

REVIEW ARTICLE

Improving saltland revegetation through understanding the "recruitment niche": potential lessons for ecological restoration in extreme environments

Edward G. Barrett-Lennard^{1,2,3}, Hayley C. Norman^{4,2}, Kingsley Dixon^{2,5}

Germination and emergence are often the most precarious stage in a plant's lifecycle: plants are particularly vulnerable to environmental stress at this time. Despite these constraints, plants colonize much of the planet including extreme environments. We argue that for many species, establishment in extreme situations is not because seed is adapted to germinate in extreme environments but because it falls into, and is spatially and temporally nurtured within, more benign "recruitment niches." This principle has importance for revegetation in extreme environments such as the world's drylands. Using examples from ground-breaking experiments conducted by CV Malcolm and colleagues between 1976 and 1982 on saltland revegetation with halophytes, we show that recruitment niches can be constructed based on an understanding of the key requirements that seeds need in their immediate environment to establish. As part of their studies, Malcolm's team developed a "niche seeder" capable of distributing and precisely placing fruits of Atriplex species in an elevated "V"-shaped mound (to decrease waterlogging), covering the fruits with vermiculite (to decrease capillarity and therefore salinity at the soil surface), and spraying the placements with black paint (to increase soil temperatures). Subsequent studies in arid environments showed that the establishment of woody plants was also improved using stones on the soil surface to develop appropriate recruitment niches. Malcolm's identification of the "recruitment niche" is an important principle of broader relevance to the revegetation of degraded landscapes in extreme environments. In addition, the development of the niche seeder is an important case study in ecological restoration.

Key words: direct seeding, niche seeder, saltbush, salinity, salt tolerance, waterlogging

Implications for Practice

- The environment around a typical germinating seed is a few millimeters thick. Plant establishment may therefore be increased in extreme environments by creating "recruitment niches" where conditions are ameliorated in soil immediately adjacent to the seed. Expensive wholesale soil remediation may therefore not be necessary.
- On saltland, establishment of halophytes was improved by placing seed into locations where fine-scale interventions decreased soil salinity and waterlogging, and increased soil temperature.
- In an arid environment, establishment was improved by the presence of rocks on the soil surface that caused seed to fall into cracks where moisture was retained.
- These examples show that if limitations to recruitment in extreme environments are known then better recruitment niches can be constructed.

Introduction

Mining can severely impair natural ecosystems in arid environments. With the conclusion of mining, rehabilitation of affected landscapes needs to occur so that soils are stabilized, they support long-term plant growth and there is a return of appropriate ecosystem functionality. Although this is the ideal, there are major knowledge gaps between science, technology, and rehabilitation practice for drylands, and on mine sites in particular (reviewed by Kildisheva et al. in press).

Seed-based restoration is most widely used in arid environments. However, the effectiveness of establishment is often unreliable, and highly wasteful of limited seed reserves, which are generally collected from wild populations (Merritt & Dixon

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¹Department of Agriculture and Food, Western Australia, 3 Baron-Hay Court, South Perth, WA 6151, Australia

²School of Plant Biology, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia

³Address correspondence to E. G. Barrett-Lennard,

email edward.barrett-lennard@uwa.edu.au ⁴Agriculture Flagship, CSIRO Centre for Environment and Life Sciences, 147 Underwood Ave, Floreat, WA 6014, Australia

⁵Department of Environment and Agriculture, Curtin University, Kent Street, Bentley, WA 6102, Australia

2011). We argue that the economy of seed use may be dramatically improved by constructing improved "recruitment niches" for seeds.

This article focuses on a case study that may have broader relevance to the restoration of arid environments—specifically the development of the principle of "niche seeding" pioneered by CV Malcolm and colleagues for the revegetation of salinized land in Western Australia and their development of a "niche seeder," in the period 1976–1982. We then consider the relevance of this principle to the revegetation of other degraded land (mine dumps) affected by exceptional aridity.

Beginning in the 1970s, Malcolm was interested in developing inexpensive reliable methods for establishing halophytic shrubs on saltland as sources of forage for sheep in the Western Australian wheatbelt. This region was experiencing "dryland salinity" because of a rise in the water table caused by a hydrological change following the industrial-scale clearing of the native eucalypt dominated forest and its replacement by annual crops and pastures (Pannell & Ewing 2006). The wheatbelt has an annual rainfall of 300-400 mm, falling mainly in winter and spring (May-October). The original forest that covered the region before European settlement had adapted to use most of this incident rain and the water table remained at depth; however, replacing this with annual crops and pastures allowed 6-12% of rain to recharge aquifers causing a rise in the water table and the mobilization of salt stored deep in the soil profile (Peck & Williamson 1987). The risk of development of a shallow water table was further affected by variation in the underlying hydrogeology of the landscape: George et al. (1997) identified 10 hazards including the presence of dolerite (clay) dykes, bedrock highs and sandplain seeps that could enhance the risks of salinity. Depth to water table became recognized as a strong indicator of the growth potential of the landscape: wheat crops would grow if the water table was deeper than approximately 2 m, but if the water table rose to 1.1-1.6 m then sites became dominated by sea barleygrass (Hordeum marinum), and sites became bare if the water table became less than 1 m deep (Nulsen 1981). At that time, more than 260,000 ha of previously productive agricultural land were severely salinized in the southwest of Western Australia (Henschke 1980).

Based on studies of the long-term survival of forage species on saltland and on sheep acceptance (Malcolm & Pol 1986; Malcolm & Swaan 1989), the target species of greatest interest for saltland revegetation was identified as Atriplex amnicola (river saltbush; syn. A. rhagodiodes), but establishment problems with this species compelled the team to also focus on A. undulata (wavy leaf saltbush), A. lentiformis (quailbrush), and Maireana brevifolia (small leaf bluebush) (Malcolm & Swaan 1989). These four species are all chenopods and have been widely used in saltland revegetation in Australia or elsewhere (Le Houérou 1992; Watson & O'Leary 1993; Barrett-Lennard et al. 2003): A. amnicola and M. brevifolia are native to Australia, whereas A. undulata and A. lentiformis are from Argentina and the United States, respectively (Malcolm & Swaan 1989). Although all these species were salt tolerant, they could not be reliably established on saltland by direct seeding.

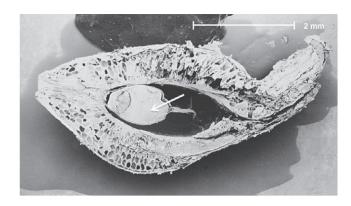


Figure 1. Cross-section of *Atriplex amnicola* fruit (scanning electron micrograph image). The seed (arrow) is enclosed between two large bracts. There is also a substantial air filled pore enclosed by the bracts and surrounding the seed.

Defining the "Recruitment Niche"

The propagule of *Atriplex* species is a fruit consisting of a single seed encased by two bracteoles. As the seed develops, the bracteoles ripen and harden, and this becomes the unit of seed dispersal (Wilson 1984; e.g. Fig. 1). *Atriplex* species typically have small seeds, limited carbohydrate stores, and therefore cannot be buried deeply as part of the planting process. Furthermore, some species (e.g. *Atriplex amnicola*) require light for germination, so fruit burial decreases establishment (for experimental data see Appendix S1, Supporting Information).

Reviewing plant establishment on saltland, Malcolm (1972) formed the view that the establishment of halophytic forages on saltland would be affected by environmental factors (e.g. salinity and soil moisture, waterlogging, and low temperatures) and by plant factors (such as seed quality); these views have been substantially supported by more recent research (see Appendix S1). In overview, the critical points are as follows. First, seed germination and plant establishment are both strongly affected by the salinity of the soil solution. In Mediterranean environments, this is highest at the start winter and toward the end of spring. This delays germination of halophytic species and increases mortality. Second, for thick-bracted fruits like those of A. amnicola, waterlogging can cause saturation of the air-filled pore between the bracts and surrounding the seed; this causes hypoxia (oxygen deficiency), which decreases seed germination. Thirdly, the low temperatures that occur in winter (often just a few degrees above 0°C) substantially decrease rates of germination. Fourthly, some Atriplex species (like A. amnicola) are dioecious, so fertilization will only occur if male and female plants are in close proximity; many fruits therefore often have a large proportion without seed.

Developing the Niche Seeding Principle

In 1976, Malcolm's team conducted a spacing trial with five *Atriplex* species: this showed that for large-framed fodder shrubs like *Atriplex amnicola*, the production of grazable biomass per hectare was largely independent of planting density.

Closely spaced plants (10,000 plants per hectare) produced small amounts of grazable biomass, whereas widely spaced plants (1,111 plants per hectare) produced larger amounts of biomass; however at all planting densities there was a similar net production of biomass per hectare (Malcolm et al. 1988). This experiment showed Malcolm that revegetation success did not require the establishment of dense plantations on saltland. Rather, establishment was only needed at widely spaced intervals in localized parts of the larger landscape, and perhaps these "recruitment niches" could be created to increase revegetation success. This led to a simple, yet fundamental shift in planting approach. A seeder was needed to create recruitment niches for salt tolerant plants at widely spaced intervals.

The prototype of the "niche seeder" was developed by Malcolm and Allen in 1976 (Malcolm & Allen 1981), and two commercial companies developed seeders based on this prototype. The major features of the seeder were: (1) a mole-board plough (or later two opposed discs) at the front of the machine, which made an elevated mound of soil approximately 20 cm high, (2) a 1 m diameter wheel in the middle of the machine which pushed a shallow V-shaped furrow into this mound, and (3) a mechanism for depositing "placements" of seed (and later vermiculite mulch and sprays of black paint) at 1–3 m intervals into the pressed V-shaped furrow.

We can trace the development of Malcolm's ideas for the niche seeding of saltland through a sequence of experiments conducted between 1976 and 1982 and subsequently published in four articles (Malcolm et al. 1980, 1982, 2003; Malcolm & Swaan 1985). Initially Malcolm's main focus was on proving the benefit to establishment of depositing saltbush fruits into the V-shaped impression in an elevated (approximately 20 cm) bank compared with applying seed directly to the soil surface. The rationale for this approach was that the V-shaped impression in the top of the bank would encourage the leaching of salt out of the seedbed and the elevation of the seed above the surrounding landscape would decrease the risk of waterlogging. The results of this trial (assessed 5-6 months after establishment) showed that there was no establishment of A. amnicola from any fruits spread directly onto cultivated ground. By contrast, placement of seed in the elevated mound gave 4.4% establishment of germinable seed on a waterlogged site sown after rain, and 5.0% establishment of germinable seed on a non-waterlogged site sown before rain. Elevation of the seedbed clearly improved establishment.

In 1979, the team adopted the raised bed of the niche seeder and conducted a new round of experiments focusing on the use of amendments to overcome ecological impediments to germination. These included applications of black paint to the soil surface to raise seedbed temperatures and chaff as a soil mulch to control salinity in the seedbed (Malcolm et al. 1982). 263 days after sowing the use of blackpaint had been successful, doubling establishment (to 11.8% of germinable seed) compared to the control on the raised mound alone (5.8% of germinable seed). On a typical sunny mid-winter day where black paint had been sprayed onto soil, the temperature rose to approximately 30°C at midday, about 5°C higher than for any other treatment measured. However, the use of chaff (as a mulch) failed, with

only 0.4% of germinable seed established. This failure may have been caused by increased competition for water in the seedbed of chaff-supplied seed placements; the authors report that the chaff contained some wheat seeds, which germinated.

In 1981, Malcolm's team tested powdered vermiculite (an inorganic mulch, used instead of chaff) in combination with black paint (Malcolm & Swaan 1985). After 33 days, 23.0% of germinable seed had established with a combination of vermiculite and black paint application on the raised bed, 13.6% of germinable seed had established with vermiculite mulch alone on the raised bed and 0.6% of germinable seed had established in the nil controls on the raised bed. Unfortunately, the site chosen for this trial was extremely saline, with an average EC value at 0-1 cm of approximately 39 dS/m during the germination phase. There was therefore substantial death of these early germinants as the season progressed, and after a year, the best treatment (vermiculite plus black paint) had a final establishment of 4.5% (Malcolm & Swaan 1985). Nevertheless Malcolm and Swaan's hypothesis that there would be synergistic benefits from the application of an inorganic mulch and black paint proved correct.

In the final year of this series of experiments, Malcolm noted that in general it was rare for new seedlings to volunteer from within established stands of A. amnicola. However, this did occur occasionally and he hypothesized that these "volunteering types" had improved genetic enhancements leading to establishment in hostile environments, and that these genotypes would also be more successful when seeded using the niche seeder. Again, the team integrated the other proven aspects of the technology—the elevated seedbed, vermiculite mulch, and black paint—with a comparison of a volunteering ecotype (accession 949—later called "Meeberrie") and a non-volunteering ecotype (accession 573). The results of this trial were the most successful that the team had. On a saline site near Cunderdin in Western Australia, the combination of elevated seedbed, vermiculite mulch, black paint, and volunteering ecotype gave an establishment of 51.5% of germinable seed after 64 days, and a final establishment of 28.4% of germinable seed after a year. By contrast, this combination of treatments with the non-volunteering ecotype had an establishment success of only 4.6% of germinable seed after 64 days, and 2.0% of germinable seed after a year.

In summary (Table 1), we can see Malcolm's team as being engaged in a process of adaptive management and continuous improvement over the period 1976–1982. In 1976, elevation of the seedbed gave a best establishment result of approximately 5% of germinable seed, but the additional warmth created by the use of black paint (in 1979) and vermiculite (in 1981) gave best establishment results of 12 and 35% of germinable seed. Finally, combining these technologies with the use of a "volunteering ecotype" gave an establishment result of greater than 50% of germinable seed (Table 1).

Commercial Adoption of the Research

What has been the long-term legacy of this research? Following the innovations of the Malcolm program, two companies

Table 1. Summary of the key hypotheses and best results from the Malcolm team's efforts to improve direct seeding on saltland (1976–1982).

Year	Hypothesis	Best Result with Atriplex amnicola	Reference
1976	Elevating seedbed (i.e. creating "niche") would increase establishment compared to cultivated ground	Approximately 5% germinable seed established after 6 months	Malcolm et al. (1980)
1979	Adding black paint to "niche" would improve establishment	Approximately 17% of germinable seed established after 63 days; 12% after 1 year	Malcolm et al. (1982)
1981	Adding vermiculite mulch and black paint to "niche" would improve establishment	Approximately 35% of germinable seed established after 64 days; 4% after 1 year	Malcolm and Swaan (1985)
1982	Adding vermiculite mulch, black paint, and a volunteering ecotype to "niche" would improve establishment	Approximately 52% of germinable seed established after 64 days; 28% after 1 year	Malcolm et al. (2003)

(Chamberlain-John Deere and Kimberley Seeds Pty Ltd) manufactured niche seeders and niche seeding of saltland occurred on approximately 5,000 hectares of land in Western Australia, mostly in the late 1980s. However, this momentum did not persist: there were three reasons for this. First, the technology was too complex for routine use. Commercial operators readily adopted the idea of the raised niche and the use of a vermiculite mulch, however, black paint sprays were not commercially adopted as the spraying mechanism was difficult to manage. Second, the niche seeding technology exacerbated establishment of competing weeds. In an elegant piece of research. Vlahos (1997) tested whether the use of herbicides could be incorporated into the niche seeding process. He tested 15 herbicides and found that Carbetamex® controlled the main grass weeds while having little adverse effect on the establishment of Atriplex amnicola. However, the use of this herbicide was prohibitively expensive for use as a blanket application across whole sites, and it was withdrawn from commercial sale shortly afterwards. Third, establishment from seed was superseded by the use of nursery-raised seedlings. By the mid 1980s commercial nurseries had begun to produce lower-cost (approximately \$AUST 0.30 each) saltbush seedlings and these were planted using tractor-drawn tree-planting machinery. In seven well-replicated comparisons of the two establishment technologies conducted across the wheatbelt of Western Australia using A. amnicola, niche seeding had an average successful establishment of 31% of seed placements with a coefficient of variation (CV) of 105%. By contrast, use of nursery-raised seedlings had a success of establishment of 82% of seedlings planted, with a CV of 39% (Barrett-Lennard et al. 1991). Niche seeding was unquestionably cheaper (costing approximately \$AUST 150/ha) than planting seedlings (costing > \$AUST 500/ha), but there was a trade-off between price and reliability of establishment (Barrett-Lennard et al. 2003). So despite Malcolm's efforts, the direct seeding of saltland did not persist as a commercial reality.

Relevance to Arid Restoration Programs

Malcolm and colleagues did directly trial their niche seeder on mine dumps in a semiarid (240 mm annual rainfall) environment with modest success (Fletcher et al. 1989). Six months after sowing with the niche seeder and a range of *Atriplex* species, there was an establishment of approximately 20% of germinable seed on a mine dump site with topsoil applied and an establishment of approximately 15% of germinable seed sown on a "bare" mine dump site without topsoil. The results were not sufficiently encouraging to justify the continued use of the seeder in such environments. However, these results should not be seen as evidence contrary to the general theme of the importance of constructing "recruitment niches" in arid environments.

We conclude this review with an example illustrating a way forward for restoration in arid environments. In such environments, seeds are often distributed naturally across the soil surface and in rocky environments, recruitment often occurs when seed falls into the cracks between rocks (e.g. Peters et al. 2008). These rocks have the effects of "mulching" the soil surface, focusing surface water toward cracks by acting as micro-water harvesting structures. They also decrease wind speeds in these cracks and therefore help create moist micro-environments. We may therefore find that better plant establishment in rockier than in bare sites. This principle can be seen in a dataset collected at Mount Magnet in Western Australia by Jennings et al. (1993). Here researchers assembled 26 mine dump spoils with a range of soil properties; these were spread over an area of 20 m² and seed of a range of genotypes (Atriplex bunburyana, A. vesicaria, Maireana pyramidata, Acacia linophylla, A. acuminata, Eucalyptus torquata, and E. striaticalyx) was spread over the soil surface of these mine spoils. Highest establishment occurred in soils of low salinity (EC_{1:5} values less than 0.5 dS/m) with pH values between 6.5 and 8.4 (Fig. 2A & 2B) with establishment maximized where there was a soil cover of 50-90% with fragments of 20-60 mm in diameter (Fig. 2C & 2D).

This experiment was conducted over a period of 10 months in 1991 in a location of climatic extremes. Examination of the meteorological records for the area showed that there were more than 30 days with maximum temperatures above 40°C, 2 days with temperatures less than 0°C, and only 8 days with rainfall above 5 mm (Bureau of Meteorology 2015). Despite this, establishment was possible on soils with the combination of acceptable pH, low salinity, and the combination of frequent rock fragments above a certain size. The researchers conducting

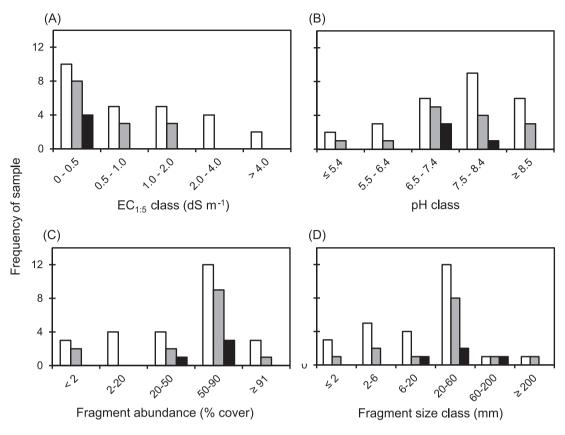


Figure 2. Effects of soil properties on numbers of plants established between sowing (9 May 1990) and final scoring (10 months later) on 26 mine dump spoils at Mt Magnet in Western Australia. (A) $EC_{1:5}$ class, (B) pH class, (C) fragment abundance class, and (D) fragment size class. Seed (*Atriplex bunburyana*, *A. vesicaria*, *Maireana pyramidata*, *Acacia linophylla*, *A. acuminata*, *Eucalyptus torquata*, and *E. striaticalyx*) was spread over an area of 20 m². Columns are: white (1–10 established seedlings), grey (11–40 established seedlings), or black (\geq 41 established seedlings).

the work were not surprised by the pH and salinity criteria for success, but the importance of abundant rock fragments was unexpected. It highlighted an important principle: plant establishment is possible in harsh environments, but it requires the presence of micro-sites (recruitment niches) where seeds are protected from sun and drying winds. These data also highlight a broader principle: recruitment niches can be created.

Challenges and Opportunities

Today, Malcolm and his team are regarded as the founders of saline agriculture in Australia. The growth of chenopod shrubs on saltland is now regarded as a core revegetation strategy that moves these previously degraded sites toward ecological restoration, that is a level of sustainable production with options for the restoration of more complex plant communities. Previously eroding soils become stabilized, increased use of groundwater by the halophytic shrubs lowers the water table decreasing surface soil salinity and waterlogging, and the management of the land for fodder production increases the growth of both the perennial fodder shrubs and annual under-storey species. In addition, the revegetated areas are used as refuges by native fauna. Furthermore, these ecological

objectives are achieved by farmers managing their saltland for commercial gain.

Malcolm's legacy has continued in more recent Australian work developing saltland pastures. One key paper catalyzing development was an economic analysis by O'Connell et al. (2006), which showed that the economic gains to farmers could be doubled if the nutritive value of the forage available to grazing sheep could be increased by 10%. This led to a new focus on increasing nutritive value in saltland pastures by incorporating: (1) *Atriplex nummularia* subsp. *nummularia* as the key fodder shrub in the system (this had higher digestible organic matter in the dry matter than *Atriplex amnicola*—reviewed by Norman et al. 2013), and (2) high nutritive value annuals into the under-storey (Norman et al. 2010).

The exact areas of land affected by secondary salinity (i.e. salinity induced by human activity) world-wide and in Australia are not completely clear. One figure for secondary salinity at the world-wide scale is approximately 80 Mha (Ghassemi et al. 1995) of which approximately 40% is on non-irrigated land (Dregne et al. 1991). For Australia, it has been estimated that approximately 17 Mha could be at risk of salinity by 2050 (National Land and Water Resources Audit 2001), but these estimates are likely to be revised downwards as decreased rainfall associated with climate change impacts on depth to

water table (George et al. 2008). Despite this uncertainty, we can say that saline incursions into non-salt adapted ecosystems are a major contributor to ecological decline and the loss of productive capability globally and in Australia.

Here, we have provided an overview of a focused research program based on the principles of "adaptive management" and how remaining engaged with outcomes of trials and integrating these into each successive phase of outcome-driven research was able to provide solutions in combating land degradation. The approaches showed that it was possible to reinstate an economic capability (a return to forage production) on land that would otherwise have been abandoned. Importantly once a level of pioneer plant cover had been established then further species enrichment became possible where a wider, more diverse and therefore ecologically resilient assemblage of species could be reinstated. However, important issues of scale still need to be addressed such as developing more effective precision seeding approaches, commercially capable seed harvesting and de-bracting processes, automated seed quality testing, seed pelleting, and regularizing seed size for automated seeding.

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Supporting Information

The following information may be found in the online version of this article:

Appendix S1. Evidence in support of statements made in section "Defining the 'recruitment niche."

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