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THE ECOLOGY OF RAGWORT (*SENECIO JACOBAEA* L.) - A REVIEW

Summary: The available literature on ragwort is reviewed. The ecological behaviour of ragwort can be explained by its tendency to act as a colonising plant, which is encouraged by pasture disturbance. Ragwort-infested pasture and closed pasture alternate with each other, and this is influenced by a number of environmental and management factors.

Introduction

Ragwort *(Senecio jacobaea* L.) is a herbaceous plant that is native to Europe, Asia and Siberia (Anon., 1981) and was first recorded in New Zealand near Dunedin in 1874 (Poole and Cairns, 1940). It is now widespread in the country, especially through the moister regions of the North Island, where the interaction of physical, biotic and management factors encourage it to act as an aggressive weed in many localities. Ragwort is important because it competes with pasture plants for space and possibly resources, and because it accumulates pyrrolizidine alkaloids that are toxic to horses, cattle, possibly deer, and to a lesser extent sheep. These alkaloids are also known to taint milk (Dickinson and King, 1978) and honey (Deinzer *et al.,* 1977). Ragwort is now classified as a class B noxious weed, and the Noxious Plants Act requires farmers to maintain a ragwort-free strip at least 20 metres wide inside their farm boundaries. Bird (1977) notes that it is illegal for landowners to allow ragwort to flower on their properties.

Population processes

Seed production

Poole and Cairns (1940) recorded data on seed production from three locations. On average, plants at Ruakura produced 1,000-2,500 capitula per season, and each capitulum contained 55 seeds (or achenes). Large plants at Piopio produced 3,375 capitula with 60 seeds per capitulum, whilst plants in Southland averaged 80 capitula with 81 flowers (not seeds) per capitulum. Results collected in the United Kingdom by Cameron (1935) revealed that plants produced between 68 and 2,489 capitula each, with 70 seeds per capitulum. The above data suggest a considerable degree of variability between localities with regard to the number of capitula, and the number of seeds produced, per plant.

Dispersal

While large numbers of seeds are usually produced, they appear to exhibit relatively poor disperal. Wind is probably the major dispersal agent. An experiment conducted by Poole and Cairns (1940) at Piopio, which involved trays being set out at various distances from a patch of ragwort plants to trap seed, found that 60% of the seeds produced were released from the seedhead, presumably by wind. The majority of these were dispersed downwind from the prevailing (north-easterly) direction, and mostly within a few metres. An almost insignificant minority were dispersed as far as 36.6 metres. The data show that the dispersal pattern of ragwort seeds in space is approximately elliptical, with the centre of the ellipse a few metres downwind from the source of the seeds. No study has yet investigated the influence of strong winds on the long-distance disperal of ragwort seeds, yet such winds, even if occasional, could still be highly important. At Arthurs Pass and near Cass, isolated ragwort plants may have been derived from seed blown by strong north-west winds from the Westland side of the main divide, possibly many kilometres (C. Burrows, pers. comm.). Sheldon and Burrows (1973) concluded that long distance dispersal of disc achenes would occur only if the dispersal unit was carried high into the atmosphere by convection currents.

Poole and Cairns (1940) also found that the weight of the seed decreased with increasing distance from the source, especially beyond 1.83 m. Unfortunately, they supplied no measure of variance to allow comparison of the significance of differences. Seeds deposited 36.6 metres from the source were on average 35% lighter than those deposited near the source. This was not coupled with a large loss in germination ability - there was only a 5% drop in percentage germination at 36.6 metres compared with seeds falling at the source. McEvoy (1984a) found that seeds from disc florets were lighter (mean:t S.E. = $199 \pm \mu g$) than those from ray florets ($286 \pm 7 \mu g$)). Those from disc florets were also more structurally adapted for dispersal, possessing a pappus (for wind carriage) and also trichomes (possibly for animal dispersal); those from ray florets possessed

neither. Furthermore, the average capitulum produced 4.46 times as many disc achenes as ray achenes. The difference between ray and disc florets with regard to dispersal potential was also noted by Green (1937), who found that after dispersal of the disc achenes the phyllories of the capitulum recurved upwards retaining the ray achenes. The data collected and observations made in the above studies suggest that ragwort seeds operate at least two strategies with regard to seed dispersal, producing seeds that are adapted to disperse little, and seeds that may disperse longer distances.

Birds have also been implicated as agents of dispersal but experiments with sparrows and zebra finches (Poole and Cairns, 1940) suggest that seed is not dispersed through droppings. Trichomes on the disc achenes may enable attachment to feathers, however. Farm animals possibly also enhance dispersal though this has never been studied. Water dispersal is a likely mechanism and it has been suggested that this agent assists dispersal along the Waipa River and South Karori Stream. In the latter waterway, Poole and Cairns (1940) noted that seedlings were often found on the lower stream bed, testimony to possible carriage of seeds by water.

Dormancy, germination and establishment

While ragwort seeds have limited dispersal powers, they are capable of considerable dormancy given the right conditions. Harper (1958) and Anon. (1977) quote dormancy periods of up to 8 and 6 years respectively. On burying -batches of seeds at depths of soil ranging from 0 to 21 cm, Thompson and Makepeace (1983) found that viability was usually still high after six years, especially at lower depths, e.g. 24070 in one case. It was predicted, through extrapolation of a fitted logarithmic model, that it would take over twenty years for well buried seeds to be reduced to I % viability. Ragwort seed dormancy is thus enforced at least to some extent by burial—similar to many other herbaceous plants noted by Wesson and Wareing (1969). In the field, frost and drought may induce dormancy and thus delay germination (van der Meidjen and van der Walls-Kooi, 1979). Baker-Kratz and Maguire (1984) noted that innate dormancy in ragwort is apparently nonexistent.

Under optimal conditions, germination is rapid - Cameron (1935) recorded that at 15 °C, seeds began to germinate on day 4 and most had germinated by day 8. Baker-Kratz and Maguire (1984) observed maximum germination occurring at 18 days after flowering in peripheral (ray and disc) achenes, and at 21 days in central (disc) achenes.

Ragwort seeds characteristically exhibit a high viability – 90% and 80% as recorded by Anon. (1977) and Cameron (1935) respectively. Schmidl (1972) records that in alternating light and dark, seeds produced in the summer showed 85% germination, while those from late flowering plants showed only 60% germination. P. Martin (unpublished) found 63% germination in autumn (April) collected seed. Van der Meidjen and van der Walls-Kooi (1979) found, over a range of temperature and moisture regimes, that maximum (92.5%) germination occurred at 15°C and 29% soil moisture content. Germination was over 80% at between l0°C and 25°C but was best if the temperature was varied diurnally with a range of 10°C. Baker-Kratz and Maguire (1984) found maximum and fastest germination occurred with alternating 20°C/30°C temperatures, with both disc and ray achenes. Van der Meidjen and van der Walls-Kooi (1979) found germination to be inhibited by sand burial depth of over 4 mm, and enhanced by 1-2 mm sand coverage (probably due to more favourable water conditions) compared with unburied seeds. Poole and Cairns (1940) obtained similar results. Seeds just covered with soil germinated faster than surface sown seeds, while seeds buried by 25 or 75 mm soil failed to germinate at all.

Induction of germination of dormant, buried seeds requires some form of local disturbance, to bring seeds nearer to the soil surface. Van der Meidjen and van der Walls-Kooi (1979) found in the Netherlands that populations in their study site were often recruited from older seeds and that large-scale germination in 1977 resulted from seeds buried over four years previously. Germination was investigated-in three different sand-dune communities, and it was found to be consistently higher in the absence of vegetation cover. It has never been determined whether this reduced germination under vegetation is due to light, microclimate or allelopathic effects exerted by the established plants. It is possible that a phytochrome effect may be operating in inhibiting germination, with high ratios of far red:red light maintaining dormancy of seeds under soil or vegetation cover. Germination of buried dormant seeds when brought nearer to the surface (e.g., by animal trampling and soil movement) and in the absence of vegetation cover, is typical of plants that inhabit open and/or disturbed habitats and are therefore transient in succession and excluded after long periods of relative stability.

Results presented by McEvoy (1984a) imply that ragwort operates at least two germination strategies.

As previously outlined, he found that disc achenes exhibited greater dispersal in space than ray achenes. In addition, he found that disc achenes germinated faster in 12-hour wetting/drying cycles at 20°C, than ray achenes. Germination of the ray achenes was found to be inhibited by the pericarp, as nicking of this enhanced germination. The germination inhibition was at least partly due to physical restriction (rather than nutrient or inhibitor blocks) because nicks in different parts of the seed coat all had different effects on the extent of germination.

McEvoy (1984b) found in Oregon, USA, that establishment of germinating seedlings was higher underneath the immediate zone occupied by the adult plant. The horizontally growing rosette inhibits surrounding vegetation, allowing the opening left in the vegetation to be colonised by offspring. This strategy contributes to the persistence of ragwort, enabling individuals of the same species to survive in the same site for more than one generation.

Crawley and Nachapong (1985) found that seeds in capitula produced on regrowth shoots of plants defoliated by the cinnabar moth *(Tyria jacobaeae* L.) showed a slight but statistically significant drop in germination compared with seeds from primary capitula, (78.8% vs 86.6%). Subsequent planting of seeds in cultivated soil demonstrated that both kinds of seeds produced similar numbers of seedlings. However, in cut-grass plots where competition was more intense, the numbers of seedlings counted was substantially less for seeds from regrowth shoots - less than 2% of that for seeds from primary capitula.

Vegetative and reproductive phase

The vegetative phase is characterised by a high mortality, especially in the earlier stages. Thompson (1985) found that in three North Island study sites, over three years, about 80% of the seedling plants entering the population in September each year died before flowering. 24% of (vegetative) rosettes died before flowering. While mortality is high, the possible agents of death have not been adequately investigated.

Ragwort is often credited as acting as a biennial, but there is evidence that it can act as an annual or perennial too. Schmidl (1972) found in Australia that 2%, 45% and 39% of his plants acted as annuals, biennials and perennials (including triennials) respectively; Forbes (1977) found figures in Scotland of 8%, 39% and 53%. In the three North Island study sites, Thompson (1985) found that no plants acted as annuals, between 5% and 20% of seedling plants acted as biennials, between 4% and 20% acted

as triennials, and between 1 % and 5% of seedling plants survived as non-flowering third year rosettes. These data show that ragwort can demonstrate a variety of strategies during its vegetative (as well as seed) stage.

Flowering is controlled at least in part by achievement of a certain minimum rosette size (van der Meijden and van der Walls-Kooi, 1979), and ragwort may regenerate after flowering, especially in conditions of disturbance. Poole and Cairns (1940), Schmidt (1972) and Forbes (1977) observed that 33%, 28% and 44% respectively of their flowering plants regenerated. Thompson (1985) found over three years, that between 1 % and 25% of flowering plants regrew while four plants flowered three times. Islam and Crawley (1983) found in the United Kingdom that the majority of their study plants survived after flowering, with only 25% of plants dying in the winter after flowering. The remainder regrew from food reserves in the rootstock in the following spring.

Ragwort can also reproduce vegetatively. Schmidt (1972) observed that within 1 1/2 years, over 35% of ragwort plants raised from seed and placed in ungrazed pasture formed multiple crowns. Portions of roots can rapidly form shoots and buds under laboratory conditions (Poole and Cairns, 1940). 15 or 30 cm root portions buried under 15 cm of soil almost always sprouted and within 2 months had grown shoots over 7 cm in length. They had all died within 6 months, however, possibly due to the failure of secondary roots to form - secondary root growth was never seen to match the observed shoot growth. Burial of ragwort plants at depths of 7.5 to 33 cm was found to give rise to only a small number of regrowth plants - 2.0% and 5.6% respectively of buried rosettes from two trials respectively regrew and the rest were found to be rotten when dug up after 5 to 9 months (Poole and Cairns, 1940). This low number of regrowths may be due to the consolidation of the Hamilton clay loam in which the rosettes were buried, combined with the wet experimental conditions that promote soil saprophytes. Poole and Cairns (1940) also found that roots of rosettes formed buds more readily (37% of root fragments) than those of flowing plants (10% of root fragments). Cairns (1938) attributed the rapid vegetative propagation that is observed in at least some field situations to an unusual ultrastructure, with the roots exhibiting an absence of a functional endodermis, and the presence instead of a pericyclic phellogen which can give rise to buds readily. Vegetative propagation is stimulated by disturbance and can result in over twenty single flowering stems

per crown; rotting of the crown enables each stem to form a single plant, as the root connection with the parent plant decays.

Changes in populations of vegetative ragwort plants can be summarised in life-path diagrams, such as those shown by Thompson (1985), for three North Island sites. These demonstrated the mortality pattern over time for cohorts of marked seedlings. However, no study has yet attempted to match the numbers of flowering plants with subsequent seedling production from these plants. Investigation of this would require the availability of seed production, dormancy, viability, germination and seedling establishment data for given plants.

Environment

Physical factors

Ragwort can grow well wherever rainfall exceeds 870 mm per annum (Poole and Cairns, 1940). In New Zealand its distribution in pastures is not influenced by temperature. Dry summer months severely check establishment, especially by seedlings that germinate in the autumn. Dempster and Lakhani (1979) found ragwort plant density to be positively correlated with July-September rainfall, and in some cases also with artificial watering during the summer, on Weeting Heath, England. A weak relationship between February-May rainfall and percentage of plants flowering was also found. Their data indicate that, in their study at least, rainfall was the principal factor controlling ragwort populations during the study period. Cox and McEvoy (1983) found in Oregon, USA, that in years with below-average rainfall, recovery from defoliation caused by the cinnabar moth was reduced. Flowering of ragwort was delayed following drought in the population studied by Poole and Cairns (1940). In the United Kingdom, ragwort is found on areas that tend not to flood during winter, and ragwort cannot survive underwater for long period (Smirnoff and Crawford, 1983). Ragwort rosettes manage to overwinter successfully in many regions of New Zealand and can therefore tolerate frost. However, Harris et al. (1976) found that plants in the eastern USA were killed by frost following recovery from a moth defoliation. Ragwort tends to be found on lighter soils (e.g. the rhyolite and derived soils of the central North Island), and performs poorly on heavy soils especially at the seedling stage (Poole and Cairns, 1940). No New Zealand records exist for the soil pH range in which ragwort can occur, but Harper (1958) states that in the United Kingdom

ragwort occurs in soils with pH readings of 3.95 to 8.20, suggesting a wide pH tolerance.

Diseases

No fungi are known that significantly harm the weed but Harper (1958) records four fungal species that are common parasites on ragwort in the United Kingdom, namely *Puccinia expansa* Link, *P. diaicae* Magn., *Sphaerotheca humuli* Burr, and *Bremia factulae* Regel. The New Zealand situation is unknown.

Herbivorous insects

Biological control of ragwort by insects in New Zealand was reviewed by Syrett (1983) and will therefore only be covered briefly here. Certain insects that naturally feed on ragwort in England were introduced to New Zealand to combat the weed, including the cinnabar moth *(Tyria jacobaeae* L.) and two seedfly species *(Pegohylemia seneciella* Meade and *P. jacobaeae* Hardy). Of these insects, only *T. jacobaeae* and *P. jacobaeae* have become properly established, and even these two are local in . distribution, failing to establish as well as was hoped. Of the native insects that attack ragwort, only the magpie moth *Nyctemera annulata* Boisduval causes significant damage, according to Miller (1971). However, the magpie moth is a foliage feeder and foliage removal does little to check ragwort (Poole and Cairns, 1940).

Grazing by stock

Cattle and horses will generally not feed on ragwort unless they are forced to, and the effects of ragwort toxicity are detrimental, frequently fatal. Sheep, however, readily browse ragwort, especially at the rosette stage (Cameron, 1935) when the plant is more succulent and has fewer poisonous alkaloids than at full bloom. Sheep may demonstrate a preference for ragwort after they have acquired a taste for it (Poole and Cairns, 1940), although it may also be detrimental. Alkaloid poisoning can show similar symptoms to facial eczema (Mortimer and White, 1975). Cameron (1935) notes that older ewes are better at reducing ragwort because they are more tolerant to the toxin and also because they eat the crown or growing portion of the rosette, whereas younger sheep often restrict themselves to the younger leaves. Amor et al. (1983) found that mean ground cover of ragwort in ryegrass/white clover/cocksfoot pasture in Victoria, Australia was in the order of 5.0-6.0% in ungrazed pasture, 1.7-2.0% in sheep-grazed pasture, and 7.8-13.2% in cattle-grazed pasture. This implies that sheep reduce ragwort ground cover directly by eating

it, while cattle encourage ragwort by eating potentially competing pasture plants and/or encouraging vegetative propagules through disturbance. No statistical tests, however, were performed on the data. Sharrow and Mosher (1982) investigated the possibility of using sheep as a ragwort control tool in cattle grazed pasture. One hundred plants were tagged and followed for one year with cattle only, and with sheep and cattle. There were no significant differences between mortality in both treatments, but in the cattle treatment significantly more plants bloomed before death than in the cattle and sheep treatment (32% vs 2%), and significantly fewer plants died as a consequence of grazing (2% vs 14%). The fact that fewer plants flowered and seeded where sheep were present suggests that sheep grazing would cause a reduction in the seed bank over time. It would have been interesting to see if there were any long-term changes in ragwort seedling emergence had the treatments been allowed to continue for longer. Poole and Cairns (1940) state that sheep alter a ragwort infestation from large rosettes and flowering plants to a number of small plants of about 7 cm diameter, which occupy a smaller percentage of the pasture area.

No study has looked intensively at the effects of different grazing regimes or stocking rates on ragwort control but it could be predicted that grazing would be more effective if it coincided with the rosette stage, checking flowering or growth. Disturbance by grazing animals later in the year might stimulate the plants to develop multiple crowns, especially if the animals are stocked at a high density.

Interactions between rag wort and pasture

Competition between pasture plants and ragwort occurs at all stages of the ragwort life cycle. Early in the life cycle the competitive balance is in favour of the pasture. Continuous pasture cover inhibits germination of ragwort seeds (see above) and probably also establishment of seedlings (Thompson, 1980). The extent of pasture cover (as affected by grazing) was found by Cameron (1935) to greatly influence the number of seedlings present in various experimental sites in England. No ragwort seedlings occurred under long grass, or short continuous turf. Overgrazed pasture, hard exposed soil, and open soil yielded respectively 212,800, 2,152,800 and 5,704,750 seedlings per hectare. Further experiments performed by Cameron revealed that the grasses *Brachypodium pinnatum* L. and *Agrostis stolonifera* (= *A. alba),* which were not greatly relished by stock, effectively exclude ragwort. Later, as the ragwort rosette

establishes, the competitive balance swings very strongly in favour of ragwort. Harper (1958) states that the established rosette competes very effectively with grasses and clovers, and only tall herbage such as a hay crop will control established plants.

The basis of competition between ragwort and pasture plants is unknown. It is also unknown whether related interference phenomena such as allelopathy occur. However alkaloids are listed by Rice (1984) as being amongst the main allelocompounds produced by plants and ragwort produces significant quantities of the alkaloid jacobine. While jacobine is usually noted because of its toxic effects on stock, it is unlikely that jacobine evolved solely to combat stock grazing because animals (especially sheep) tend to graze rag wort at its most susceptible phase, and because defoliation has little effect on the survival and persistence of ragwort.

Control

Pasture management

Ragwort can be kept in check or controlled to acceptable levels by promoting a dense, continuous and competitive pasture sward. This can often be successfully achieved through appropriate grazing management (see above). Factors promoting the competitiveness of pasture such as irrigation and fertilisation probably also suppress ragwort. However, the only study reported along this line is that of Thompson (1986) who conducted two experiments to investigate the effects of fertilisers on ragwort. It was found that added superphosphate or urea reduced ragwort densities, presumably by promoting a dense pasture; fertiliser plus 2,4-D performed better still.

If a site has a history of problem ragwort, or is near another densely infested site, maintenance of a dense pasture sward over a long period of time will be necessary because of the long-term dormancy of ragwort seeds, and their powers of dispersal.

Mechanical removal

Mechanical means of controlling ragwort have proven to be largely inadequate because of the weed's ability to regenerate from small fragments. Poole and Cairns (1940) found that chipping out plants enhances ragwort growth by encouragement of new meristem formation. Pulling plants out or cutting them down were also impraticable control measures. Flame throwers successfully killed 93% of seeding ragwort plants, and seeds on the burnt plants did not retain their viability.

Chemical control

Effects on ragwort

Several herbicides have been tried on ragwort, with varying degrees of success. Generally young plants are killed more easily, older ones being more resilient. 2,4-D controls younger plants but performs poorly on late rosette, budding or flowering plants, according to Black (1976) in a Canadian study. With older plants, many of the seeds are still viable after spraying (Balfour, 1955).. Picloram has been found to be superior to 2,4-D at controlling ragwort rosettes (Coles, 1967) or ragwort in general (Thompson, 1974, 1977). MCPA was found by Thompson and Saunders (1984) to provide inferior control to 2,4-D but Forbes (1978) in Scotland found that 2,4-D, MCPA, and 2,4,5-T all gave virtually complete (>98%) control. Glyphosate can suppress ragwort but not all the subterranean portions are necessarily killed (author's observations). Makepeace and Thompson (1982) found glyphosate to be slightly inferior to 2,4-D/picloram for ragwort control, while Thompson (1983) found glyphosate to be superior to 2,4-D/picloram and 2,4-D/dicamba for controlling flowering plants, and inferior to those two with regard. to controlling bolting stage ragwort plants.

Side effects on pasture

Generally the most harmful side effect of most herbicides used against ragwort is their influence on clover. Forbes (1982) and Honore, Rahman and Dyson (1980) found 2,4-D inhibited clover production in pasture. Thompson (1974) observed picloram inhibited clover more than 2,4-D. MCPA was as damaging as 2,4-D to clover (Honore *et al.,* 1980) or even more damaging (Thompson and Saunders, 1984). There are several so-called 'clover-safe' herbicides which are less injurious to clover. Forbes (1982) in Scotland used six such herbicides but only asulam gave over 90% ragwort control which still made it less effective than MCPA or 2,4-D. Thompson (1977) found asulam much less effective than granulated forms of five other (non clover-safe) herbicides including dicamba and picloram.

Pasture grass species tend to be more resistant than clover to damage by herbicides (exept where a clover-safe herbicide is used). Thompson (1974) using 2,4-D and Honore *et al.* (1980) using 2,4-D or MCPA, observed inhibition in pasture dry matter production, although this might be, to some extent, a consequence of inhibition of clover productivity.

Control of mature rag wort plants

Ragwort is more difficult to kill at the later stages of its life cycle and higher rates of herbicides are required. This may influence pasture growth, especially of clover, but mature ragwort plants can be controlled by localised spot-spraying. Makepeace and Thompson (1982) obtained good results using a rope wick applicator to apply 2,4-D, picloram or glyphosate to individual plants. The newly established plants require less herbicide to kill them, but being more numerous and obscure, often require spraying over the whole pasture. It has been suggested by Matthews and Thompson (1977) that it is unnecessary to kill flowering plants, thus giving rise to the so-called Matthews technique for controlling ragwort (referred to as the Australian 'Mitchell technique' in Watt's (1987) review). The approach is to allow the mature plants complete their life cycle in an ungrazed situation so that the majority of crowns and roots die. Subsequent establishment will then depend entirely on seed, emerging seedlings being controlled either by light rates of 2,4-D, applied below the levels that severely inhibit clover, or by management techniques such as grazing or maintenance of a dense pasture. No quantitative data are available on the relative benefits of the Matthews technique over the spraying of mature plants, either in the short or long term.

Ecological strategies

The ecology of ragwort can be summarised in a number of ways but only two will be described here, namely the r-K continuum and Grime's (1974) system. Grubb's (1985) scheme, in which plants are classified according to their responses to habitat, disturbance and competition, is more complex but also more specific.

The r-K continuum is a scheme in which a given plant is placed relative to two extremes: 'r-adapted' plants that are typically short-lived 'colonisers'; and 'K-adapted' ones that are typically long-lived 'climax' plants. The studies that have been discussed in this review suggest that ragwort tends towards the r end of the r-K continuum. However, it is not representative of the extreme of the r-type plants. Characteristics of its r-type tendencies are:

* The seeds of ragwort are small.
* Ragwort is relatively short lived. Normally it is a biennial but it can tend towards perennation in continued disturbance.
* Vegetative growth is rapid.
* Plants are poor competitors during establishment.

* Dormancy is enforced and not innate.
* The dispersal curve is relatively steep, with most seeds being distributed near the parent plant.
* Ragwort is an early successional plant that establishes during periods of disturbance (e.g. overgrazing, stock trampling, pasture suppression). During periods of relative stability ragwort is transient, but as it has limited powers of regeneration under its own canopy, it may persist for a few generations.

Ragwort fits reasonably well into an r-K continuum but occupies several different points on it. The seeds produced are of two types, and show different dispersal and dormancy abilities. Adult plants can act as annuals, biennials or perennials.

The r-K classification has often been criticised for being too simple to reflect complex ecological situations. An alternative approach is the three-pronged scheme of Grime (1974) which states that all plants can be classified according to their abilities as ruderals, competitors and stress tolerators. Ragwort acts as a ruderal but not as much as most annual weeds. It does, however, typically colonise in disturbed situations and is relatively transient during periods of long-term stability. With regard to competition, ragwort is intolerant of pasture during establishment, but at the rosette stage becomes a vigorous competitor. Ragwort is relatively tolerant of some stresses, like cattle grazing and high temperature, but not of others such as sheep grazing and drought. Just as ragwort occupies more than one location on the r-K continuum, so it occupies more than one position on Grime's ruderal/competitor/stress tolerator triangle, according to the plant's age and environmental conditions. Grime (1974) calculated indices of competitiveness and stress tolerance for 100 herbaceous plant species in the Sheffield region (U.K.), one of which was ragwort. With regard to
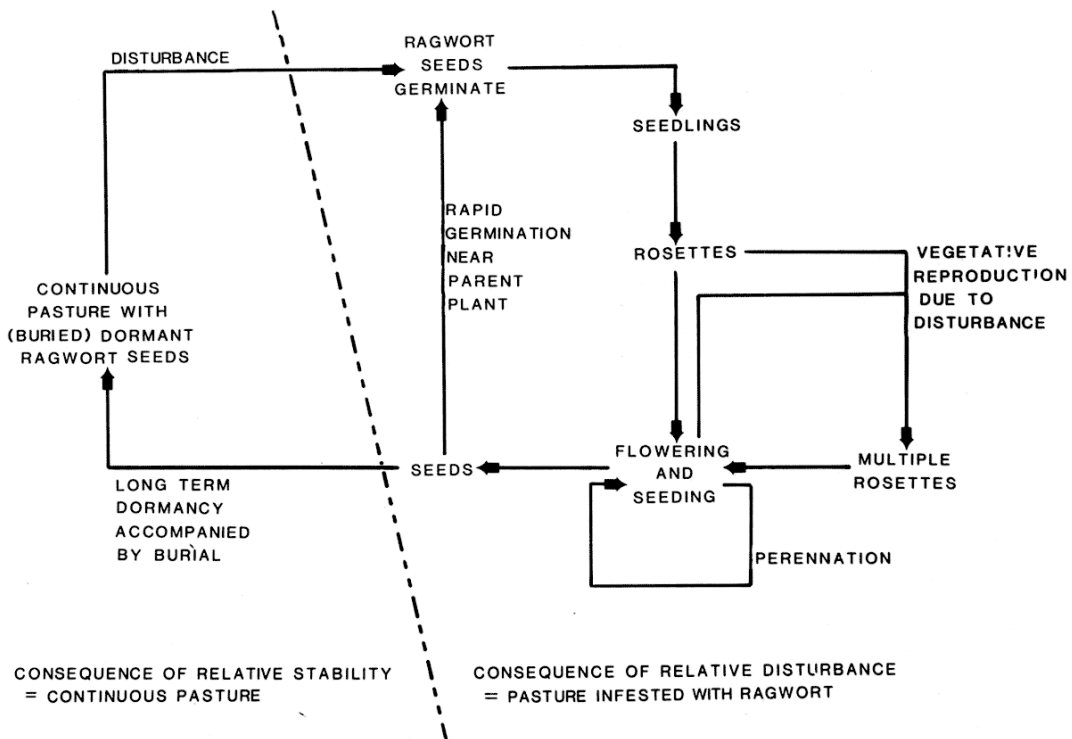

Figure 1: *The life history of ragwort in a pasture, as influenced by disturbance.*

competitiveness, ragwort was ranked 64th along with 13 other species, and in terms of stress tolerance, it was ranked 49th together with 10 other species.

In conclusion, Fig. 1 summarises the ecology of ragwort in the pasture environment. Ragwort-infested pasture exists in a dynamic state with closed pasture, which a Clements-type view of succession could regard as the 'climax'. Disturbance by trampling or grazing will then encourage dormant seed banks to germinate, including buried seed brought to the surface by livestock trampling or erosion, or seeds exposed due to depletion of the pasture vegetation cover. The ray achenes will tend to germinate under or near the parent plant and exhibit some dormancy; the disc achenes may disperse further and germinate faster. Continual disturbance will enhance the persistence of ragwort, by encouraging seeds to continually germinate and possibly propagate vegetatively. Relative continued 'stability' will lead to a continuous pasture cover forming again, accompanied by the disappearance of ragwort (but with ragwort seeds being buried and acquiring dormancy in anticipation of germination stimuli provided by later disturbance). While the extent of disturbance appears to be important in determining the extent of ragwort infestations, other factors which directly influence the plant also determine its success. These include interactions with climate and soil conditions, as well as with livestock and herbivorous insects (see above). However, the relative importance of these factors as they influence populations of ragwort is not entirely known. Dempster's and Lakhani's (1979) model encompassed the interactions of rainfall, defoliation by cinnabar moth populations and ragwort abundance, and provides a useful first step. However, further work is required. In particular, the model must be tested in other environments, the effect of competition from pasture included, and if necessary the empirical relationship with rainfall replaced by a more mechanistic and general treatment of soil moisture.

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