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Recovery of soil and vegetation in semi-arid Australian old fields

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ABSTRACT

Due to the harsh environmental conditions of arid and semi-arid regions, recovery of native plant communities after abandonment from cultivation is hypothesised to be slow and unlikely to return to pre-disturbance condition. We examined vegetation and soil parameters along a ∼100 year chronosequence of agricultural field abandonment in semi-arid grasslands in south-eastern Australia to quantify resilience. Native species richness, abundance and composition converged towards those of uncultivated grasslands, and there was a replacement of initial exotic dominance by native perennial grasses. Thus, the vegetation did not enter an alternative stable state and the community variables studied showed some resilience. However, many native species failed to recolonise, and native species richness, composition and abundance remained significantly different from uncultivated grasslands over the span of the study. Soils demonstrated post-abandonment recovery, with differences to uncultivated grassland in most nutrients becoming non-significant by ∼50 years, and soils did not appear to be the main driver of vegetation patterns with time-since-abandonment. The basic patterns of community reassembly did not appear to be fundamentally different from temperate northern hemisphere old field succession and suggest that secondary succession in Australian semi-arid grasslands may be constrained by seed availability rather than environmental conditions.

1. Introduction

In many areas of the world, land abandonment after cultivation is a common practice, and one which is predicted to increase (Ramankutty and Foley, 1999). The resulting old fields therefore allow regional comparisons of plant community reassembly with time-since-abandonment (Cramer and Hobbs, 2007). However, most successional studies have taken place in the temperate northern hemisphere and their findings may be less applicable in semi-arid regions or the southern hemisphere (Cramer and Hobbs, 2007). As well as contributing to conservation management and restoration plans, the study of succession can address basic ecological questions such as how communities assemble. Niche-based (deterministic) assembly models predict that local communities with similar environmental conditions should have similar species composition and successional trajectories, due to trait based filtering of the species pool, and that site history will have little effect (Chase, 2010; MacDougall et al., 2008). Dispersal-based (stochastic) models predict that local communities should have considerable variation in species composition among locations, driven largely by dispersal limitation and stochastic colonisation (Chase, 2010; MacDougall et al., 2008).

Succession is no longer thought to be necessarily linear and deterministic, and old field successional theory now combines ideas such as resilience, ecosystem assembly, ecological filters and thresholds, states and transitions, feedback loops, and contingencies (Cramer and Hobbs, 2007). The concept of resilience is a useful one as it is a quantitative measure of the recovery of a particular ecosystem variable (e.g. species richness, floristic composition, evenness) to the pre-disturbance state (Lavorel, 1999). Successional change in the temperate northern hemisphere often demonstrates a relatively rapid and predictable trajectory in community structure, composition and diversity, driven to at least some extent by species interactions (e.g. Foster and Tilman, 2000; Pickett et al., 2001). In contrast, recovery of native vegetation may be a slow process in arid and semi-arid regions, and vegetation dynamics in these environments are generally considered more likely to be controlled by abiotic conditions than biotic interactions, due to limited opportunities for many species to establish or for particular species to dominate (Hobbs et al., 2006). A trajectory towards pre-disturbance condition is less likely in areas of high environmental harshness because environmental constraints on establishment and growth are stronger than in more temperate systems (Hobbs et al., 2006), and the likelihood of alternative stable states may increase because

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smaller pools of species with similar traits increases the likelihood of priority effects (Didham et al., 2005). Indeed, due to the large yearly variability in recruitment success and plant cover in semi-arid systems, community assembly could be more prone to stochastic outcomes (MacDougall et al., 2008).

Additionally, the effects of cultivation on the physical, chemical, and biological properties of the soil can persist for decades or even centuries after abandonment (e.g. Foster et al., 2003; Walker et al., 2004), particularly in arid and geologically old regions, because of a lower ability to recycle nutrients or retain water after the native vegetation has been removed (Cramer et al., 2008). These legacies can affect the establishment and growth of native species, and may lead to the passing of abiotic thresholds, when a return to pre-cultivation species composition is unlikely (Cramer et al., 2008). In particular, increased soil fertility in old fields may slow or arrest succession (e.g. Foster et al., 2003; Standish et al., 2007; Walker et al., 2004); fertilisation experiments have shown reductions in native species richness due to increased invasions of exotic species and/or increased biomass of resident exotics (e.g. Foster and Gross, 1998).

Accordingly, biotic conditions may also have important consequences for succession in semi-arid systems. The interaction of limited seed dispersal and competition with exotic species may be especially important in altering or delaying the trajectory of succession (Cramer et al., 2008). Community reassembly is also dependent on the life-history characteristics (e.g. seed production and dispersal, establishment, longevity) of the current dominants and on those of the colonising species (Foster and Tilman, 2000; Grime, 1979). The level of adaptation of the native community to agricultural disturbance can be an important constraint on recovery and, in areas where agriculture represents a novel disturbance and where there is a pool of well-adapted exotic species, a trajectory back to a pre-disturbance state may be unlikely (Cramer and Hobbs, 2007). As such, the evolution of Australian grassland communities in the absence of hard-hoofed mammals and large-scale soil disturbance from glaciation and volcanism probably affects their ability to recover from cultivation (Wong et al., 2010). Thus, it is unclear if patterns of community reassembly and generalisations derived from classic successional studies hold in semi-arid regions or the southern hemisphere.

This study documents post-abandonment vegetation and soil dynamics in semi-arid south-eastern Australian old fields. Western Australia and south-eastern Australia are the major cultivation zones of the continent (Ramankutty and Foley, 1999) and the native vegetation of these regions has been severely degraded by grazing, clearing and cultivation. Old fields in Western Australia show little capacity for recovery due to a combination of increased soil fertility, competition from exotic annual grasses, seed limitation and harsh environmental conditions (Standish et al., 2006, 2007; Yates and Hobbs, 1997). In the current study region, $<5\%$ of the native grasslands remain (McDougall and Kirkpatrick, 1993) and the remnant communities are of immense conservation significance. However, only one old field study has been undertaken in this region; using a state-and-transition framework, Wong et al. (2010) concluded that the exotic-dominated state that forms after abandonment is unstable and demonstrates a directional change into a stable state resembling that of uncultivated grassland, but is characterised by a lack of several native species. The objective of the current study was to increase the understanding of successional processes in semi-arid grasslands in southern Australia by sampling across four study areas and two years. In particular, we: (1) examine the recovery of several community and soil variables compared to those of adjacent uncultivated grasslands (i.e. their resilience); (2) examine patterns of exotic species; (3) assess the role of the soil in post-cultivation vegetation dynamics; and (4) discuss the results in relation to common patterns in temperate and other semi-arid regions.

2. Methods

2.1. Study region

The study was undertaken in four grassland remnants on the Northern Plains in southern Australia (36°4′ S, 144°24′ E), approximately 200 km north of Melbourne, Victoria. The study region is dominated by a mosaic of grey (Rochester and Restdown Clays) and red (Koga and Koyuga Clay-loams) soils (Skene and Harford, 1964). The two soil types support distinct, but overlapping, vegetation communities and only the red soils are considered in this study. The climate is semi-arid, with an average annual rainfall of 395 mm, but with considerable yearly variation (163–871 mm over the last 100 years; http://www.bom.gov.au/climate/averages/). Sixty percent of annual precipitation falls in winter and (potential) evaporation exceeds precipitation in all months except June and July. The study region experienced severe drought during the sampling period, particularly in 2006, when rainfall was ~40–50% below-average. Seasonal average maximum temperatures range from 31 °C in summer to 15 °C in winter. Seasonal average minimums range from 14 °C in summer to 4 °C in winter.

Grasslands in the Riverine Plain have been transformed from C_4 grasslands and shrublands to C_3 grasslands by mechanisms such as overgrazing, exploitation and drought (Garden et al., 2001; Moore, 1953; Robinson and Dowling, 1976). They are now dominated by the native perennial C_3 grasses *Austrodanthonia* and *Austrostipa*. The inter-tussock spaces support a rich flora, predominantly from the *Asteraceae* and *Chenopodiaceae*. The vegetation is low and open, with cover of the dominant grasses ranging from ~15–20%, lower than that of more temperate south-eastern Australian grassy ecosystems (Williams, 1956). Exotic species richness is also lower in the Northern Plains (~23% of total species richness) than in other more temperate Australian grasslands (35%) (McDougall and Kirkpatrick, 1993).

2.2. Field methods

To investigate patterns of community reassembly following mechanical disturbance, we used space-for-time substitution (Pickett, 1989; Walker et al., 2010) over 16 sites from four study areas across the Northern Plains, representing an approximately 100 year chronosequence of agricultural field abandonment. The use of chronosequences can be problematic, particularly if site factors co-vary with age (Walker et al., 2010). However, a chronosequence is necessary for this study due to the assumed length of time required for semi-arid grassland recovery and the lack of long-term vegetation monitoring in these grasslands. Similarities in post-abandonment management (see below) and environment make these sites a valid chronosequence, and differences in site histories are assumed to be of secondary importance to time-since-abandonment in explaining reassembly. Local variation was minimised by repeating the chronosequence at each study area. Additionally, non-age-related variability among stages was addressed by replication within each chronosequence stage (Walker et al., 2010).

Sites were grouped into five age-classes (time-since-abandonment): (1) very recent (1–5 years), (2) recent (~20 years), (3) intermediate (~40–50), (4) long (80–100 years), and (5) uncultivated grassland. The four study areas containing the chronosequence were: Glassons Grassland Reserve (GGR), Kinypanial Grasslands (KG), Korrick Korrick Grassland Reserve (KKGR), and Terrick Terrick National Park (TTNP). Sites from the recent, intermediate and uncultivated age-classes were present at all study areas, while sites from the very recent and long uncultivated age-classes were only present at two study areas (Appendix 1). Management histories were established from land holders and managers. It was not possible to determine exact site histories, such