Asian Journal of Environment & Ecology

18(3): 1-13, 2022; Article no.AJEE.88158
ISSN: 2456-690X

Do Woody Plants Facilitate Herbaceous Plants in Dryland New Zealand?

Amadou S. Camara [a,b*]

[a] *Department of Botany, University of Otago, P.O. Box 56, Dunedin 9054, New Zealand.*
[b] *EUCLID (Pôle Universitaire Euclide / Euclid University) Headquarters Gambia, PMB 819, Brusubi, The Gambia.*

Author's contribution

The sole author designed, analysed, interpreted and prepared the manuscript.

Article Information

DOI: 10.9734/AJEE/2022/v18i330314

Open Peer Review History:
This journal follows the Advanced Open Peer Review policy. Identity of the Reviewers, Editor(s) and additional Reviewers, peer review comments, different versions of the manuscript, comments of the editors, etc are available here: https://www.sdiarticle5.com/review-history/88158

Original Research Article

Received 15 April 2022
Accepted 23 June 2022
Published 30 June 2022

ABSTRACT

Aims: Woody plants are postulated to facilitate understory herbaceous plants in arid and semi-arid environments worldwide, the so-called 'nurse plant' effect, but this mechanism. has been little studied in the drylands of New Zealand. Indigenous dryland plants postulated to have grown under woody shrubs in New Zealand before European settlement may benefit from their recovery, or even their replacement by exotic substitutes. The aim of this study was to investigate woody pant facilitation of understory herbaceous plants in dryland New Zealand.
Study Design: In this study I investigated the effects of canopies of four shrub species – *Kunzea serotina*, *Discaria toumatou*, *Rosa rubiginosa* and *Coprosma propinqua* – on herbaceous plant species richness, in the presence and absence of rabbit grazing (for *K. serotina*).
Place and Duration of Study: The study was conducted in the drylands of Central Otago, New Zealand, from August 2007 to January 2009.
Results: Herbaceous plant species richness was lower under canopies of *K. serotina*, possibly because the dense canopy shaded the understorey plants. It was higher under *C. propinqua*, *D. toumatou* and *R. rubiginosa* canopies than in their adjacent open grasslands, but for all three species this effect was seen only in winter. Woody plant canopy protection of understorey herbaceous plants against winter frost may explain the effects. Grazing significantly decreased herbaceous plant species richness. Since *D. toumatou*, *R. rubiginosa* and *C. propinqua* showed facilitative effects on herbaceous plant species richness they are possible agents for the restoration of dryland vegetation.

**Corresponding author: E-mail: ascamara33@gmail.com;*

Conclusion: I conclude that control of grazing and the protection of these three woody species could be a good management strategy for the maintenance of a predominantly indigenous dryland mixed herbaceous and woody vegetation in Central Otago.

Keywords: Woody; herbaceous; drylands; facilitate; species richness; grazing.

1. INTRODUCTION

The effects of woody plants on the herbaceous understorey species in dryland areas have been prominent among the plant interactions studied over the past few decades. These studies, however, have been contradictory. Some have reported a positive effect, i.e., plant establishment, and/or growth, and/or species richness being higher under the woody plant canopy than in adjacent open grassland [e.g. 1-11]. Others have reported inconsistent or negative results, with is less establishment/growth/species richness [e.g. 12-18].

The issue is not well understood in New Zealand, but it is particularly relevant for the understanding and restoration of its drylands, which constitute about 20% of the total land area [19] and are particularly vulnerable to degradation. Some threatened herbaceous plant species are postulated to have grown under former New Zealand woody canopy and might therefore benefit from the restoration of the woody ecosystem [20], but little is known about which dryland species might benefit from shaded woody habitats [21]. Moreover, restoration might be prevented by grazing by introduced mammals such as the European rabbit *Oryctolagus cuniculus*.

Human disturbance and mammalian grazing do not have a very long history in New Zealand [22]. Before occupation by Polynesian people after 1200 AD, the occurrence of fire was low [23]. In the 1850s, European pastoralists introduced grazing mammals such as sheep and cattle, and feral pests: rabbits and plants [24].

The present study sets out to examine this question by survey and experiment, addressing three questions:

(1) do different shrub species facilitate recruitment of native herbaceous plant species and do they facilitate their recruitment differently?
(2) does the effect of shrubs on recruitment of herbaceous plants vary with time and scale of observation? and
(3) does grazing reduce the recruitment of herbaceous plant species?

2. MATERIALS AND METHODS

2.1 Study Environment

The study area is in an inter-montane basin of Central Otago, New Zealand, within the sub-humid moisture range. The study was situated at the Luggate Long-term experimental site (Luggate), in the Upper Clutha (45^o S, 169^o E, [25]), in the northwest corner of Central Otago. The site is located on a fluvio-glacial outwash terrace [26]. The annual rainfall was 495.6 mm in 2007 and 605 mm in 2008 [27]. The study area is dominated by terraces of outwash gravel deposited by meltwater streams during Pleistocene glacial advances in the Upper Clutha catchment. The outwash materials are typically sandy, fine-coarse gravel with occasional boulders and a veneer of loess (windblown silt) on the terrace surface. The maximum daily temperatures usually are 25-30 ^oC in summer (December-February) and less than 5 ^oC in winter (June-August), sometimes with severe frosts [28]. Within- and between-year weather variations are large with soil moisture deficiency periodically extending into drought. During the study (2007-2009), recorded wind speed averaged 31.6 km/h in summer, 15.1 km/h in winter and 24.7 km/h in spring.

The study site is a dry grassland with a mosaic of shrubland. The vegetation consists of a mixture of native and exotic grasses and forbs with remnants of native subshrubs and shrubs. Prominent species were grasses *Anthoxanthum odoratum* and the native *Festuca novae-zelandiae* [28]. Other species include the native shrubs such as *Kunzea serotina*, *Coprosma petriei, Discaria toumatou* and *Carmichaelia petriei,* and the exotic *Rosa rubiginosa*. Nomenclature in this manuscript follows the Allan Herbarium [29].

2.2 Research Design

2.2.1 Effects of shrub canopy on herbaceous plant species richness

The aim of this investigation was to examine the environmental effects of shrub canopy (via shade, temperature, etc.), aspect (north, south, west, east) and mammalian herbivory on the herbaceous plant species richness.

Sixteen *K. serotina* shrubs were randomly selected from a relatively uniform *Kunzea serotina*-dominated plot of 200 m by 200 m. To be eligible for selection, shrubs had to be 1.8 - 4.0 m canopy diameter and with no neighbouring *K. serotina* of more than 0.5 m height within 2 m radius of the outer edge of the tree canopy. Shrubs were classified as small when less than 4.0 m^2 in canopy area and those 4.0 m^2 and over, as large, calculating the shrub canopy area as an ellipse when the two axes are not identical. Shrub architecture was classified as follows: canopy 10 cm or less above ground was classified as dense-canopy where more than 10 branches and dense leaves, and fewer than 10 branches with sparse leaves sparse-canopy: (1) small sparse-canopy (2) small dense-canopy and (3) Large sparse-canopy.

Eight of the sixteen shrubs were randomly selected and fenced in late winter 2007 to examine effect of rabbit herbivory. A wire meshed rabbit-proof fence was erected 2 m radius from the outermost edge of the canopy in the north and south aspects, and 1 m from it in the west and east aspects, and laid on the ground for 15 cm outside to prevent access. The average canopy area of the *K. serotina* shrubs selected was 4 m^2. Since the shrubs differed in size, the plots (square fence area) ranged in size from 17.9 m² to 31.9 m², with an average of 24.7 m².

2.3 Data Collection

For all the sixteen selected shrubs, plant species richness was monitored using a 25 cm by 25 cm quadrat placed on the ground, on all four aspects both under a *K. serotina* canopy and in the adjacent open grassland, where the quadrat was placed halfway between the outermost edge of the canopy and the fence or the boundary of the plot. In each quadrat, the number of plant species was recorded on nine occasions at approximately 60-day intervals from late winter (27 to 31 August) 2007 to mid-summer (15 to 19 January) 2009. Occurrences of all other vascular plant species in the 200 m by 200 m study area were also recorded.

2.3.1 Effects of canopy of other shrub species on herbaceous plant species richness

In order to examine whether different shrub species can have different effects on their understorey herbaceous plant species, herbaceous plant species richness was also monitored under three other shrub species. An area of 200 m by 160 m adjacent to the study area was included to monitor *D. toumatou* (Rhamnaceae) and *R. rubiginosa* (Rosaceae) in late autumn (15 to 19 May) 2008. A third species, *C. propinqua* (Rubiaceae), situated in an area of 100 m by 50 m, about 600 m northeast of the other plots was first monitored in late winter (29th August to 2 September) 2008. In these areas, ten *D. toumatou*, *R. rubiginosa,* and *C. propinqua* plants were selected randomly from all plants of these species that met the criteria as for *Kunzea serotina*. The plot dimensions for *D. toumatou* and *R. rubiginosa* were also defined as in *K. serotina*. The average canopy area and the average plot area of *D. toumatou* plants selected was 1.1 m^2 and 16.4 m², *R. rubiginosa* 2.8 m² and 22.5 m², *C. propinqua* 1.8 m^2 and 19.0 m², respectively.

Herbaceous plant species richness was measured as described for *Kunzea serotina* plots. For all three shrub species, herbaceous plant species richness was then monitored at approximately 30-day intervals up to the end of the investigation in mid-summer (15 to 19 January) 2009, as described for *K. serotina* plots. *D. toumatou* and the *R. rubiginosa* plots were measured five times, and *C. propinqua* plots four times.

2.3.2 Intensity of grazing by rabbits

In order to determine grazing intensity, the resident rabbit population was estimated by spotlight transect counts [30-32], since they can be spotlight transect counts can be consistent and more cost-effective [33].

A 350 m transect was marked across the *Kunzea serotina* study area to count rabbits using a spotlight at night. However, no rabbits were sighted along the transect during two nights of spotlight counting on the 29th and 30th August 2007. Therefore, a total count of all rabbits was done the following morning, by walking across

350 m x 200 m the study area and counting all rabbits sighted. The total counts were then done at approximately 60-day intervals during plant sampling. The rabbit population density was 4.29 per ha.

2.4 Data Analyses

The herbaceous plant species richness was analysed by experimental period and shrub species. Herbaceous plants were sampled under only *Kunzea serotina* canopy and in the open grassland from August 2007 to March 2008. *Discaria toumatou* and *Rosa rubiginosa* were included in the sampling in May 2008 and *Coprosma propinqua* in August 2008. Therefore, herbaceous plant species richness under shrubs were analysed from when the shrub species were included in sampling. To decrease the rate of type I error, a Bonferroni correction was applied, with the original α value (0.05) divided by the number of shrub species (4) resulting in an adjusted α value of 0.0125.

Herbaceous plant species richness data were analysed using Analysis of Variance (ANOVA) in the Teddybear software [34] to test if there were statistically significant differences between the experiment treatments in a split-plot design. The treatments were canopy cover (canopy or open grassland), grazing (grazed or ungrazed) and aspect (north, east, south or west). As indicated earlier, for *K. serotina*, there were 16 plots: 8 grazed and 8 ungrazed. For the other three species (*D. toumatou*, *R. rubiginosa* and *C. propinqua* pl), there were 10 plots each with no grazing treatment.

The grazing ratio was calculated by dividing mean abundance in the grazed plots by mean abundance in the ungrazed plots.

Species-accumulation curves were calculated and the size of the florule estimated by Chao-type estimators (Chao 1) based on 100 randomized samples, using EstimateS software (version 7.5.1, [35]).

3. RESULTS AND DISCUSSION

3.1 Results

3.1.1 Herbaceous plant species richness

The tendency through the study was for species richness to be lower under *Kunzea serotina* canopies than in the adjacent grassland, significantly so from October 2007 to March 2008 and May 2008. The difference was greater in the ungrazed plots (Figs. 1, 2). The opposite trend was seen in *Rosa rubiginosa*, with significantly higher herbaceous plant species richness under the canopy than in open grassland, and even more clearly in *D. toumatou* (Fig. 2, Appendix 1).

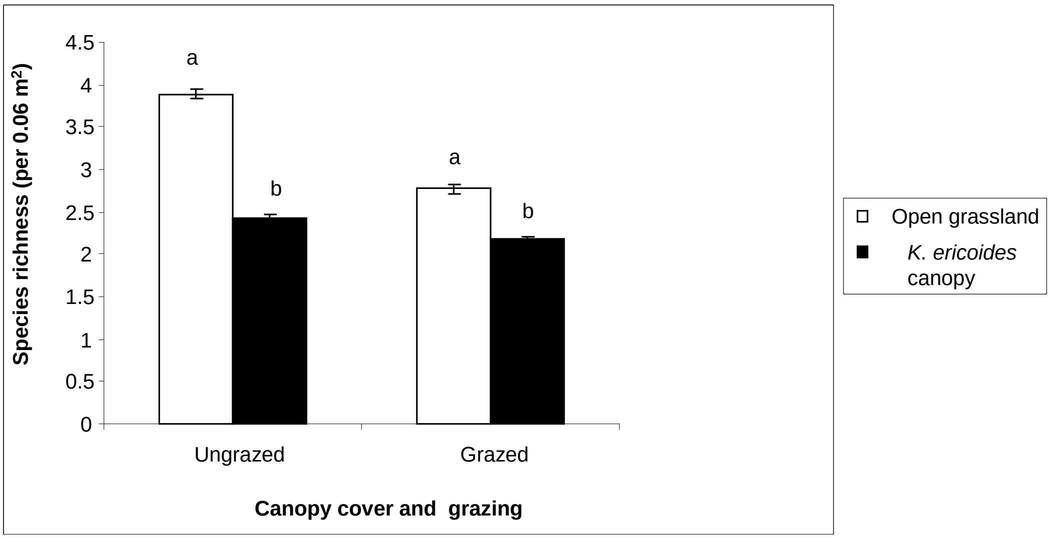

Fig. 1. Effects of canopy cover and grazing on herbaceous plant species richness (mean, n = 32 for each type of canopy cover per grazing treatment), October 2007 to March 2008. For each grazing treatment, types of canopy cover sharing a letter are not significantly different from each other (*P* > 0.0125, ±1SE)

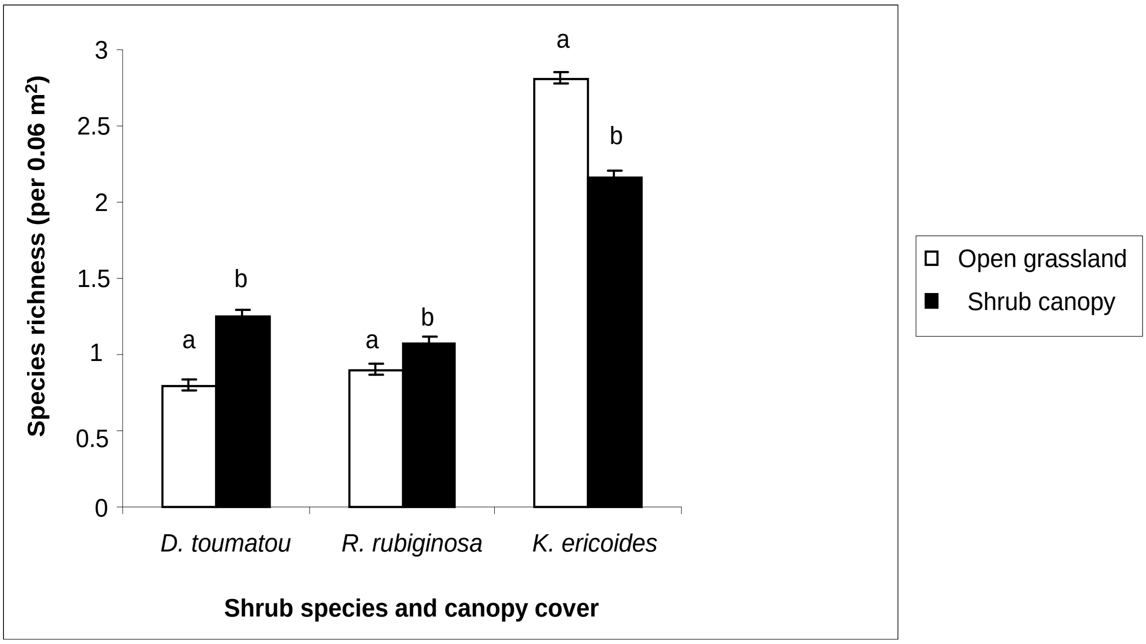

Fig. 2. Effects of shrub species and canopy cover on herbaceous plant species richness (mean, n = 40 for each type of canopy cover per shrub species), May 2008. For shrub species, types of canopy cover sharing a letter are not significantly different from each other (*P* > 0.0125, ±1SE)

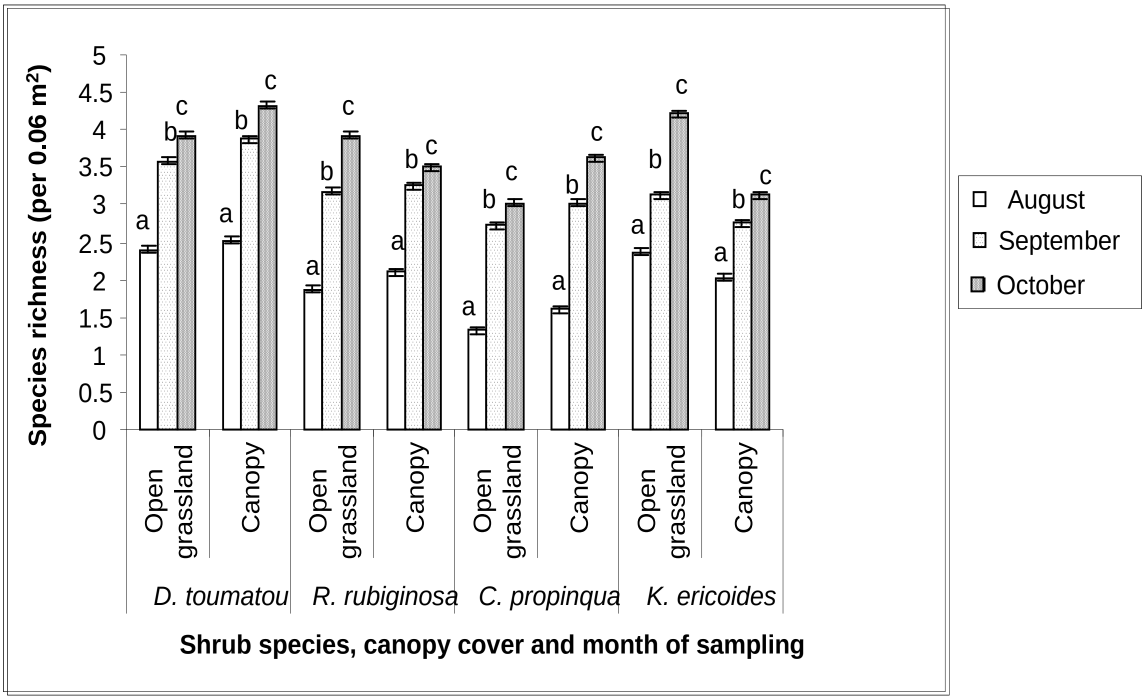

Fig. 3. Effect of shrub species, canopy cover and month of sampling on herbaceous plant species richness (mean, n = 120 for each type of canopy cover per species except for *K. serotina* where n = 96), August 2008 to October 2008. For each aspect, types of canopy cover sharing a letter are not significantly different from each other (*P* > 0.0125, ±1SE)

Table 1. Cumulative species richness, diversity and similarity in *K. serotina* plots

Plot	Canopy cover		Open grassland	
	Species richness	Chao 1 estimate	Species richness	Chao 1 estimate
Kunzea serotina	36	38	34	35
Discaria toumatou	22	22	23	23
Rosa rubiginosa	30	35	31	31
Coprosma propinqua	29	30	30	41

Herbaceous plant species richness was significantly higher in October and March (3.1 in October and 3.2 in March) than in January (2.2; Appendix 2). In the period August to October 2008, herbaceous plant species richness increased significantly with month of sampling for all four species (Fig. 3, P = 0.017, Appendix 3).

3.1.2 Species pool [or florule] under a shrub canopy and in the open grassland

Contrary to the mean number of species per sample (see results on herbaceous plant species richness), areas under a *Kunzea serotina* canopy supported higher total number of herbaceous plant species (cumulative species richness) than the adjacent open grassland. Areas under a *K. serotina* canopy also supported higher herbaceous plant species diversity than the adjacent open grassland (Table 1). The ungrazed plots of *K. serotina* supported higher cumulative herbaceous plant species richness and species diversity than the grazed plots.

However, the open grasslands of the *Discaria toumatou* plots and the *Coprosma propinqua* plots supported higher cumulative herbaceous plant species richness and species diversity than areas under canopy (Table 1).

For the *Rosa rubiginosa* plots, the open grassland supported higher cumulative herbaceous plant species richness but lower species diversity than the adjacent areas under canopy.

3.2 Discussion

3.2.1 Do different shrub species studied facilitate the recruitment of native herbaceous plant species and do they facilitate their recruitment differentially?

Positive (facilitative) effects of woody plants on recruitment and species richness of understorey plants have been demonstrated by previous workers [2-8,36]. This hypothesis of a facilitative effect of woody plants on understorey herbaceous plant species, however, was not always supported by the experiment results of the current study. Evidence of a facilitative effect varied with aspect and time of measurement. At the beginning of the experiment in late winter (August) 2007, areas under *Kunzea serotina* canopy supported a higher herbaceous plant species richness on the northern and southern aspects than on the western and eastern aspects. While recruitment of herbaceous plant species increased from mid-summer (January 2008) to through to mid-autumn (March 2008), *K. serotina* canopy seemed to suppress the recruitment of herbaceous plant species during the same period.

3.2.2 Facilitation

Belsky et al. (2) compared herbaceous plant productivity under isolated trees of *Acacia tortilis* and *Adansonia digitata*, and in open areas in the semiarid Tsavo National Park, Kenya. Belsky et al. (2) reported that that the above-ground net primary productivity was higher under the tree canopies than in the open grassland, although the two species did not significantly differ in primary productivity. Belsky et al. (2) attributed the higher herbaceous plant productivity under the trees to greater fertility of the soils in the canopy zone. In contrast, in the current study, evidence of facilitation of understorey herbaceous plants by shrubs differed with shrub species and time of sampling. In late autumn (May 2008), *Discaria toumatou* and *Rosa rubiginosa* facilitated herbaceous plant species richness but the reverse was true for *Kunzea serotina* (Fig. 3). For all four shrub species; *K. serotina*, *D. toumatou*, *R. rubiginosa* and *Coprosma propinqua*, recruitment of herbaceous plant species increased from late-winter (August) through to October (mid-spring). *D. toumatou*, *R. rubiginosa* and *C. propinqua* facilitated the recruitment of herbaceous plants but the opposite was true for *K. serotina* (Fig. 3). In contrast to Belsky et al. (2), higher soil fertility under shrub canopy may not be the main explanation for the higher herbaceous plant species richness under a canopy. Camara [37] reported that soils under *K. serotina* canopy showed higher concentrations of nitrogen and phosphorus than those in the open grassland but the opposite was true for herbaceous plant species richness. The higher concentrations of total nitrogen and available phosphorus in soils under canopies of *D. toumatou*, *R. rubiginosa* and *C. propinqua* (nitrogen only) than soils in the adjacent open grassland [see 37; 38] can explain the higher herbaceous plant species richness found under shrub canopy than in the adjacent open grassland.

The higher species richness of herbaceous plants cannot be explained only by soil fertility. Facelli and Brock [5] studied the effects of *Acacia papyrocarpa* on vegetation and soils in South Australia and reported that some bird-dispersed plant species were more often under the canopy of *Acacia* than in open grassland areas [5]. Similarly, Duarte et al. [8] reported that in southern Brazil the mean number of forest species seedlings was higher under the canopy of a nurse plant, 1.6, compared to 0.1 for the open grassland. They argued that by providing perching for birds the forest trees enhanced colonization by other species. However, since few birds (less than ten) were encountered during the current study, perching for birds may not be an important agent of herbaceous plant species colonisation in the area. Moreover, none of the herbaceous plants found in the study area are fleshy-fruited or known to be bird-dispersed.

Protection against heat stress could also explain the higher herbaceous plant species richness under a shrub canopy than in the adjacent open grassland [1,4,6,7]. Phillips [1] reported that areas under the canopy of *Artemisia tridentata* (Great Basin Sagebrush) supported a higher number of seedlings of *Pinus monophylla* (Pinyon pine) than open grassland areas. These results were confirmed by Callaway et al. [4] working on the same species. Callaway et al. [4] argued that shrubs not only reduce mortality through the amelioration of heat stress and desiccation, but they also indirectly facilitate Pinyon pine seedlings by reducing herbivory [4]. In a related study, Camara [37] found that from late winter through to mid-spring, canopies of *Kunzea serotina* reduced PAR transmission by 70%, *Coprosma propinqua* by 57%, *Discaria toumatou* by 44% and *Rosa rubiginosa* by 36%, which may facilitate the establishment of understorey herbaceous plant species. Similarly, soil water content was generally higher under the canopies of all the four shrub species than in the open grassland which could also minimise water stress for herbaceous plant species under a shrub canopy [37].

3.2.3 Interference

Some workers have reported negative effects of woody canopy plants on understorey herbaceous plant species in drylands [4,16,13,14,17,18], as outlined in the introduction. Negative effects of woody canopy plants on understorey herbaceous plant species could be due to the inhibition of annuals by shrubs [17] or by seasonal resource fluctuation [16,13,14,18].

Facelli and Temby [18] compared annual plants under a shrub canopy and in open grassland areas in South Australia and reported simultaneous negative and positive effects. In a related study in the current study area, Camara [37] found that, in mid-summer (January 2009), areas under canopies of *Kunzea serotina, Discaria toumatou* and *Coprosma propinqua* supported lower frequency of herbaceous species than the adjacent open grassland. In contrast, areas under a *Rosa rubiginosa* canopy did not differ in frequency of herbaceous plants from the adjacent open grassland [37]. The negative effects of the canopies of the shrub species on the recruitment of understorey herbaceous plant species could be an indication of interference between the woody and the herbaceous species. However, since canopies of the same shrub species had positive effects on herbaceous plant species richness at other times, seasonal fluctuation of resources such as solar radiation, soil temperature and soil moisture may also be operative [see 37].

3.2.4 Do effects of shrubs on recruitment of herbaceous plants vary with time and scale of observation?

Different shrub species can have different effects on the recruitment of understorey herbaceous plant species. Greenlee and Callaway [16] studied *Lesquerella carinata* a perennial herb usually associated with bunchgrass and reported a negative interaction between the two species in a wet year, and facilitative effects of bunchgrasses on *Lesquerella* in a very dry year. Similar results of seasonal variation in the net outcome of plant interactions have been reported in South Australia by Hastwell and Facelli [18]. They reported that shade had a positive effect on seedling survival of a shrub species (*E. tomentosa*) in summer but a negative effect in winter and spring. They also reported that seedlings growing under the shade showed higher relative growth rate (RGR) than seedlings growing in the open [18]. They ascribed their findings to the theory that positive interactions increase with the severity of the environment.

Not all year-to-year variation in the net outcome of plant interactions follows the postulated pattern of increased positive interactions (facilitation) with increase in environmental severity. Tielbörger and Kadmon [14] reported that in the Negev desert of Israel, the net effect of shrubs on understorey annual plants shifted from negative to positive when annual rainfall increased [14], contrary to the theory of positive interactions increasing with environmental severity [39]. In contrast, in the current study, effects of the shrubs on the recruitment of understorey herbaceous plant species shifted from positive in winter to negative in summer. The positive effect in winter could be due to the shrubs protecting the understorey herbaceous plant species from winter frost. The shift to a negative effect in summer could be an indication that the benefits to an herbaceous plant of being in the grassland, outweigh those of being under a shrub canopy.

Effects of a shrub canopy on recruitment of herbaceous plant species can vary with scale of observation. A positive effect of a woody plant canopy at the small (sample) scale may not reflect a positive effect at the large (cumulative) scale. Areas under a shrub canopy can have lower herbaceous species richness than adjacent open areas in a grassland at the sample scale, but higher cumulative herbaceous species richness if herbaceous plants of the open grassland are more similar than those of the areas under the shrub canopy. Camara [40] in the Negev Desert, Israel, reported that shrub patches supported lower herbaceous species richness at the sample scale, but higher cumulative herbaceous species richness over time, than microphytic crust patches. In the current study, for the *Kunzea serotina* plots, while the open grassland sometimes supported higher species richness than adjacent areas under the canopy, at the cumulative scale (total under a canopy or in the adjacent grassland) the areas under a canopy supported higher species richness. Areas under a canopy also supported higher species diversity than those of the adjacent open grassland. The lower species diversity of the adjacent open grassland could explain the discrepancy between species richness at the sample scale and cumulative species richness, in the open grassland. The open grassland supported a higher species richness at the sample scale but showed a higher similarity, resulting in a lower cumulative species richness than adjacent areas under a shrub canopy.

3.2.5 Does grazing reduce the recruitment of herbaceous plant species?

Grazing can have both negative [41] and positive [42,43,44,45] effects at the level of the individual plant. Grazing may also have a negative effect at the plant community level [46,47,48]. However, if dominant plant species competitively exclude less-dominant ones, grazing can have a positive effect on species richness at the plant community level.

Plants can either avoid or tolerate herbivory [49,50,51]. The effect of grazing on plants could depend on the evolutionary history of the plant species. The vegetation of the dry grasslands of Central Otago evolved in the presence of probable avian grazing but absence of mammalian grazing up to the time of European settlement. Since European settlement, mammals such as the European rabbit and sheep have been the major herbivores in the area [24]. Mammalian grazing coupled with frequent fires at the time of European settlement, initiated modification of the grassland vegetation resulting in the spread of exotic plant species and reduction in the distribution of palatable native species [52]. Anecdotal evidence suggests that rabbit population in the study area is significantly increasing. The rabbit population has been estimated at 4.29 per ha in the study area. Rabbit grazing was, therefore, expected to have a negative effect on the recruitment of herbaceous plant species. Natural recruitment of herbaceous plant species was higher in the ungrazed than in the grazed plots, at the end of the experiment in mid-summer (January) 2009. Consistent with our hypothesis, grazing had a negative effect on natural recruitment of herbaceous plant species. The negative effect of grazing on herbaceous plant species richness could be due to a decrease in diversity and productivity [47,48] and the absence of competitive exclusion by dominant species.

4. CONCLUSION AND IMPLICATIONS FOR RESTORATION

The success of the restoration of a predominantly indigenous dryland mixed herbaceous and woody vegetation can depend on the choice of species tolerant to shade and defoliation. Effects of a shrub canopy on the recruitment of understorey herbaceous plant species ranged from mainly negative and scale-dependent (*Kunzea serotina*) to inconsistent but mainly positive (*Discaria toumatou* and *Coprosma propinqua*), and mainly positive (*Rosa rubiginosa*). Grazing generally decreased the natural recruitment of understorey herbaceous plant species. Since *D. toumatou, R. rubiginosa* and *C. propinqua* showed mainly facilitative effects on the recruitment of understorey herbaceous plant species, they may be good candidates for the restoration of a predominantly indigenous dryland mixed herbaceous and woody vegetation in Central Otago.

In the study area, protection against grazing is probably more important for understorey herbaceous plant species than protection against intense solar radiation and desiccation. Control of grazing coupled with the use of shrubs as 'nurse plants' could be a good starting point for the restoration of a predominantly indigenous dryland mixed herbaceous and woody vegetation in Central Otago, New Zealand.

ACKNOWLEDGEMENTS

I am very grateful to the University of Otago and the Miss E. L. Hellaby Indigenous Grasslands Research Trust for funding part of this study. I sincerely acknowledge the support of my supervisors Prof. J. Bastow Wilson and Dr. Peter R. Espie as well as the guidance of Prof. Katharine Dickinson and Emeritus Prof. Sir Alan Mark. My sincere thanks and appreciation also go to the University of Otago Research Committee through the University of Otago Postgraduate Publishing Bursary, for funding the preparation of this manuscript. I would also like to thank the reviewers for their comments.

COMPETING INTERESTS

Author has declared that no competing interests exist.

REFERENCES

1. Phillips FJ. A study of pinyon pine, Botanical Gazette. 1909;48:216-223.
2. Belsky AJ, Amundson RG, Duxbury JM, Riha SJ, Ali AR, Mwonga SM. The effects of trees on their physical and, chemical and biological environments in a semi-arid savanna in Kenya. Journal of Applied Ecology. 1989;26:1005-1024.
3. Callaway RM. Effect of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. Ecology 1992;73:2118-2128.
4. Callaway RM, Delucia EH, Moore D, Nowak R, Schlesinger WH. Competition and facilitation: Contrasting effects of *Artemisia tridentata* on desert vs. montane pines. Ecology. 1996;77:2130-2141.
5. Facelli JM, Brock DJ. Patch dynamics in arid lands: Localized effects of *Acacia papyrocarrpa* on soils and vegetation of open woodlands of South Australia. Ecography. 2000;23:479-491.M.
6. Lenz TI, Facelli JM. Shade facilitates an invasive stem succulent in a chenopod shrubland in South Australia. Austral Ecology. 2003;28:480-490.
7. Barchuk AH, Valiente-Banuet A, Diaz MP. Effect of shrubs and seasonal variability of rainfall on the establishment of *Aspidosperma quebrancho-blanco* in two edaphically contrasting environments. Austral Ecology. 2005;30:695-705.
8. Duarte LDS, Dos-santos MMG, Hartz SM, Pillar VD. Role of nurse plants in Araucaria Forest expansion over grassland in south Brazil. Austral Ecology. 2006;31:520-528.
9. Barchuk AH, Iglesias MDR, Boetto MN. Spatial association of *Aspidosperma quebracho-blanco* juveniles with shrubs and conspecific adults in the Arid Chaco, Argentina. Austral Ecology. 2008;33:775-783.
10. Soliveres S, Eildridge DJ, Hemmings F, Maestre FT. Nurse plant effects on plant species richness in drylands: The role of grazing, rainfall and species specificity. Perspectives in Plant Ecology, Evolution and Systematics. 2012;14(6):402-410.
11. Fegundes M, Weisser W, Ganale G. The role of nurse successional stages on species-specific facilitation in drylands: Nurse traits and facilitation skills. Ecology and Evolution. 2018;8(10):5173-5184.
12. Tielbörger K, Kadmon R. The effect of shrubs on the emergence, survival and fecundity of four coexisting annual species in a sandy desert ecosystem. Ecoscience. 1995;2:141-147.

13. Tielbörger K, Kadmon R. Relationships between shrubs and annual communities in a sandy desert ecosystem: A three year study. Plant Ecolog. 1997;130:191-201.
14. Tielbörger K, Kadmon R. Temporal environmental variation tips the balance between facilitation and interference in desert plants. Ecology. 2000;81:1544-1553.
15. Callaway RM, Delucia EH, Moore D, Nowak R, Schlesinger WH. Competition and facilitation: Contrasting effects of *Artemisia tridentata* on desert vs. montane pines. Ecology. 1996;77:2130-2141.
16. Greenlee J, Callaway RM. Effects of abiotic stress on the relative importance of interference and facilitation. The American Naturalist. 1996;148:386-396.
17. Facelli J, Temby AM. Multiple effects of shrubs control the distribution and performance of annual plants in arid lands of South Australia. Austral Ecology. 2002;27:422-432.
18. Hastwell GT, Facelli JM. Differing effects of shade-induced facilitation on growth and survival during the establishment of a Chenopod shrub. Journal of Ecology. 2003;91:941-950.
19. Rogers G, Walker S, Lee B. The role of disturbance in dryland New Zealand: Past and present. Science for Conservation, Department of Conservation, Wellington, New Zealand. 2005;258.
20. Walker S, Price R, Rutledge D. New Zealand's remaining indigenous cover: Recent changes and biodiversity protection needs. Landcare Research Contract Report: LC0405/038(unpubl.), prepared for the Department of Conservation; 2005a.
21. Walker S, Rogers G, Grant G, Stephens T, and Lee B. Research needs for the conservation of dryland biodiversity- A scoping report. Landcare Research Contract Report: LC0405/150, prepared for the Chief Scientist, Department of Conservation, Wellington, New Zealand; 2005b.
22. Mark AF Indigenous grasslands of New Zealand. In: R.T. Coupland and D.W. Goodall (eds). Ecosystems of the world Volume 8B. Grasslands. Elsevier, Amsterdam, The Netherlands. 1993;361-410.
23. Anderson A. The chronology of colonization in New Zealand. Antiquity. 1991;65:765-795.
24. Wardle P. Vegetation of New Zealand. Cambridge University Press. Cambridge, U. K; 1991.
25. Wilson JB. Relations between native and exotic plant guilds in the Upper Clutha, New Zealand. The Journal of Ecology. 1989;77:223-235.
26. Wardle M, Bruce DL, Rance BD, Roozen DA, Grove P. Lindis, Pisa, and Dunstan Ecological Districts- a survey report for the Protected Natural Areas programme. New Zealand Protected Natural Areas Programme Series No 36. Otago Conservancy, Department of Conservation, Dunedin, New Zealand; 1994.
27. National Institute for Water and Atmospheric Research (NIWA) Rainfall data for Wanaka Automatic Weather Station; 2010.
Available:https://data.niwa.co.nz
(Accessed February 2010).
28. Walker S, Wilson JB. Test for nonequilibrium, instability and stabilizing processes in semiarid plant communities. Ecology. 2002;83: 809-822.
29. Allan Herbarium Nğa Tipu o Aotearoa. New Zealand Plant Names Database Landcare Research, New Zealand; 2000.
Available:http://nzflora.landcareresearch.co.nz
(Accessed 8 March 2010).
30. Frampton C, Warburton B. Methods for monitoring rabbit populations: A review. Contract Report, LC9394/77. Landcare Research, Lincoln, New Zealand; 1994.
31. Norbury G, Reddiex B. European rabbit. In King M (eds). The handbook of New Zealand mammals second edn. Oxford University Press, Melbourne. 2005;131-150.
32. Casey PA, Morley CG. Assessing growth rates of European rabbit populations using spotlight transect counts. Journal of Wildlife Management. 2002;66:131-137.
33. Polamores F. Comparisons of 3 methods to estimate rabbit abundance in a Mediterranean environment. Wildlife Society Bulletin. 2001;29:578-585.
34. Wilson JB. Teddybear a statistical system manual. Department of Botany, University of Otago, Dunedin, New Zealand; 2007.
35. Colwell RK. EstimateS 8.0 user's guide. University of Connecticut, Storrs, CT, U. S. A; 2006.
36. Holzapfel C, Tielbörger K, Parag HA, Kigel J, Sternberg M. Annual plant-shrub

interactions along an aridity gradient. Basic and Applied Ecology. 2006;7:268-279.
37. Camara A. The role of shrubs and rabbit herbivory in the ecological restoration of the drylands of south-central New Zealand. Unpublished PhD thesis. University of Otago, Dunedin, New Zealand; 2011.
38. Camara AS. Do woody plants create ‘fertile islands’ in dryland New Zealand? New Zealand Journal of Ecology. 2021;45 (1):3419.
39. Bertness MD, Callaway R. Positive interactions in communities. Trends in Ecology and Evolution. 1994;9:191-192.
40. Camara AS. The effect of shrub cutting and grazing on shrub growth and herbaceous plant communities in the Negev Desert. Unpublished MSc thesis. Ben-Gurion University of the Negev, Sede-Boqer, Israel; 2005.
41. Belsky AJ. The effects of grazing: Confounding of ecosystem, community and organism scales. The American Naturalist. 1987;129:777-783.
42. Owen DF, Wiegert RG. Do consumers maximize plant fitness? Oikos. 1976;27:488-492.
43. Owen DF, Wiegert RG. Mutualism between grasses and grazers: An evolutionary hypothesis. Oikos. 1981;36:376-378.
44. Owen DF. How plants may benefit from animals that eat them. Oikos. 1980;35:230-235.
45. Dyer MI, Detling JK, Coleman DC, Hilbert DW. The role of herbivores in grasslands. In: J. R. Estes, R. J. Tyrl and J. N. Brunken (eds). Grasses and grasslands: systematics and ecology. University of Oklahoma Press, Norman. 1982;255-295.
46. Perevolotsky A. Conservation, reclamation and grazing in the northern Negev: contradictory or complementary concepts? Pastoral Development Network, Network Paper 38a. London: Overseas Development Institute; 1995.
47. Pickett STA, Shachak M, Boeken B, Armesto JJ. Management of Ecological systems. In: Hoekstra TW, Shachak M (eds) Arid Lands Management- Toward Ecological Sustainability. Illinois University Press. 1999;8-17.
48. Zaady E, Yonatan R, Shachak M, Perevolotsky A. The effects of grazing on abiotic and biotic parameters in a semiarid ecosystem: A case study from the northern Negev desert, Israel. Arid Land Research and Management. 2001;15:245-261.
49. Rosenthal JP, Kotanen PM. Terrestrial plant tolerance to herbivory. Trends in Ecology & Evolution. 1994;9:145-148.
50. Mauricio R, Rausher MD, Burdick DS. Variation in the defense strategies of plants: Are resistance and tolerance mutually exclusive? Ecology. 1997;78:1301-1311.
51. Strauss SY, Agrawal AA. The ecology and evolution of plant tolerance to herbivory. Trends in Ecology and Evolution. 1999;14:179-185.
52. Walker S, Lee WG. Alluvial grasslands in southeastern New Zealand: vegetation patterns, long-term and post-pastoral change. Journal of the Royal Society of New Zealand. 2000;30:72-103.

APPENDIX

Appendix 1. Analysis of Variance (ANOVA) for herbaceous plant species richness in May 2008. Significant probability (P) values are in **bold**. P values > 0.1 are shown as not significant (ns). Interactions above two factors are shown only when P < 0.1.

Plot

Source of variation	SS	DF	MS	F	P
Shrub species	99.94	2	49.97	58.28	**< 0.001**
Canopy cover	0.01	1	0.01	0.01	ns
Shrub species x canopy cover	11.48	2	5.74	6.69	**0.003**
Error	42.87	50	0.86		
Total	154.36	55	2.81		

Sub-plot

Source of variation	SS	DF	MS	F	P
Aspect	124.70	3	41.57	77.98	**< 0.001**
Shrub species x aspect	30.25	6	5.04	9.46	**< 0.001**
Canopy cover x aspect	5.44	3	1.81	3.40	**0.019**
Error	79.96	150	0.53		
Total	256.50	168	1.53		

Appendix 2. Analysis of Variance (ANOVA) for herbaceous plant species richness from October 2007 to March 2008. Significant probability (P) values are in **bold**. P values > 0.1 are shown as not significant (ns). Interactions above two factors are shown only when P < 0.1.

Plot level 1

Source of variation	SS	DF	MS	F	P
Grazing	41.25	1	41.25	10.86	**0.008**
Error	37.97	10	3.79		
Total	89.17	15	5.94		

Plot level 2

Source of variation	SS	DF	MS	F	P
Canopy cover	90.65	1	90.65	49.99	< **0.001**
Aspect	18.74	3	6.25	3.45	0.021
Canopy cover x grazing	15.76	1	15.76	8.69	**0.004**
Canopy cover x aspect	16.39	3	5.46	3.01	0.036
Error	126.95	70	1.81		
Total	330.83	112	2.95		

Plot level 3

Source of variation	SS	DF	MS	F	P
Month of sampling	67.73	2	33.86	33.27	**< 0.001**
Error	162.83	160	1.02		
Total	345.33	256	1.35		

Appendix 3. Analysis of Variance (ANOVA) for herbaceous plant species richness in August 2008 to October 2008. Significant probability (P) values are in **bold**. P values > 0.1 are shown as not significant (ns). Interactions above two factors are shown only when P < 0.1.

a) Plot

Source of variation	SS	DF	MS	F	P
Shrub species	94.11	3	31.37	14.78	**< 0.001**
Canopy cover	0.01	1	0.01	0.00	ns
Shrub species x canopy cover	31.05	3	10.35	4.88	**0.003**
Canopy cover x aspect	15.16	3	5.21	2.45	0.064
Error	577.27	272	2.12		
Total	743.85	303	2.45		

b) Sub-plot

Source of variation	SS	DF	MS	F	P
Month of sampling	445.26	2	222.63	318.64	**< 0.001**
Shrub species x month of sampling	9.29	6	1.55	2.22	**0.040**
Shrub species x canopy cover x month of sampling	10.94	6	1.82	2.61	**0.017**
Error	380.08	544	0.69		
Total	886.67	608	1.46		

Peer-review history:
The peer review history for this paper can be accessed here:
https://www.sdiarticle5.com/review-history/88158