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RESEARCH

Do woody plants create 'fertile islands' in dryland New Zealand?

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Abstract: Woody plants in arid and semi-arid environments may enhance soil nutrient status, the so-called 'fertile island' effect, but this mechanism has never been tested in the drylands of New Zealand. In this study I investigated effects of *Kunzea serotina*, *Discaria toumatou*, *Rosa rubiginosa*, and *Coprosma propinqua* on soil properties in the drylands of central Otago, New Zealand. Soils had significantly higher organic matter under *C. propinqua* and significantly higher nitrate and phosphorus concentrations under *K. serotina* than soils in the adjacent open grassland. A bioassay using oat (*Avena sativa*) growth indicated higher fertility in soils from under *K. serotina* than from under grassland. A review of 28 other studies revealed that fertile island effects of woody plant species on soil nitrogen and phosphorus concentrations decreased significantly with increases in annual precipitation. The occurrence of fertile islands under only two of the four shrub species in the current study in a dry sub-humid environment is consistent with this trend of decreased fertile island effect with increased annual precipitation. The higher concentration of nitrogen in soils under woody plants such as *C. propinqua* may be explained by the plants depositing organic matter on the surface, but some species such as *K. serotina*, *D. toumatou*, *R. rubiginosa* and *C. propinqua*, may also preferentially establish in areas of high soil phosphorus availability. I conclude that the occurrence of fertile islands under woody plants may be due to both effects of the woody plant canopy, and the plants preferentially establishing in areas of high soil fertility.

Keywords: drylands, arid, semi-arid, organic matter, nitrogen, phosphorus, nitrate

Introduction

The soils under woody plant canopies in savannah and shrub-savannah often differ in nutrient status from those in grassy/bare areas (Callaway & Pugnaire 2007). In some cases nutrients are lower under woody canopies, which has been ascribed to increased nutrient uptake by plants (e.g. Davis 1994; Giddens et al. 1997). However, the soils under woody canopies are often nutrient enriched (Belsky et al. 1989, 1993; Ryel et al. 1996; Facelli & Brock 2000; Barritt & Facelli 2001; Graham et al. 2004), especially in arid and semiarid ecosystems: the 'fertile island' (Garner & Steinberger 1989; de Graaff et al. 2014) or 'resource island' (Callaway 2007) effect. Fertile island effects have been attributed to the transfer of nutrients by animals, modification of the micro-environment, the input of organic matter via litterfall, trapping of airborne particles, and nitrogen fixation (Belsky et al. 1989; Facelli & Brock 2000; Graham et al. 2004; Callaway 2007).

Despite such studies, the mechanisms explaining the formation of fertile islands are poorly understood (Schlesinger et al. 1996; Ochoa-Hueso et al. 2018). Moreover, to my knowledge, prior to the current study, the fertile islands effect had not been investigated in the subhumid drylands of New Zealand. The fertile islands effects in subhumid drylands may be different to those in other climates because lower annual precipitation may increase the dependency for shelter.

The main questions I address in this study are:

(1) do soil properties under the shrubs differ from those beyond in the adjacent grassland, and do different plant species affect soil properties differently?

(2) does the strength of fertile island effects vary along the rainfall gradient, and

(3) if fertile islands exist, are they the result of shrub modification of the environment or of shrubs preferentially establishing in areas of high soil nutrients? This question is addressed through literature review.

The study area is in an inter-montane basin of Central Otago, New Zealand, the driest part of New Zealand (Hubbard & Wilson 1988), within the Luggate Long-term experimental (LLT) site, on a glacial outwash terrace. It is situated about 10 km southeast of Wanaka and lies in the dry sub-humid moisture range (Leamy & Saunders 1967). Such a moisture range makes this one of the wettest types of dryland. The annual rainfall recorded at Wanaka Airport during the study, was 496 mm in 2007 and 605 mm in 2008 (NIWA 2010). The study site supports a dry mixed indigenous and exotic grassland interspersed with shrubs of *Kunzea serotina*, *Discaria toumatou*, *Rosa rubiginosa* and *Coprosma propinqua*, and is part of the short tussock grasslands defined by Newsome (1987). The vegetation consists of a mixture of native and exotic grasses and forbs with remnants of native subshrubs

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and shrubs. Nomenclature in this manuscript follows the Allan Herbarium (2000).

Methods

Experimental design

In order to answer the above research questions, four shrub species were selected for the study. Individuals of the four species: *Kunzea serotina* a native evergreen, *Discaria toumatou* a native deciduous, *Rosa rubiginosa* an exotic deciduous and *Coprosma propinqua* a native evergreen shrub, were randomly selected. All the shrubs selected (10 of each species) were above 50 cm height. Half of the *K. serotina* shrubs were ungrazed, with wire meshed rabbit-proof fences erected in August 2007, 2 m from the outer edge of the canopy on the north and south aspects of a shrub and 1 m from it on the east and west aspects; the rest were exposed to grazing (i.e. unfenced). For *D. toumatou*, *R. rubiginosa* and *C. propinqua* all the shrubs examined were exposed to grazing. The average canopy areas of the shrub species used were: *K. serotina* 4.0, *D. toumatou* 1.1, *R. rubiginosa* 2.8, and *C. propinqua* 1.8 m^2. Shrubs of less than average canopy area were classified as small and those of average, or above, as large. The *K. serotina* and *D. toumatou* shrubs with canopy 10 cm or more above the ground with more than 10 branches and dense leaves were classified as dense-canopy, and those with fewer than 10 branches and sparse leaves, sparse-canopy. The *K. serotina* shrubs were thus divided into two groups according to their architecture: small sparse-canopy and small dense-canopy. The *D. toumatou* shrubs were also grouped according to their architecture into four categories: small dense-canopy, small sparse-canopy, large dense-canopy and large sparse-canopy.

Soil fertility bioassay

Seeds of common oat *Avena sativa* were grown both on soils from under *Kunzea serotina* canopy (from the trees selected above), and soils from the adjacent open grassland. However, no testing was conducted to determine whether fencing changed any effects on soil fertility. In addition, two standard soil mixtures—high fertility (S1) and low fertility (S2)—were made up. For high fertility, soils under canopy and in the open grassland were mixed with an equal volume of washed beach sand, and for each 1-litre pot, calcium carbonate: $CaCO_3$ (0.5 g) and NPK: Yates fertilizer (0:10:0) (3 g). For low fertility, washed beach sand was thoroughly mixed with an equal volume of horticultural vermiculite. About 1.8 g of common oat (*Avena sativa* L.) seed were sown into each of the 52 pots (2 types of shrub canopy cover × 10 replicates × 2 pseudo-replicates and 2 standard mixtures × 6 replicates). The bioassay was conducted in a thermo-regulated glasshouse (20 °C) and the pots were arranged in a completely randomised design and re-randomized every week. All containers were watered daily. After five weeks of growing, the aboveground biomass of all the pots was harvested and oven-dried at 80°C for 48 hours.

Soil analysis

The methods for analyzing soil properties are a modification of those described by Belsky et al. (1989) and Facelli and Brock (2000). Soil samples were taken under the selected shrubs of *K. serotina* (October 2007), *D. toumatou* (May 2008), *R. rubiginosa* and *C. propinqua* (both January 2009) and in the adjacent open grassland, from 2.5–7.5 cm depth and for *K. serotina* and *D. toumatou* additionally from 7.5–12.5 cm depth. For each selected *R. rubiginosa* and *C. propinqua* tree, one sample was taken from 2.5–7.5 cm depth under the canopy and one other sample was taken in the open grassland during each sampling period. For each selected *K. serotina* and *D. toumatou* tree, one sample was taken from 2.5–7.5 cm depth and one other sample from 7.5–12.5 cm depth under the canopy as well as in the open grassland during each sampling period.

Soil organic matter was calculated as the loss in soil weight after burning at 500°C for two hours. Soil pH was measured using an electronic pH meter (Orion 420 A) in a 1:2.5 soil:water solution. Phosphate was extracted with 0.5 M sodium bicarbonate solution at pH 8.5 using the Olsen's method (Rowell 1994). Soil nitrate content was analysed by flow injection analysis (FIA) (Foss 2000a, 2000b) and total nitrogen soil using the var MAX CN machine (Elementar Group).

Rainfall

The net outcome of the interaction between woody and herbaceous plant species can vary with the amount of precipitation (Tielbörger & Kadmon 2000). A standard rain gauge was installed at the centre of the study area in September 2007. Rainfall data were collected every 60 days during field work. Rainfall data for Wanaka Airport (2006, 2007, 2008 and 2009), about 3 km west of this study area, were downloaded from the National Institute for Water and Atmospheric Studies website (https://data.niwa.co.nz).

Review of 'fertile islands'

A review of 28 other studies on fertile islands was conducted to establish whether their strength varied along the rainfall gradient. A Google scholar search for studies was conducted on the internet using the terms "fertile islands" "islands of fertility" "fertile islands in drylands" and "islands of fertility in drylands". The reference lists of some of these studies were also used to identify other relevant studies for the review. Data collected from these 28 studies include: annual rainfall (in millimeters), total nitrogen in soil (g kg^{-1}) and available phosphorus concentration of soil (mg kg^{-1}); under woody plants and those in the open grassland. The mean values of total nitrogen in soil and available phosphorus concentration were calculated across all replicates. Moreover, all studies were weighted equally.

Data analysis

The soil fertility bioassay data were analysed using one-way ANOVA with Teddybear software (Wilson 2007) comprising canopy, open, low fertility and high fertility. A Tukey's test (Tukey's Honest Significant Difference test) was used to investigate which treatments differ from which others. Soil properties data were analysed statistically using a split-plot ANOVA with grazing and shrub architecture as the plot and canopy cover and soil depth (2.5–7.5 cm and 7.5–12.5 cm) as sub-plot and their interactions. The data for Olsen's P were log-transformed prior to analysis to meet the assumptions of ANOVA. The lowest value above 0 was added to each datum before log-transformation. A separate analysis was conducted for each woody plant species because data for different species were collected at different times. 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. For the review of fertile islands the data on total nitrogen in soil and available phosphorus concentration were plotted against annual rainfall to establish any relationships.

Results

Soil fertility bioassay for *Kunzea serotina* plots

Soils from under *K. serotina* canopy supported a significantly higher dry weight of *A. sativa* than soils from the adjacent open grassland (Table 1; $P = 0.05$, $F_{3, 28} = 5.4$, see Appendix S1 in Supplementary Materials), almost as high as the high-fertility standard. The open grassland soils did not differ significantly from the low-fertility standard (Table 1).

Shrub canopy effects on soil properties

Kunzea serotina

Soils under *K. serotina* were significantly more fertile than those in the adjacent open grassland in terms of total nitrogen (canopy 0.13%, grassland 0.12%, Table 2, $P = 0.003$, $F_{1, 18} = 11.81$, see Appendix S2), nitrate (canopy 1.3 ppm, grassland 0.89 ppm; Table 2; $P = 0.003$, $F_{1, 18} = 11.37$; see Appendix S3) and Olsen P (canopy 9.56 mg kg^{-1}, grassland 5.10 mg kg^{-1}; Table 2; $P < 0.001$; $F_{1, 18} = 27.46$: see Appendix S4). However, these effects were not uniform. Total nitrogen was higher under the canopy only in the absence of grazing (Fig. 1; interaction $P < 0.001$), and this grazing effect was seen only under dense-canopy shrubs although this was not significant (interaction $P = 0.032$). Nitrate was higher in grazed plots (1.54 ppm) than in the ungrazed plots although this effect was not significant (0.74 ppm) ($P = 0.048$, $F_{1, 6} = 6.17$; Appendix S3). The upper topsoil contained more nitrate (1.28 ppm) than the lower topsoil though not significantly so (1.01 ppm) ($P = 0.034$, $F_{1, 18} = 5.27$; Appendix 3) and higher Olsen P (2.0 mg kg^{-1} in the upper topsoil, 1.75 mg kg^{-1} in the lower topsoil although this effect was not significant; $P = 0.027$, $F_{1, 18} = 5.83$; Appendix S4).

Discaria toumatou

Soils of plots with small dense-canopy *D. toumatou* shrubs contained significantly more total soil nitrogen than soils of plots with the other three shrub architectures (Fig. 2; $P < 0.001$, $F_{3, 6} = 129.27$; see Appendix S5).

Rosa rubiginosa

Soils under *R. rubiginosa* did not significantly differ in any soil property from soils in the adjacent open grassland.

Coprosma propinqua

Soils under *C. propinqua* canopy were significantly more

Table 1. Effects of *Kunzea serotina* canopy cover and fertilizer treatment on *Avena sativa* L. dry weight (mean ± SE). Low = standard low fertility and High = standard high fertility.

Group	*A. sativa* weight (g)
Canopy	2.65 ± 0.11
Open	2.18 ± 0.09
Low	2.39 ± 0.13
High	2.79 ± 0.08

Table 2. Effects of *K. serotina* canopy on soil nutrient concentration ($\bar{x}$ ± SD).

Soil nutrient	*K. serotina* canopy	Open grassland
Total nitrogen (%)	0.13 ± 0.01	0.12 ± 0.01
Nitrate (ppm)	1.3 ± 0.74	0.89 ± 0.46
Olsen P (mg/kg)	9.56 ± 3.99	5.10 ± 3.01

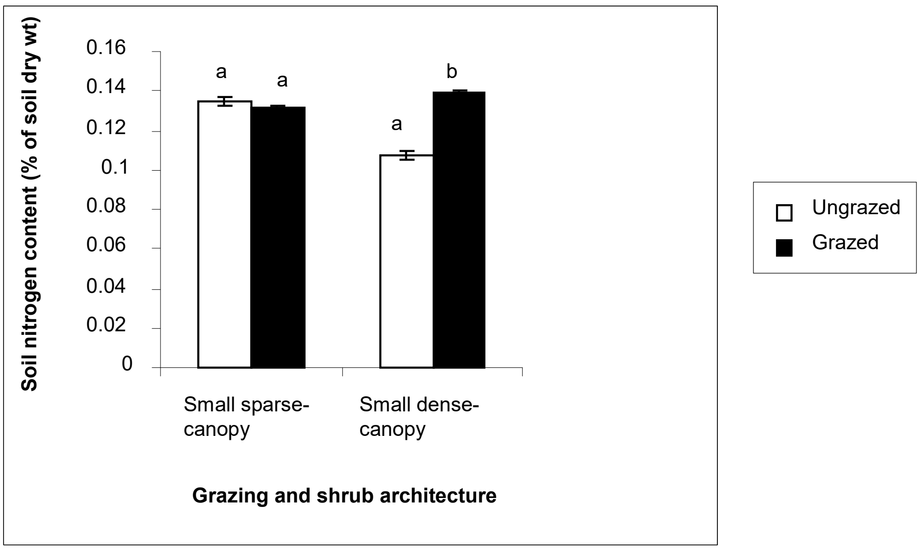

Figure 1. Effects of grazing and *Kunzea serotina* architecture on soil nitrogen content. For each type of shrub architecture, grazing treatments sharing a letter are not significantly different from each other ($P > 0.0125$, ± 1 SE).

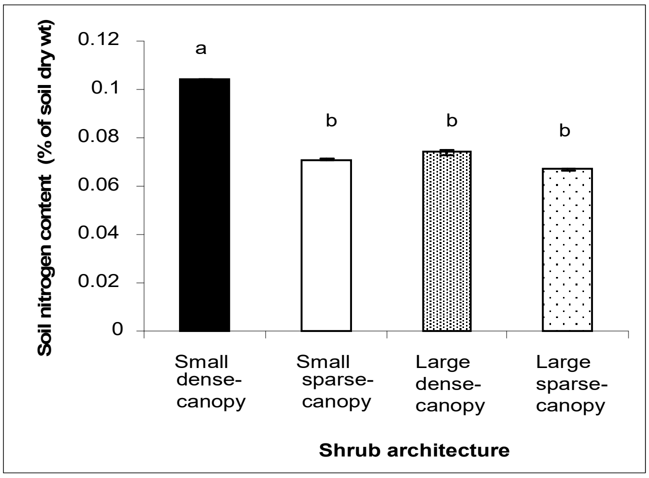

Figure 2. Effect of *Discaria toumatou* architecture on total nitrogen. Shrub architectures sharing a letter are not significantly different from each other ($P > 0.0.0125$, ± 1 SE).

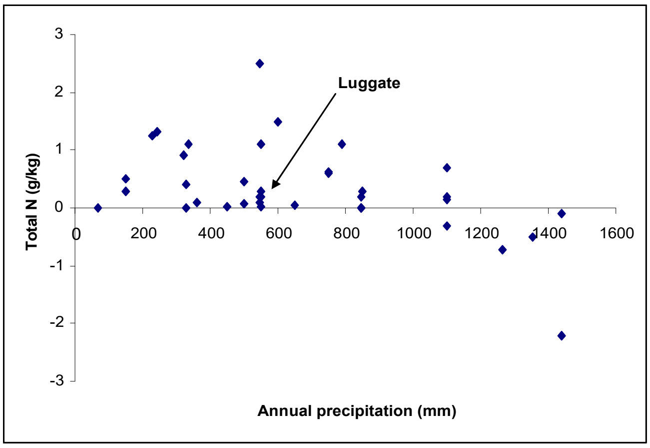

Figure 3. Relationship between total nitrogen concentration in soil (difference between soils under woody plants and those in adjacent open grasslands) and rainfall. Positive values represent higher nitrogen concentration in soils under woody plants and negative, higher concentration in soils in open grasslands.

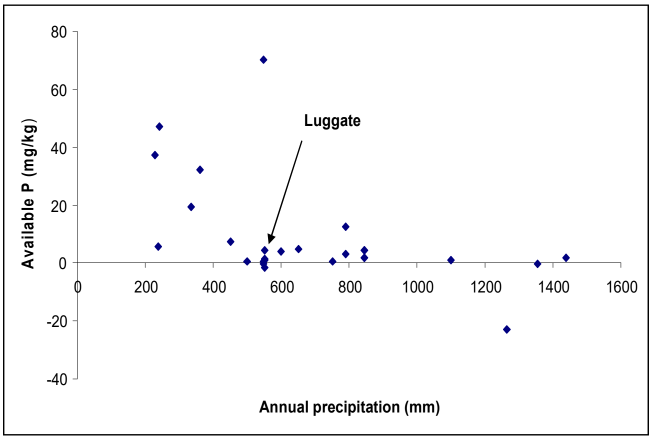

Figure 4. Relationship between available phosphorus concentration of soil (difference between soils under woody plants and those in adjacent open grasslands) and rainfall. Positive values represent higher phosphorus concentration in soils under woody plants and negative, higher concentration in soils in open grasslands.

fertile than those in the adjacent open grassland in terms of a higher organic matter content (canopy 7.25%, grassland 6.25%; $P = 0.008$, $F_{1,8} = 12.37$; see Appendix S6) and higher nitrate content though not significantly so (canopy 0.21 ppm, grassland 0.15 ppm; $P = 0.049$, $F_{1,8} = 5.37$; see Appendix S7). Canopy cover did not significantly affect total soil nitrogen (Appendix S8). *C. propinqua* shrub size affected the soil, with higher contents of organic matter although this effect was not significant (large shrubs 7.50%, small shrubs 6.50%; $P = 0.027$) and total nitrogen (large shrubs 0.40%, small shrubs 0.25%; $P = 0.013$).

Review of 'fertile islands' along rainfall gradients

Fertile island effects under woody plants have been reported almost exclusively in semi-arid and arid areas, from 150 mm precipitation p.a. (Santong River, China; Li et al. 2007), to 790 mm (Northern Tablelands, Australia; Graham et al. 2004). From the literature (Appendix S9), the size of the effect decreases as precipitation increases, with negative effects sometimes occurring above 1000 mm. This trend is significant for total soil nitrogen ($R^2 = 0.25$, $P < 0.01$) and available phosphorus ($R^2 = 0.25$, $P < 0.01$) (Figs. 3, 4). The findings of the current study, 1.1 g kg^{-1} higher soil total nitrogen and 4.46 mg kg^{-1} higher soil available phosphorus concentrations under a *Kunzea serotina* canopy than in the adjacent open grassland, conducted in an area of 550 mm annual precipitation, are at the lower range of what previous workers have found for 'fertile islands' (Appendix S9), but within the range expected for that precipitation (Figs. 3, 4).

Discussion

Do soil properties under the shrubs differ from those in the adjacent grassland, and do different plant species affect soil properties differently?

It was hypothesised that soils under the canopies of the four shrub species are more fertile than soils in the adjacent open grassland. The fertile islands effect was demonstrated only for soils under *K. serotina* and *C. propinqua* and not for those under *D. toumatou* and *R. rubiginosa*. This difference may be explained by the denser canopies of *K. serotina* and *C. propinqua* than those of *D. toumatou* and *R. rubiginosa*. Camara (2011) reported that canopies of *R. rubiginosa* and *D. toumatou* transmitted a higher percentage of photosynthetically active radiation (64% and 56%, respectively) than those of *C. propinqua* (43%) or *K. serotina* (30%), attesting to the relatively denser canopies of the latter two. *C. propinqua* and *K. serotina* may therefore deposit more litter and thus organic matter per unit ground area than *R. rubiginosa* and *D. toumatou*. Although mycorrhizal symbiosis may increase phosphorus concentration under all four shrub species studied relative to the open grassland (Mao et al. 2019), modification of the environment by *K. serotina* and *C. propinqua* may also cause fertile islands under their canopies. Although actinorrhizal symbiosis may increase nitrogen concentration under *D. toumatou* compared to the open grassland, *D. toumatou* is a deciduous species like *R. rubiginosa*. Soil samples were taken under canopies of these two species during the fully-leafed period of the year, which may affect any occurrence of fertile islands under their canopies. During the fully-leafed period, fewer leaves may be deposited as litter for eventual mineralisation compared to during the leafless period.

The outcomes of my study partly supported the theory of 'fertile islands' for *K. serotina*, with higher fertility in the bioassay, which can be explained by the higher concentration of total nitrogen (for the ungrazed plots), Olsen P, and nitrate. *Coprosma propinqua* shrubs also showed the effect in higher organic matter content and nitrate concentration. Similar effects were seen under *D. toumatou* (higher carbon, nitrogen, nitrate, and Olsen P), but none were significant, and there was little sign of a fertile island effect under *R. rubiginosa*.

Higher concentrations of total nitrogen (0.11–20 g kg^{-1}) and higher concentrations of available phosphorus (0.4–93.0 mg kg^{-1}) in soils under woody plant canopies than soils in adjacent open grasslands have been reported (Belsky et al. 1989; Facelli & Brock 2000; Chambers 2001; Appendix S9). For instance, Belsky et al. (1989, 1993), working at two sites in Kenya (400–500 mm and 750 mm annual rainfall), reported that soils under *Acacia tortilis* and *Adansonia digitata* showed higher concentrations of total nitrogen (0.03 g kg^{-1}) and available phosphorus (13.50 mg kg^{-1}) than soils in the adjacent open grassland (0.01 g kg^{-1} and 6.00 mg kg^{-1}, respectively) for the arid site. However, the difference between soils under the two woody plants and those in the adjacent open grassland in soil nutrient content was smaller at the higher rainfall site (Appendix S9).

Higher nutrient and carbon concentrations under shrubs and trees can be caused by uptake from deeper layers in the soil, or from solubilisation, and then the deposition of leaf and stem litter (Belsky et al. 1989), from animal deposits if defecation tends to occur under shrubs (Frank et al. 2000; Clark et al. 2005) and from the decomposition of cadavers if animals tend to die under shrubs, as they often do (Vass et al. 1992; Carter et al. 2007). Mark and Whigham (2010) reported that soils in a century-old sheep graveyard, in the high-alpine zone of south-central South Island New Zealand, showed higher concentrations of phosphorus and nitrate than soils of adjacent areas, with effects on vegetation composition. However, no signs of animal dung and no cadavers were seen under shrubs in this study.

Is the fertile island effect the result of shrub modification of the environment or of shrubs preferentially establishing in areas of high soil nutrients?

The fertile islands effect may be caused by woody plants modifying the environment or by plants preferentially establishing in soils of relatively high fertility or both. However, deposition of faeces by animals and their cadavers add nutrients to soil, which may also mediate the occurrence of fertile islands. The occurrence of fertile islands should, therefore, be examined in the broader context of soil development and growth of vegetation, and the deposition of nutrients particularly by the arthropod fauna, birds and mammals.

Soil development and growth of vegetation

Concentrations of soil nutrients such as nitrogen and phosphorus change during soil development. Nitrogen and phosphorus occur both in inorganic forms and in organic matter in the soil (Rowell 1994). Inorganic nitrogen comes mostly from precipitation but biological fixation is also an important source of inorganic nitrogen. The initial stage of soil development is directly related to the growth of vegetation, which deposits organic matter on the surface, causing depth gradients in concentrations of carbon, nitrogen and many phosphorus fractions in the soil profile (Stevens & Walker 1970). Moreover, most of the phosphorus in young soils is in the inorganic form, which is mostly converted into organic phosphorus as the soil ages (Turner et al. 2007). Therefore, the effect of plants on concentrations of nitrogen and phosphorus in soil can change with the ages of the soil and the plant. In the current study, soils under large *C. propinqua* shrubs showed higher concentrations of organic matter and total nitrogen compared to those under small *C. propinqua* shrubs. In another study, Facelli and Brock (2000) did not report any difference in soil nutrients between soils under young *Acacia papyrocarpa* trees and soils in adjacent open grassland areas in semi-arid (230 mm annual rainfall) Australia, but under old *A. papyrocarpa* trees the soils showed higher organic matter content and higher concentrations of total nitrogen and total and available phosphorus. Moreover, soil nitrogen concentration decreased, but levels of organic matter and total and available P under a former canopy remained high for up to 50 years after the death of the plant (Facelli & Brock 2000). The persistence of high available phosphorus concentration suggests that plants may preferentially establish in areas of high phosphorus availability, but the decrease in total nitrogen also suggests that *A. papyrocarpa* may have an important effect on soil nitrogen concentration. Therefore, it seems that there are causes (drivers) and effects of fertile islands. Patches of high soil fertility are required for shrub germination and establishment, but once established the shrubs may maintain and/or increase soil fertility (Facelli & Brock 2000). Although plants may establish in patches of high soil fertility, plant modification of the microenvironment also appears to make an important contribution to the occurrence of an associated 'fertile island'.

Do fertile islands vary along a rainfall gradient?

The findings of the current study (1.1 g kg^{-1} higher soil total nitrogen and 4.46 mg kg^{-1} higher soil available phosphorus concentrations) under a *Kunzea serotina* canopy than in the adjacent open grassland, conducted in an area of 550 mm annual precipitation, are at the lower range of what previous workers have found for fertile islands (Appendix S9), but within the range expected for that amount of precipitation (Figs. 3, 4).

Conclusion

The ecological mechanisms behind the fertile islands are varied and not well understood. The review (Appendix S9) implies that the fertile islands are not restricted to arid and semiarid areas although they appear to be most prevalent under such climatic regimes. Further, the review showed that although fertile islands occur in many areas along rainfall gradients, they are more common in areas receiving less than 800 mm annual rainfall. The current study was conducted in a dry sub-humid area receiving 550 mm average annual rainfall during the study with a long-term average (1981–2010) of 594 mm (Macara 2015) and so falls within the range of fertile islands reported in previous studies.

More research needs to be conducted along the rainfall gradient in different ecosystems using different woody plant species to more adequately test the fertile islands theory. For instance, seeds of dryland woody plants could be sown in both fertile and infertile soils and their growth monitored. Another line of enquiry could be the use of shrub removal and addition experiments to compare soils and the growth of understorey herbaceous species under live woody plants with those from where woody plants were recently removed and also in the adjacent open grassland. Although such studies could improve our understanding of the mechanisms behind the fertile islands effect, these would need to be long-term experiments.

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Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Analysis of variance (ANOVA) showing the effects of *Kunzea serotina* shrubs or grassland on soil fertility.

Appendix S2. ANOVA showing effects of *Kunzea serotina* shrub canopy on soil nitrogen content.

Appendix S3: ANOVA showing effects of *Kunzea serotina* canopy on soil nitrate content (log-transformed).

Appendix S4: ANOVA showing effects of *Kunzea serotina* shrub canopy on Olsen available phosphorus (log-transformed).

Appendix S5: ANOVA for total nitrogen in *Discaria toumatou* plots.

Appendix S6: ANOVA for soil organic matter content under *Coprosma propinqua*.

Appendix S7: ANOVA for soil nitrate under *Coprosma propinqua*.

Appendix S8: ANOVA for total nitrogen under *Coprosma propinqua*.

Appendix S9: Review of ‘fertile islands’ along the rainfall gradient.

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