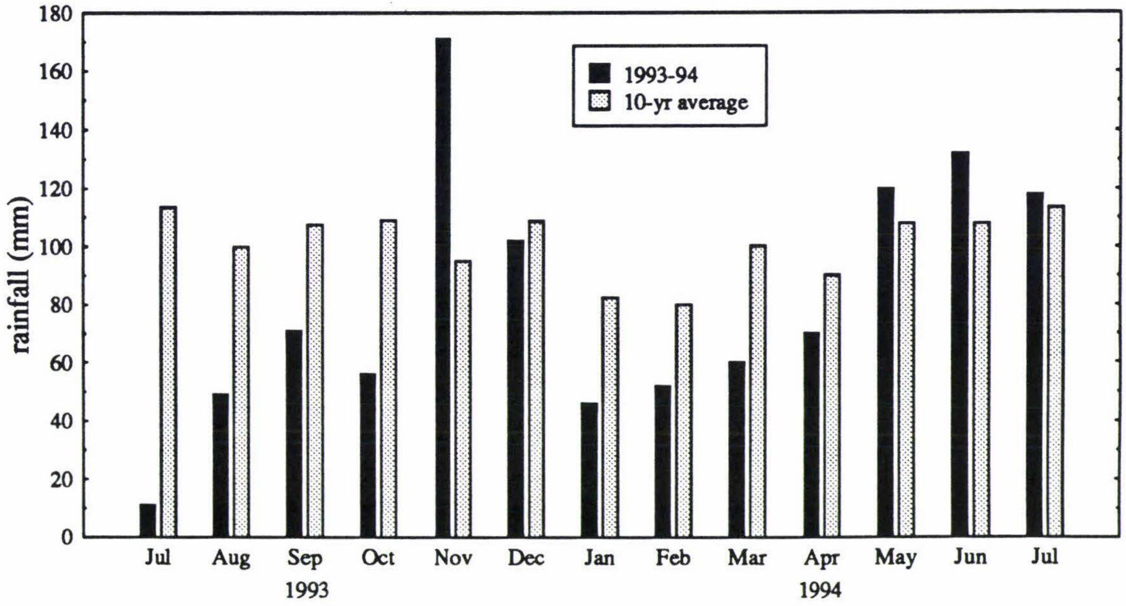

Figure 4.3. Average monthly rainfall recorded near the experimental site at Ballantrae.

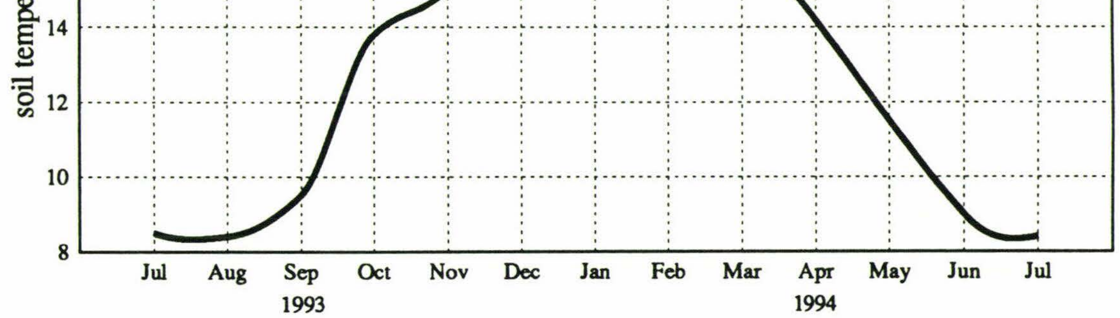

Figure 4.4. Average soil temperature (10 cm) recorded daily near the experimental site at Ballantrae.

Table 4.2 also shows that soil temperature and seedling emergence are highly correlated as well, but in this case negatively (r = -0.85). It is, however, unlikely that soil temperature has inhibited seed germination. Van der Meijden and van der Waals-Kooi (1979) demonstrated that ragwort seed germination is actually improved if temperature rises from 10°C to 20°C. In this trial, average soil temperature was within this range when emergence was minimal (January to April). However, soil temperature may have affected germination from the bare soil indirectly, by increasing soil water evaporation. This hypothesis seems to be partly confirmed by the negative correlation (r = -0.66) shown on Table 4.2. Note, however, that only 44% of the variation in soil moisture was attributable to the annual fluctuation in temperature.

Low temperatures from July to September 1993 and from June to July 1994 did not inhibit seed germination. Van der Meijden and van der Waals-Kooi (1979) found that ragwort seed germination is only significantly checked by temperatures below 5°C (Section 2.4.1).

Table 4.2. Relationships between seedling emergence, soil moisture, soil temperature and rainfall. Correlations were obtained on a monthly basis.

	soil moisture	soil temperature	rainfall
seedling emergence (bare soil)	0.86 [1] 74% [2] *** [3]	-0.85 72% ***	0.31 9% ns
soil moisture	——	-0.66 44% *	0.37 14% ns

[1] r (Pearson product-moment correlation coefficient).

[2] r^2 (coefficient of determination).

[3] $P > \rho$ under H_0: $\rho = 0$ or $P > F$ under H_0: $\beta = 0$ (see Steel and Torrie 1981). *** = $P < 0.001$, * = $P < 0.05$, ns = not significant (*ie* $P > 0.05$).

There was no apparent relationship between rainfall and seedling emergence (Table 4.2). However, if soil moisture does affect seedling emergence as discussed earlier, it is obvious that rainfall will also affect seedling emergence, since it is one of the factors which determine the amount of water stored in the soil. Nevertheless, rainfall and soil moisture content were very weakly correlated in this trial (Table 4.2). As the site was moderately steep (approx. 60% inclination), part of this lack of relationship would be explained by runoff. Probably a more significant part would be accounted for by the evapotranspiration, since it is more variable throughout the year (McLaren and Cameron 1993). Thus, soil moisture content would be more useful than rainfall for predicting ragwort seedling emergence.

The seedling emergence from bare ground represented in Fig. 4.1 can be regarded as the potential seedling emergence for that environment. This information can be used to predict the immediate consequences of a disturbance to the herbage cover in terms of subsequent ragwort seed recruitment. While a disturbance in February or March, for instance, will not cause any short-term problem, the same disturbance in September may result in a serious ragwort invasion. However, it should be noticed that this trial only monitored the effects for the period of one month after treatment imposition. Thus, we may speculate that a disturbance (*eg* overgrazing) in February (when pasture growth is minimal) is likely to show its effects later in the year (from April onwards), when soil moisture increases, giving seeds the chance to germinate before pasture has had time to become dense again.

4.6. Summary

The results of this trial can be summarized as follows:

(i) Ragwort seedling emergence was significantly greater on bare soil than under the pasture cover, provided soil moisture was not limiting.

(ii) No seedlings emerged where cover was dense and unbroken. In the covered treatment, seedlings were only seen when there were gaps (though small) in the canopy.

(iii) Bare soil and intact pasture produced different patterns of seedling emergence over the year. On bare soil, emergence reached a peak in September and another in June. Variations in seedling emergence under intact pasture were not significant throughout the year.

(iv) Soil moisture content appears to be the most important factor affecting seedling emergence, provided soil is not covered by pasture.

(v) Care must be taken in interpreting the lack of emergence in February and March. Disturbance to pasture cover at this time of the year may not stimulate seed germination immediately but might favour seedling establishment as soon as soil moisture is no longer limiting.

The Influence of Treading by Cattle on Emergence and Early Establishment of Ragwort Seedlings on a Hill Country Pasture

5.1. Introduction

If germination of ragwort seeds is favoured by soil and vegetation disturbance (Cameron 1935; Poole and Cairns 1940; Harper and Wood 1957; van der Meijden and van der Waals-Kooi 1979; McEvoy 1984a)[1] and moist soil conditions (Poole and Cairns 1940)[1], it is reasonable to presume that a severe treading during winter would favour the appearance of a large number of seedlings.

The risk of treading damage to pasture arises from the need to concentrate animals into mobs for feed rationing purposes in winter. Hence, according to Sheath *et al.* (1987), a common-sense compromise between controlled feeding and pasture damage is required, particularly with beef cattle on hill country. Alternatives like the use of "sacrifice paddocks" are sometimes advocated to minimise damage (Smethan 1973). However, removing all animals from paddocks and feeding them in a confined area (sacrifice paddock) may not be practical in some situations, especially on large farms.

For beef and sheep farms "block grazing" may be more appropriate. In this system the area fenced is as square as possible to discourage animals from walking up and down along fence lines. However, if the soil is too wet block grazing will not prevent treading damage (Smethan 1990).

Sheath *et al.* (1987) argue that there is no experimental evidence that justifies options like "sacrifice paddocks". However treading studies in New Zealand pastures by D.B. Edmond conducted from the 1950s to 1970s (reviewed by Brown and Evans 1973) did reveal advantages,

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[1] See also Chapter 4

through direct and indirect effects on pasture plants, in removing animals from paddocks, particularly at high soil moisture levels. On the other hand the same studies also uncovered a positive aspect of treading if perennial ryegrass and white clover are wanted in the pasture (which is generally the case), as these two species will be favoured over other pasture species that cannot tolerate trampling.

The investigation of treading in New Zealand is mostly limited to the effects on pasture plants and on soil properties. A few studies have shown that treading can be used positively to control weeds (*eg* Hartley *et al.* 1980; Hartley 1981), but apparently no experimental work has been carried out to study whether treading stimulates the recruitment of weed seeds. However, seedling invasions have been observed following the imposition of grazing treatments intended to control weeds (*eg* Sanders 1990).

If treading during winter was demonstrated to stimulate the germination of ragwort seeds, alternatives like block grazing, sacrifice paddocks or others could be more easily justified and farmers would have another factor to take into consideration when deciding whether to invest time and money in measures such as these. Furthermore, it would constitute important information for the understanding of the occurrence of this weed.

5.2. Objectives

As implied above, the objective of the experiment reported in this chapter was to determine whether a severe treading during winter would stimulate the emergence of ragwort seedlings. If so, seedlings would be monitored during their early life to determine whether they successfully established.

5.3. Methods and materials

A hill country pasture, adjacent to the area where Experiment 2 (Chapter 4) was carried out, was split into three blocks. Every block contained a complete set of six treatments designed to isolate the effect of treading from possible confounding effects caused by the presence of herbage cover and the action of grazing (*ie* the pure removal of foliage by animals).

Accordingly, treatments consisted of combinations of treading, grazing and herbage cover, each of which could either be present or absent (structured as a 2 x 2 x 2 factorial design). However, two of the eight combinations were impossible, *viz* those involving grazing with no herbage cover (Table 5.1). Note that Treatment 6 did not involve any disturbance during treatment imposition, thus was regarded as a control treatment.

Table 5.1. Combinations of treading, grazing and herbage cover at two contrasting levels, *viz* presence ("yes") or absence ("no").

Treatment	treading	grazing	herbage cover
1	YES[1]	YES	yes
2	YES	no	yes
3	YES	no	NO
4	no	no	NO
5	no	YES	yes
6 (control)	no	no	yes
impossible	no	YES	NO
impossible	YES	YES	NO

[1] Capital letters signify that the level of that factor would cause a disturbance.

An area 27 x 49 m was fenced off with a single electric wire supported by plastic tread-in posts. The same kind of fencing was used to divide the area into three blocks, each one measuring 9 x 49 m (Fig. 5.1) to be grazed by 27 heifers (9 heifers per block) at a stocking rate of 205 heifers ha^{-1} (Plate 5.1).

Treatments involving the complete removal of the herbage cover (Treatments 3 and 4) and grazing without treading (Treatment 5) were conducted in small plots for practical reasons. Therefore all treatments were evaluated using small observation units of 40 x 40 cm (small squares in Fig. 5.1), so that the area sampled and consequently assessed would be equal for all treatments. The time that would be necessary to locate, identify and count seedlings in the pasture was another reason for the adoption of small plots.

Plate 5.1. General view of the experimental area when grazing had just begun.

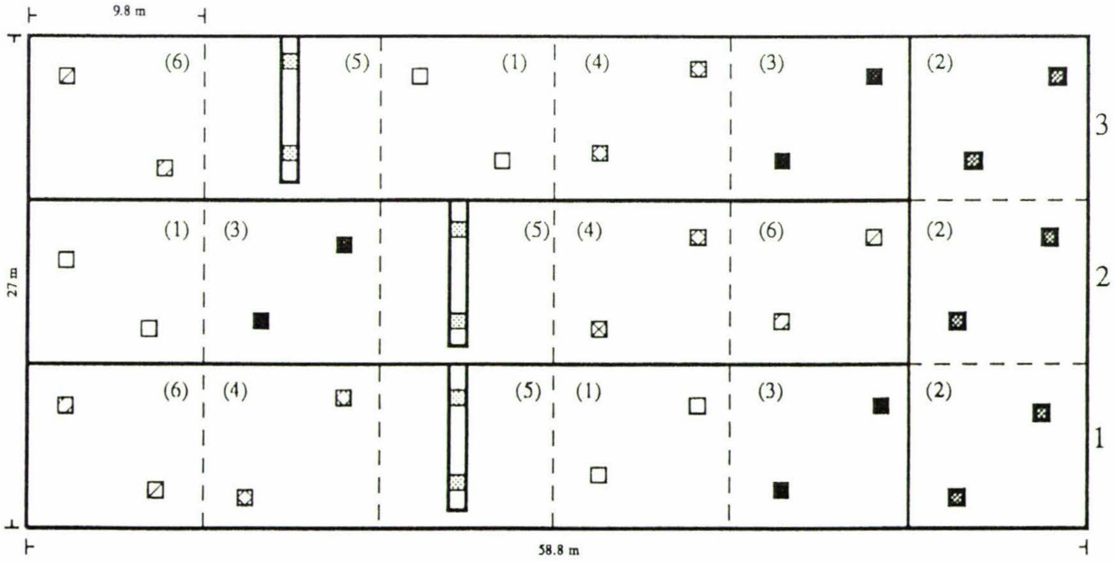

Figure 5.1. Diagram of the experimental area. Numbers 1, 2 and 3 on the right indicate blocks. Continuous lines represent the electric fencing. Small squares represent the observation units ("sub-samples"). Numbers in parentheses represent treatments.

The different kinds of disturbance were achieved in the following way:

Treatment 1 (treading and grazing). No special preparation was needed. As with all other treatments, plots were marked by pegs before bringing the animals into the fenced area.

Treatment 2 (treading only). Animals were forced to walk around without stopping to graze. However, the area allocated for each treatment (9.0 x 9.8 m) was too small to forcibly move animals. Therefore, the three replicates of Treatment 2 were fenced as a single area, thus this treatment could only be assigned to one of the extremes of the blocks, which was done randomly (Fig. 5.1).

Treatment 3 (treading on bare soil). Pasture was clipped at ground level with an electric clippers, leaving plots completely denuded. In contrast to Experiment 2 (Chapter 4), no herbicide was applied as the bare soil was only needed during treatment imposition. However, pasture was clipped exactly the same way in both experiments (see Plate 4.1).

Treatment 4 (bare soil not trodden). The same as Treatment 3 but protected from treading by cages.

Treatment 5 (grazing without treading). A fence line was especially set up (Fig. 5.1 and Plate 5.2) to allow cattle to graze underneath an electrified wire without treading on the plots, leaving a path at the end of the fenced strip to allow the same animals to have access to the other treatments (except Treatment 2).

Treatment 6 (control, no grazing, no treading). Pasture was left intact and caged against any damage from animals during treatment imposition.

All treatments (except Treatment 2) were imposed over a three-day period commencing on 28 August 1993. The initial pasture cover throughout the three blocks was 2100 kg DM ha^{-1} (determined by visual assessments) with an average height of 12 cm. Animals were removed when the desired level of soil disturbance had been achieved and were then (31 August) shifted to Treatment 2 where they were made to walk for about one hour without stopping to graze. Gravimetric soil moisture content was 42% during the period of treatment imposition. This moisture level was not enough to allow the soil to be actually pugged in any treatment, which would have been a more typical effect of winter treading.

When animals were removed from the experimental area all fencing and cages were also removed and treading was assessed by a vertical point quadrat, recording the proportion of the ground that had been depressed or stirred by the hooves. This had the purpose of checking whether treading had been uniformly achieved in Treatments 1, 2, and 3, both in terms of average trodden area per treatment and type of soil disturbance (*ie* depressed vs stirred). Differences between treatments in stirring and depression of the soil were considered to be worth analysing as stirring might have brought seeds to the surface than depressing. An analysis of variance (using the SAS "GLM" procedure) was performed on data as randomized complete block design.

All plots were grazed by bulls (approximately 25 bulls ha^{-1} for 3 days) 8, 14, and 19 weeks after treatment imposition and by ewes (approximately 150 ewes ha^{-1} for 3 days) after 21 weeks as part of the normal pasture management of the farm.

The effect of treading on the germination of ragwort seeds was assessed by counting seedlings that emerged inside the 40 x 40 cm plots on three consecutive occasions: 4 October 1993, 15 December 1993, and 31 January 1994, *ie* 5, 15, and 22 weeks after the imposition of the treatments.

To further minimise the effect of a probable heterogeneous distribution of seeds in the soil (already partially addressed by randomization and blocking of treatments), four soil samples were taken from each plot to a depth of 2 cm using a tiller corer 5 cm in diameter soon after the last count. Pots were filled with sand and soil samples were laid in thin layers of approximately 4-5 mm on top of the sand. These pots were maintained in a glasshouse under an automated mist irrigation system with an average temperature of 20°C for a period of 30 days. Seedlings were counted and removed every week. Seedling numbers obtained in the glasshouse from each pot were added to the highest number of seedlings recorded in the field from each corresponding plot, producing an estimation of the number of viable seeds present at the start of the trial. These estimates have been used to express the results as "percentage seedlings", *ie* the number of seedlings found at each assessment divided by the estimated total number of viable seeds in the soil.

Note that this "percentage seedlings" is not the same as "percentage seed germination", since the number of seeds that germinate but do not produce a visible seedling (*ie* die prior to emergence) is unknown. Neither is it equivalent to "percentage emergence" used in Chapter 4, as it comprises the number of recently emerged seedlings plus previously counted seedlings minus the ones which died.

5.4. Results

Pasture was uniformly grazed down to 700 kg DM ha^{-1} (2.5 cm height) in Treatment 5, reduced by treading to 300 kg DM ha^{-1} in Treatment 2 and by grazing and treading to a negligible residual in Treatment 1. Grazing after the imposition of treatments did not affect ragwort seedlings.

5.4.1. ***Type of soil disturbance*** There was no significant difference in the overall treading damage (the sum of depressed and stirred ground area) between the three trodden treatments (Table 5.2). See Plate 5.3 for an indication of the treading effect.

Table 5.2. Analysis of trodden area (%) immediately after the imposition of the treatments. Number in parentheses refers to treatment.

	Overall[1]	Depressed	Stirred
	(3) 78.43 a	(3) 78.43 a	(2) 12.74 a
	(2) 72.55 a	(1) 64.71 b	(1) 2.94 b
	(1) 67.65 a	(2) 59.81 b	(3) 0.00 b
$P > F$	0.1526	0.0090	0.0079
r^2 (%)	61.20	74.46	68.96
CV (%)	11.88	12.12	106.08

[1] Depressed plus stirred. Treatment means within a column sharing the same letter are not significantly different (LSD$_{0.05}$).

Trodden treatments showed similar proportions of stirred and depressed areas. Nevertheless, soil in Treatment 2 was more stirred than Treatments 1 and 3, while soil in Treatment 3 was depressed more than in Treatments 1 and 2 (Table 5.2).

Plate 5.2. A view of Treatment 5 showing a strip of pasture fenced with electric wire to restrain animals from walking on plots but allowing them to graze underneath the fence.

Plate 5.3. Plot showing damage achieved by treading (Treatment 1).

5.4.2. ***Percentage seedling*** Variances of the treatments were not homogeneous. Transformations were attempted but no significant changes in the data could be achieved. Because of the large occurrence of zeros in Treatment 6, weighted analysis of variance was not found to be an appropriate alternative. Instead, the following nonparametric analyses (performed by the SAS "NPAR1WAY" procedure) were carried out: (a) the Kruskal-Wallis *k*-sample test (Kruskal and Wallis 1952) to test the null hypothesis that the populations all had the same location, and (b) the Wilcoxon two-sample test (Wilcoxon 1945) to test the location of each pair of treatments. Both (a) and (b) were carried out separately for each time (*ie* 4 October 1993, 15 December 1993, and 31 January 1994). Unfortunately, the use of these nonparametric procedures meant a loss of power to discriminate amongst treatments. It was also a more laborious analysis as each pair of treatment had to be tested individually (multiple comparisons are not possible without a common variance).

Although mean "percentage seedlings" (defined in Section 5.3) is used to represent the effects of treatments, note that the procedures described above actually test the sum of ranks of each treatment (Steel and Torrie 1981) rather than their means. According to the Kruskal-Wallis test, there were significant differences between treatments at all times with the following probabilities: $P < 0.001$ (4 October), $P < 0.01$ (15 December), and $P < 0.05$ (31 January).

The least seedlings emerged in undisturbed pasture (Treatment 6), while all three forms of disturbance caused increases in ragwort seedling emergence (Fig. 5.2). The largest seedling numbers were found where soil was denuded of herbage cover (Treatments 3 and 4).

By 15 December 1993 differences in seedling numbers between treatments were less marked, though all treatments still had significantly more seedlings than the control treatment (Fig. 5.2).

There was a clear distinction between the trend followed by Treatments 3 and 4 (the only denuded treatments) and that followed by the other disturbance treatments (*ie* Treatments 1, 2, and 5), particularly after 15 December. The slope of the lines between 15 December and 31 January in Fig. 5.2 indicate that seedlings disappeared faster in Treatments 3 and 4 than in any other treatment. However, their percentage seedling mortality (Table 5.3) was similar to the other treatments.

By the final assessment the population of ragwort seedlings had been reduced in all treatments

(Fig. 5.2). Nevertheless Treatments 2 and 3 still had statistically more seedlings than the control treatment.

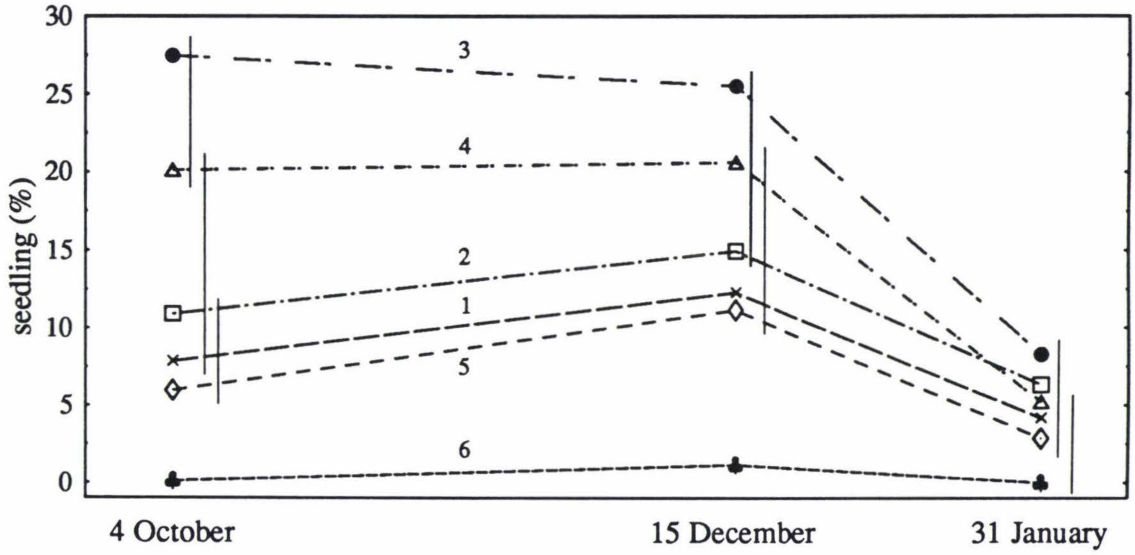

Figure 5.2. Ragwort seedling populations resulting from different types of disturbance to herbage cover on 31 August 1993. Numbers close to the lines represent treatments: 3 (trodden, bare), 4 (bare), 2 (trodden only), 1 (trodden, grazed), 5 (grazed only), and 6 (no disturbance). Treatments linked by the same vertical lines are not significantly different according to the Wilcoxon two-sample test (*ie* P > 0.05). See definition of "percentage seedling" in Section 5.3.

Although percentage seedling values have the advantage of taking into consideration the heterogeneity of seed distribution in the soil, they do not express the size of the seedling population. This information has been provided in Table 5.3.

An average seed population of 2955 viable seeds m^{-2} was obtained following the 30-day exposure of soil to light in the glasshouse. The maximum population estimate was 14,543 viable seeds m^{-2}. Note that only the surface 2 cm of soil was tested.

5.5. Discussion

5.5.1. ***Type of soil disturbance*** Based on the information provided in Table 5.2, it can be concluded that treading was uniformly achieved in all treatments in terms of average trodden area. Differences in type of treading between treatments did not seem to be associated with seedling emergence. Also, there was no evidence that the action of stirring the soil with hooves caused greater seedling emergence than the action of depressing. Table 5.2 shows in fact that the greatest seedling emergence (at the first assessment) occurred in Treatment 3, where there had been no stirring of the soil (Table 5.2). However the effect of stirring or depressing actions of hooves on seedling emergence could only be positively established if we had treatments involving several intensities of grazing and clipping so that, through a partial correlation, the effects of treading on seedling emergence could be separated from the effects of defoliation.

Table 5.3. Population of ragwort seedlings from October 1993 to January 1994.

Treatment	seedlings m^{-2}			seedling mortality[1] (%)
	4 October	15 December	31 January	
3 (trodden, bare)	572	631	229	64
4 (bare)	442	378	60	84
2 (trodden only)	388	540	219	59
1 (trodden, grazed)	217	320	109	66
5 (grazed only)	159	241	45	81
6 (no disturbance)	1	11	0	100

[1] Between 15 December and 31 January.

5.5.2. ***Effects of the different disturbances*** The stimulation of ragwort seed germination by all three forms of disturbance could be explained largely by the reduction of the above ground biomass, a common feature of all disturbed treatments. Treatments in which herbage cover had been completely removed (Treatments 3 and 4) had the largest seedling populations, while the control treatment (Treatment 6), which was not disturbed during treatment imposition, had the smallest number of seedlings (Fig. 5.2, 4 October). The other three Treatments (1, 2, and 5), in which cover removal was not as complete as in the denuded treatments, resulted in an intermediate number of seedlings. Of these three treatments (1, 2, and 5) the least emergence occurred in Treatment 5 where disturbance only reduced pasture height and did not leave patches of bare soil[2].

While the complete removal of herbage cover (Treatment 4) caused statistically the same effect as treading (Treatment 2), their combination (Treatment 3) produced a significantly larger number of seedlings. The significant difference between Treatments 2 and 3 suggests that an interaction occurred between cover removal and treading, thus indicating that treading had an effect other than the simple damage to the herbage cover.

The majority of seedlings that emerged in the trodden treatments were found on the inner border of hoof prints. Apparently, these seedlings originated from seeds lying close to a trodden patch as shown in Fig. 5.3. This would explain the additional effect observed in Treatment 3 that caused it to be significantly different from Treatment 2. Seeds that were pushed down along with the soil probably remained at a similar depth relative to the new (depressed) surface (Fig. 5.3), which explains why there was no seedling emergence on the actual depressed area. Moreover, soil above these seeds would be more compacted after treading.

Between 4 October and 15 December the change in seedling density was the net result of seedling emergence and seedling mortality. However, between 15 December and 31 January changes were entirely determined by seedling mortality, as no new seedling emergence was detected[3]. Observations suggested that seedling mortality was mainly due to competition from pasture plants which had recovered fully from all treatments. Seedlings disappeared faster in Treatments 3 and 4 because an even, dense cover was formed just a few weeks after treatment imposition. This apparently resulted from a uniform light interception by the remaining plant parts (*eg* stolons), as these plots were thoroughly denuded of herbage cover. Pasture in the other disturbed treatments did not grow as vigorously and never covered the ground completely.

The presence of a thick layer of dead plant material (1.5-2 cm on the bottom of the sward) hindered the lateral expansion (tillering) of pasture plants needed for the elimination of the gaps

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[2] Though the statistical analysis did not show any significant difference between treatments 5, 1, and 2, the consistent trend followed by these treatments between the first and the last assessment suggests that their location was not attributed to chance. If a more powerful test could have been used perhaps those differences would have been detected.

[3] Although seedlings were actually counted only three times, the site was visited every week. These frequent visits made this and other observations possible.

where ragwort seedlings were growing. This was observed in treatments which were not clipped to ground level (*viz* 1, 2, 5, and 6). In these treatments, 15 weeks (31 August to 15 December) were needed for the suppression of ragwort seedlings to become noticeable (Fig. 5.2), which only happened when pasture plants closed the gaps from above.

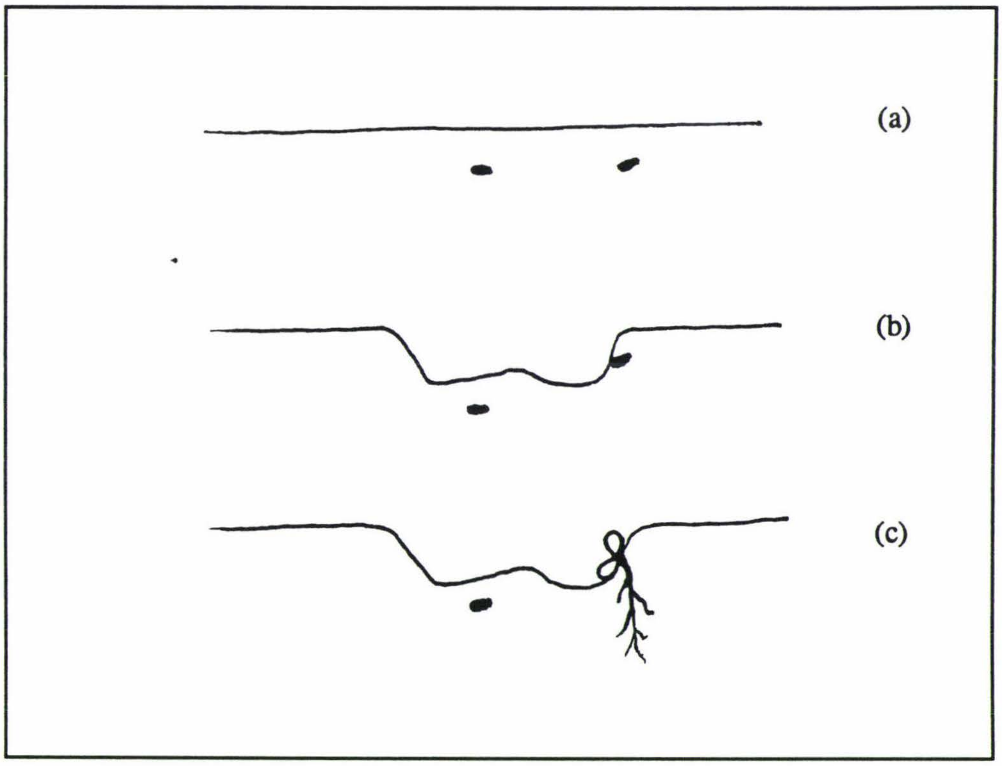

Figure 5.3. Germination of ragwort seeds favoured by a depression on adjacent soil caused by hooves. (a) Position of two photodormant seeds in the soil profile before treading. (b) Soil after being depressed by a hoof. (c) Germination favoured by lateral exposure of seed to light (see Chapter 3).

A thick layer of plant litter may be useful as a protection against the establishment of ragwort seedlings, as long as it is not broken up (*eg* by hooves). However, if this layer does get broken up it may actually help the establishment of ragwort by maintaining a "safe site" for the seedlings (as discussed above). A safe site (Harper 1977) not only provides seeds with the necessary conditions for germination but also offers protection against competitors, predators, etc (see Chapter 6 and 7).

Despite the reduction in seedling density recorded between 15 December and 31 January, the actual number of seedlings per m^2 recorded in the disturbed treatments during the last assessment was still very high (Table 5.3), particularly in Treatments 1, 2, and 3. However, in terms of percentage seedling values, only Treatments 2 and 3 remained significantly higher than the control treatment (Fig. 5.2).

Notice that relative ranking of Treatments 2 and 4 (on 15 December) and Treatments 1 and 4 (on 31 January) differed depending on the way seedling numbers were expressed (see Fig. 5.2 and Table 5.3). This shows that there was a considerable variation in the natural distribution of seeds in the soil, which consequently justified the use of percentage seedling values.

It should be stressed that the disturbance imposed in this trial lasted for only three days (only one hour in Treatment 2) and that soil moisture was relatively low as well. This moist hill-country area would be wetter in an average winter (see Fig. 4.2). Also paddocks may be heavily trodden more than once during this time (probably lasting for more than three days as well). Therefore, ragwort seedling emergence could often be higher than the values recorded in this trial.

If the subsequent summer is dry, an unusual situation for these moist hill-country areas but very common in other New Zealand pastures (see Chapters 6 and 7), seedlings may not survive. If so, winter treading could even be desirable, at least with respect to ragwort problems, as the soil seed bank would be partly depleted of viable seeds.

The vast majority of the seedlings observed in this experiment originated from seeds rather than from vegetative parts (only three seedlings were found to be vegetative regrowths). This was expected as there were no ragwort plants in the area prior to treatment imposition. Seedlings originating from regrowth would probably have more chance of surviving in a dry summer.

Of the six treatments, the combination of treading and grazing (Treatment 1) would certainly be the most common case in normal pastures. However all of them can actually be found within a farm. Treading only (Treatment 2) is seen on tracks, for instance. Treading on bare soil (Treatment 3) and untrodden bare soil (Treatment 4) would happen in small gaps in the pasture arising from the death of some plants. A soil slip could also be an example of Treatment 4, but usually no soil seed bank would be left after a slip. Grazing without treading (Treatment 5) is found in patches, probably more commonly in a continuous grazing system and/or on certain banks where animals cannot walk but can reach them to graze and also along fence lines. A paddock closed for hay or silage making, for instance, could be a real example of no disturbance for some time, with subsequent grazing (Treatment 6). It is likely that all these patterns (disturbed and undisturbed) occur in a single paddock, which would partly explain why some areas of a paddock are sometimes highly invaded by ragwort while others are ragwort-free. The proportion of each pattern would certainly depend on grazing method, grazing duration, stocking rate, animal species and distribution of seeds in the soil as well.

5.6. Summary

The main results of this experiment can be summarized as follows:

(i) Only 3 days of intense grazing and treading in late winter were sufficient to cause significant increases in the ragwort seedling population.

(ii) Fewest ragwort seedlings emerged where pasture was not disturbed.

(iii) Any of the forms of disturbance studied resulted in significant increases in ragwort seedling numbers.

(iv) Seedling emergence was greater when pasture had been denuded of cover.

(v) A large seedling mortality was observed as a consequence of full recovery of pasture from the disturbance. This was even more noticeable in treatments which were previously denuded of herbage cover, as pasture became denser and more competitive than in treatments which had a considerable layer of dead plant material on the bottom of the sward. Additionally, seedling mortality occurred sooner in previously denuded treatments.

(vi) This layer of plant litter was observed to help prevent seed germination provided it was undamaged. However, when it was broken up by hooves it served as a protection for seedlings.

(vii) The main effect of treading on seedling emergence was largely explained by a reduction of the above-ground biomass. A smaller effect was explained by soil movement which allowed previously covered seeds to be exposed to light.

Dynamics of Ragwort Seedling Populations on a Dairy Farm

6.1. Introduction

As mentioned earlier (Sections 2.4.2 and 4.1), previous studies which have considered the establishment of ragwort have either used sown seeds (Cameron 1935; Poole and Cairns 1940; van der Meijden and van der Waals-Kooi 1979) or have failed to identify seedlings at early stages (Forbes 1977; Thompson 1985). Apparently, Forbes (1977) and Thompson (1985) were not able to monitor young ragwort seedlings because of (a) deficient mapping techniques and (b) long time intervals between assessments (one month and three months respectively).

Studies which have attempted to understand the emergence of ragwort seedlings in pastures (Cameron 1935; Poole and Cairns 1940; Phung and Popay 1981; McEvoy 1984a) have not considered the importance of seasonal changes in the environmental conditions that may influence seed germination and seedling survival. In New Zealand, peak seedling emergence under grazed conditions is claimed to occur in autumn, soon after the seed rain (Poole and Cairns 1940; Thompson 1985). However, these observations are mostly anecdotal.

Despite the occurrence of ragwort in hill country pastures (Radcliffe 1969), particularly in bull beef systems (Betteridge *et al.* 1994; see also Chapters 4 and 5), it is on dairy farms that the species is generally regarded as an important weed (Bourdôt *et al.* 1994).

6.2. Objectives

The trial reported in this chapter was designed to study the emergence and fate of ragwort seedlings under the normal conditions of a commercial dairy farm, *ie* without intentionally interfering with any element of the system.

To help understand the dynamics of seedling populations, a number of factors that might influence seed germination and seedling survival were monitored for the period of one year.

6.3. Methods and materials

6.3.1. ***The farm*** The trial was conducted on a commercial dairy farm (owned by Mr J. Tait-Jamieson) close to the Manawatu River, 6 km from Palmerston North. Ragwort was conspicuous throughout the whole farm, but some paddocks were more infested than others. The property is run as an organic farm, thus herbicides are not used for the control of ragwort. Instead, the farmer has been relying on biological control using ragwort flea beetle and cinnabar moth (see Section 2.6.3) and also has been running some sheep (rotationally grazed) on part of the farm with the purpose of keeping the species in check. Ragwort seeding is largely reduced by mowing pasture every year for silage making. However, seed production is abundant in paddocks which are not mowed.

6.3.2. ***The sites*** Three sites were selected within the farm ranging from the most productive to the poorest pasture. The selection was based on information provided by the farmer regarding the performance of individual paddocks over the years.

The sites were:

> Site 1. A paddock with a dense, productive sward regarded by the farmer as one of his best pastures. Of the three sites, Site 1 had the smallest ragwort population at the beginning of the trial (July 1993). Average ragwort density (rosettes) was approximately 400 plants ha^{-1}.
>
> Site 2. A paddock 600 m from Site 1 where pasture was of an intermediate quality between Sites 1 and 3. Ragwort density was approximately 1600 plants ha^{-1}.
>
> Site 3. This was located 650 m from Site 2 (approx. 1210 m from Site 1) close to the Manawatu River (180 m from the river banks). It was the poorest pasture on the farm, particularly in summer when herbage growth, according to the farmer, was severely affected by drought. Ragwort density was 8300 plants ha^{-1}.

To help characterize the sites, 25 soil samples (7.5 cm deep) were taken from each paddock in February 1995 and tested for pH, nutrients and organic matter content (Table 6.1). Additionally, the botanical composition of each site was visually assessed (also in February 1995) to provide a general description of each sward by giving scores (1 to 5, allowing 1.5, 2.5 etc) to randomly selected 40 x 40 cm quadrats. The scores were subsequently transformed into percentage values (Table 6.2).

Table 6.1. Soil pH, nutrient concentration and organic matter content of Sites 1, 2 and 3. Phosphate and sulphate values are expressed as $\mu g\ g^{-1}$ (air-dry). Exchangeable cations (K, Ca and Mg) and CEC (cation exchange capacity) as meq 100 g^{-1}.

Site	pH	Olsen P	SO_4	K	Ca	Mg	CEC	OM (%)
1	5.7	16	6.0	0.95	14.3	2.18	27	10.37
2	5.5	18	5.0	0.86	8.4	1.58	21	6.77
3	5.7	10	4.5	0.93	7.8	1.38	20	7.21

6.3.3. ***Measurements*** On each site, five 1 x 1 m permanent quadrats were laid out. The position of each quadrat was marked by four wooden pegs (30 cm each) which were buried in the soil leaving only 2 cm above the surface. Initially, each peg had a yellow plastic tag attached to its top to help locate and identify the plots. However the tags soon had to be removed as they attracted the attention of the cows. Despite that, there was no difficulty in finding nor in identifying the plots particularly because the sites were visited every week.

6.3.3.1. ***Weekly observations*** The quadrat frame was divided into 25 subunits (20 x 20 cm). The attributes described below were measured/estimated once a week within 5 subunits per quadrat. Every week, new subsamples were randomly selected before going to the field.

(i) Herbage mass (kg DM ha^{-1}) - Since no destructive method could be used, herbage mass was estimated by eye appraisal. The accuracy of visual assessments (carried out by only one observer) was checked against values obtained by cutting the herbage to ground level, washing and drying in an oven at 100°C overnight (Frame 1981). Since the assessments were highly correlated ($r = 0.89$, $P < 0.01$ in winter and $r = 0.82$, $P < 0.05$ in summer) the visual estimation of the herbage mass was considered satisfactory. Alternatives like the rising plate meter or the electronic capacitance probe could not be used because of the interference of the frame on the readings and also because of the small size of the sub-samples (20 x 20 cm).

Table 6.2. Botanical composition (percentage cover) of Sites 1, 2, and 3 visually estimated in February 1995. The dominant species for each site are indicated by shading.

Species	Site 1	Site 2	Site 3
Achillea millefolium, yarrow	3	14	3
Agrostis capillaris, browntop	—	30	45
Anthoxanthum odoratum, sweet vernal	—	—	15
Bellis perennis, daisy	tr[1]	1	—
Bromus hordeaceus, soft brome	9	2	—
Bromus catharticus, prairie grass	—	1	—
Cirsium arvense, Californian thistle	5	—	—
Cynosorus cristatus, crested dogstail	—	2	3
Dactylis glomerata, cocksfoot	—	5	1
Holcus lanatus, Yorkshire fog	2	4	—
Hypochaeris radicata, catsear	1	3	10
Lolium perenne, perennial ryegrass	58	25	5
Lotus pedunculatus, lotus	—	tr	—
Paspalum dilatatum, paspalum	—	—	5
Plantago lanceolata, narrow-leaved plantain	4	2	10
Ranunculus repens, creeping buttercup	4	—	—
Ranunculus sardous, hairy buttercup	—	1	—
Rumex obtusifolius, broad-leaved dock	4	3	1
Senecio jacobaea, ragwort	3	4	—
Taraxacum officinale, dandelion	1	1	—
Trifolium repens, white clover	6	2	2
Trifolium pratense, red clover	—	tr	—
Number of species	13	18	11

[1] tr = trace (percentage cover < 1%)

(ii) Sward surface height (cm) - This was measured with an ordinary ruler in the centre of the selected frame subunits (no error due to parallax was expected from the use of a ruler since the observer was lying on the ground).

(iii) Trodden ground area (%) - The percentage ground area damaged by hooves was visually estimated by giving scores from 1 to 5, using half values (*eg* 3.5) when in doubt between two whole numbers (I. Gordon, pers. comm.). Score 1 was given to swards bearing no evident signs of treading and score 5 was given to sward samples which were almost entirely damaged by hooves (this was rarely found). Note that a trodden patch could either be covered by foliage or denuded.

(iv) Bare soil (%) - The percentage ground area lacking herbage cover (live or dead). The assessment followed the same method described in (iii).

(v) Ground area covered by dung (%) - This was included for two purposes: (a) to check possible (marked) changes in animal behaviour due to the atypical presence of pegs and people (either by excessive defecation on the area or its absence); and (b) to explain a sudden disappearance of ragwort seedlings (vi) as well as some erratic values of any of the above attributes (i to iv) that might be found.

(vi) Ragwort seedling density (seedlings m^{-2}) - This parameter represents the absolute number of seedlings per m^2 in each assessment (*ie* the net result of seedling emergence and death) and included recently emerged seedlings (*ie* seedlings emerged within one week) as well as seedlings emerged earlier.

Additionally, soil samples were collected every week to provide information on seasonal fluctuation in the soil moisture content. Five samples (15 cm deep) were collected per site (approx. 2 m away from each plot) and placed in individual plastic bags. The moisture content was obtained by the gravimetric method (Rundel and Jarell 1989). To allow the comparison between sites, three soil samples (15 cm deep) were taken from each site and placed in two pressure plates, one at -100 kPa and the other at -1500 kPa. After one week, soil was oven dried to obtain the gravimetric moisture corresponding to each of the pressures above (see

McLaren and Cameron 1990). Values were choosen to indicate two important stages: (a) an average water potential (-100 kPa) when most plants start to spend energy to absorb water from the soil (Taylor and Ashcroft 1972) and (b) the water potential (-1500 kPa) generally associated with the permanent wilting point, *ie* when plants are wilted day and night (McLaren and Cameron 1990).

6.3.3.2. *Mapping of seedlings* As indicated above (vi), simply counting the number of ragwort seedlings in a random sample every week was not an accurate way of monitoring emergence and mortality of seedlings. Though a larger number of seedlings in a given week (compared to the previous week) would certainly be a result of emergence, the exact figure would be unknown due to the likely occurrence of death as well.

To overcome the problem we needed a technique which allowed us to map seedlings often enough to detect major changes but did not demand too much time so that a larger number of samples could be taken. Sarukhán and Harper (1973) used a pantograph for mapping of *Ranunculus* spp. within a sward. The instrument had a pen at one end and a pin at the other. When the pin was made to move over the plant's leaves (following their edges), the pen registered the movement on transparent paper which lay on a board beside the quadrat. By superimposing two consecutive maps, it was possible to identify new seedlings as well as seedlings that disappeared between observations. Although in theory the technique would produce exactly what we needed, in practice it had several drawbacks: (a) the procedure could not be carried out in humid weather (not to mention a rainy day), because the paper expands with excessive moisture and becomes uneven; (b) it requires two operators; (c) demands too much time; (d) the material is awkward for transportation; (e) the pantograph is difficult to operate when the sward is high; and also (f) the soil surface has to be as flat as possible.

Based on this method, we developed a simple technique that did the same job but with much less effort and time involved. Instead of using a pantograph, a board and paper, we used a sheet of transparent glass (45 x 45 cm), transparent acetates (those used on overhead projectors), adhesive tape and waterproof pens of different colours (Plate 6.1, p. 89).

To map seedlings (Plate 6.2, p. 89), the glass was placed upon the quadrat and a sheet of acetate was laid on the glass and fixed with adhesive tape. Seedlings were drawn with a black pen and the four corners of the subunit in question were also marked on the acetate. The date, subunit and plot identification were recorded on it as well. In the following observation (a fortnight later), the previous map was laid again (to help find "old" seedlings faster) and a new acetate was placed on the top of it. On the new map, seedlings from the earlier map which were still present were marked with a black pen and linked with a blue line. If a seedling which had been recorded on the previous map was not found, its place was marked with a red cross on the new map. If a seedling was later found to have been wrongly identified as ragwort (which happened only a few times) it was then marked with a green cross. Initially, hoof prints were also mapped for comparison with the pattern of seedling emergence. However, because of intensive treading, this became very difficult to carry out and was soon abandoned. It could have been useful if treading was more controlled.

The main source of error (though small) in this method was due to parallax: the taller the pasture the further apart was the glass from the seedlings. However, because the glass was heavy, herbage was greatly lodged during the observations, thus the distance was never too great. On subunits close to the edges of the 1 x 1 m quadrat it was easier to view seedlings at a right angle to the ground (*ie* perpendicularly), but on inner positions it became more difficult and uncomfortable. Nevertheless, the subunits to be mapped were selected at random and followed through till the end of the trial. Mapping was carried out from August 1993 to June 1994.

6.3.3.3. ***Soil seed bank*** In February 1994, prior to the ragwort seed rain, the soil seed bank of all three sites was sampled in order to obtain information about the densities of ragwort seeds. From around each plot, 4 soil cores (5 cm diameter and 2 cm deep) were taken (a total of 20 cores per site). The soil was placed in a glasshouse to stimulate seed germination following the same method described in Section 5.3.

6.3.3.4. ***Rainfall and soil temperature*** Average monthly rainfall and soil temperature data (10 cm deep, recorded daily at 9 a.m.) were obtained from the Palmerston North AgResearch Meteorological Station which is approximately 6.5 km from the farm and approximately 700 m from the Manawatu River.

6.4. Results

6.4.1. ***Seedling density*** Ragwort seedling density varied greatly between sites and also throughout the period of study. It was much greater at Site 3 for most of the year (Fig. 6.1a), but was similar between Sites 1 and 2 (Fig. 6.1b), except in August and November 1993 and in May and June 1994. Note that this data is the average number of seedlings found in each assessment, not seedling emergence (see Section 6.3.3.1, item vi).

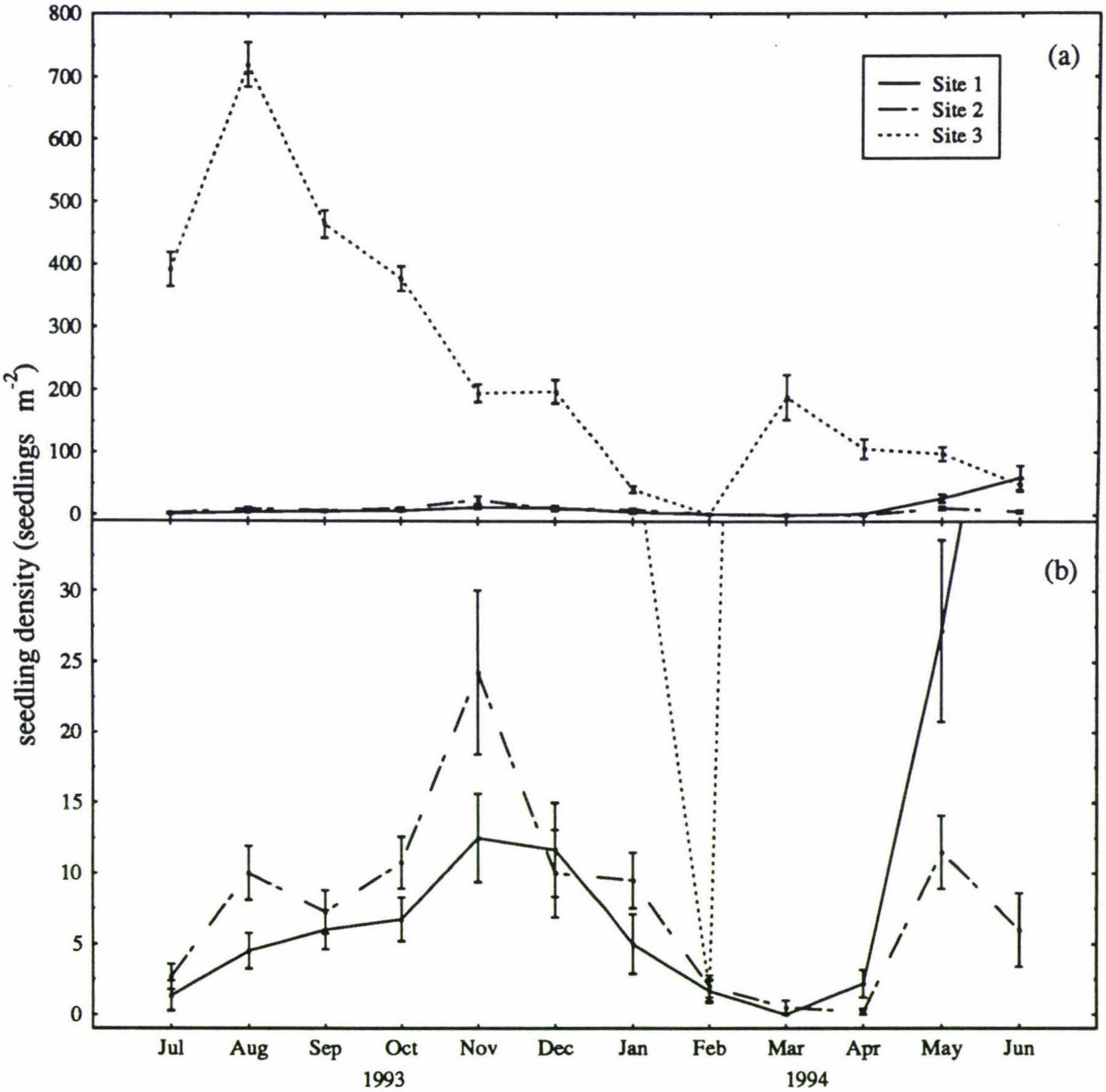

Figure 6.1. Density of ragwort seedlings (±SE) recorded weekly from July 1993 to June 1994. Graph (b) shows data from Graph (a) in larger scale to allow better comparison between Sites 1 and 2. Values are monthly means.

The peak seedling density also differed markedly between sites. While seedling numbers at Site 3 peaked in August, Site 2 peaked in November and Site 1 in June. However, the overall pattern of seedling density was very similar between Sites 1 and 2, except for the decline observed between May and June on Site 2.

6.4.2. *Seedling emergence* As described in Section 6.3.3.2, seedling emergence was obtained from the mapping of ragwort seedlings. As expected from the seedling density figures (Section 6.4.1), Site 3 presented the highest emergence values, except from December to February (Fig. 6.2a).

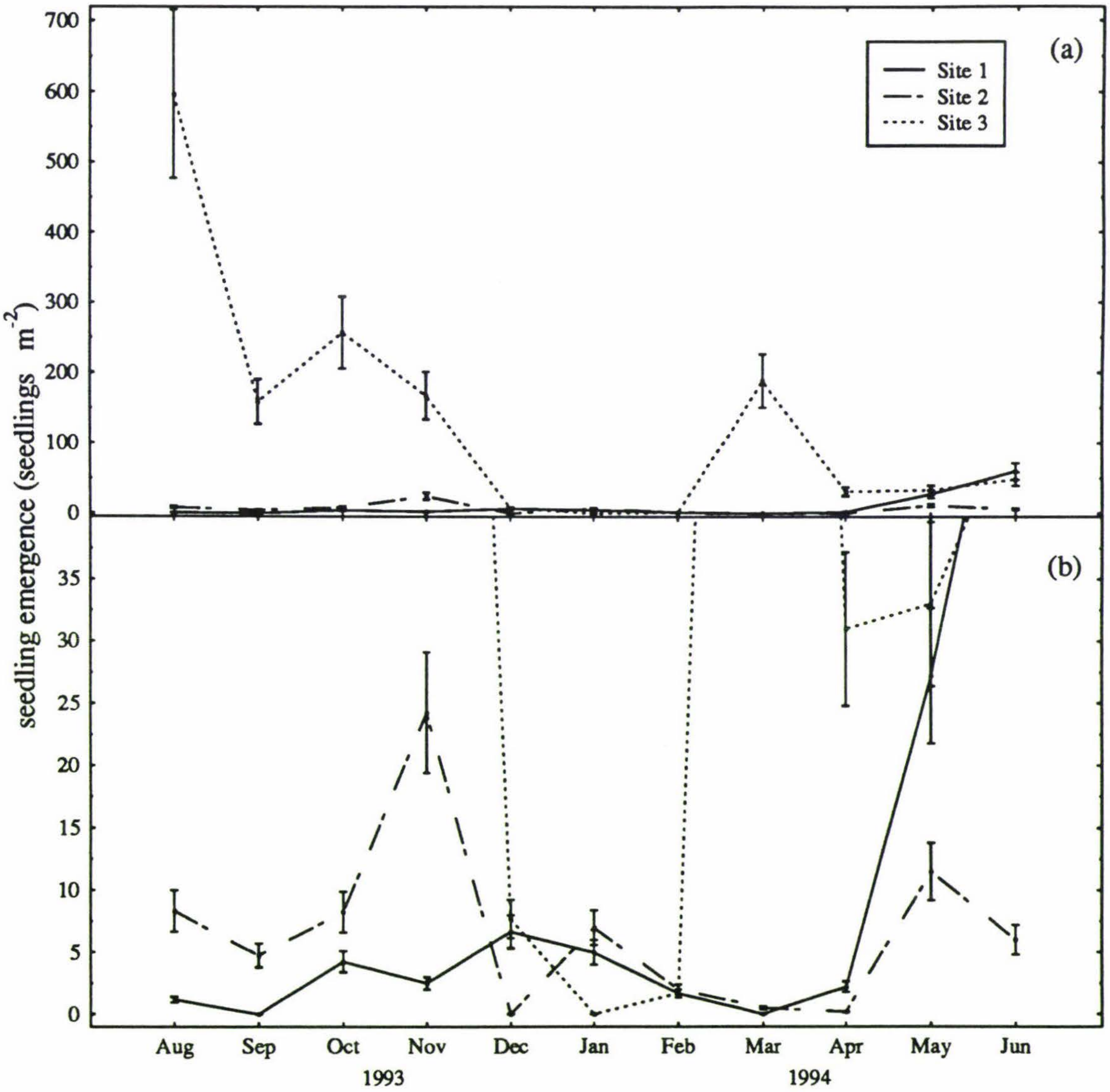

Figure 6.2. Emergence of ragwort seedlings (±SE) recorded fortnightly from August 1993 to June 1994. Graph (b) shows data from Graph (a) in larger scale to allow better comparison between Site 1 and 2. Values are monthly means.

At Site 3, the highest emergence was reached in August but two other peaks were also observed over the year, one in October and another in March (Fig. 6.2a). However, seedling emergence reached its highest peak at Site 1 in June and Site 2 in November (Fig. 6.2b).

6.4.3. ***Seedling mortality*** The mortality of ragwort seedlings, also obtained from mapping (Section 6.3.3.2), is shown in Fig. 6.3. Similarly to seedling density and emergence, mortality varied between sites and throughout the year. The figures are somewhat proportional to the size of each seedling population, thus Site 3 presented the highest average mortalities, reaching peaks in September (the highest), December and April-May. The largest mortality recorded on Site 2 was reached in December, coinciding with one of the peaks of Site 3. At Site 1, mortality was higher in September (coinciding with Site 3) and in November (contrasting with the other two sites). After November, mortality decreased steadily and was nil from January onwards.

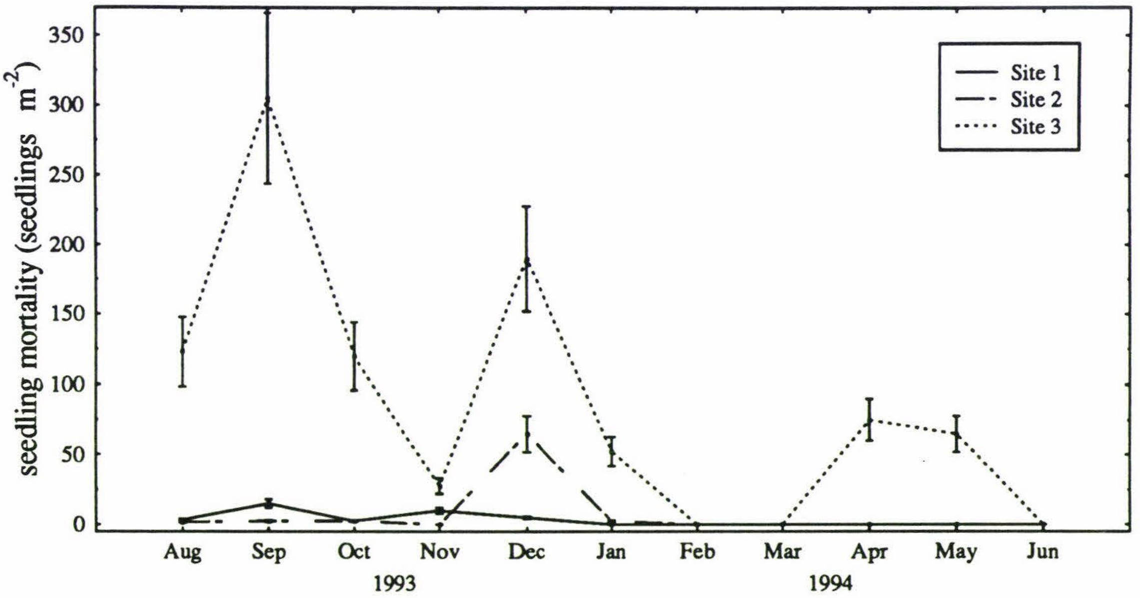

Figure 6.3. Mortality of ragwort seedlings (±SE) recorded fortnightly from August 1993 to June 1994.

6.4.4. ***Herbage mass*** Visual estimation of herbage mass (see Section 6.3.3.1, item i) recorded on a weekly basis is shown in Fig. 6.4. Because the weekly observations were independent of any farm management decision, assessments were carried out at any growing stage (*ie* varying from pre-grazing to post-grazing). Herbage mass was predominantly higher on Site 1 for most of the year. Maximum average values recorded were 2100, 1910 and 1720 kg DM ha^{-1} for Sites 1, 2 and 3 respectively. All three sites had a minimal herbage mass in July. The minimum average herbage cover found on Site 1 was 1215 kg DM ha^{-1}. On Sites 2 and 3 it was 790 and 770 kg DM ha^{-1} respectively. Curves for Sites 1 and 3 followed a similar pattern, while Site 2 differed markedly from Sites 1 and 3 between September and October and from March to April.

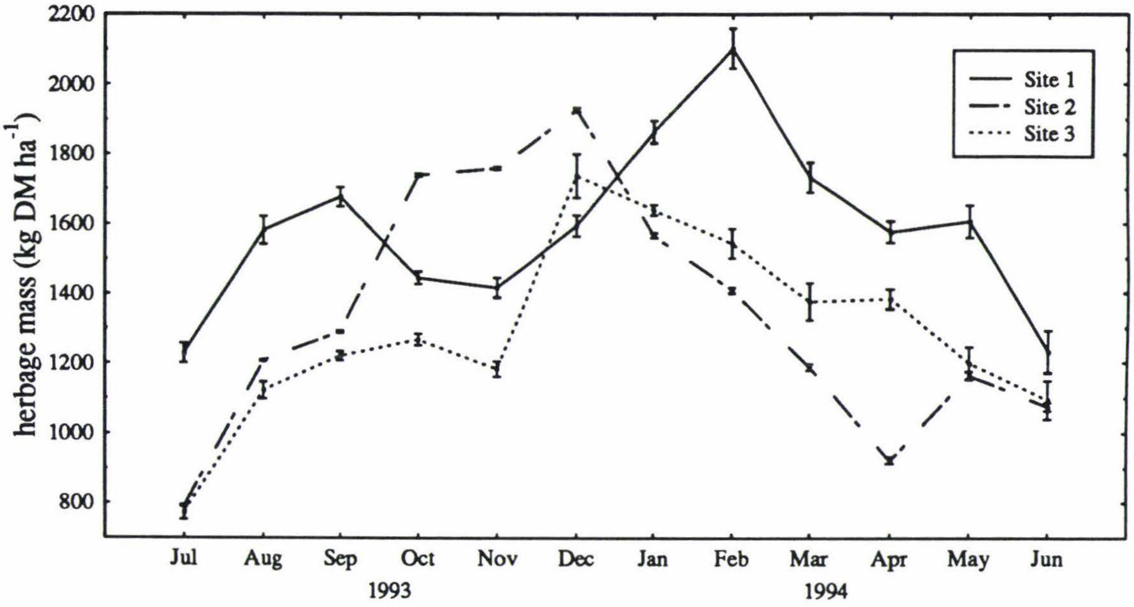

Figure 6.4. Herbage mass (±SE) recorded weekly by eye appraisal from July 1993 to June 1994. Values are monthly means.

6.4.5. ***Sward surface height*** Fig. 6.5 shows that average sward height values followed a similar pattern to that of the herbage cover. Average values ranged from 2.1 cm (Site 3 in July) to approx. 12.5 in Sites 1 and 2.

6.4.6. ***Herbage bulk density*** Estimates of mean herbage bulk density (Hodgson 1990) were derived by dividing herbage mass (Section 6.4.4) by sward surface height (Section 6.4.5). As shown in Fig. 6.6, bulk density was inversely proportional to sward surface height, *ie* the shorter the pasture the higher the bulk density and vice versa.

6.4.7. ***Trodden ground area*** The most intensive treading was recorded in July on Sites 2 and

3 (Fig. 6.7). Though Site 1 was also severely trodden in July, it was more intensively trodden in August and October. From December to April neither of the sites suffered visible effects of treading. However, on the three sites, treading increased in May (though negligibly on Site 1) and decreased again in June.

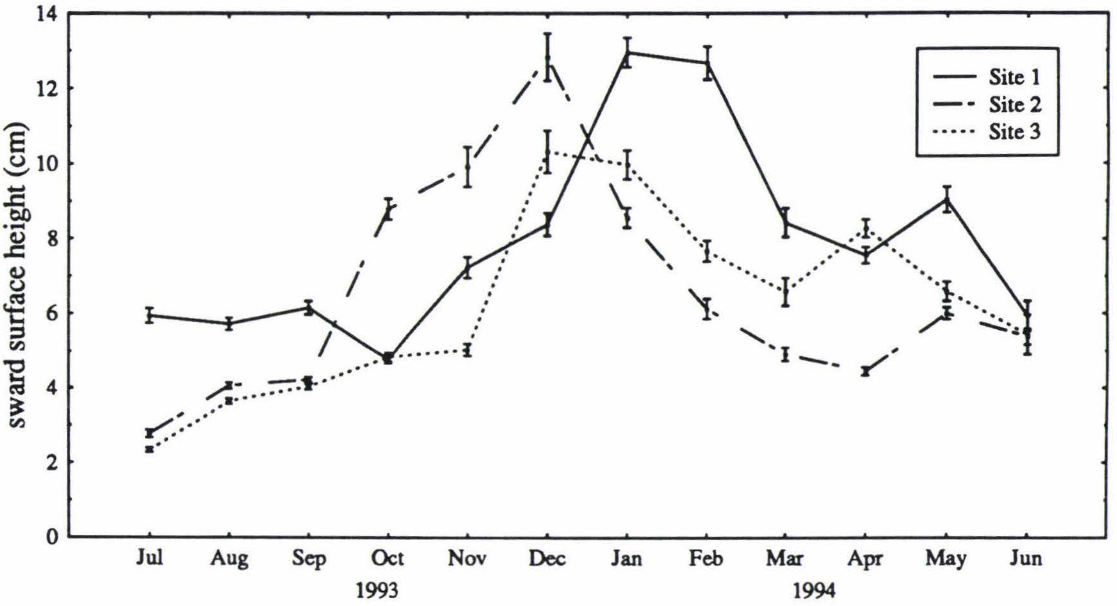

Figure 6.5. Sward surface height (±SE) measured weekly from July 1993 to June 1994. Values are monthly means.

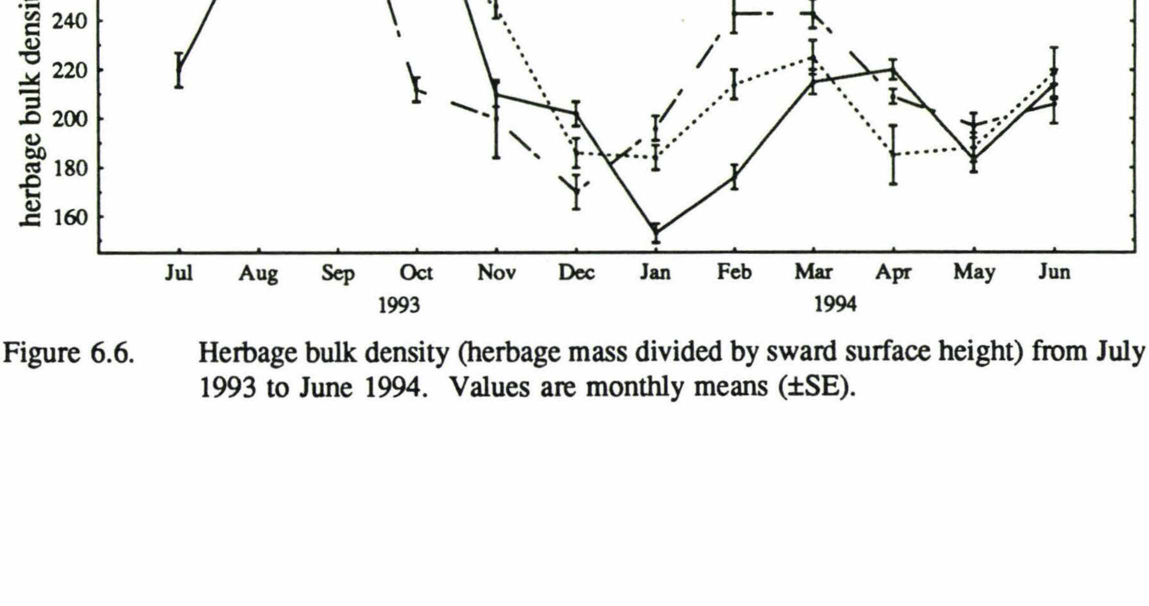

Figure 6.6. Herbage bulk density (herbage mass divided by sward surface height) from July 1993 to June 1994. Values are monthly means (±SE).

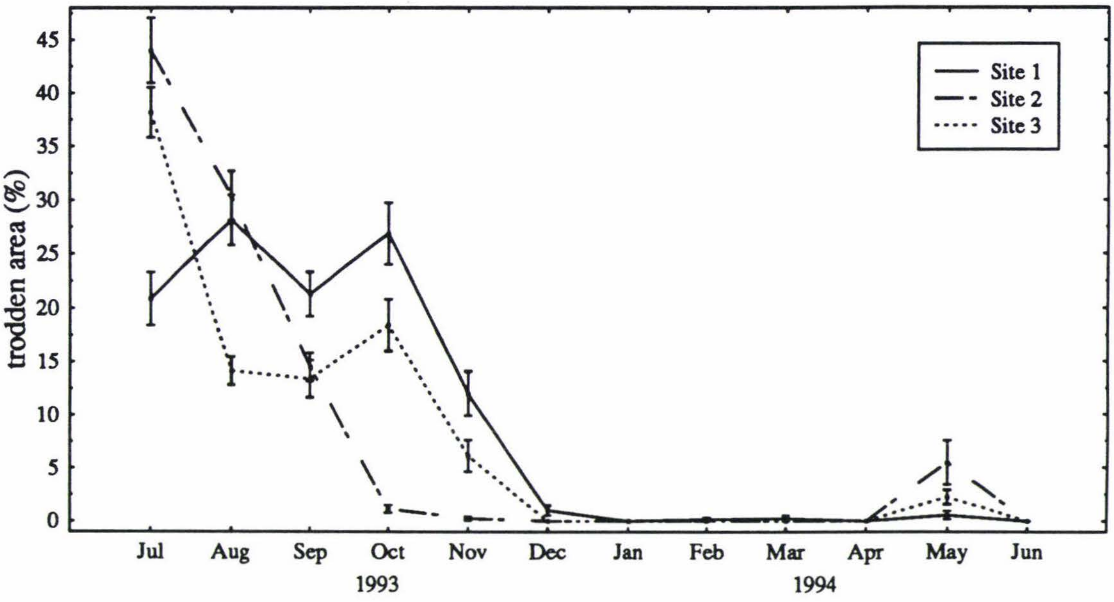

Figure 6.7. Ground area trodden by livestock from July 1993 to June 1994. Values are expressed as monthly means (±SE) and were derived from weekly assessments.

6.4.8. ***Bare soil*** The mean percentage ground area found denuded of herbage cover throughout the year is shown in Fig. 6.8. Sites 2 and 3 presented a similar trend over the year, while Site 1 produced quite a different pattern. This was markedly so from January to March and between May and June.

6.4.9. ***Ground area covered by dung*** Dung cover varied from nil to 6.8% of the ground. It was generally higher on Site 3, though variability of the data was high (Fig. 6.9).

6.4.10. ***Soil moisture content*** Site 1 had a consistently greater water content than Sites 2 and 3, while the latter were similar to each other (Fig. 6.10). Nevertheless, Site 3 did tend to be drier.

Comparisons between sites should be based on the amount of water actually available to the plants. Because of differences in organic matter content (Table 6.1) and perhaps also in clay, sand and silt, equal moisture contents do not necessarily mean equal availability of water (McLaren and Cameron 1990). To account for this, the soil moisture content at -100 and -1500 kPa (Taylor and Ashcroft 1972; Rundel and Jarell 1989; McLaren and Cameron 1990) are provided in Fig. 6.10 (a) and (b) respectively.

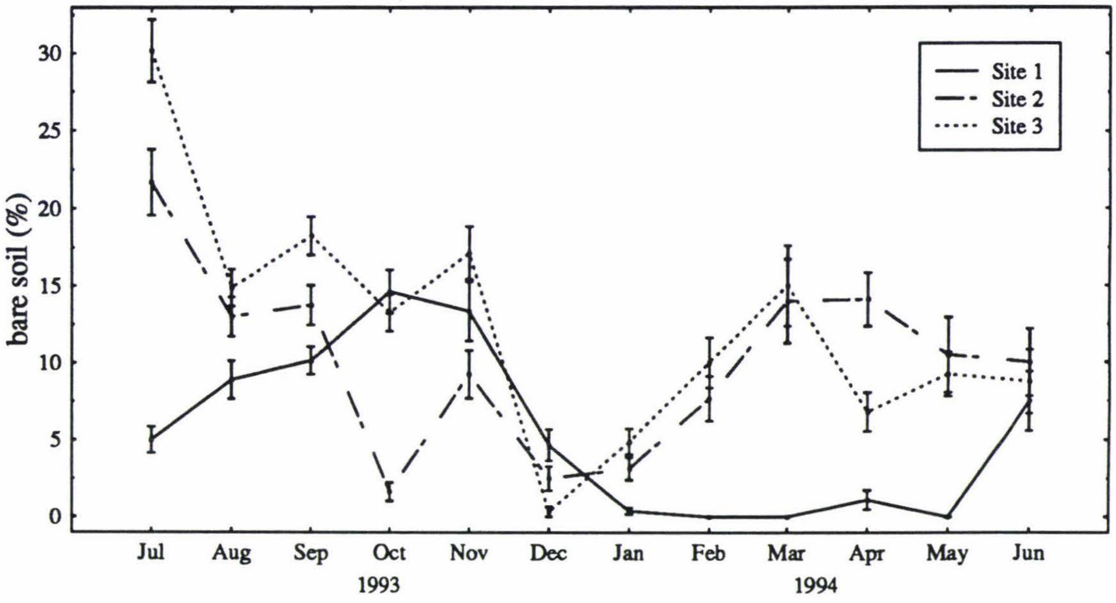

Figure 6.8. Percentage of bare soil (±SE) assessed weekly from July 1993 to June 1994. Values are monthly means.

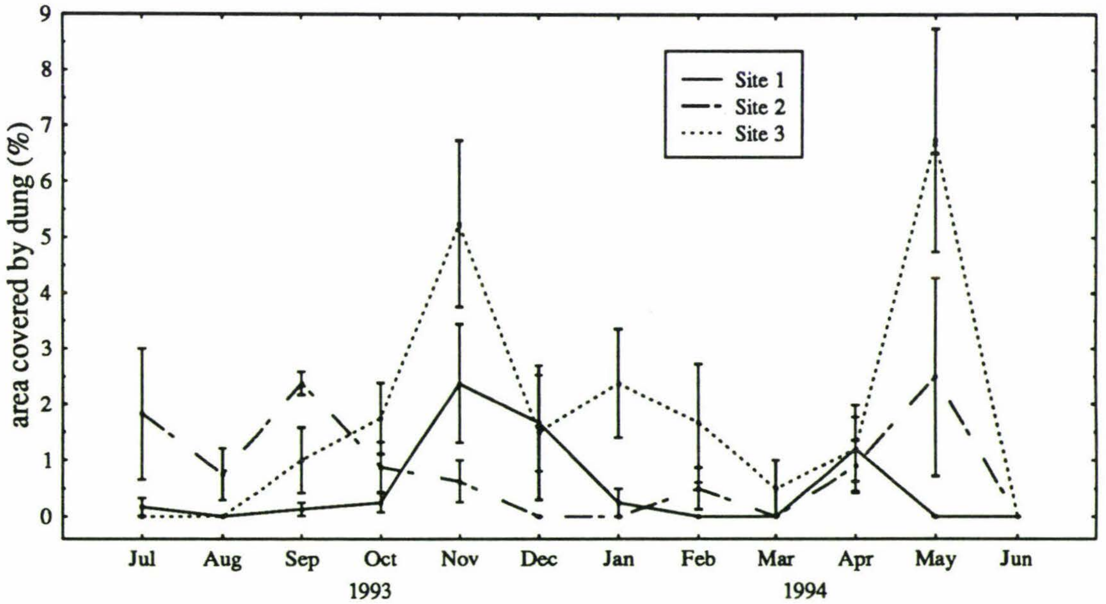

Figure 6.9. Percentage ground area covered by dung (±SE) from July 1993 to June 1994. Values are expressed as monthly means and were derived from weekly assessments.

6.4.11. ***Soil seed bank*** As expected, the amount of ragwort seeds in the soil seed bank of Site 1 was much higher than at the other two sites (Fig. 6.11).

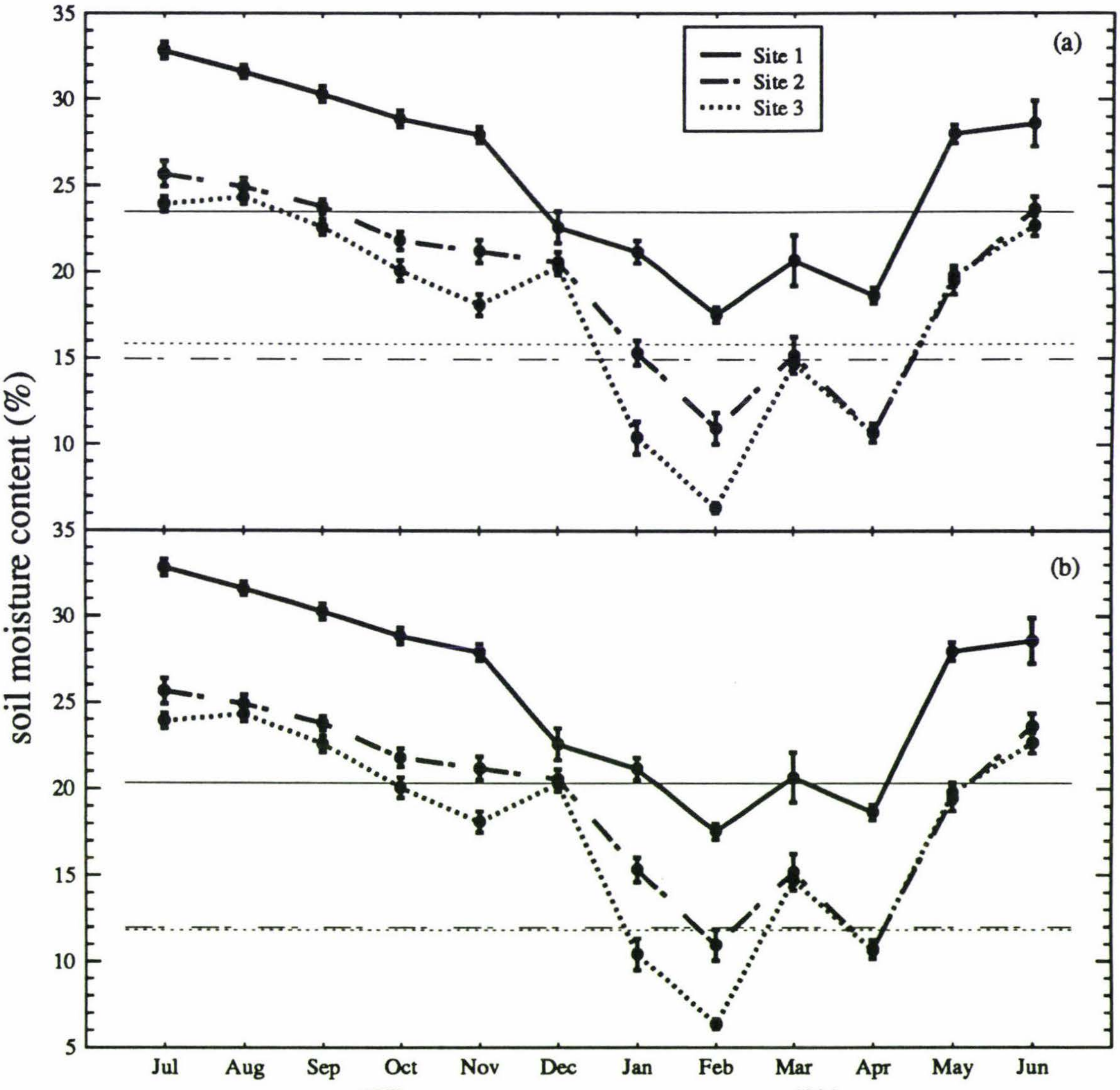

Figure 6.10. Gravimetric soil moisture content (±SE) recorded weekly from July 1993 to June 1994. Horizontal lines represent the soil moisture content at -100 kPa (a) and at -1500 kPa (b) (see Section 6.3.3.1). NB: values are average soil moisture content.

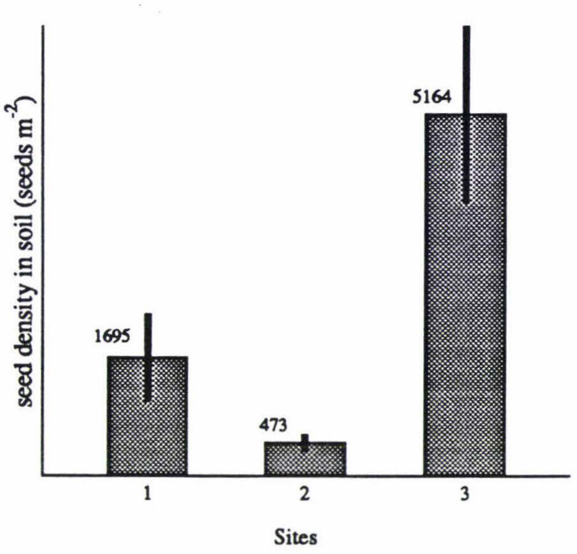

Figure 6.11. Population of viable ragwort seeds (±SE) found in February 1994 prior to the seed rain.

6.4.12. *Rainfall and soil temperature* As at Ballantrae (Chapters 4 and 5), rainfall was generally below average during most of this study (Fig. 6.12). Soil temperature is shown in Fig. 6.13.

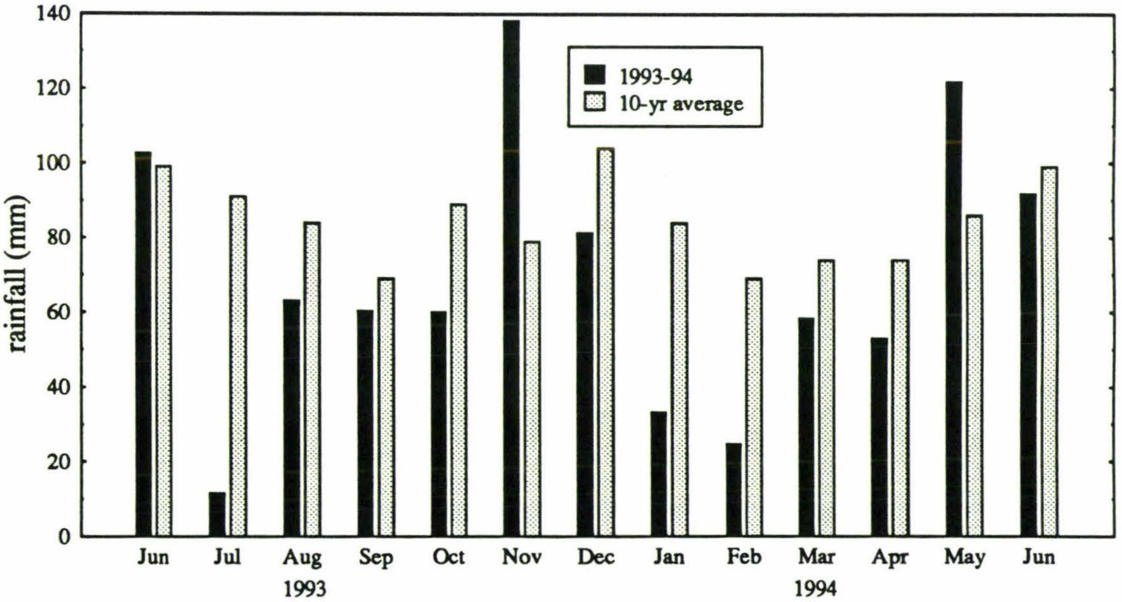

Figure 6.12. Average monthly rainfall recorded at the Palmerston North AgResearch Meteorological Station.

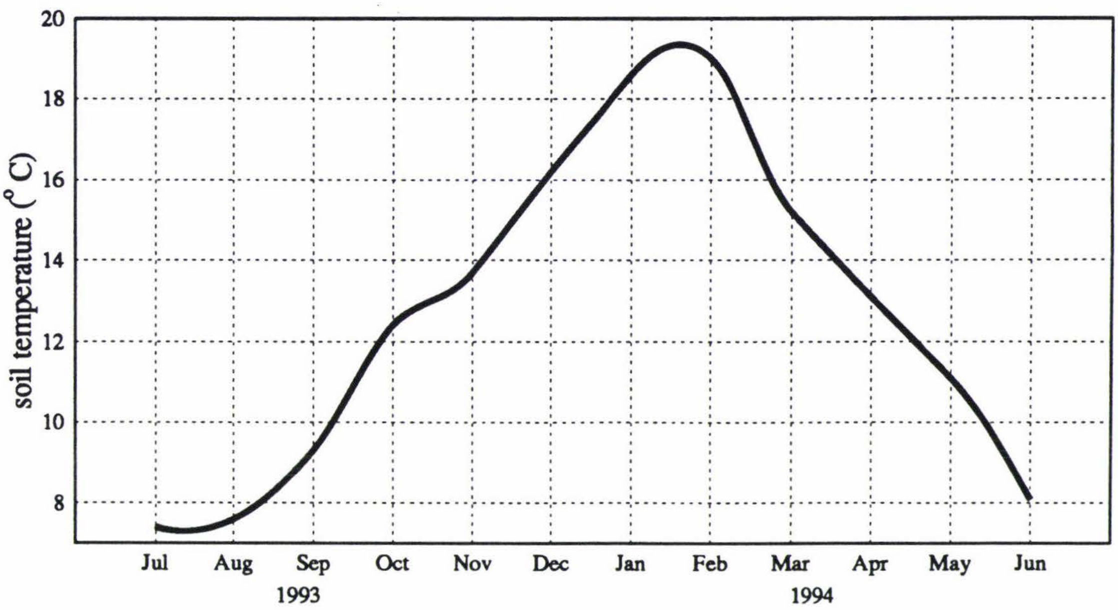

Figure 6.13. Average soil temperature (10 cm deep) recorded daily (9 a.m.) at the Palmerston North AgResearch Meteorological Station.

6.4.13. ***Other observations*** Because the visits to the sites were frequent and regular it was possible to notice a number of other factors that might also have some direct or indirect influence on the behaviour of ragwort on the farm (see Table 6.3).

Table 6.3. Some additional observations carried out from July 1993 to June 1994.

Month	Site 1	Site 2	Site 3
July-August	(a) Sward dominated by grasses.	(a) Sward with similar proportions of grasses and white clover.	(a) Sward dominated by white clover; (b) A large amount of earthworm casts was accumulated on the soil surface. This was so intensive that any open space had a layer at least 5 mm thick, frequently thicker than 10 mm. Depending on weather conditions, these casts became dry and hard within one or two days after being produced. A large number of ragwort seedlings were covered by casts (Plate 6.3, p. 89) and none was seen to break through them, *ie* once covered they died.

October	(a) Proportion of white clover increased, but grasses were still dominant; (b) marked increase in pasture growth since early month; (c) ewes grazed the paddock for 2 weeks.	(a) Sward dominated by white clover; (b) marked increase in pasture growth since early month; (c) paddock shut for silage making; (d) ragwort plants started bolting; (e) high accumulation of plant litter.	(a) Marked increase in pasture growth since early month; (b) some ragwort seedlings killed by treading; (c) seedlings within a whole plot were killed by cattle urine.
November	(a) Californian thistle became conspicuous particularly at the end of the month.	(a) Paddock was mowed at the beginning of the month; (b) mowed again at the end of the month.	(a) Water stress started to become apparent in some plants (wilting); (b) ragwort started bolting (end of the month); (c) ragwort seedlings recovered from water stress after some rain; (d) casts increase again all over the site; (e) paddock excluded from grazing but never mowed.
December	(a) Paddock mowed at the beginning of the month.	(a) Mowed for silage at the end of the month.	(a) Most species in full flowering (including ragwort).
January	(a) Apparently, no water stress; (b) Californian thistles growing vigorously; (c) ragwort starting to flower.	(a) Recovered well from mowing (early month); (b) tiller density increased due to frequent mowing (good quality pasture: leafy and growing vigorously).	(a) Water stress became apparent again (early month); (b) plants (except catsear and yarrow) markedly wilted; (c) a few patches of less wilted plants; (d) white clover clearly more susceptible than any other species in the paddock (aerial parts died); (e) sward started to open up; (d) ragwort flower heads started to mature (end of the month).
February	(a) Large patches of water-stressed pasture.	(a) Paddock was grazed in the second week of the month (first time since October); (b) silage was fed (end of the month).	(a) Catsear and yarrow were the only green material in the paddock; (b) rainfall at the end of the month did not make any visible difference.
March	(a) Silage was fed; (b) paddock grazed by lambs; (c) site visibly not so dry as Sites 2 and 3.	(a) paddock grazed by sheep (only); (b) dry patches showed signs of recovery.	(a) Catsear and yarrow still the only green plants (early in the month); (b) pasture recovering from drought (later in the month); (c) sward was grass dominant; (d) more ragwort seedlings emerging under clumps of grasses than on open patches between them.

April	(a) paddock grazed by sheep.	(a) plants trampled but because of dryness no hoof prints were noticeable.	(a) Pasture recovered fully by the first week; (b) some seedlings showed signs of insect feeding (this was very rare); (c) ragwort seedlings wilted on the second week.
May			(a) Many white clover seedlings emerged; (b) paddock was grazed (first time since November); (c) larger ragwort seedlings (originated vegetatively after drought) became rosettes; (d) ragwort seeds were shed uniformly over the whole site; (e) rank material decreased; (f) white clover started to regrow (end of the month); (g) sward grew denser; (h) casts increased and once again were seen to smother many ragwort seedlings.
June	(a) Some casts apparent but far less than on Sites 2 and 3; (b) sward became denser and dominated by grasses.	(a) casts all over; (b) sward dominated by white clover.	(a) silage was fed (mid-month); (b) sward was grass dominant; (c) casts increased even more; (d) old ragwort stems started to disappear.

6.5. Discussion

6.5.1. *Reliability of the visual estimates of herbage mass* Traditionally, the estimation of herbage mass by eye appraisal has been discouraged. Frame (1981) stated that "the method is not objective, is subject to operator bias and cannot be considered to be precise even though it is possible to make large numbers of estimates per treatment for subsequent statistical analysis". However the author did acknowledge some improvements in the accuracy of the visual assessments.

As explained in Section 6.3.3.1 (i), due to the characteristics of this trial, the only feasible way of obtaining information about changes in herbage mass was by eye appraisal. Despite the disadvantages of the method, it did seem to produce meaningful data. When sward surface height values were plotted against the visual estimates of herbage mass the pattern formed

Plate 6.1. Material used to collect data in the field. Note especially the use of a sheet of plain glass and acetate for mapping.

Plate 6.2. Mapping of ragwort seedlings.

Plate 6.3. Earthworm casts covering part of a ragwort seedling at Site 3 (August 1993).

apparently followed the model $ln(Y) = \beta_0 + \beta_1\ ln(X)$. To test how well this model would fit the data, the SAS "GLM" procedure was used as described by Steel and Torrie (1981). The curve obtained in this way is shown in Fig. 6.14 along with the significance of the slope and variability of the data.

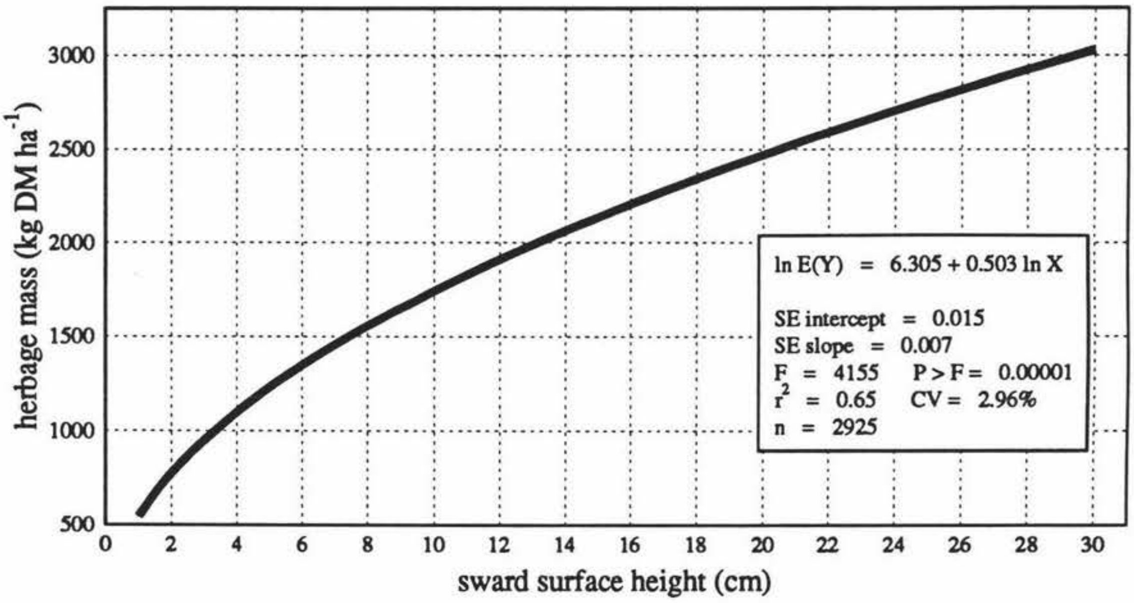

Figure 6.14. Relationship between sward surface height and herbage mass (visually estimated) obtained from pooled data (Sites 1, 2, and 3) collected from July 1993 to June 1994.

Evidence that the eye appraisal of herbage mass was a reliable method is that the coefficient of determination (Fig. 6.14) was similar to those obtained under New Zealand conditions by Webby and Pengelly (1986) when sward surface height was regressed against herbage mass derived by cutting. Also the extremely high significance of the slope of the curve as well as the small CV and standard errors give further evidence that the visual estimates of herbage mass can, at least in this trial, be used with reasonable confidence[1].

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[1] For additional information on the relationship between sward surface height and herbage mass under New Zealand conditions see L'Huillier and Thompson (1988).

6.5.2. General considerations about the establishment of causation The patterns of ragwort seedlings density (Fig. 6.1), seedling emergence (Fig. 6.2) and seedling mortality (Fig. 6.3) were not a simple function of any of the factors considered as potential determinants of seedling dynamics, *ie* herbage mass (Fig. 6.4), sward surface height (Fig. 6.5), herbage bulk density (Fig. 6.6), treading (Fig. 6.7), bare soil (Fig. 6.8), soil moisture (Fig. 6.10), rainfall (Fig. 6.12) and soil temperature (Fig. 6.13).

Unlike Experiment 2 (Chapter 4), where seedling emergence was found to be largely governed by one factor (*viz* the availability of water in the soil), this trial is apparently marked by complex interactions. In Experiment 2, only one factor accounted for most of the fluctuation in seedling emergence over the year because herbage cover was absent in one treatment. Also the participation of grazing animals was only allowed up to 30 days prior to the assessment of seedlings (see Section 4.3).

It is important to notice that seedlings were counted and mapped at the same time that all other factors were assessed. However, any causal relationship that might be found between, say, sward height and seedling emergence must consider a time-lag between them. Thus the emergence observed in October, for instance, might be related to the sward height recorded in September. If this was not so, establishing cause and effect would be just a matter of working out a multiple regression and judging the importance of each factor by the size of their sum of squares (*ie* how much each factor contributes to the total variation in the seedling population). What makes this analysis particularly difficult to carry out is that we cannot assume that the time-lag would be the same between seedling emergence or mortality and any of the factors thought to determine them.

6.5.3. Seedling emergence One way of trying to understand the factors which governed the emergence of ragwort seedlings in this trial is by concentrating on marked changes such as the occurrence of peaks or the absence of emergence.

The emergence recorded in August on Site 3 (Fig. 6.2) is an important event to be considered given its magnitude. Apparently, it was largely determined by events that happened in July. In this month several factors were highly favourable to seed germination: (a) average herbage mass (Fig. 6.4) and (b) sward height (Fig. 6.5) were remarkably low (the lowest ever recorded during the period of study); (c) soil moisture was not limiting (Fig. 6.10); and (d) the average proportion of bare soil was the highest recorded in the whole trial (Fig. 6.8). Most of the bare soil found in July was caused by treading damage to plants (Fig. 6.7). Though treading was more intense on Site 2 than on Site 3 (July), Site 3 had more bare soil than Site 2 because of the greater presence of white clover in its sward (Table 6.3). When white clover was heavily trampled it tended to disappear faster than the grass species.

A number of points indicate that the differences in emergence between sites recorded in August was mostly caused by bare soil (particularly in July): (a) herbage mass and sward height were very similar on Sites 2 and 3, while seedling emergence on Site 2 was only 1.3% of that achieved on Site 3; (b) soil moisture could not account for any difference between sites since it was not limiting in either of them[2]; (c) the proportion of bare soil was highest on Site 3, intermediate on Site 2 and low on Site 1, *ie* in the same order as with seedling emergence. Though the proportion of bare soil on Site 2 (July) was not so different from that of Site 3 (considering the large difference in their seedling emergence), Site 2 had much less viable seeds per m^2 than Site 3 (Fig. 6.11). Because Site 3 had a huge ragwort seed population in its soil, a small disturbance to vegetation could result in a large number of seedlings emerging per m^2 and, consequently, Site 2 would need more bare soil to achieve similar seedling emergence to that of Site 3.

Thus it seems probable that the overall greater emergence observed at Site 3 was partly determined by the larger amount of seeds in its soil seed bank. However, it is also clear that the size of the soil seed bank was just one component of the equation, otherwise the emergence curves (Fig. 6.2) would be approximately parallel with distances from each other determined by the availability of seeds in the soil.

The lower emergence observed in September on Site 3 (compared to August) can be attributed to the decrease in treading damage observed in August (Fig. 6.7). As a consequence of less treading and an increase in the above ground vegetation (Figs. 6.4 and 6.5) the amount of bare soil was largely reduced in that month as well (Fig. 6.8).

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[2] Note that sites were never waterlogged. Even if it had happened, ragwort seed germination is not hindered by excessive moisture (see Section 2.4.1).

The shape of the bare soil curve from July to October at Site 3 (Fig. 6.8) was very similar to the emergence curve from August to November (Fig. 6.2). However, the same does not hold at the other sites, particularly at Site 2. The only apparent reason for a peak emergence in November at Site 2 was the increase in bare soil in the same month.

The next noteworthy event is the overall reduction in seedling emergence over summer. During this period seeds had a large number of factors working against their germination: (a) herbage mass (Fig. 6.4) and sward height (Fig. 6.5) increased significantly; (b) soil moisture content was greatly reduced (Fig. 6.10); (c) because soil was dryer, no treading damage occurred (Fig. 6.7) and (d) the proportion of bare soil decreased (Fig. 6.8). Probably all these factors operated in conjunction, though soil moisture was outstandingly low. Surprisingly, seeds were able to germinate even when the soil was drier than a water potential of -100 kPa (Fig. 6.10a). However, seedling emergence ceased when the soil water potential was -1500 kPa or drier (compare Fig. 6.10 with Fig. 6.2).

Seedlings started emerging again at Site 3 when the soil became moister than -1500 kPa (see Figs. 6.10b and 6.2) in March. Apparently, Site 2 had similar conditions for germination in March (including bare soil and even lower herbage mass), but no emergence was noticed. However, at Site 1 no emergence occurred in March because the soil had been totally covered by vegetation since January (Fig. 6.8). At Site 3, emergence dropped again in April when the soil became drier than -1500 kPa (Figs. 6.2 and 6.10b).

Emergence at Sites 1 and 2 reached similar values to Site 3 (April) when the soil became drier than a water potential of -1500 kPa. During this period, the proportion of bare soil was increasing at Site 1 and had already been high at Sites 2 and 3 since mid-summer (Fig. 6.8). The increase in bare soil found between December and March was clearly associated with the death of many plants which were under severe water stress (see also Table 6.3). This happened independently of any overgrazing. Site 3, for instance, was excluded from grazing between November and May, but bare soil increased markedly in the same period.

The steady increase in seedling emergence between April and June observed at Site 1 was probably a combined effect of an increase in soil water content (Fig. 6.10b), a decrease in herbage mass (Fig. 6.4) and sward height (Fig. 6.5) and an increase in the proportion of bare soil (Fig. 6.8), which resulted from treading (Fig. 6.7).

The emergence curves obtained in this trial (Fig. 6.2) were different from the pattern of emergence observed in the second experiment (Chapter 4) carried out at Ballantrae (Fig. 4.1). Apparently, the only common feature between them was the large reduction in emergence during the driest months of the year.

6.5.4. ***Seedling mortality*** Most of the time the causes of seedling death could be easily identified. Predation, commonly pointed out as an important cause of death in young seedlings (Harper 1977), was noticed on only one occasion and in just a few seedlings. Thus, from our observations, predation was not an important factor.

The main determinants of seedling death were: (a) treading; (b) earthworm casts; (c) water stress and (d) smothering by neighbouring plants (usually grasses). Sometimes one of these factors was the major determinant of seedling mortality, but at other times death was attributable to more than one factor.

6.5.4.1. ***Treading*** Seedlings were many times seen to disappear after a heavy trampling. They were very resistant when treading occurred on soil at intermediate levels of moisture content. However they were very susceptible to hoof damage when soil was too wet (only noticed soon after rainfall, mostly in July and August) and also easily killed when soil was too dry, hence too hard.

Besides the actual observations, Fig. 6.15 also indicates that treading killed existing seedlings. In general terms it shows that the larger the trodden area, the smaller the seedling density, *ie* the greater the mortality. Apparently, seedlings were more frequent when the trodden area was not greater than 25% of the ground.

Treading (Fig. 6.7) was observed to kill seedlings (Fig. 6.3) mainly in July (Sites 2 and 3), October (Site 3) and May (Site 3). The increase in treading in October at Sites 1 and 3 was partly a consequence of concentrating the livestock when some paddocks (Site 2 and some other paddocks on the farm) were closed for silage making. This is also the reason why the treading curve is so different on Site 2 between October and December compared to the other sites. Similarly, it also explains the higher herbage mass (Fig. 6.4) and sward height (Fig. 6.5) recorded on Site 2 between September and December.

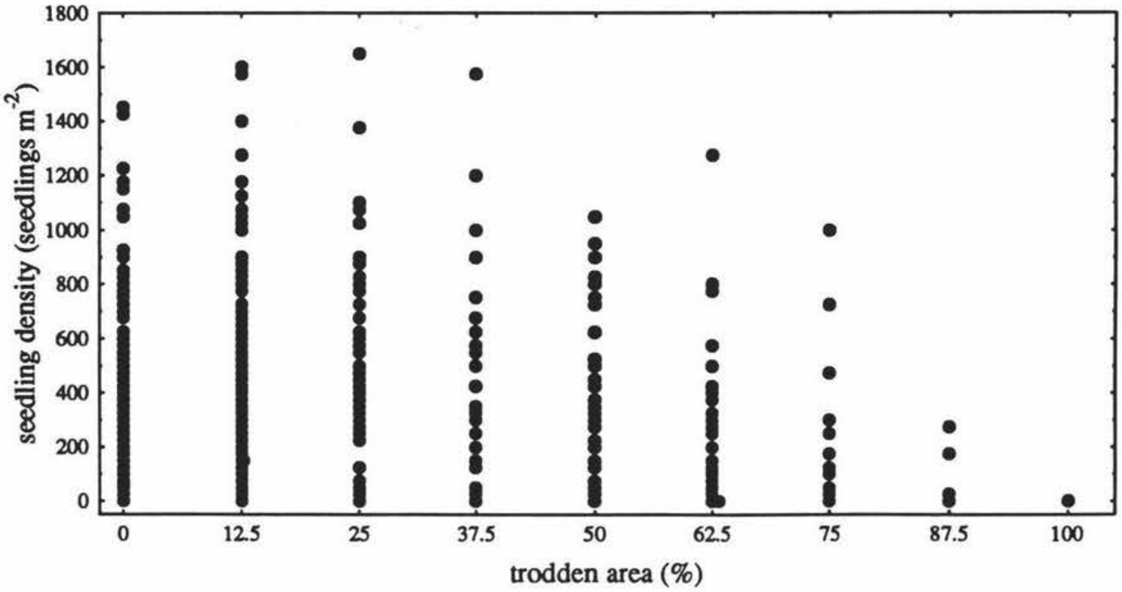

Figure 6.15. Scatter plot of trodden area (obtained from scores transformed in percentage values) and seedling density (pooled data).

6.5.4.2. *Earthworm casts* As outlined in Table 6.3, casts left by earthworms were one of the main causes of seedling death. Plate 6.3 shows a ragwort seedling (approx. 4 weeks old) partly covered by casts. They were mainly abundant at Site 3 (particularly in August, November, May and June), less noticeable at Site 2 (observed mainly in June, but also in August) and almost absent at Site 1 (except some casts in June). Their presence was clearly associated with seedling mortality (Fig. 6.3) only at Site 3 (probably because of the greater abundance of both casts and seedlings). This happened mainly in August and May.

Although no attempt was actually made to identify which species of earthworms were present, a few points allow us to state that the casts were made by earthworms rather than by caterpillars of porina moth (*Wiseana* spp.): (a) casts did not contain silken threads, which is a characteristic symptom of porina (Helson 1974); (b) the number and volume of casts was very high at certain times of the year, which would consequently be a result of a high infestation of porina yet (c) there was no damage to pasture which could be associated with porina feeding; (d) the form of the casts were generally sub-spherical ranging from a few millimetres to > 1 cm in diameter (see Plate 6.3), but paste-like slurries of irregular shapes were also seen, which, according to (Lee 1985), are characteristic of some earthworm species which produce surface casts; and (e) some earthworms were sometimes found in the soil cores collected weekly for determining soil moisture, while no porina larvae were ever seen.

It seems unusual that Site 3, which was the driest of the three sites had apparently more earthworm activity than Site 1, for instance. However, since not all species cast on the soil surface (Lee 1985), Site 1 might have different species of earthworms.

Although earthworms are beneficial if they contribute to the death of ragwort seedlings, they also accelerate the decomposition of the surface organic mat (Stockdill and Cossens 1984), which, as discussed in Chapters 4 and 5, helps prevent the germination of ragwort seeds. This is probably a reason why there was greater ragwort seedling emergence at Site 3. The site actually had much less plant litter accumulated on the soil surface than the other sites, and sometimes no organic mat was present (*eg* July and August). Consequently, the higher amount of bare soil on Site 3 must also be related to the earthworms.

6.5.4.3. ***Water stress*** This was the most important cause of seedling mortality because no seedling was able to survive it. It literally determined the disappearance, from mid-summer to mid-autumn, of all seedlings emerged since July. Deaths related to water stress started in December (Sites 2 and 3), but complete disappearance of seedlings was noticed in February (Site 3), in March (Site 1) and in April (Site 2). Additionally, all ragwort plants (including a few rosettes which had not flowered) died back. Apparently, this does not happen every year. As shown in Fig. 6.12, most of the period of study was drier than average. Note also that such mortality was only severe at Site 3.

Perhaps at Site 3 ragwort plants behaved more closely to annuals, flowering and seeding within a shorter period than at the other sites (Table 6.3), because of the drier conditions.

6.5.4.4. ***Competition exercised by neighbouring plants*** Ragwort seedlings showed an enormous capacity to survive underneath a closed canopy. They were never seen to emerge under such conditions, but when neighbouring plants closed the gaps from above, some of the ragwort seedlings remained for several months without any apparent growth. In these conditions seedlings presented an extraordinary plasticity, expanding the leaves (very often the cotyledons) to maximize light interception and to compensate, the leaves became very thin. This was only noticed in seedlings up to 4 true leaves. Older seedlings (phenologically) did not seem to have any problem in receiving the necessary amount of radiant energy.

By plotting herbage mass against seedling density (Fig. 6.16) it seems that most seedlings are found when herbage mass is between 500 and 2000 kg DM ha^{-1}. Note that seedling density decreases gradually either at higher or lower herbage masses. When sward surface height is plotted against seedling density (Fig. 6.17) it appears that seedlings cannot survive in a very short pasture (apparently below 2 cm). Since the change in seedling density is marked at about 2 cm and is gradual at the other extreme, it seems that seedlings can cope with tall pastures better than with very short ones. Seedlings were found in pastures up to 24 cm high, but were more abundant when pasture is shorter than 7 cm, approximately.

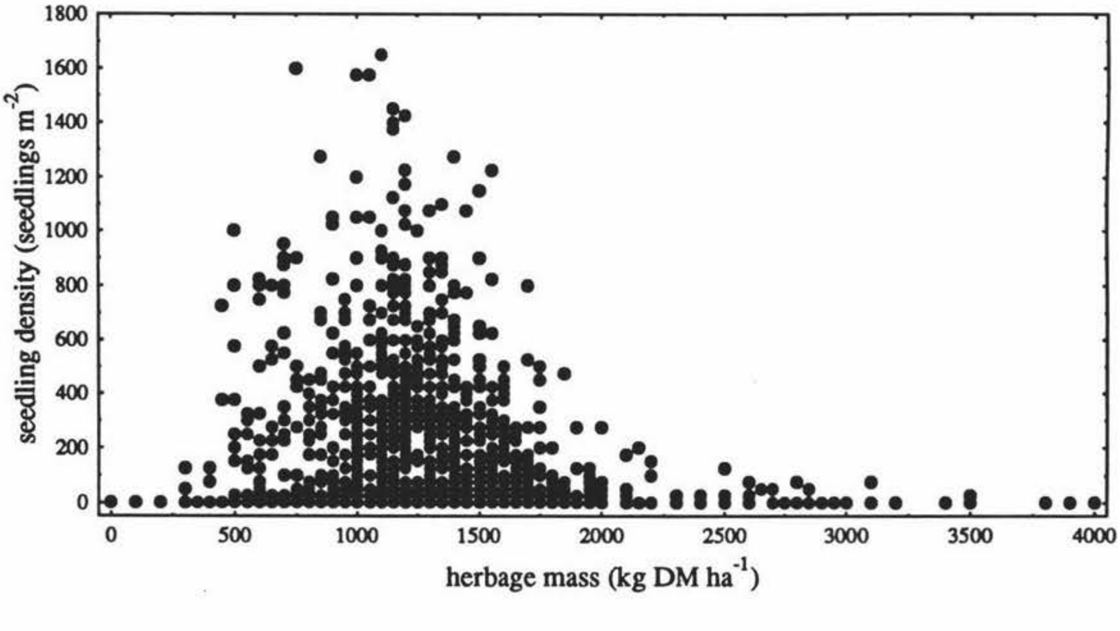

Figure 6.16. Scatter plot of herbage mass and seedling density (pooled data).

As with bulk density (Fig. 6.18) both extremes seem unfavourable to seedling survival, since changes in seedling density are abrupt at both sides. Apparently, seedlings are more frequently found when pasture has a bulk density between 125 and 440 kg DM ha^{-1} cm^{-1}. However, when the fluctuations in bulk density (Fig. 6.6) are compared with seedling mortality (Fig. 6.3) there is no apparent causal relationship. Perhaps one reason is that bulk density (Fig. 6.6), on average, has not achieved values below 125 kg DM ha^{-1} cm^{-1} nor above 440 kg DM ha^{-1} cm^{-1}.

The reason for the disappearance of seedlings when pasture is above 2000 kg DM ha^{-1}, or 7 cm or 440 kg DM ha^{-1} cm^{-1} is probably associated with competition from other plants. Conversely, when pasture is short, with low mass and low bulk density, there is less plant material above and around the seedlings. Since they were seen to be killed by cattle hooves, this probably indicates the minimal above ground protection against treading damage necessary for survival.

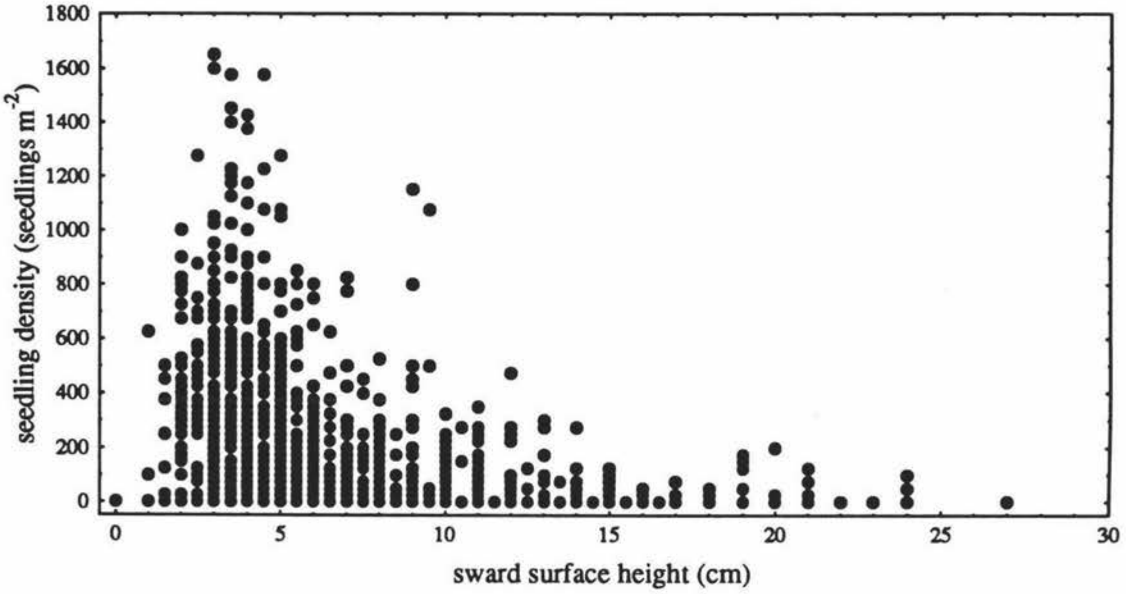

Figure 6.17. Scatter plot of sward surface height and seedling density (pooled data).

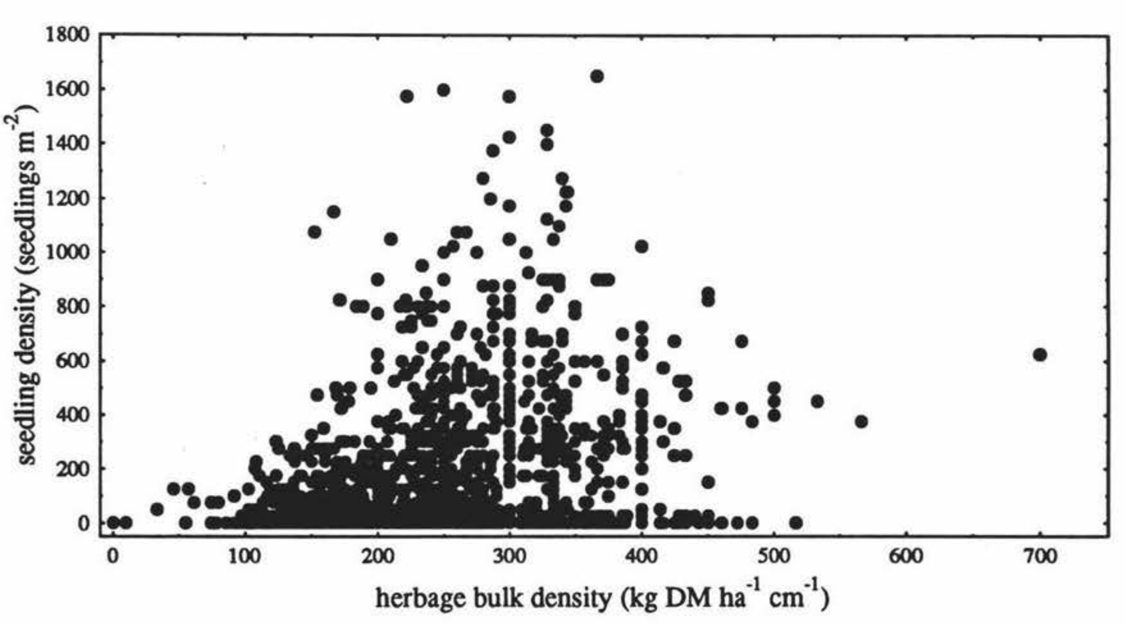

Figure 6.18. Scatter plot of herbage bulk density and seedling density (pooled data).

6.6. Final remarks

Herbage bulk density was considered in this trial because it was easily obtainable and did not require any extra field observations. Tiller density measurements would have been a more useful estimate of the herbage density given the purpose of relating it to seedling behaviour. Changes in bulk density not only reflect changes in tiller density but also changes in the internal arrangement and composition of plant biomass. However monitoring tiller density was not feasible in this trial. Although it could have been assessed nondestructively, it would have demanded too much time.

A similar comment should be made regarding the use of leaf area index (LAI), which would have a large influence on seedling emergence and survival. It would give direct information about the amount of light that seeds and seedlings received at different times of the year. However, we needed a quick way of assessing it and the only nondestructive method, which seems to be the point quadrat analysis (Frame 1981), is a time demanding procedure. Perhaps even better would be measuring irradiance and red/far-red light ratio arriving on the soil surface.

All these possibilities were ruled out because of time constraints. Even without them the weekly assessments lasted almost two entire days. Results obtained in this trial suggest that in years and areas subjected to severe drought, the most important period of seedling emergence is soon after the soil moisture returns to levels which allow germination to take place (in this trial this happened in May). Although the number of seedlings that emerge in winter and spring is considerable, most of them will probably die from water stress in summer. Therefore, strategically, seedling emergence in autumn is more important, as seedlings have time to become more mature by summer, when their deeper roots will help them survive dry conditions (see also Chapter 7).

6.7. Summary

The experiment reported in this chapter was marked by a number of important details that would be difficult to list in a concise way. However the main results can be summarized as follows:

(i) Ragwort seedling density varied markedly over the year and also between the three sites studied.

(ii) Differences in magnitude of emergence between sites were partly explained by different amounts of ragwort seeds in the soil seed banks at each site. However, this did not account for any of the fluctuations observed over the year. Also, the site which was intermediate in soil seed population (viable seeds) had often the smallest seedling density. This indicates that a large amount of ragwort seeds in the soil does not necessarily results in a large number of seedlings, *ie* that seedling emergence can be controlled.

(iii) Bare soil and soil moisture were apparently the most important determinants of seedling emergence. Seedlings only emerged when the soil was moister than -1500 kPa (average monthly water potential).

(iv) Seedling density was generally lower when the sward was short and with low herbage mass. However this was not always the case. Emergence was generally more associated with bare soil than with either of these two factors. Nevertheless, seedling survival was related to herbage mass and sward height (*ie* the higher the pasture or the greater its mass, the lower the density of ragwort seedlings).

(v) Bare soil resulted from treading damage and from the death of plants caused by water stress. Treading was only important in wetter months.

(vi) At one of the sites, all ragwort seedlings died from water stress in summer. During the same period, at least the top part of almost all mature ragwort plants died as well.

(vii) A large number of ragwort seedlings died after being covered by earthworm casts. Casts were more abundant in May, June, August, and November, but seedlings were more intensively buried in May and August.

(viii) Other causes of seedling mortality were treading (during wetter periods) and competition from neighbouring plants. Only a very small number of seedlings were seen to have been eaten by insects.

(ix) Some ragwort seedlings survived several months underneath the pasture canopy without any apparent growth. In this situation, seedlings showed a great plasticity by developing wide, thin leaves (some times the cotyledons).

(x) Where seedlings are not likely to survive the summer drought, the most important period of emergence is probably late autumn/early winter. Seedlings emerged at that time would have more chance of surviving summer as they would have developed deeper root systems.

General Discussion and Conclusions

7.1. Integrating the results

The behaviour of ragwort seeds and seedlings was studied under different conditions, ranging from the controlled environment of growth chambers to a commercial dairy farm where nothing was manipulated (see Chapters 3, 4, 5 and 6).

The results of the first experiment (see Chapter 3) demonstrated that the germination of ragwort seeds is highly increased under the incidence of white light when its ratio of red to far-red light (R:FR) is greater than 1. In the field (see Chapters 4, 5 and 6), seedlings were only found in areas that were completely denuded of herbage cover or within small gaps in the pasture canopy, *ie* where R:FR was high (see Section 3.5.1). Not a single seedling was ever seen to emerge where the ground was densely covered, either by living plants or by their litter. Apparently, the results obtained in the laboratory are applicable to the field situation.

Considering that 13.8% of the viable seeds collected from a soil seed bank produced visible seedlings in the growth chambers in complete darkness, it would seem reasonable to expect that a similar proportion of seeds would germinate in the field without the need for light (*ie* red light). However, as stated above, none were ever seen to emerge where red light was expected to be scarce (*ie* where sun light was filtered by plant material). The reason is apparently simple: seeds which germinated in darkness (13.8%) had previously received a high R:FR in the field (see Section 3.5.2), which could only happen if they were on (or very close to) the soil surface without any cover above them. Thus, it was concluded that these seeds were originally in open areas.

Fluctuations in ragwort seedling emergence were demonstrated to be very site specific. However, previous observations (mostly anecdotal) have pointed to a general peak emergence in autumn (Poole and Cairns 1940; Thompson 1985). In our trials, autumn emergence was very small compared to emergence recorded in June, August and September (see Chapters 4 and 6). We argue that the importance of the autumn emergence is not dependent on its size, but on its timing, at least in areas of dry summers. In the dairy farm trial (see Chapter 6) all seedlings which had emerged within the experimental period (*ie* after July 1993) died during summer from water stress. Autumn-emerged seedlings would have more time to grow deeper roots before the summer drought strikes, thus increasing their chances of survival. In the dairy farm, some seedlings that already existed when the trial started (thus were not being monitored) were seen to regrow after the summer drought. Nevertheless, these could be seedlings that had originated vegetatively rather than autumn seedlings. Unlike the dairy farm, on the hill country farm (see Chapter 4) where rainfall is more abundant, seedlings were not seen to die over summer.

The number of seedlings originating vegetatively from all field studies was insignificant. If pasture in Experiment 3 (see Chapter 5) also had ragwort plants (not only seeds in the soil), perhaps the number of vegetative regrowths would be higher as a consequence of the heavy treading, which would certainly have damaged ragwort crowns and roots.

In all the field experiments (see Chapters 4, 5, and 6) some seedlings were seen to survive for long periods (greater than three months) when subsequently shaded by neighbouring plants. In the dairy farm, where they were carefully monitored, some seedlings remained with 3-4 true leaves from August 1993 until February 1994, when they died during the summer drought. This ability of some seedlings to survive under a fairly closed canopy greatly increases their chances of establishment. As pointed out by Harper (1977), such seedlings form a seedling bank remaining "dormant", like seeds in the soil seed bank, until growth can be resumed as a consequence of more favourable conditions (*eg* increased light intensity following hard grazing). Poole and Cairns (1940) also noted that some ragwort seedlings remained small for several months underneath the pasture canopy (see Section 2.4.3).

The third experiment (Chapter 5) indicated that treading may stimulate the germination of ragwort seeds by reducing the above ground biomass, which was shown in the second trial (Chapter 4) to inhibit germination. In the dairy farm trial (Chapter 6) we noticed that seedling emergence was more closely related to the proportion of bare soil than to the area of ground actually trodden. This happened because not all trodden area became bare. Additionally, treading was only a major cause of bare soil in winter, when plants were more severely damaged. At other times, bare soil resulted chiefly from the water stress suffered by pasture plants.

7.2. The importance of this study to understanding of the species

Perhaps we should reinforce that a few points make this study different from previous work discussed in Sections 2.4.1, 2.4.2 and 2.4.7: (a) in our trials, ragwort seedlings originated from seeds naturally occurring in the soil seed bank of grazed pastures, rather than from sown seeds collected from seed heads; (b) the study of the sensitivity of seeds to light conditions (carried out in laboratory) also used seeds from the soil seed bank; (c) in the field, seedlings were carefully mapped right from the moment of emergence, hence leaving no doubt about their origin (*ie* whether from seed or crown/root segments) nor about their age (*ie* when they had emerged); (d) seedling emergence and establishment was also studied under natural conditions, *ie* in a real farm situation.

Because of these factors, we can be reasonably confident that what we observed is very close to what actually happens in the field. However, because the trials were carried out no longer than one year and also within a relatively narrow range of environments, care must be taken before trying to extrapolate the results to other environments or even to the same kind of environment but in different conditions (*eg* not so dry over summer).

The results from our experiments corroborate the claim that ragwort seedling establishment is prevented by the presence of a dense sward (Cameron 1935; Poole and Cairns 1940; Harper 1958; Schmidl 1972; Popay 1980; Phung and Popay 1981; Rahman *et al.* 1993). The first experiment (Chapter 3) demonstrated that ragwort seeds, like many weed seeds, require light (red light) for germination. This partly explains the absence of seedling emergence under a closed canopy. Experiment 1 (Chapter 3) was the first trial designed to establish whether ragwort seed germination is actually light dependent. Previous observations (Maguire and Overland 1959; van der Meijden and van der Waals-Kooi 1979) did not allow any conclusive judgement.

Also, it was the first time that the effect of treading on the emergence and establishment of ragwort seedlings was studied (see Chapter 5). As expected, treading did stimulate the emergence of seedlings, however not by moving the soil and uncovering buried seeds, but mainly by damaging the herbage cover. The trial also showed that seeds which were stimulated by soil movements were those uncovered laterally by hooves (see Fig. 5.3).

In general, seedlings are naturally sensitive to water stress (Harper 1977). However, the death of all ragwort seedlings in summer (Chapter 6) is an important observation (see Section 7.3). Also, the high mortality caused by earthworm casts was unexpected. Though it seems likely when we consider the large amount of soil that may be pushed out of earthworm burrows in a year (Lee 1985), the extent of seedling mortality caused by these casts had not been anticipated.

7.3. Some implications for farm practice

The results of the last experiment (Chapter 6) indicate that different paddocks within a single farm are likely to require different strategies to avoid the establishment of ragwort. Similarly, different times of the year would also require different actions. As conditions suitable for germination of seeds and the establishment of seedlings varied within one farm, presumably differences between regions of New Zealand in such conditions are even greater. Nevertheless, some of the results obtained in our study do seem to allow broad generalisation to be made.

If most seedlings were known to die over summer, stimulating emergence through treading in winter/early spring might be an efficient way of depleting the soil seed bank of ragwort seeds without increasing the problem[1]. However, no one would know how dry the next summer would be. Although this does not necessarily invalidate the practice, since seedlings could still be treated with herbicides, given the size of some soil seed banks (see Chapter 5), treading would have to be frequent and intensive to exert some significant impact on the seed population. Frequent and intensive treading would hardly seem an intelligent way of managing a pasture, particularly because of soil compaction, decrease in herbage production (Watkin and Clements 1978) and the possibility that other weeds would become established without dying over summer.

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[1] This was first suggested by a farmer during a field day about the control of ragwort, when some of these results were presented.

Ideally, seeding should always be avoided. Mowing was seen to prevent seeding reasonably well on the dairy farm (Chapter 6). However, cutting usually prolongs the life of ragwort plants (Harper 1958). Additionally, if cut material is used for silage (as reported in Chapter 6) it should be considered that livestock are unable to select the plants in the form of silage and also that the alkaloids diffuse through the entire mass of silage (see Section 2.5.1). Although no animals were seen to suffer from the symptoms of intoxication by pyrrolizidine alkaloids during the year we monitored the events on the dairy farm, sub-clinical doses of ragwort are thought to be a common cause of poor animal performance (Anon. 1975).

Although the density of ragwort seedlings that may be achieved at a given site is potentially determined by the amount of seeds in the soil seed bank, the above ground conditions, generally determined by pasture management, is also very important. This was observed at the dairy farm (Chapter 6). Although Site 1 had many more seeds per m^2 than Site 2, for most of the year its ragwort seedling density was lower than at Site 2 or very similar to it. Overall, Site 1 had a higher average herbage mass (Fig. 6.4) and lower proportion of bare soil (Fig. 6.8), though the area trodden on Site 1 (Fig. 6.7) was sometimes greater than at Site 2 (or even at Site 3). Apparently, the higher proportion of grasses and lower contribution of white clover at Site 1 (see Tables 6.2 and 6.3) was one reason for its better performance against ragwort seedlings. As discussed in Section 6.5.3, white clover tended to be more severely damaged by treading than grasses (particularly perennial ryegrass). Thus, areas covered by grasses more rarely became bare as a consequence of treading. It would appear then that a pasture (known to contain ragwort seeds in the soil) with a high proportion of white clover should be managed more carefully to avoid treading damage. We would not, at this point, claim that grass dominant pastures should be aimed at during times of the year when treading is more likely to cause greater damage. This would require a more comprehensive study which would have to consider the consequences to animal production as well. Nevertheless, considering the biology of ragwort, the damage to white clover caused by herbicide application might help prevent subsequent invasion of ragwort seedlings (at least in the short term) if grasses are in turn stimulated.

Apparently, ragwort seedlings would emerge more abundantly after a dry summer even if drier paddocks were de-stocked. We noticed that bare soil increased at Site 3 over summer (Fig. 6.8) despite the absence of livestock for several months (Table 6.3). Emergence was high in March, when soil moisture increased again and pasture had not yet recovered. This observation is not new. However, it has generally been associated with overgrazing during summer (Popay 1980). Certainly a dry pasture being trampled and defoliated without subsequent regrowth will result in even more bare soil, but, as we observed, it is likely to happen without the presence of animals as well. For this kind of paddocks, irrigation could be a good alternative. It would not only maintain the soil covered through appropriate herbage growth but also increase herbage production. Drought resistant cultivars might be a cheaper and more practical alternative, however in really dry situations (as observed at Site 3) pasture would most likely still open up.

If summer is not too dry, herbage plants will tend to maintain the soil more covered. Consequently, there will not be much bare soil in autumn that would stimulate seedling emergence. Additionally, pasture plants would tend to recover faster (compared to plants which suffered from drought) when soil moisture increases, thus further minimizing the chances of ragwort emergence.

7.4. Further work

A number of questions have been raised which could not be followed up during the study. Some of them would merit further investigation.

In Experiment 1 (Chapter 3) a large number of seeds still germinated when soil was moved from the growth chambers to the glasshouse. The only plausible explanation was that temperature would have been variable within the glasshouse, while in the growth chambers it was constant. Thompson *et al.* (1977), studying the germination of several species (not ragwort) demonstrated that alternating temperatures sometimes substitute for the need for light as a trigger of germination. They also showed that the amplitudes of diurnal fluctuations of soil temperature are smaller under an established sward than in gaps denuded of herbage cover. Thus, although our trial has demonstrated that light does stimulate the germination of ragwort seeds, alternating temperatures could also be important. In practice, since light quality and fluctuations of temperature are affected by the presence of vegetation, management for one factor will also work for the other.

From our observations (Chapter 6), it seems that ragwort seedlings are negatively associated with grasses. The paddock where less seedlings were recorded (Site 1) was generally dominated by grasses, while in the paddock where more seedlings were found (Site 3), white clover was more abundant during some parts of the year. Because we did not properly monitor the changes in botanical composition over the year, this could not be positively established. Perhaps this could be studied by treading pastures (preferably more than once) with different white clover contents (*ie* varying from pure ryegrass to pure white clover pastures) and monitoring subsequent emergence and survival of ragwort seedlings. From our observations, pastures with higher clover content are likely to be more affected by treading (*ie* result in greater proportion of bare soil) than pastures dominated by ryegrass. The same design could be used for assessing the effect of a dry period on subsequent development of bare areas and emergence of ragwort seedlings.

The mortality caused by earthworm casts (Chapter 6) might also merit further attention. It would be important to know whether this occurs in other places. After being confirmed, the apparent negative aspect of earthworms should also be checked, *ie* greater earthworm activity is also related to less accumulation of plant litter on the soil surface (Stockdill and Cossens 1984), which was shown to lead to greater seedling emergence (Chapters 5 and 6).

Another point which was not answered by our study was the recovery of ragwort plants after a summer drought. We believe that some of the plants which regrew in autumn 1994 were seedlings which had emerged in autumn 1993 and thus had deeper root systems than younger seedlings. However, because our mapping only started in August this could not be determined. If this was confirmed, our hypothesis that seedlings emerging in autumn are strategically more important than seedlings emerging later in the year might also be confirmed.

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