Facilitation and Fertile Islands:
linking canopy effects with plant interactions.

Graeme T. Hastwell

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Department of Environmental Biology
University of Adelaide, Australia

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Contents

Abstract

Plant community composition and soil nutrient levels under tree canopies frequently differ from that found in the open spaces between trees. While there is some evidence suggesting that these differences may be due to factors associated with the presence of trees, rather than simply being the result of pre-existing heterogeneity, the processes giving rise to this phenomenon are poorly understood. The issue of biogenic modification of the environment is of considerable theoretical interest and has important implications for the management of natural resources. Consequently, this thesis investigates the question of whether trees generate heterogeneity in resources and plant community composition, and seeks to identify some of the canopy processes that may be responsible.

I investigated the association between woody perennial plants and heterogeneity in soil resources and plant communities in an arid chenopod shrubland. A field survey revealed that soil nutrient levels (organic carbon, total nitrogen and available phosphorus) were higher under canopies of the small clonal tree *Alectryon oleifolius* than in areas outside canopy edges. Soil nutrient levels and plant litter densities were also positively correlated with canopy size. Nutrient levels differed with aspect, while correlations between nutrients changed with distance from the trunk, suggesting that shading by canopies influences nutrient cycling processes.

A second survey found that whereas the soils and plants under the smallest trees did not differ from those found in open areas, species composition and soil organic carbon levels under larger trees did differ. This is consistent with fertile islands being created by cumulative biological processes. Evidence suggested that fertile islands may develop when shrubs establish in the shade of trees and trap litter, thereby concentrating nutrient cycling.

I used artificial canopies to test the effects of shade and rainfall redirection on emergence of the annual forb *Carrichtera annua* and the perennial grass *Danthonia caespitosa*. Although emergence rates were very low, significantly more seedlings

emerged in shaded plots than in unshaded plots, and emergence was sometimes higher under larger canopies than smaller canopies. No effects of rainfall redirection were detected.

I tested the effects of shading on *Enchylaena tomentosa* seedlings in order to verify the prediction that facilitation becomes stronger as environmental stress increases. Patterns of survivorship and growth differed. As predicted, shading reduced mortality rates in summer, but not during winter and spring. However, while shading consistently increased *E. tomentosa* growth rates, the difference between shaded and unshaded seedlings did not differ between seasons. Thus facilitation of growth did not change as stress increased.

I used graphical models linking modification by plants with plant performance to investigate the strength of interactions along environmental gradients. These models show that facilitation will not always be stronger under adverse conditions, and that it may show complex patterns of change.

My results confirm that modification of soil resources and plant community composition occurs in the vicinity of *A. oleifolius*. The magnitude of this modification increases with canopy size, and varies with both distance and direction from the tree trunk, suggesting that modification is the result of cumulative processes with shading being an important factor. Support for this view was provided by experimental tests of the effects of shading on emergence of *C. annua* and *D. caespitosa*, and on growth of *E. tomentosa*. Clearly, tree canopies are an important source of heterogeneity in both physical resources and plant community composition. Their effects on neighbouring plants increase with canopy size, while the generation of heterogeneity in soil resources appears to depend on both size and time.