The demography of *Carduus nutans* as a native and an alien weed

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Summary

Comparative demographic and phenological studies of nodding thistle, *Carduus nutans*, populations were carried out in both native (European) and Australian localities over at least three years or until the population became extinct. Seed banks under established thistle populations were at least 100 times greater in Australia. Germination was largely restricted to spring and autumn in Europe, but occurred in all seasons in Australia. Most plant mortality occurred soon after germination and was far higher in Australia where seedling densities were also higher (>500 cf <55 m^{-2}). In Australia a higher proportion of the winter and summer recruits survived to flowering than autumn and spring recruits. Most plants in both regions behaved as biennials, flowering after their first winter. Flowering plant density (× 2), capitula per plant (× 3) and actual seed rain (× 100) were greater in Australian thistle populations, where the flowering season was also nearly 50% longer. These differences are discussed in relation to this thistle's greater importance as a weed in Australia, and to provide insight into its potential control strategies.

Introduction

The recent Biology of Australian Weeds chapter on *Carduus nutans* ssp. *nutans* L. (Popay and Medd 1995) provides a comprehensive review of this noxious weed. In summary, *C. nutans* is endemic to Europe, Siberia, Asia Minor and North Africa, and has become a serious weed in North and South America as well as in Australasia. It was first introduced to Australia in the late 1940s as a seed contaminant, which happened repeatedly until it was declared a prohibited contaminant in the 1960s. It is spread over tens of thousands of square kilometres in Tableland New South Wales, and it also occurs sporadically in Queensland, Victoria and Tasmania. It has the potential to spread further, especially in New South Wales (Popay and Medd 1995). As part of a prerequisite for a biological control program, basic ecological studies were mounted in both its native range, and in Australia. These data were to determine which ecological factors were having a controlling influence on the population dynamics of *C. nutans* in the two areas where the plant has a contrasting weed status. The Australian data were also to provide baseline data to assess the impact of any organism released to control the weed.

Materials and methods

Study sites for thistle populations (usually 20 × 30 m) were selected in both France and Australia. The procedures adopted in France for demography / phenology and soil seed bank determination have been detailed in Sheppard *et al.* (1990, 1994). Similar procedures were used in Australia, excepting that 10 permanent quadrats (0.5 × 0.5 m) were used. The plant populations at these sites were monitored every six weeks over several years. On each visit any seedling recruitment was recorded. The growth of individual plants was assessed on each visit. Each plant was given a unique number and had its position in the quadrat determined. Additional visits were undertaken each fortnight in the flowering season. Data collected on these visits included measurement of flowering capitula. The season of recruitment and time to flowering were used to classify plants / cohorts into summer annuals (germinated in spring and flowered in the next summer), winter annuals (germinated in autumn and flowered in the next summer), biennials (completed whole life-cycle in more than one, but less than two calendar years and triennials (completed life-cycle in more than two years). The number and sizes of capitula matured per plant and per square metre were used to measure the potential seed rain (see Woodburn and Cullen 1993), whilst in France the actual seed rain was measured by collecting mature capitula before seed fall and counting the numbers of viable in the laboratory. The proportion of the seed rain destroyed by insects in the capitula was estimated from the difference between actual and potential seed rain. The maximum annual soil seed banks were estimated in France and Australia by washing and sieving 100 random soil cores (10 cm deep and 3.2 cm diameter) from each study area in late autumn following the seed rain.

Results

Details of one French site, and part of one Australian site are presented in Figure 1a and b. For ease of visual display these data have been summed over two recording times, corresponding by and large to a season, and then averaged. Detailed results are to be found for part of another French site in Sheppard *et al.* (1990). Differences in plant and population measurements over all sites are summarized in Table 1.

Recruitment, survival and life history

Germination followed rainfall in both regions. In France germination was therefore limited to spring, summer and autumn (Figure 1a), but recruitment in summer was not observed at all sites (Sheppard *et al.* 1990). In Australia recruitment occurred throughout the year and at much higher densities than in Europe (Figure 1b) due to the higher soil seed bank (see below). Most plant mortality occurred soon after germination. Plant survival was higher in France than in Australia for both seedlings to rosettes, and from rosettes to flowering (Table 1). Competition resulting from high seedling densities recorded in Australia (often >500 m^{-2}) would have contributed to this. In Australia, higher proportions of the winter and summer recruits survived to flowering than autumn and spring recruits. In France, survival to flowering was higher among autumn recruits than spring recruits largely because the hot dry southern French summers induced higher mortality in the smaller spring germinated rosettes (Sheppard *et al.* 1990). In certain years densities of flowering plants fell to similarly low levels corresponding to very dry periods in either region, but in good 'thistle years' the difference in flowering plant density was 6.8 times greater in Australia than in Europe. In both regions, plants mostly took between one and two calendar years to complete development; one cohort flowered in its third year in Australia (triennial). Winter annual cohorts occurred in both regions, but were more common in France. Also, two of nine cohorts followed in France, (same year different sites), behaved as summer annuals. *C. nutans* has a vernalization requirement for floral development (Popay and Medd 1995). Summer annual cohorts were possible because the spring recruitment was vernalized as seedlings. This life history was not observed in Australia.

Flowering period

Individual plants and populations flowered for longer in Australia (Table 1), and the average number of capitula produced $plant^{-1}$ was greater in Australia than in France for similar life history strategies. Biennial plants produced more capitula than either of the two annual flowering strategies (Sheppard *et al.* 1990). Despite these differences large biennial plants of similar reproductive potential did occur in both regions (Table 1).

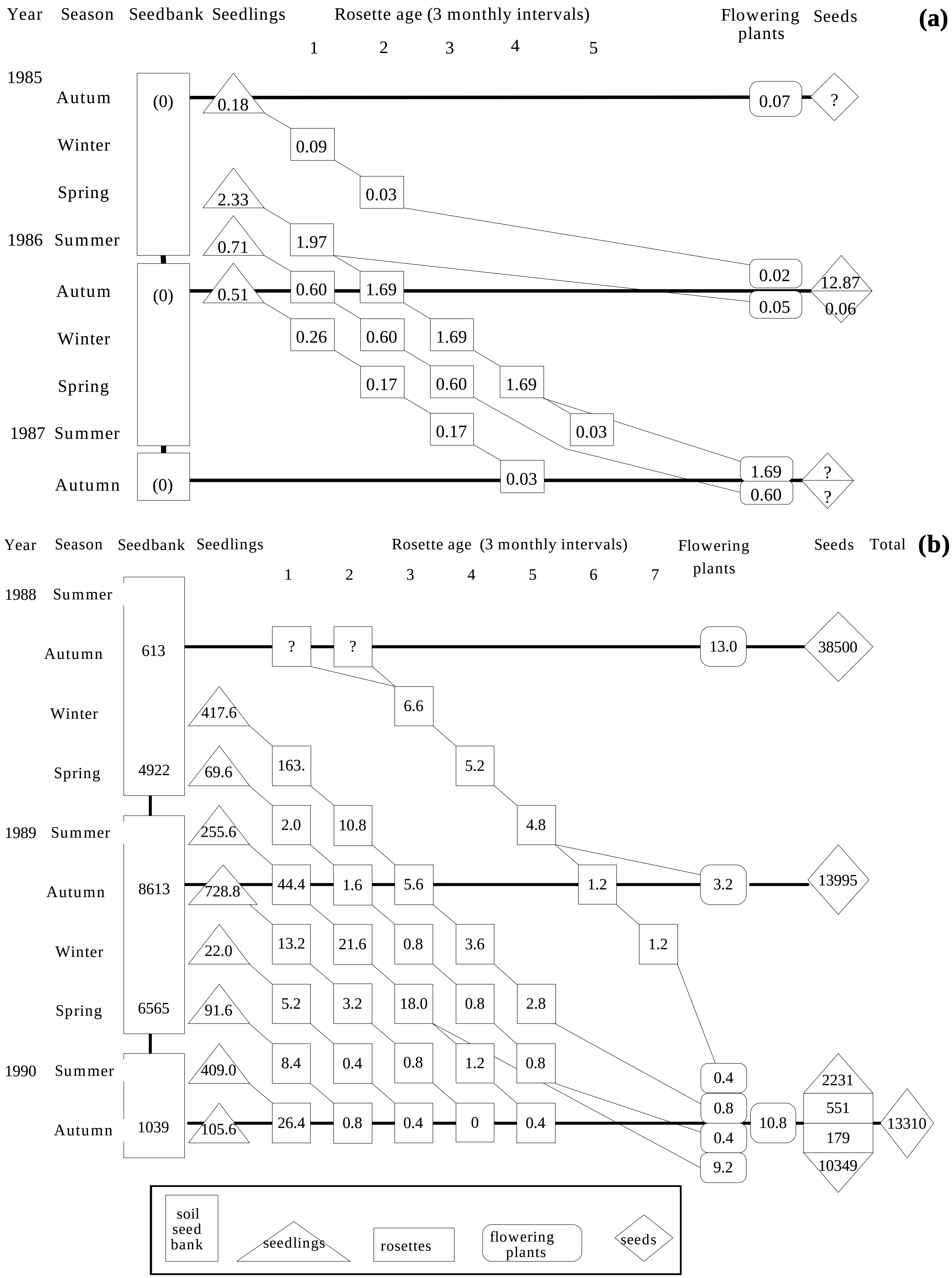

Figure 1. Demography of the different developmental stages of *C. nutans* for cohorts germinating during differing seasons. The numbers are individuals per square metre. Figure 1a show data from France, 1b show data from Australia.

Table 1. Summary of population demography/phenology of *C. nutans* in Europe and Australia (numbers are expressed as per square metre unless indicated otherwise).

Attribute	France	Australia
Seed bank range	undetectable–140	3000–13 000
Prop. seedbank that recruits	0.02–0.67	0.02–0.23
Recruitment	spring, (summer) and autumn	all seasons
Seedling density	0.18–54.3	2.4–728.8
Seedling survival (prop.)	0.69 (0.12–0.93)	0.26 (0.02–0.83)
Rosette survival (prop.)	0.58 (0.22–1.0)	0.16 (0.0–0.61)
Flowering type (prop of cohorts followed)	summer annuals (0.18) winter annuals (0.27) biennials (0.55) triennials (0)	summer annuals (0) winter annuals (0.1) biennials (0.8) triennials (0.1)
Flowering plant density	0.03–4.7	0.02–13.0
Flowering period of population (months)	4 (June–September)	7 (November –May)
Flowering period of individuals (weeks)	8 (2–14)	10.2 (2–19)
Av. no. mature capitula / biennial plant	7 (2–93)	29.3 (2–120)
Potential seed rain	13–4261	171–38 500
Actual seed rain	0.4–240	171–38 500
Actual (potential) seed production / plant	0–1116 (6978)	57–24 334
Proportion seed destroyed	0.82–0.99	0

Seed production and seed banks

Potential annual seed rain was 10 times greater in Australian than in French populations, although the observed seed rain and the existing seed bank under a range of high density populations was two orders of magnitude greater in Australia than in France. The high seed banks in Australia suggest that the weed is rarely seed limited in this region. This is supported by the observation that a lower proportion of the seed bank successfully germinates and recruits in any given year in Australia than in France. The seed bank decay rates could not be estimated as no sites were available where seed rain had been prevented over several seasons. The proportion of the seed rain that enters the bank may also explain why the population dynamics of this weed varies between the two regions as this will indicate the levels of post-dispersal seed predation, for example. However, the seed bank sampling protocol used was not sufficiently detailed to allow accurate assessment of this parameter in France.

Discussion

These data provide some understanding as to why this plant is a more serious weed in Australia than in its native range. In Australia, there is a longer flowering season and a higher seed production per plant resulting from both the greater plant size and the absence of any specific seed predators (Sheppard *et al.* 1994). This has enabled the plant to lay down large soil seed banks which in established thistle infestations always stabilize an order of magnitude greater than in the weed's home environment. Other factors not specifically measured here, such as higher post dispersal seed predation and shorter seed survival in the soil, may also be important (Sheppard 1996). The large seed bank leads to higher densities of seedlings and ultimately of flowering plants, as seed limitation (the successful occupancy of all germination microsites) no longer inhibits recruitment. Australian thistle infestations appear to be above the threshold where seed-limitation is important. They are also not in a situation where populations tend to be limited by the chance that a seed will successfully produce a flowering plant. Evidence for this are the lower proportion of the seedbank that successfully recruits in any given year in Australia and the lower survival to flowering than in France. Modelling the dynamics found in these thistle populations will help determine the level of seed production control necessary to force Australian *C. nutans* populations below the threshold where they become seed limited (Shea 1996).

Successful weed control will have been achieved if the dynamics of this weed in Australia are manipulated such that they are similar to those found in the French populations studied. This requires a reduction in the size of the seed bank either directly, by using such practices as will reduce seed bank persistence (e.g. regular cultivation) or indirectly by using biological control agents (Woodburn and Briese 1996) to reproduce in Australia the levels of seed predation observed in Europe. This will reduce both the rate at which seed banks are replenished, as well the spread of the weed. Additional practices, such as spray-topping and graze-topping, (to reduce seed production), and better pasture management (to reduce the availability of suitable germination microsites and increase the levels of pasture competition), will also contribute to this goal.

Acknowledgments

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