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Interference between pasture plants and thistles—a review

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Summary

The proposition that thistles may be controlled in pasture biologically by interference from neighbouring pasture plants is reviewed. Central to this approach is the hypothesis that the species composition and vegetation cover of a pasture influence birth and death rates in thistle populations, and hence also, population size. Experiments conducted mainly in New Zealand, Australia, USA and UK with species of *Cirsium, Carduus, Silybum* and *Onopordum* confirm that pasture grasses and legumes exert powerful inhibitory influences over seedling emergence and seedling and rosette survival in thistles. Pasture grasses, particularly perennial species, are generally more effective than legumes. This appears to be related mainly to their higher cover density, implicating competition as a mechanism, although there is some evidence that allelopathy may also operate. *Lolium perenne, Holcus lanatus* and *Phalaris aquatica* are particularly effective inhibitors of thistles. Pasture gaps play a key role in thistle seedling emergence and it is concluded that pasture management that promotes a dominant perennial grass component and an absence of small gaps is most likely to prevent thistle invasions. Research is needed on how grazing management and other factors including soil fertility and soil moisture influence the creation and closure of pasture gaps and the balance between grasses, legumes and thistles in pastures.

Introduction

Spatial and temporal variation in the size of thistle populations in pastures is commonly observed and often appears to be related to pasture cover and species composition. This observation has lead to the general hypothesis that interference from sown pasture species plays a dominant role in regulating population size in these weeds. Thistle control recommendations promoting interference from pasture species have arisen from this hypothesis for *Cirsium vulgare* (Scotch or spear thistle) (Anon. 1978), *Carduus nutans* (nodding or musk thistle) (Cregan and Scarsbrick 1977, Popay *et al.* 1979), *Carduus tenuiflorus* (slender or winged thistle) and *C. pycnocephalus* (slender winged or shore thistle) (Bendall 1973), *Onopordum acanthium* (Scotch or cotton thistle) and *Onopordum illyricum* (Illyrian thistle) (Gammie 1972), and *Silybum marianum* (variegated thistle) (Anon 1978, Michael 1968a). The ecological evidence supporting these control recommendations is reviewed in this paper and suggestions for the direction of future research on this topic are made.

Evidence for pasture interference from experiments in which pasture cover is manipulated

Cirsium spp.

Forcella and Wood (1986) investigated the effect of two levels of pasture interference on the demography of a natural population of the biennial *C. vulgare* in an annual pasture composed of *Bromus rubens, Lolium rigidum* and *Trifolium subterraneum* at Canberra, Australia, by leaving 1 ha of the pasture ungrazed for three years, and grazing 0.5 ha with sheep when forage was available. The thistle plants in the grazed pasture were, on average, larger, with more flower heads per plant and more seeds per head than plants in the ungrazed pasture. Significant population effects were evident by the second year. In the third year 14 times as many seeds were shed, and there were 18, 5 and 40 times as many seedlings, rosettes and adult plants respectively in the grazed pasture when counted in April or May. Estimates of the average annual transition probabilities between these life history stages for the three years showed about 50% of rosettes present in one year survived to become adults in the next year regardless of grazing. By contrast, the transition from seeds produced in one year to seedlings the next year was 1.5 times greater in the grazed pasture (0.149 compared to 0.098), but the transition most affected by pasture interference was that from seedling to rosette which was five fold greater in the grazed pasture (0.01 compared to 0.002). Seedling mortality began in the autumn in both grazed and ungrazed pastures, but proceeded at a greater rate during the winter in the ungrazed pasture in each of the three years.

Silverton and Smith (1989) planted seeds of *C. vulgare* in the winter into a permanent grass pasture in England under two levels of summer grazing (using sheep) and all combinations of some or no winter and spring grazing; these grazing regimes had been imposed for two years prior to the experiment. The percentage seedling emergence was determined during the next six months, and at the same time that the seedlings were counted for the final time in the summer, naturally-occurring rosettes were censused in each of the grazing treatments. Spring grazing increased the mean seedling emergence overall from 3.5 to 8.5%, and also resulted in a three fold increase in rosette numbers. Using seedling emergence as a covariate in the analysis of rosette numbers, 77% of the variance in rosette numbers was accounted for, indicating that the main effect of grazing on thistle rosette numbers was indirect, through a grazing-mediated interference with germination conditions. Possible mechanisms are alteration of light quality at the soil surface and/or changes in day/night temperature fluctuations (Phung and Popay 1981). Silverton and Smith (1989) concluded that the close relationship between emergence of sown seed and the number of rosettes established a year or more earlier indicates that seedling emergence is likely to be the most important transition in determining population size in *C. vulgare* in pasture.

Bullock *et al.* (1994) expanded the above demographic by determining the fates of individuals of *C. vulgare* in nine different life history classes over six years. Seed survival and seedling emergence were determined from sown seeds, and other life history stages were quantified by mapping and following the fates of naturally occurring individuals under the different grazing regimes. Heavier summer grazing, or grazing in the winter, increased seedling emergence 1.5 and 2.3 fold respectively, while winter grazing, in addition, increased seedling and small and medium-size rosette survival 2.7, 2.9 and 1.6 fold respectively. These effects were considered to have arisen through the relaxation of interspecific competition due to the preferential grazing of the pasture grasses. This hypothesis was supported by the finding that winter grazing, and heavier summer grazing, decreased the frequency of microsites in the pastures with a canopy, or with litter, by 20 and 80% respectively, and increased the frequency of sites with bare ground 1.5 fold. Matrix analysis of thistle life tables for the experimental paddocks showed that winter and spring grazing, and heavier summer grazing, increased the finite rate of population increase (λ), 3.1, 1.7 and 1.7 fold respectively. The hypothesis that the thistle populations had the capacity to grow faster as the level of pasture interference was reduced by increased grazing intensity, was supported by a significant correlation of λ values calculated for each of the 16 different grazing treatments (paddocks) with the six-year average population size for the paddocks. Five of these 16 λ values were <1, predicting that these populations should decline in size as a result of the level of interference from the pasture plants induced by the particular grazing regimes.

The effect of interference from pasture plants on the seedling emergence of *Cirsium arvense* L. (Californian or perennial thistle) has been investigated in dairy pastures in Victoria, Australia by Amor and Harris (1975). At one site seeds were sown in summer into plots of pasture consisting of *Lolium perenne* L., *Dactylis glomerata* L. and *Trifolium repens* L. that were either cut monthly to a height of 3 or 15 cm. Seeds were also sown onto, or shallowly into, pasture bared by a paraquat/diquat treatment. No seedlings emerged on pasture plots, but 13 and 3% of sown viable seeds emerged as seedlings from shallowly-buried and surface-sown seeds respectively on bared plots in the spring. Similar results were obtained in another dairy pasture in which seeds were sown either onto the surface of a *L. perenne*/*T. repens* pasture set stocked with 3.75, 4.25, 5, 5.75 or 6.5 cows per hectare, or into a lightly grazed pasture or into a wet pasture. Seeds were also shallowly buried or surface-sown on bared plots. Again there was no emergence in any pasture. However 7% of the shallowly buried seeds emerged as seedlings on the bare soil. These results suggest that pasture plants have a powerful inhibitory action against the germination of *C. arvense* seeds. The light requirement of the seeds (Bakker 1960), may not be fulfilled under pasture. Observations of patch size in the thistle in two lightly grazed pastures and two heavily grazed pastures suggested that the rate of vegetative spread was lower the higher the grazing pressure. It would seem that the reduced level of pasture interference which accompanies heavy grazing, while usually increasing population size in the biennial *C. vulgare*, is overshadowed in *C. arvense* by some opposing force, possibly that of being eaten (Mitchell and Abernethy 1993). However the dry matter production of *C. arvense* was relatively insensitive to increased interference from neighbouring pasture plants (compared to other weeds) in a Swedish study when the row spacing of pasture grasses and legumes was decreased from 50 to 10 cm (Hallgren 1976).

Together these studies provide good evidence that the presence of neighbouring pasture plants can limit population size in the biennial *C. vulgare* and that the life history stage most susceptible to pasture interference is the transition from seed to seedling (emergence) (Silverton and Smith 1989, Bullock *et al* 1994,). The seedling to rosette transition (Forcella and Wood 1986, Bullock *et al.* 1994) and the rosette to adult transition may also be sensitive, although perhaps to a lesser extent. These results support a control recommendation that maximizes pasture interference by maximizing pasture height or cover at the time of year when seedling emergence of *C. vulgare* is occurring. By contrast, population size in the perennial *C. arvense* may be much less affected by pasture interference (Amor and Harris 1975, Hallgren 1976). Population growth in this species depends entirely upon recruitment of shoots from adventitious buds on a creeping root system, and the initial reliance of these shoots on stored root reserves, rather than on current photosynthesis, provides an explanation for a lower sensitivity than seedlings to interference from pasture.

Carduus spp.

Feldman *et al.* (1968) sowed seeds of *C. nutans* in Nebraska, USA, in spring and summer, into 15-year-old pastures of four different types (species composition), each under three different grazing regimes (ungrazed, rotationally or continuously grazed). There was no overall effect of grazing intensity on seedling emergence, but the presence of more *C. nutans* plants on the grazed plots (relative to the ungrazed plots) in each of the two years after both sowings, was interpreted as a result of a higher survival rate of rosettes under a relaxed level of pasture interference. Medd and Lovett (1978) showed that the relative growth rate (RGR) of *C. nutans* seedlings is reduced by shading and concluded that the light compensation point (1.7% full daylight) may be reached for this species under a pasture canopy. Low RGR results in small size, and small *C. nutans* rosettes have higher mortality in pasture than larger rosettes (Popay *et al.* 1979). Thus relaxed competition for light is a possible explanation for the greater survival of *C. nutans* in grazed pasture. In Virginia, USA, Kok *et al.* (1986) sowed one or four *C. nutans* seeds per square metre with or without seeds of *Festuca arundinacea* (tall fescue) into cultivated soil. The growth of the thistles was greatly depressed in the tall fescue (relative to no tall fescue), as indicated by an 83% reduction in stem dry weight measured 10 months after sowing. Fecundity was also severely reduced as evidenced by an 89% reduction in seeds produced per plant, a consequence of reductions in the size and number of inflorescences per plant. These results were interpreted as the result of intense competition from the tall fescue. In a related study by these authors, seeds of *C. nutans* sown into the tall fescue pasture a year after it was sown, germinated poorly and all seedlings died before developing four leaves.

Studies in New Zealand in which the fates of *C. nutans* plants in pasture have been followed have revealed high mortality of seedlings and young rosettes during winter after emergence in the autumn (Popay and Thompson 1979, Popay and Thompson 1980). For example, Popay and Thompson (1980) found that of 200 rosette-stage thistles present in a pasture in autumn, 83% died during winter and spring before flowering began. The hypothesis that this mortality is due, at least in part, to interference from pasture species, is supported by studies showing greater survival in pastures desiccated by herbicide. Edmonds and Popay (1983) transplanted *C. nutans* seedlings into sheep-grazed pasture composed of the grasses *Lolium perenne*, *Cynosurus cristatus*, *Bromus mollis*, and *Anthoxanthum odoratum*, with and without prior desiccation by paraquat. Thirty five times as many seedlings from an early autumn planting survived to flowering in the desiccated pasture (relative to intact pasture).

Other studies in New Zealand in which pasture cover has been removed by herbicide indicate that the transition from seed to seedlings may also be influenced strongly by pasture plants. Popay and Kelly (1986) counted *C. nutans* seedlings emerging from intact pasture and pasture bared monthly by paraquat from autumn one year until the following autumn. Three times as many seedlings emerged on the bare pasture. In addition, there were both spring and autumn emergence peaks on the bare pasture, whereas all seedling emergence was confined to the autumn in the intact pasture. The results indicated that the presence of pasture prevented seedling emergence in the spring, and halved the numbers of seedlings emerging in the autumn. Martin and Rahman (1988) obtained similar results using the same experimental approach. When Kelly and McCallum (1990) sowed seeds of *C. nutans* into a pasture composed of *Lolium perenne* and *Trifolium repens* that was either kept clipped to a height of 1 cm or allowed to grow to a greater height under sheep grazing, they found that 6% of the seed emerged as seedlings in the clipped pasture but only 0.94% in the taller pasture. Thus the transition from seed to seedling was reduced 83% in the taller pasture. Furthermore, in related studies comparing life history transitions between two regions in NZ contrasting in susceptibility to the thistle, Kelly and McCallum (1990) found that the seed to seedling transition was an order of magnitude lower in the region where the thistle is not a problem, whereas other transitions differed little between the regions. This lead the authors to suggest that the seed to seedling transition is the single most important stage in the life-cycle of *C. nutans*, and that pasture interference during the time when this transition is occurring, will reduce population size.

By contrast, grazing experiments by Bendall (1973) in Tasmania, Australia, with *Carduus pycnocephalus* L. and *C. tenuiflorus* Curt. provide no evidence that pasture interference directly affects the demography of these thistles. While the survival of these thistles in *Lolium perenne*, *Bromus* sp., *Cynosurus echninatus*, *Trifolium repens* pasture grazed by sheep was significantly lower when winter grazing was not preceded by autumn grazing, when autumn grazing was withheld without being followed by winter grazing, there was no effect on thistle survival. The former results were explained by etiolation of the thistles in presence of ungrazed grass in the autumn, making them palatable and readily eaten (and killed) by the sheep during winter (or spring) grazing.

Overall, the above studies provide evidence of a powerful influence of pasture plants over the transition from seed to seedling in the annual/biennial/triennial *C. nutans* (Popay and Kelly 1986, Martin and Rahman 1988, Kelly and McCallum 1990). The transition from seedling to flowering plant is also significantly reduced in this thistle by interference from pasture plants (Edmonds and Popay 1983), probably by mortality at both the seedling (Kok *et al.* 1986) and rosette stages (Feldman 1968, Popay and Thompson 1980). Pasture interference can also reduce fecundity by depressing growth of surviving thistles (Kok *et al.* 1986). These results support control recommendations for *C. nutans* that maximize pasture cover especially during the seedling emergence phase. Direct effects of pasture interference on population size in the annuals *C. pycnocephalus* and *C. tenuiflorus* have not been proven, but etiolation in long grass facilitates death by grazing.

Pasture species composition effects

Cirsium vulgare

Forcella and Wood (1986) established two seedlings of *C. vulgare* with two of either *Lolium rigidum* or *Trifolium subterraneum* in pots under two nitrogen levels in glasshouse conditions, and imposed clipping treatments on the *L. rigidum* and *T. subterraneum* to simulate grazing. Pots containing four plants of *C. vulgare* only were included as controls. When the swards were not clipped, the dry weights of the thistle plants were the same in mixture with *L. rigidum* and *T. subterraneum* regardless of fertility, and by 10 weeks, were reduced 55% by interference from these pasture plants. However, when the competing grass and clover plants were clipped, differences occurred. Under low fertility, the dry weight of the thistle was 35 and 58% lower when *L. rigidum* was the competing species (relative to *T. subterranean*) when clipping occurred throughout or during the last five weeks of the experiment respectively. The *L. rigidum* was also the better competitor under high fertility and resulted in 61 and 48% lower thistle dry weights when clipping occurred during the first or last five weeks respectively. Fisher and Davies (1991) provide further evidence that pasture species vary in their abilities to interfere with *C. vulgare*. In a study to compare the effects of sown ground covers on invading weeds in set-aside fallows in the UK, they sowed swards of either *Lolium perenne*, *L. perenne* plus *Trifolium repens*, or *Festuca rubra* into an arable field. An unsown treatment was included. Both the frequency and cover of *C. vulgare* were lower in sown swards. Averaging over years 2, 3 and 4 of the study, the percentage ground cover of *C. vulgare* was reduced, in comparison to the unsown sward, 96, 94 and 85% by the three swards respectively. The frequency of occurrence of *C. vulgare* was reduced 86, 92 and 64% respectively. These results together suggest that *L. perenne* interfered more than *F. rubra* with population growth in *C. vulgare*.

Wardle *et al.* (1992) planted seeds of *C. vulgare* into 92 day old swards of the six grasses *Dactylis glomerata* L., *Phalaris aquatica* L., *Bromus catharticus*, *Lolium perenne* L., *Festuca arundinacea* Schreb, *Holcus lanatus* L. and the four legumes *Medicago sativa* L., *Trifolium pratense* L., *T. subterraneum* L. and *T. repens* under greenhouse conditions. *H. lanatus* had the most effect on the percentage emergence of *C. vulgare* seeds, reducing this to 35% from 53% on bare soil; a reduction of 34%. There was a significant negative correlation between the pasture cover of the 10 swards and the percentage emergence of the thistle seeds, implying that the mechanism of germination inhibition is related to foliage cover. Greater differences were found between these ten pasture species in their ability to reduce the growth of *C. vulgare*. In general the grasses, as a group, tended to reduce thistle growth more than the legumes, reducing shoot dry weight, measured 80 days after sowing, when the thistles were still rosettes, by 83 to 94% (relative to bare soil). The results suggested that *H. lanatus* and *L. perenne* are the most effective inhibitors of growth in *C. vulgare*, while *M. sativa*, *T. subterraneum* L. and *T. repens* are the least effective. In contrast to seedling emergence, there was no correlation between thistle growth (dry matter, plant diameter) and cover of the pasture species, suggesting that the mechanism of the inhibition of *C. vulgare* may not involve shoot competition.

Overall the evidence from these three studies suggest that grasses are better able to reduce the growth of *C. vulgare* plants, than are legumes.

Carduus nutans

Research in New Zealand has revealed that pasture species also vary greatly in their relative abilities to inhibit *C. nutans*. Nicholson *et al.* (1990) sowed *C. nutans* in replacement series with either *Lolium perenne* or *Trifolium repens* at two total densities under greenhouse conditions. Per plant dry weight of *C. nutans* declined in mixture with *L. perenne* but increased in mixture with *T. repens* suggesting that *L. perenne* had a competitive advantage over the thistle, whereas *T. repens* did not. Relative yield totals were not different from unity, implying competition between the pasture species and *C. nutans* for the same pool of limiting resources.

In the experiment described above for *Cirsium vulgare*, Wardle *et al.* (1992) also sowed *C. nutans* seeds into swards of the same grasses and legumes under greenhouse conditions. The total percentage emergence of *C. nutans* was reduced 55 and 61% (relative to emergence on bare soil) by *L. perenne* and *H. lanatus* respectively, whereas the other grasses and legumes had no effect on emergence. They concluded that this effect was probably due to a reduced red:far red light ratio under the canopies (Phung and Popay 1981, Black 1969); the difference between the species being explained, at least in part, by differences in their cover as measured by the point intercept method. There was no correlation between the emergence responses of *C. nutans* and *Cirsium vulgare* to these 10 pasture species, implying that the mechanism of emergence inhibition must vary between the two thistles. All ten pasture species reduced the seedling growth of *C. nutans* although the legumes exerted much less effect than the grasses, as was also the case for *C. vulgare*. The growth responses of *C. nutans* and *C. vulgare* were highly correlated, suggesting (in contrast to seedling emergence), that a particular pasture species will be equally effective in suppressing seedling growth in both thistles. *L. perenne* and *H. lanatus* were particularly effective.

Since there was no correlation between *C. nutans* seedling growth and canopy cover of the ten species, as was also found for *C. vulgare*, Wardle *et al.* (1992) suggested that competition for light was not the mechanism for thistle inhibition. They concluded that allelopathy is a more likely mechanism, at least for *C. nutans*, because they found strong positive correlations between *C. nutans* root growth (and root/shoot ratio) in a previous residual alleopathy study, and root and shoot growth, and seedling emergence in the current study. In the previous study Wardle *et al.* (1991) grew the same 10 pasture species separately in boxes for 3–5 months and then sowed *C. nutans* seeds into the soil from under each species at various times up until 162 days after removing the pasture plants. Residual allelochemical effects were identified for all six grasses in the 162-day-old soil. These effects ranged from 64 to 87% reduction in *C. nutans* shoot growth in the soil from beneath *D. glomerata* and *H. lanatus* respectively. Root growth was also significantly reduced in soil from some species and germination of *C. nutans* was reduced 50% by soil from beneath *L. perenne*. By contrast all four legumes demonstrated stimulatory effects, particularly in terms of thistle root and shoot growth.

In order to test the hypothesis that grasses have a greater capacity to interfere with seedling emergence and subsequent growth of *C. nutans*, Wardle *et al.* (1995) sowed monocultures of each of the six grasses and four legumes compared in previous studies, into a dairy pasture with a history of *C. nutans* infestation, after killing the existing pasture with herbicide. The experiment ran for 27 months from March (autumn 1990) during which time *C. nutans* seedlings were counted and removed two-monthly, regular point intercept (cover) estimates of pasture composition were made, and the fates of some tagged *C. nutans* plants were followed. Seedling emergence was generally lower in the grass than in the legume swards. These results are consistent with those of Wardle *et al.* (1992), showing that grasses inhibit emergence more than legumes. Across all swards, emergence was negatively correlated with the cover of grasses (sown or volunteer) and also with the cover of *Poa annua*, a species which invaded particularly in the grass-sown plots. Other measures of *C. nutans* performance also negatively correlated with the cover of grasses in the plots were the fraction flowering as annuals, plant diameter and capitulum number per plant. These correlations suggest, contrary to the conclusion made by Wardle *et al.* (1992), that shoot competition, at least from grasses, is an important interference mechanism under field conditions. The intense interference from the grasses prevented thistles from reaching sufficient size to flower in their first year, and resulted in a higher fraction of thistles dying as rosettes in the grass swards, relative to the legume swards.

The results of these glasshouse and field studies on interference between pasture plants and *C. nutans* reveal that grasses inhibit seedling emergence and subsequent growth and survival of rosettes to a significantly greater level than legumes. It also appears that pasture species vary in their abilities to inhibit emergence and growth of *C. nutans* by virtue of the amount of cover they produce. This implies that canopy cover alters the germination conditions, probably through reducing the ratio of red:far red light, and also that competition is involved in inhibiting growth and survival. Thus, while legumes may often be an essential component of pastures, it appears that newly-sown pastures should be grass dominant if control of *C. nutans* is an objective.

Silybum marianum

In an experiment in New South Wales, Australia, to measure the relative effectiveness of perennial and annual pasture species in preventing the establishment of the annual, *Silybum marianum*, Michael (1968a) sowed seeds of *Phalaris aquatica*, and *Lolium rigidum* with and without seeds of *Trifolium subterraneum*, *T. subterranean* alone and *Medicago sativa* alone into cultivated soil with a history of *Silybum marianum* infestation in preceding crops and pastures. When assessed in the first spring following autumn sowing the perennial species, *P. aquatica* had reduced the fresh weight and population density of *S. marianum* 74 and 39% respectively relative to the 'not sown' control. The other perennial, *M. sativa*, had completely prevented the occurrence of the thistle. By contrast the annuals, *L. rigidum* and *T. subterranean* had no effect. In the second spring after sowing, dry weights of the thistle were still lowest in the *P. aquatica* and the *M. sativa;* 98% reduction relative to the not sown treatment. The ability of *M. sativa* and *P. aquatica* to make rapid growth after late summer or autumn rains, at the time when *S. marianum* is germinating, was suggested as a mechanism for their success in controlling the thistle. Pook (1983) found that the light compensation point of *S. marianum* (and *Onopordum* sp.) was 2.4% full (cool season) daylight, and suggested that while this represents a degree of shade tolerance, heavy shading during the cool winter season by persistent pasture species could contribute to control of these thistles.

Onopordum spp.

The effects of pasture interference on *Onopordum acanthium*, *O. illyricum* and hybrids between these two biennial thistles appears to have received less attention by researchers than *Carduus* and *Cirsium* sp. Michael (1968b) sowed *Bromus inermis*, *Dactylis glomerata*, *Festuca arundinacea*, *Lolium perenne*, and *Phalaris aquatica*, (including not-sown controls) in the autumn (and spring) in New South Wales, Australia, into cultivated soil previously supporting a *Trifolium subterranean* pasture heavily infested with *Onopordum* sp. These five perennial grasses diverged significantly in their abilities to influence thistle population size with both times of sowing. Differences between the pastures appeared in the first year and persisted for at least seven years. In the spring of the seventh year after sowing, the population density of *Onopordum* plants that exceeded 100 mm diameter, and the dry matter yields of the populations, were lower in the *F. arundinacea* and *P. aquatica* pastures relative to the other three pastures (and the volunteer pasture) indicating that these two grasses had interfered more than the others with population size and plant growth in the thistle. Since both thistle population density and dry matter yield in spring were highly correlated to the cover of the grasses in the previous winter, differences in competitive abilities between the grasses probably explain the effects.

Pasture gap effects

Cirsium spp.

Gaps in pastures probably play a crucial role in the ability of pasture plants to interfere with the population dynamics of *C. vulgare*. Silverton and Smith (1989) found evidence for this by planting seed of *C. vulgare* into artificial gaps of varying diameter created in a mown grassland in England by cutting the sward to ground level. Percentage seedling emergence of sown seeds increased with gap diameter four fold from zero to 10 cm, but tended to decline with greater gap diameter. Panetta and Wardle (1992) found a similar relationship when they planted seeds of *C. vulgare* into gaps created in a *Lolium perenne–Trifolium repens* pasture on a dairy farm in New Zealand. In this case percentage seedling emergence increased 13 fold from a gap diameter of zero to 2 cm, and declined with increasing gap diameter up to 10 cm. Seeds sown into large (3 m^2) bared plots had a probability of producing seedlings similar to those sown into the intact pasture. There was however no response to gap size under glasshouse conditions, leading Panetta and Wardle (1992) to conclude that differences in diurnal temperature fluctuations or soil moisture content between gap sizes, rather than reductions in red:far red ratios of foliage filtered light (Black 1969), may control the gap size response of *C. vulgare*. This hypothesis is supported by the results of Phung and Popay (1981) which showed that increasing pasture cover, while reducing both germination and the red:far red ratio under fluctuating temperature conditions, did not reduce germination under constant temperature. These two studies suggest that there is an optimum gap size for seedling emergence in *C. vulgare*. Survival of seedlings may also be influenced by gap size. While there is no direct evidence for this with *C. vulgare*, Louda *et al.* (1990) found that the survival of transplanted seedlings of the native *Cirsium canescens* Nutt. in prairie grassland in Nebraska, USA, was reduced by 89% within nine weeks of planting, in 15–20 cm diameter gaps within clones of *Panicum virgatum* L. compared to survival in large open spaces between clones. Louda *et al.* (1990) suggested that competition between the thistle and the grass for water was the most likely mechanism for this effect, although they could not discount differences in the light levels and physical conditions.

Silverton and Smith (1989) explored the relationship between gap density and the population dynamics of *C. vulgare* by altering the gap density and seed aggregation parameters of a simple model which simulated the expected population density after 50 years, of a monocarpic perennial weed, capable, like *C. vulgare*, of establishing only in gaps of a specified size. The model showed the existence of a gap density threshold below which the population becomes extinct, and above which small changes in gap density lead to very large differences in population density. These results imply that sudden outbreaks of *C. vulgare* might be expected as gaps become more frequent through over grazing or through poor persistence of pasture plants.

Carduus nutans

Gaps in pasture have been considered to play a crucial role in the recruitment also of *Carduus nutans* seedlings (Ivens 1979). This was confirmed by the study of Panetta and Wardle (1992) in which the field emergence of sown *C. nutans* seeds increased with gap diameter up to 10 cm, above which it declined. This response was explained by a greater amplitude of temperature fluctuations experienced by seeds in medium size gaps promoting germination, and faster drying of soil after rainfall in larger gaps reducing germination. Reduced red:far red ratio of canopy filtered light may also partly explain the initial increase in germination with increasing gap size since Phung and Popay (1981) found *C. nutans* seedling emergence was increased on bare ground (relative to under a pasture canopy) under both fluctuating (glasshouse) and constant (growth room) temperature conditions.

Conclusions

The main conclusions that can be drawn from the studies reviewed here on the role of pasture interference in the population ecology of thistles are:

i. Pasture grasses and legumes can exert powerful inhibitory influences over seedling emergence and seedling and rosette survival in thistles, thereby regulating population size.
ii. Pasture grasses are, as a whole, more effective than legumes at inhibiting these demographic processes.
iii. Grasses (and legumes) vary in their inhibitory abilities and this seems to be determined largely by their foliage cover density although allelopathy may also operate.
iv. Perennial grasses exert greater inhibitory effects than annual grasses. *Lolium perenne*, *Holcus lanatus* and *Phalaris aquatica* appear to be particularly effective.
v. Pasture gaps promote thistle seedling emergence, and the optimum size appears to be in the range of 2–10 cm diameter.

The general rule that emerges, at least for the annual and biennial thistles, is that thistle population size will be limited most in pastures composed predominantly of perennial grasses that are managed in a manner that prevents the occurrence of small to medium size gaps particularly during times of the years when the seed to seedling (autumn) and seedling to rosette (winter/spring) transitions are occurring. Sindel (1991) reached a similar conclusion. The empirical evidence supporting this general rule for thistle control is very strong. Future research should focus on how grazing management and other factors including soil fertility and soil moisture (Sindel 1991), influence the creation and closure of pasture gaps and the balance between grasses, legumes and thistles in pastures.

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