Plant facilitation under trees and shrubs along a degradation gradient

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Abstract

Traditionally the presence of large numbers of woody plants in rangelands is thought to reflect declining rangeland health and reduced pastoral productivity. However, an increasing body of evidence suggests that shrubs may provide an important ecological role by providing habitat for understorey plants, particularly in overgrazed and degraded rangeland. To test this we examined the role of trees and shrubs in facilitating understorey growth along a gradient representing three degradation states in semi-arid Australia. There was a significant difference in plant composition under tree and shrub canopies and in the open along the degradation gradient. We recorded significantly greater plant richness (Chao2–adjusted) under shrubs (17.1 species) than under trees (12.4) or in the open (8.2). Larger shrub canopies

supported more species, and this effect was more pronounced with increasing degradation. Our results indicate that the sub–canopy area of woody shrubs likely facilitates the growth and survival of a diverse and productive understorey community. Studies of the relative effects of trees and shrubs on soil surface processes are needed to enhance our understanding of the importance of woody plants as facilitators of plant growth in semi-arid environments.

Introduction

The encroachment of woody plants into grasslands, and the conversion of savannas and open woodlands into shrubland has been a widespread and widely-reported phenomenon over the past century (Archer et al. 1995). Encroachment, which is synonymous with woody thickening and woody weed invasion, alters soil hydrological properties and the spatial distribution of soil nutrient pools (Schlesinger et al. 1996). The generally negative perception of native shrubs as invaders is highly context–dependent (Colautti and MacIsaac 2004). It is based largely on the effects that shrubs have on reducing pastoral productivity in agricultural, production–based systems. Large areas of Australia's semi-arid woodland are now occupied by native shrubs (e.g. Eremophila, Acacia, Senna, Dodonaea), and considered by land managers to be at densities that negatively affect pastoral production.

Shrubs may also be important ecologically by providing habitat for understorey plants. In arid and semi-arid environments, stressors such as low rainfall and reduced nutrient pools provide strong mechanisms for promoting facilitative relationships between nurse plants (trees and shrubs) and their protégés (groundstorey plants; Brooker et al. 2008). The strength of the facilitatory response under nurse plants is thought to be stronger in areas of environmental harshness i.e. where resource availability declines (Bertness and Callaway 1994).

We examined the role of trees and shrubs for facilitating the growth of groundstorey plants in a semi-arid woodland along a gradient in disturbance. We used a grazing gradient ranging from heavily grazed sites close to water, to grazing remote, long ungrazed sites, to examine the relative facilitatory effect of trees and shrubs. We expected greater abundance and richness of plant species under woody (shrub and tree) canopies than out in the open and stronger facilitatory effects with increased degradation.

Methods

The study was conducted in the semi-arid woodlands (283 mm rainfall) near Wentworth, NSW. The soils were calcareous earths (calcarosols) with low levels of soil C and N and high pH. Twelve sites were measured along a gradient representing three degradation states: 1) long-ungrazed, undisturbed National Park sites, 2) recently reserved (recovering) sites, and 3) currently grazed, highly disturbed (degraded) sites. Within each site we measured the cover and abundance of all perennial plants within thirty 0.25 m^2 quadrats placed either in the open, or beneath the canopies of shrubs and trees (n=90 quadrats/site). We measured the canopy area of all shrubs and trees. We used a rarefaction analysis to correct for differences in the number of individuals encountered (Gotelli and Colwell 2001) using EstimateS (Colwell 2009). The Chao 2 estimate of total richness was used as the open plots tend to asymptote faster than those of the tree or shrubs. Univariate data were analysed using a range of Mixed Models ANOVAs using Minitab statistical software. Plant compositional data were analysed using Permanova (Anderson and Gorley 2008) and Indicator Species Analysis (McCune and Mefford 1999).

Results

We recorded significantly more species under shrubs (17.1 ± 3.1, mean ± SE species) than under trees (12.4 ± 1.5 species) or in the open (8.2 ± 1.2 species) using abundance–adjusted (Chao2) richness ($F_{2,22}$=4.87, P=0.018). There was no significant difference, however, in abundance–adjusted richness among the three degradation states (P=0.11; Fig. 1). Overall, perennial plants were about 3.5–times more abundant under shrubs (8.79 ± 0.78 plants m^{-2} canopy) than under trees (2.52 ± 0.21 plants m^{-2} canopy, $F_{1,165}$=90.69, P<0.001, log_{10}-transformed data). This effect changed along the degradation gradient, with 3 to 5–times more plants under shrubs at currently grazed and recovering sites, but similar numbers under shrubs at long ungrazed sites (condition by microsite interaction: $F_{2,57}$=4.64, P=0.014). For shrubs, larger canopies supported more plants in both currently grazed (R^2=0.36) and recovering sites (R^2=0.20), but not at long ungrazed sites. For trees, however, the opposite trend occurred, i.e. the effect on increasing canopy size on abundance was more influential at long ungrazed sites (Table 1).

Table 1. Relative importance of tree and shrub canopies for supporting understory plants across the degradation gradient. The R^2 value expresses the strength of the relationship between canopy area and abundance of perennial plants (adjusted to m^2 of canopy); ns = not significant.

Treatment	Tree		Shrub	
	Effect	R^2	Effect	R^2
Long-ungrazed	Increase	0.42	Unchanged	ns
Recovering	Increase	0.16	Increase	0.20
Degraded	Unchanged	ns	Increase	0.36

We found significant differences in plant composition under tree and shrub canopies and in the open along the degradation gradient ($F_{2,9}$=1.70, P=0.045), with only long ungrazed sites differing from currently grazed sites (t=1.68, P=0.029). The condition by microsite interaction ($F_{2,57}$=4.64, P=0.014) indicated that, for recovering and long ungrazed sites, a different suite of plants occurred beneath trees than either beneath shrubs or in the open. In the degraded currently grazed sites, however, any differences between trees and shrubs had disappeared. Indicator species analysis revealed that, although there were some significant effects, no species were strong indicators of a particular patch type (shrubs, tree, open).

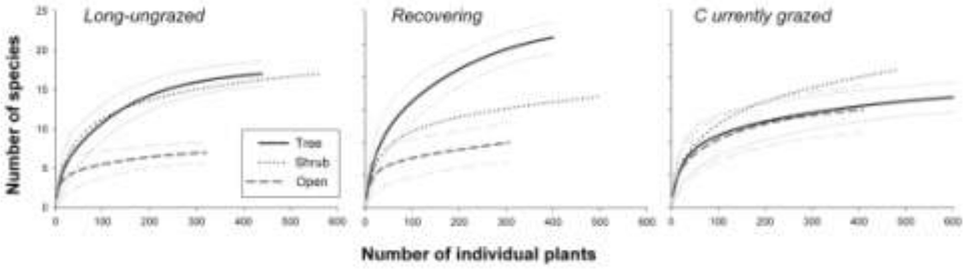

Fig. 1. Species accumulation curves for trees, shrubs and open microsites along a degradation gradient

Discussion

Overall, there were no significant differences in the number of species found along the degradation gradient. The relative strength of shrubs as facilitators however generally increasing as sites becomes more degraded. There was generally greater plant richness under woody plant canopies than in the open, particularly at long ungrazed sites. Any differences in microsites however tended to disappear at the most degraded end of the gradient (Fig. 1). This effect resulted mainly from reduction in the habitat value of shrub and tree canopies with degradation, though there were also slight increases in richness with degradation in open areas. Increased soil disturbance by livestock could have created a greater range of microsites in the open, supporting relatively disturbance–tolerant species such as Maireana sclerolaenoides and Sclerolaena diacantha, both of which were significant, though weak, indicators of degraded sites.

Another interesting trend was that richness under trees at recovering sites was substantially higher than that at either end of the gradient (Fig. 1), suggesting support for the intermediate disturbance hypothesis. Indeed, sub-canopy environments of trees have been shown to be shaded, and along with a continuous cover of leaf litter, and reduced evaporation and evapotranspiration, are favourable sites for drought – tolerate species (e.g. Jackson and Ash 2001; Hastwell and Facelli 2003; Warnock et al. 2007).

For plant abundance, the relative importance of canopies as habitat for plants also changed along the degradation gradient. While the influence of tree canopy size on plant abundance declined with increased degradation, it increased for shrubs (Table 1). Thus shrubs with larger canopies supported a larger number of plants for a given crown coverage than those with smaller canopies. The answer could lie in the facilitatory effects of canopies on environmental conditions. Shrubs are important for moderating a range of environmental conditions due to their effects on soil porosity. This results in enhanced biological processes around the roots, greater rates of infiltration and therefore potentially greater water holding capacity, and changes in light and temperatures under the canopies (Barchuk et al. 2005). Some of the shrubs in our study area also produced nitrogen (Senna spp.), which would result in the regulation of nutrient flow pathways (Vetaas 1992).

The relative importance of trees declined with increasing degradation in our gradient. The sub-canopy environment of the trees in our study (Casuarina cristata) was characterised by a deep layer of litter, which could mitigate against plant establishment, except where litter depth is shallow. Trees with very large canopies are generally used more by livestock for camping than trees with smaller canopies (Dean et al. 1999). Larger trees are more likely to have a deeper litter layer, with potential allelopathic effects, which are known to reduce seedling emergence (Barritt and Facelli 2001). Shrub canopies, however, produce substantially less litter than trees, and less likely to be used for camping. Thus their inhibitory effect on vascular plants is likely to be less. The positive effect of shrub canopies would be to filter solar radiation, lowering soil surface temperatures and reducing levels of evapo-transpiration, but in the absence of a deep layer of litter.

Taken together, the sub-canopy area of shrubs is likely to facilitate the growth and survival of a diverse and productive groundstorey vegetation (Maestre et al. 2009). Our data are consistent with the notion that facilitation, at least in terms of plant abundance, is strengthened in harsh environments (Brooker et al. 2008), but only for shrubs. Studies of the relative effects of trees and shrubs on soil surface processes are needed to enhance our understanding of the importance of woody plants as habitat for plants in semi-arid environments.

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