

Establishment of native perennial shrubs in an agricultural landscape

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Abstract Native vegetation has been destroyed or dramatically modified throughout agricultural regions of southern Australia. Extensive restoration of native perennial vegetation is likely to be crucial in these areas for the persistence of native plant and animal species, to ameliorate dryland salinity and soil degradation, and to maintain long-term agricultural production. The long-term resilience of these systems will be dependent on the ability of key functional taxa, such as perennial shrubs, to recruit and persist. In this study, we examine the factors limiting establishment of two perennial shrubs in formerly cropped land, the rare *Maireana rohrlachii* and the common *Maireana decalvans*. Field and laboratory observations suggest that establishment of both species is not limited by life-history traits following cultivation. Both species established and persisted under varying levels of plant competition. Similarities existed between species in their initial germination rates. Weak differences were found between species in the growth and survival rates under different levels of competition. The main difference between the two species was in the decline of germinability of fruits with increasing fruit age. From the data, it is difficult to determine what factors limit the establishment of perennial shrubs in these landscapes. The main hypothesis that can be advanced is that establishment of shrub species appears to be limited by propagule availability and this is likely to be a function of past and present grazing management rather than cultivation per se. Further investigation of these land-use practices may give greater insight into the factors affecting the establishment of this life form across these landscapes.

Key words: chenopod grassland, competition, disturbance, low rainfall, resilience.

INTRODUCTION

Throughout the low rainfall regions of southern Australia (<450 mm year⁻¹), shrubs (particularly chenopods) are used by graziers to fill feed gaps for domestic stock during the late summer–autumn period, and in drought years (Leigh & Mulham 1966, 1967; Cunningham *et al.* 1981; Graetz & Wilson 1984; Millsom 2002). However, farming practices such as cultivation and intensive livestock grazing have changed the dominant vegetation in these landscapes from perennial shrubs and summer-active native perennials grasses, most with C₄ metabolic pathways, to winter-active exotic annual and perennial grasses with C₃ metabolic pathways (Williams 1961, 1969; Foreman 1997). This shift in the dominant functional groups and therefore, growth patterns, can lead to landscape-scale change in water use due to a decrease in the effective length of the growing season (Clarke *et al.* 2002). Loss of perennial shrubs and summer-

active grasses also reduces habitat complexity and shifts the seasonal availability of refugia for faunal assemblages (Morton 1990).

The land-use practice that has had the most detrimental impact on native plant persistence in dryland areas of Australia is cultivation (Arnold *et al.* 1999; Dorrough *et al.* 2004; Wong 2004). Following cultivation, the establishment of native plants is likely to be influenced by the availability of propagules in the surrounding landscape, soil factors, competitive interactions between plant species and climate (Pulliam 2000). For example, heavy cracking soils do not provide favourable conditions for plant establishment and growth (Watt 1982; Abu-Irmaileh 1994), while cultivation can modify soil structure and nutrient availability in a way that favours fast-growing ruderals (Brown 1991; Kleijn & Verbeek 2000). Indeed, the competition exerted by exotic monocultures, such as cereal crops, and subsequent establishment of annual pastures may be a major factor limiting the re-establishment of native plants following cultivation (Weiner *et al.* 2001). The exotic annual grasses that typically dominate grazing areas following cultivation

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are likely to reduce soil moisture availability for germinating native seeds and plants, thus limiting shrub establishment (Eliason & Allen 1997). In low rainfall environments, successful native plant establishment is likely to be driven by episodic rainfall events that result in periods of above-average soil moisture (Lenz & Facelli 2003). The outcomes of these inter-specific interactions and therefore, colonizing ability, are likely to be a consequence of life-history traits (Leishman & Westoby 1992). Therefore, investigation of life-history traits may provide insights into the processes underlying establishment of native vegetation (Williamson & Fitter 1996; Radford & Cousens 2000). Life-history traits believed to be of importance in determining colonization success are those that influence germination responses, seedling establishment and survival (Radford & Cousens 2000).

The development of resilient natural and agricultural systems depends on the ability of ecosystems to reorganize and renew following disturbance (Pettersson *et al.* 1998). It has been argued that broad-scale restoration of native vegetation in agricultural landscapes is required to increase the resilience of these systems. This 'active restoration' aims to halt biodiversity losses, reduce impacts of dryland salinization, slow soil degradation (Hobbs & Harris 2001) and sustain livestock production (Millsom 2002). In low-rainfall landscapes of southern Australia, perennial shrub species have been argued to be central to the resilience of natural and agricultural landscapes. However, research into the natural regeneration of chenopod grasslands is currently lacking. Further understanding of these processes will aid in planning and implementing landscape-scale restoration.

In this study, we examine the patterns and processes of establishment of chenopod shrubs under cultivation in the Patho Plains region of northern Victoria. We contrast the life-history traits of two *Maireana* species, the common *Maireana decalvans* and the rare *Maireana rohrlachii*, to gain insights into the processes of shrub establishment in these highly used agricultural landscapes. In particular, we ask (i) is the establishment of a rare and a common shrub affected by competition in a post-cultivation environment? and (ii) is establishment success of the species influenced by the life-history traits of germination, survival and growth?

METHODS

Study area

The study was undertaken on the Patho Plains, a subregion of the Riverine Plains of northern Victoria, Australia (36°12'28"S, 144°25'24"E). The region con-

sists of fertile arable soils that have been subject to varying degrees of agricultural disturbance after European settlement (Diez & Foreman 1996). Summers are hot and dry with mean temperature of the hottest month (January) in excess of 30°C (Bureau of Meteorology 2005). Long-term mean annual precipitation is 395 mm with the highest and lowest monthly mean precipitation occurring in August (40 mm) and January (24 mm), respectively. During the study period (28 May 2003 to 28 December 2003), the region received 124% (308 mm) of mean precipitation with December receiving 223% (58 mm) of mean monthly precipitation <http://www.apsru.gov.au/apsru/Products/HowOften/datadrill.htm> (accessed June 2006). Thus, the vegetation can be assumed to be subject to a water deficit for most of the year as potential evapotranspiration exceeds rainfall in almost all months. The average number of frost days recorded at Rochester, 43 km west of the Patho Plains, is 10.2 year⁻¹ and they occur predominantly in the winter months of June to August (Bureau of Meteorology 2005).

Study species

The study focused on two species within the genus *Maireana* (Chenopodiaceae). This genus is endemic to Australia, with 21 of the 57 species occurring in Victoria (Walsh 1996). *Maireana* species are mainly herbaceous and shrubby perennials of unknown longevity. The distribution of the genus is generally limited to the lower rainfall regions and they can dominate semiarid and arid plant communities (Mitchell & Wilcox 1998).

To estimate the abundance and distribution of shrubby *Maireana* species in the Patho Plains area, a database of floristic quadrats collected between 1983 and 2003 by Victorian government departments, universities, other state agencies and private consultants was accessed using the Flora Information Service, Department of Sustainability and Environment (2003). All available data for quadrats greater than 1 m² and less than 100 m² for the Patho Plains subregion of the Victorian Riverine Plains bioregion were compiled. A total of 583 multispecies quadrats were examined and the number of quadrat occurrences of each *Maireana* shrub species noted. From this information, arbitrary categories of rare (present in less than 1% of quadrats) and common (present in more than 10% of quadrats) were assigned to *M. rohrlachii* and *M. decalvans*, respectively.

The two species selected for more detailed investigation in a field experiment were the rare *M. rohrlachii* and the common *M. decalvans*. Both species are medium-sized shrubs (to 1 m height), that have winged fruit and rely on wind dispersal. Their responses to management factors such as grazing, and

cultivation, as well as to droughts, have not been studied or reported in the literature.

Field sampling and experiments

To determine whether differences in the life history of *M. decalvans* and *M. rohrlachii* influence their potential for establishment after cultivation, seed germinability and seedling establishment were quantified in laboratory and field experiments.

Germinability

Fruit of *M. decalvans* and *M. rohrlachii* were collected from the Pine Grove district within the Patho Plains in January 2003 using a portable 12 V vacuum cleaner. Fruit was collected from at least two populations and from at least five individuals within each population, dried at 30°C for 5 days, and stored in the dark until use.

Germination trials were conducted in a Thermoline controlled-temperature growth cabinet using randomly selected fruit following the recommendations of the Flora Bank Guideline 8 (Mortlock 1999). The fruit was washed in a 1% sodium hypochlorite solution, rinsed and then soaked for 2 h in distilled water. Ten fruit were placed on two sheets of Whatman filter paper saturated with distilled water in 90-mm Petri dishes, which were sealed with Parafilm to reduce evaporation.

Germination was assessed under two temperature regimes: (i) 14 h light at 30°C and 10 h dark at 15°C to represent average summer conditions; and (ii) 12 h light at 20°C and 12 h dark at 10°C, to represent average autumn conditions. Each treatment was replicated 10 times.

Germination was recorded at 3, 7, 14 and 20 days after the start of the experiment. A preliminary germination test showed that 100% of viable fruits germinated within 14 days so no assessments were made after 20 days. Fruit was recorded as germinated once the radical had emerged through the fruit (McIntyre 1990; Morgan & Lunt 1994; Morgan 1998). The germination trials were conducted on fruit that had been stored for 3, 6 and 12 months to examine whether dormancies were induced or relaxed with time-since-collection.

Field establishment and competition

To examine the role of plant competition on the establishment of *M. decalvans* and *M. rohrlachii*, a field trial was established in a paddock in the Pine Grove district (144°25'24"E, 36°12'28"S) that had had a long

history of cultivation (C. Peat, pers. comm., 2003). A 60 m × 20 m area was selected and existing plant competition removed with an application of glyphosphate at 1.1 kg a.i. ha⁻¹.

A total of 60, 1.42 m × 8 m plots were established in a ten-by-six configuration. There was a 4-m buffer between the ends of plots and a 0.6-m pathway between plots. The 20 treatments consisted of the factorial combination of four seeding rates of *Triticum aestivum* (Wheat) and five *Maireana* treatments, which were a factorial combination of two *Maireana* species and two *Maireana* seeding rates plus a nil *Maireana* control. Within each of the three replicate blocks, the 20 treatments were randomly allocated to plots.

Per cent vegetation cover in each plot was estimated before the treatments were imposed. *Triticum aestivum* cv. Silver Star was sown on 28 May 2003 with an 1.42 m eight-row cone seeder at rates of (i) 0; (ii) 50; (iii) 100; and (iv) 200 seeds m⁻¹ of drill row; which corresponded to 0%, 25%, 50% and 100% of the commercial seeding rate of 90 kg ha⁻¹. Superphosphate was drilled at the same time into all plots at a rate of 15 kg ha⁻¹ of phosphorus.

Fruits of *M. decalvans* and *M. rohrlachii* were spread evenly by hand over each plot at one of two sowing rates, low (30 fruits m⁻²) and high (60 fruits m⁻²); each plot was lightly raked to improve soil-fruit contact. The site was then fenced to exclude stock grazing.

Maireana plant density, height and survival were recorded from a 1 m × 6 m internal area of each plot to eliminate edge effects and ensure uniformity of competition. All individuals that had germinated at the first sampling (100 days after sowing) were marked and re-sampled on days 170 and 214 after sowing to determine their survival. Wheat density of each plot was assessed at day 170 after sowing by counting the number of tillers along three randomly chosen 0.5 m lengths of drill row in each plot and expressed as number m⁻¹ drill row.

Data analyses

Germinability

The effects of the light/temperature regimes, fruit storage time and species on total germination were examined using an analysis of variance with a normal distribution. Lag times and germination rates to 50% (t_{50}) and 90% (t_{90}) of final germination were calculated. Lag time was defined as the number of days from the start of experiment to when the first fruit had germinated. The germination rates t_{50} and t_{90} were defined as the time in days from the beginning of the experiment for 50% and 90% of final germination to be achieved (Morgan 1998). Lag times and

Table 1. Analysis of variance table of germinability of *Maireana* seed as a function of species, temperature regime and storage period

Source	d.f.	SS	F-value	P-value
Species (Spp)	1	162.29	62.59	<0.001
Storage period (SP)	2	348.26	67.16	<0.001
Temperature regime (TR)	1	40.71	15.70	<0.001
Spp × SP	2	48.57	9.37	<0.001
Spp × TR	1	3.00	1.16	0.285
SP × TR	2	59.66	11.50	<0.001
Spp × SP × TR	2	29.24	5.64	<0.001
Residual	100	259.28		

germination rates were plotted for each treatment combination for all three storage periods.

Field establishment and competition

Initial assessments indicated that wheat establishment rates were not uniform across the wheat seeding treatments. As a result, generalized linear models were used to assess the establishment, height and survival of *Maireana* species with the *a priori* explanatory variables of wheat density and *Maireana* species. Initial analysis of the data indicated that there was no density effect of seeding rate on the establishment or survival of seedlings per 100 seeds. For all further analysis, the establishment success was standardized and analysed as seedlings per 100 seeds. Establishment success (seedlings/100 seeds) was modelled assuming a normal distribution with interactions between the variables wheat tiller density at day 170, *Maireana* species, and initial vegetation cover as explanatory variables. Plant height was modelled using generalized linear models assuming a normal distribution, and wheat tiller density at day 170, sampling date, and *Maireana* species were used as explanatory variables. Survival was examined using generalized linear models for a binomial distribution with logit link transformation. Interactions and the additive effects of wheat tiller density at day 170, sampling date, and *Maireana* species were tested.

RESULTS

Germinability

Germinability varied significantly with species, fruit storage time, and between the light/temperature treatments (Table 1). The germination of both species significantly declined with storage time, with a more rapid decline apparent for *M. rohrlachii* (Fig. 1). The

lag times for both species appear to be similar under average summer conditions, with a trend towards a more rapid germination by *M. decalvans* under average autumn conditions (Fig. 2).

Field establishment and competition

Initial establishment was a function of wheat tiller density interacting with *Maireana* species (Table 2), with the establishment of *M. decalvans* negatively correlated with wheat density, while that of *M. rohrlachii* was positively correlated (Fig. 3). Initial vegetation cover also proved to be an important factor affecting establishment (Table 2), as establishment rates were inversely correlated with levels of vegetation cover in both species. Wheat density had negative effects on seedling height. This was more pronounced for *M. decalvans* (Table 3, Fig. 4), particularly at the second sampling date, as indicated by the significant interaction between wheat density and sample date in Table 3. Figure 5 shows that the height of *M. decalvans* seedlings was greater than that of *M. rohrlachii*, with surviving *M. decalvans* seedlings taller by the final sampling date. The effect of competition from wheat on seedling height was significant across species (Table 3) although this appeared to be driven by the increased effect seen in the second sampling period (Fig. 6). There was a weak trend towards higher survival of *M. decalvans* seedlings (mean proportion across all treatments: *M. decalvans* = 0.815 ± 0.047 , *M. rohrlachii* = 0.693 ± 0.046) and a weak negative trend of declining survival in both species with increasing wheat density (Table 4).

DISCUSSION

The ability of perennial native shrubs to establish following disturbance by cultivation may provide an indication of the resilience of low rainfall chenopod grassland systems of southern Australia. The results of the present study suggest that although landscape abundance may vary between species, this may only be weakly related to establishment characteristics such as germination rates, early seedling survival and response to competition. Indeed, we suggest that the impacts of historical processes (e.g. grazing and drought interactions), particularly in refuge sites, may be the most important factors for understanding the current landscape abundance of plant species. This has significant implications for how the productive capacity and resilience of these systems can be managed in the long term.

The low abundance of several *Maireana* species in the Patho Plains allows for a comparison between the establishment characteristics of rare and common

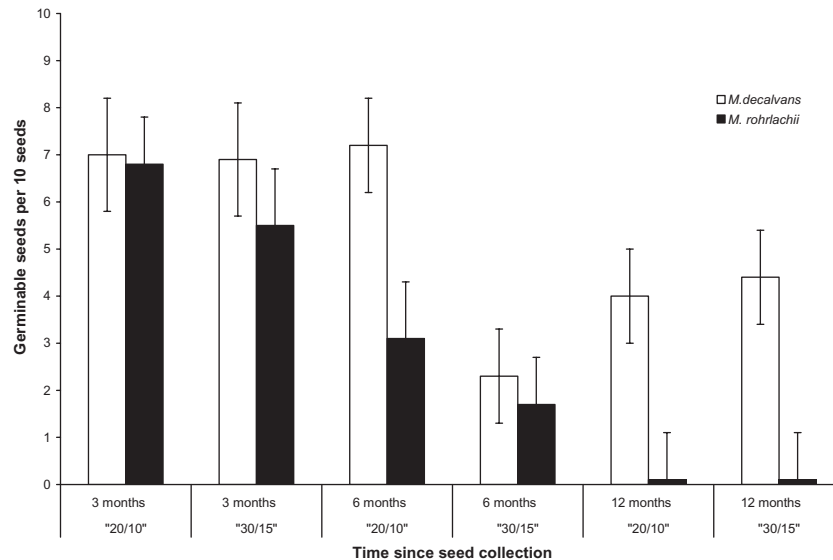


Fig. 1. Mean number of germinable seeds (± 2 SE) (per 10 seeds) of *M. decalvans* and *M. rohrlachii* after three storage periods (months), germinated at two temperature regimes (Autumn – 12 h light at 20°C and 12 h darks at 10°C: '20/10', summer – 14 h light at 30°C and 10 h dark at 15°C: '30/15').

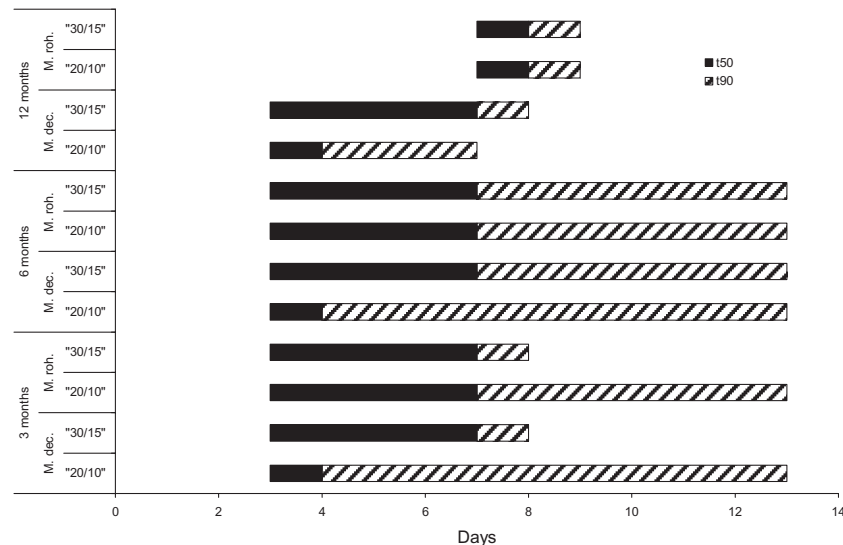


Fig. 2. Germination time (days) t_{50} – solid bar (0–50% of final germination) and t_{90} – hatched bar (50–90% of final germination) at three storage periods (3, 6 and 12 months), germinated at two temperature regimes '20/10': '30/15', for *M. decalvans* and *M. rohrlachii*.

species within this region. Factors affecting establishment are likely to include availability of viable propagules, germination success and competitive abilities of seedlings (Leishman & Westoby 1992; Perrins *et al.* 1993; Tilman 1999). The availability of viable propagules, in turn, is dependant on soil seed banks, germination rates and seed production (Leishman & Westoby 1992; Radford & Cousens 2000).

Comparison of the germination traits of the common *M. decalvans* and the rarer *M. rohrlachii*

showed little variation between species. However, the germinability of the rare *M. rohrlachii* clearly declined over time with few viable seed remaining after 12 months of storage. The likelihood of this species forming a persistent soil seed bank (Leishman & Westoby 1992) must therefore be assumed to be lower than that of *M. decalvans*. The ability to form a seed bank, and to re-establish from that seed bank, is an important factor in regularly disturbed environments (McIntyre & Martin 2001). Differences between the

Table 2. Summary of generalized linear model of *Maireana* seedling establishment rate (seedlings/100 seeds) as a function of wheat density (tillers m⁻¹ drill row), *Maireana* species and initial vegetation cover

Source	d.f.	SS	F-value	P-value
Wheat density (WD)	1	0.07	0.02	0.902
Species (Spp)	1	9.18	2.04	0.160
WD × Spp	1	51.86	11.54	0.001
Initial vegetation cover	1	61.19	13.62	<0.001
Residual	43	193.27		

Table 3. Summary of generalized linear model of *Maireana* seedling height (mm, log₁₀(x + 1) transformed) as a function of *Maireana* species, wheat density (tillers m⁻¹ drill row) and sampling date

Source	d.f.	SS	F-value	P-value
Wheat density (WD)	1	3.98	63.22	<0.001
Species (Spp)	1	0.23	3.67	0.056
Sampling date (SD)	2	30.61	242.78	<0.001
WD × Spp	1	0.55	8.70	0.003
Spp × SD	2	0.59	4.72	0.009
WD × SD	2	0.62	4.94	0.007
Residual	532	33.50		

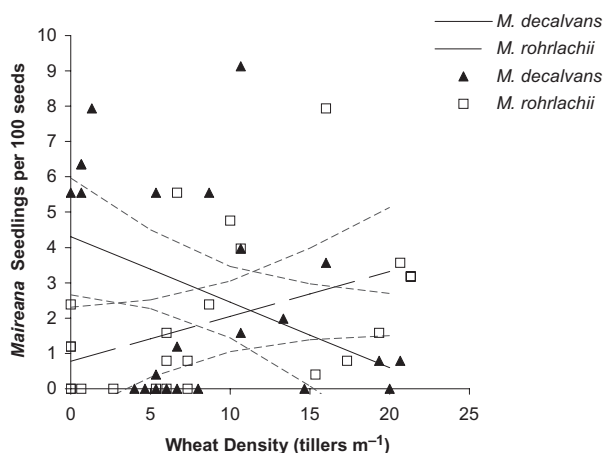


Fig. 3. Predicted mean (± 2 SE) establishment success (seedlings/100 seeds) of *M. decalvans* and *M. rohrlachii* under a range wheat tiller densities.

two species were also observed in their germination lag times as well as in their t_{50} and t_{90} times. The tendency of *M. decalvans* to germinate quickly and *en masse*, as opposed to the slower and more gradual response of *M. rohrlachii*, could provide some basis for the rarity of the latter species. The lag and t_{50} rates of both species are, however, rapid when compared with other species from similar grassy habitats (Morgan 1998) and the difference between the two species had little effect on their establishment in the field. In summary, the dif-

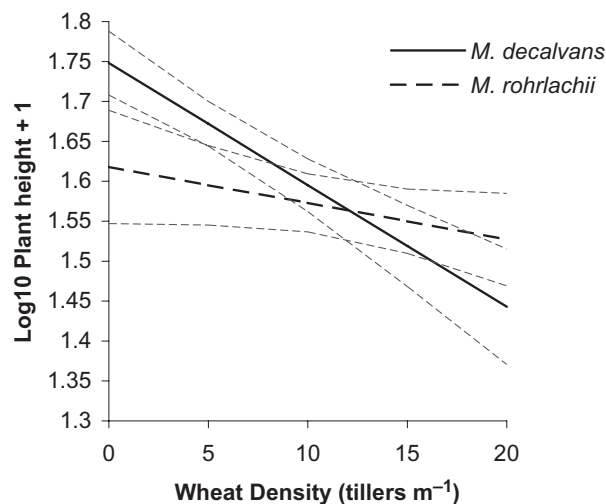


Fig. 4. Predicted mean (± 2 SE) height (mm, log₁₀(x + 1) transformed) of *M. decalvans* and *M. rohrlachii* under a range of wheat tiller densities. Predicted values were calculated while holding all other terms in the model constant.

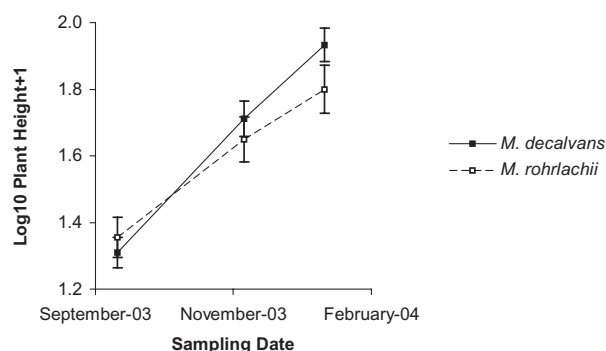


Fig. 5. Predicted mean (± 2 SE) height (mm, log₁₀(x + 1) transformed) of *M. decalvans* and *M. rohrlachii* at three sampling dates.

ferences in germination attributes are apparently not sufficient to result in variation in field establishment rates and alone do not provide a convincing explanation of the dramatic differences in landscape abundance and distribution of these two species.

Following the investigation of germination success, the response of the two *Maireana* species to varying levels of competition from wheat suggested that *M. decalvans* may achieve slightly greater densities in areas with low levels of competition. This may indicate that *M. decalvans* is a species that is better adapted to regular disturbance (Lavorel *et al.* 1997), although compared with many invasive and disturbance-tolerant species (Lavorel *et al.* 1997), this response was weak. Even so, at the greatest level of competition from wheat, *M. decalvans* still established and survived. By contrast, the establishment rate of *M. rohrlachii* was similar across a range of competition levels, indicating

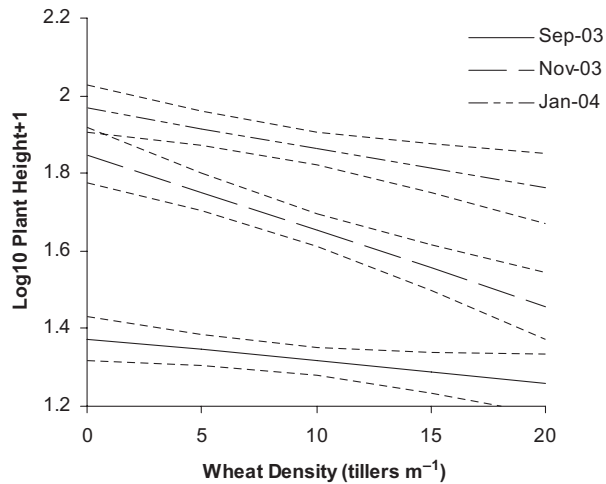


Fig. 6. Predicted mean (± 2 SE) effects of wheat tiller density on plant height at three sampling dates, averaged over two *Maireana* species.

Table 4. Summary of generalized linear model of survival of *Maireana* seedlings as a function of *Maireana* species, wheat density (tillers m^{-1} drill row) and sampling date

Source	d.f.	SS	F-value	P-value
Wheat density	1	0.22	3.31	0.074
Species	1	0.24	3.48	0.067
Date	1	0.45	6.62	0.013
Residual	62	4.36		

that it may be less influenced by competition than by other factors. The differences in species establishment under varying levels of competition was not enough to explain the marked imbalance in their frequency in the region.

In the field experiment, both species were capable of establishing when sown with wheat, although the growth rate was significantly higher for the more common *M. decalvans*. High seedling growth rates may infer a competitive advantage in sites dominated by rapidly growing exotic annuals (Lavorel *et al.* 1997), although rapid and tall growth may lead to increased selectivity by domestic stock in this region (Foreman 1996).

CONCLUSION

The ability of species to persist and establish under intensive land use will determine the longer-term composition of landscapes. The diversity and abundance of *Maireana* species in the Patho Plains is likely to have been influenced by past land-use practices that may have altered the ability of individuals and populations to persist and recruit.

Species that readily invade disturbed sites may differ in life-history traits from non-invasive species (Radford & Cousens 2000). Attributes considered to give a species an advantage include plant height and shade tolerance (Perrins *et al.* 1993), performance as pasture species (Lonsdale 1994) and habitat-specific adaptations (Radford & Cousens 2000). It has also been suggested that the ability to be invasive is often inferred not by a single difference, but by many minor variations in plant life histories (Radford & Cousens 2000). The ability to untangle the impacts of past and current land-use practices from natural environmental fluctuations on the abundance of a species in the landscape is often extremely difficult (Drake 1990). From the results of the current study, it would be hard to explain the reasons for the low abundance of *M. rohrlichii* in this agricultural landscape. While the two species showed significant differences in their germination rates over time, this appeared to have little impact on their establishment under field conditions. The major difference evident between the two species is their abundance in the regional species pool. The argument that a species fails to establish because propagules are not present or abundant is circular in logic, yet often the basis used in the interpretation of data from studies into colonization and invasion (Radford & Cousens 2000; Foster & Tilman 2003; Foster *et al.* 2004). Given the assumption of the relatively uniform distribution of *M. rohrlichii* across the study area before European settlement, the reasons for its rarity in the agricultural landscape remain to be unravelled. Historical and/or current grazing management practices, particularly during droughts, may be critical (Westoby *et al.* 1989; Seabloom & Richards 2003). Anecdotal evidence suggests that minor modifications to grazing management practices, such as including a rest from grazing, particularly during recruitment episodes, may be sufficient to allow this species to persist in these areas (E. O'Brien, unpubl. data 2003), and research in this area is required.

The results of this study suggest that some chenopod shrubs are able to successfully establish in cultivated pasture and hence, there is potential to maintain these perennial woody species in the landscape in the long term. This, however, may be dependant on the intensity and frequency of cultivation events. However, shrub species remain rare in the landscape and are observed only within sites that have been uncultivated for a long time. Importantly, it may be hypothesized that the persistence of some components of the shrub assemblage may be driven by historical factors rather than life-history traits related to establishment ability. As a result, it can be hypothesized that targeted introduction of species (i.e. shelter belts and habitat islands within paddocks), rather than broad-scale active replanting, in combination with subtle adjustments in

current land management practices, may improve the long-term persistence of these species.

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