REVIEW

Nitrogen cycling in gorse-dominated ecosystems in New Zealand

Guna N. Magesan^{1,3*}, Hailong Wang¹ and Peter W. Clinton²

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Abstract: The legume gorse (*Ulex europaeus*) is one of the most widespread nitrogen (N) fixing species and is also one of the most invasive weeds of New Zealand. Despite its widespread occurrence, little research has been undertaken on N cycling in gorse ecosystems. This lack of knowledge is important since gorse covers up to 900 000 ha in New Zealand and there is a potential for a large environmental impact from the cycling of large amounts of N fixed by gorse entering waterways and water bodies. We undertook this overview to summarise the current understanding of N cycling in gorse-dominated ecosystems and identify knowledge gaps and provide recommendations for future research in New Zealand. Specifically, we describe some key biological processes associated with N cycling under gorse-dominated ecosystems. Gorse is capable of fixing up to 200 kg ha⁻¹ N annually during the period of rapid dry-matter accumulation. External factors such as temperature, fertiliser application, moisture, pH and atmospheric CO₂ can affect biological N fixation in legumes, but such information is scarce for gorse. Gorse produces large quantities of litter, and N concentrations are generally higher in gorse litter than in the litters collected under other shrubs and trees. During and after litter decomposition, N is released into the surrounding soil, resulting in higher N concentration in the soils under gorse sites compared with under other species. This is due to the ability of gorse to fix N and produce large quantities of litter. The contribution of gorse-infested land to surface water eutrophication is also discussed because gorse has invaded large areas within the catchment of some significant lakes in New Zealand. From this review a good understanding of N cycling under gorse ecosystems has emerged. To better understand the wider environmental impact of gorsedominated ecosystems in New Zealand, further research is needed including monitoring and modelling the impact of climate change on N fixation, leaching and C sequestration in gorse-dominated ecosystems.

Keywords: catchments; leguminous weeds; litter decomposition; N fixation; nitrate leaching; water quality

Introduction

In most natural ecosystems, nitrogen (N) is the primary nutrient that limits plant production (Vitousek et al. 1997). Human-induced activities and disturbance have helped increase contributions to the N cycle, through energy and fertiliser production, and mobilisation of N from long-term storage pools (Galloway 1998; Goulding et al. 1998). This extra reactive N can affect ecosystem processes such as N deposition and soil acidification, and microbiologically mediated soil processes such as mineralisation, immobilisation, nitrification, denitrification, and emission of nitrous oxide and methane (Goulding et al. 1998; Fageria & Stone 2006).

Of all sources, biological N fixation is the most 'environmentally friendly' approach to supplying N to ecosystems (Jensen & Hauggaard-Nielsen 2003). Leguminous and actinorhizal plants form nodules with their respective host plants and fix N in association with rhizobia or *Frankia* (Franche et al. 2009). *Rhizobium*—legume symbioses represent the major mechanism of biological N fixation compared with the N-fixing heterotrophs and associative bacteria and actinorhizal plants (Zahran 2001). Through symbiotic fixation, these N-fixing plants provide high inputs of N to the ecosystem (Watt et al. 2003; Augusto et al. 2005). Such N supply increases soil fertility and builds up the soil N pool

through the decomposition of N-rich litter, and the release of N from roots and nodules (Ehrenfeld 2003; Goldstein et al. 2010) can contribute significantly to the global N cycle (Colebatch et al. 2002). The quantity of symbiotic N fixation remains difficult to assess as it varies from species to species, and depends on environmental conditions (Fageria & Stone 2006; Jackson et al. 2008).

Nitrogen-fixing species are typically pioneer species (McQueen et al. 2006; Goldstein et al. 2010) colonising disturbed ecosystems, including those that are fire prone (Arianoutsou & Thanos 1996). In New Zealand, gorse (*Ulex europaeus*) is one of the most widespread legume species. Egunjobi (1969) reported the superiority of gorse over other legume species in its ability to accumulate N. Wardle and Greenfield (1991) reported that introduced N-fixing species such as gorse generally have high fixation rates when compared with indigenous N-fixers. It is important to estimate the N benefit from biological N fixation, and understand soil N turnover (Ehrenfeld 2003; Ganjegunte et al. 2005).

Widespread concern about increasing concentrations of nitrate in surface water has focused attention on N leaching in recent years (Goldstein et al. 2010). A number of studies have been carried out to identify the source and extent of N leaching on a catchment scale in New Zealand (Quinn & Stroud 2002). However, the contributions from leguminous weeds such as

¹Scion, Private Bag 3020, Rotorua 3046, New Zealand

²Scion, PO Box 29237, Fendalton, Christchurch 8540, New Zealand

³Present address: Maori Research Institute, PO Box 12103, Rotorua 3045, New Zealand

^{*}Author for correspondence (Email: guna.magesan@maoriresearchinstitute.co.nz)

gorse and broom (*Cytisus scoparius*) have not received much attention despite their widespread distribution.

In this review, we focus on N cycling under gorsedominated ecosystems in New Zealand, and aim to offer insights on the importance of study of leguminous weeds, identify knowledge gaps, and highlight the topics for future research.

Gorse as a weed

Gorse is a perennial, evergreen, leguminous shrub and is native to Western Europe and north-west Africa. It was deliberately introduced to New Zealand as a hedge plant and as a fodder crop for domestic stock (Lee et al. 1986). As gorse is tolerant of a large range of climates and soil types, it has spread, covering large areas of marginal and unproductive land, over-grazed pastures, and roadsides (Matthews 1982; Lee et al. 1986; Weir et al. 2004; McAlpine et al. 2009; Sullivan et al. 2009) and has colonised around 900 000 ha or approximately 3.6% of New Zealand (Sandrey 1985). In 1900 gorse was declared a noxious weed (Moss 1960). Rees and Hill (2001) reviewed published data on the demography of gorse in New Zealand.

Gorse is regarded as a weed because of its invasiveness, and economic and environmental impacts (Gaynor & MacCarter 1981; Isern 2007). The main biological features that contribute to its weed status are its vigorous growth, N-fixation ability, prolific seed production, longevity of seeds in the soil, its sprouting ability after cutting or fire, and the low palatability of mature plants to stock (Clements et al. 2001; Hill et al. 2001; Sixtus et al. 2003). In pastoral areas, gorse reduces the potential for grazing by cattle and sheep (Krause et al. 1988), while in New Zealand plantation forests gorse can increase the cost of site preparation and at the same time reduce growth of forests by competing for water, light and nutrients (Richardson et al. 1996). Gorse can also suppress native plant communities (Lee et al. 1986; McQueen et al. 2006; Yelenik et al. 2007) or alter subsequent vegetation succession (Bellingham et al. 2005; Sullivan et al. 2007). In New Zealand, gorse is becoming established as the dominant species responsible for the initial post-disturbance shrub community, replacing native mānuka (Leptospermum scoparium) and kānuka (Kunzea ericoides) scrub communities (Harris et al. 2004). This may have implications for N cycling and further successional changes and potential environmental consequences of N fixation and ecosystem N processes.

In general, there are two seeding periods each year (Hill et al. 2001; Tarayre et al. 2007) following two main flowering periods (autumn and spring—summer). Gorse is a prolific seed producer and an average seed bank population in the top 6 cm of soil is about 6000 seeds m⁻² (Zabkiewicz & Gaskin 1978; Partridge 1989). The seeds have a hard, water-resistant coating that allows them to remain dormant in the soil for at least 30 years (Sixtus et al. 2003; Gonzalez et al. 2010). The ability to produce large seed banks helps gorse to persist.

Human-induced disturbance can facilitate invasion by weeds. When there are high numbers of gorse seeds present in the soil, disturbance of any form – and fire, in particular – is likely to favour recruitment of gorse over native species, as gorse germination is strongly promoted by heat (Zabkiewicz & Gaskin 1978; McAlpine et al. 2009).

A voluminous body of literature on gorse deals predominantly with control measures: mechanical, chemical,

fire, and grazing in various combinations. The success and efficacy of these measures are not covered in this overview. MacCarter & Gaynor (1980), Gaynor & MacCarter (1981) and Richardson & Hill (1998) have produced comprehensive literature reviews on the impact of gorse and its control in New Zealand and Australia.

Benefits of gorse

Although considered a weed, gorse does offer some benefits. It has been used for hedges and stock feed in large areas of the country; it also stabilises, develops, and enriches soils. In New Zealand, where gorse flowers for almost the whole year (Miller 1970; Hill et al. 2001), it provides the honey industry with an important source of early-spring pollen for bees (Sandrey 1985). It is a source of fodder for goats and sheep (Lambert et al. 1989). In the past, gorse has been used as a source of protein in animal food (Bao et al. 1998). In some situations, gorse has acted as a nursery crop for native seedlings (Hackwell 1980; Lee et al. 1986; Wilson 1994) while some studies have noted its useful function in biological conservation as a pioneer transient successional species in the re-establishment of indigenous forest vegetation (Druce 1957; Healy 1961; Harris et al. 2004; Sullivan et al. 2007). Gorse contains volatile oils, giving it a high fuel load (Anderson & Anderson 2009), which needs to be explored to see if gorse can be used for biofuel/biodiesel production. Gorse is considered a promising candidate as a biomass source, and it has a total xylose content of 12%, thus qualifying it as a suitable material to extract xylan-derived compounds (Ligero et al. 2011). Xylan is a generic term used to describe a wide variety of highly complex polysaccharides.

Biological N fixation by gorse

Biological N fixation is a process in which inert atmospheric N₂ gas is converted into plant-available N. It is the result of a structurally and physiologically highly organised, host-specific mutualistic interaction between bacteria and legumes (Fustec et al. 2010). In this symbiotic association, the host plant supplies the bacteria with carbohydrates for energy, and the bacteria reciprocate by supplying the plant with fixed-N compounds (Graham & Vance 2003; Fageria & Stone 2006). A major portion of biological N is fixed by species of *Rhizobium* and *Bradyrhizobium*, and they constitute the predominant symbionts for most legume species throughout the world (Gage, 2004). Weir et al. (2004) showed that all introduced weeds in New Zealand, including gorse, were aligned with *Bradyrhizobium* species. Table 1 gives some introduced weeds in New Zealand with their N-fixation estimates.

N-fixing species contribute to ecosystem N budgets. In general, background resource levels influence nodulation, fixation, and plant growth (Goergen et al. 2009). The amount of N fixation in the nodule depends on nutrient availability, soil pH, moisture and temperature (Graham & Vance 2003; Fustec et al. 2010). Here we discuss our understanding of the impacts of some of these factors on N fixation of gorse.

Fertiliser N supply can affect N fixation in gorse. It is well documented that externally applied N inhibits both nodulation and N fixation in legumes (Dixon & Wheeler 1983; Goergen et al. 2009). In other words, as N levels

Table 1. Nitrogen-fixing rates by exotic species in New Zealand. Note that estimations of fixation will vary with the methods used, and thus are only indicative (adapted from McQueen et al. 2006).

Species	Estimated annual N fixation (kg ha ⁻¹)	Reference
Alder (Alnus spp.)	40–300	Silvester 1976
Gorse (<i>Ulex europaeus</i>)	100-200	Egunjobi 1969
Tree lupin (Lupinus arboreus)	160	Gadgil 1982
Broom (Cytisus scoparius)	111	Watt et al. 2003
White clover (<i>Trifolium repens</i>) (in pasture)	4–88	Augusto et al. 2005

increase, nodule weight, density and fixation rates decrease and dependence on mineral N increases (Streeter 1985). For example, MacConnell and Bond (1957) reported that external application of ammonium ions decreased the mean dry weight of gorse nodules per plant. Thornton et al. (1995) grew gorse plants over two seasons, manipulating the rate of N fixation from the air by varying exogenously applied N in the form of either nitrate or ammonium ions. ¹⁵N was used as a tracer to estimate total root uptake, and N fixation to the N content of new shoot growth, in the second season. When nodulated gorse plants were grown in sand, N fixation from the air provided the main source of N for plants supplied with a low level of N-containing fertiliser but not for those supplied with abundant N-containing fertiliser. Goergen et al. (2009) reported from their greenhouse experiment that additional water and N increased biomass production, but plants grown without N had the largest, most active nodules.

Biological N fixation is a phosphorus (P) demanding process, so most legumes are also highly dependent on P-supply by arbuscular mycorrhizal fungi in natural ecosystems (Azcón et al. 1991). Studies have shown that inputs of P enhance the growth of gorse (Cheaïb et al. 2005); result in an increase in the abundance and biomass of N-fixing shrubs (Augusto et al. 2005); and promote the production of nodules and the N-fixing activity of leguminous shrub species (O'Toole et al. 1984; Augusto et al. 2005). These can result in a higher N-fixation flux and a better supply of N and P for gorse species, which then acquired a competitive advantage over non-fixing species. Augusto et al. (2005) estimated that the annual N-fixation flux of gorse understorey ranged from 0.5 to 5.1 kg ha⁻¹ N in mature pine stands of south-western France. But in young open pine stands, annual gorse understorey fixation ranged from 8.1 to 57.4 kg ha⁻¹ N and increased with P fertiliser application. They suggested that the difference between mature and young pine stands was probably due to increasing light interception of the tree canopy, weed control operations, and the vegetation succession of the understorey. The ability of woody legumes to acquire P is thus of paramount importance to their role as N-fixers (Adams et al. 2010).

Symbiotic N fixation and ammonium assimilation can cause acidification of soils under legumes (Jensen &

Hauggaard-Nielsen 2003). However, such information is not available for gorse.

Nitrogen availability may become increasingly important in governing ecosystem processes as atmospheric CO₂ increases and temperature increases through global change (Jackson et al. 2008). Several studies have shown that N fixation can be enhanced under CO₂ enrichment (Schortemeyer et al. 2002) and the soils under N-fixing species can play a major role in land rehabilitation and C sequestration strategies (Resh et al. 2002). Although it is recognised that woody legumes can be highly responsive to atmospheric CO₂ (Adams et al. 2010), little is known of how gorse and its capacity to fix N may be influenced by global change phenomena. While N fixation is commonly temperature dependent, this remains unexplored for gorse.

Dry matter accumulation

Egunjobi (1969) studied nine ecosystems in New Zealand, including gorse. He found that young gorse grows very quickly, and that gorse was superior to other species in its ability to accumulate dry matter, and N content. Gorse had high annual dry matter accumulation compared with other shrubs. The quantity of dry matter (above ground) produced in the first year was comparable with pasture production on the same soil type. After the first year, rapid production and accumulation of dry matter continued, lasting some 4–5 years. Mean annual accumulation of dry matter was 15 000 kg ha⁻¹. After the first 5 years, productivity appeared to fall, and between 7 and 10 years, the mean annual accumulation of dry matter was only approximately 10 000 kg ha⁻¹. Egunjobi (1969) reported that annual biomass accumulation decreased with age (c. 3000–4000 kg ha⁻¹ for sites between 16 and 33 years old).

In another field study, Lambert et al. (1989) studied 11 scrub species in New Zealand and found that gorse had a high survival rate, and was the most productive shrub in the trial. Gorse produced the most dry matter, and more than 85% of its annual production was in spring and summer. However, the major proportion of the dry matter was in stem material rather than in the leaf material.

Dry matter production does not necessarily increase with added fertiliser (Egunjobi 1971a,b) but occasionally added phosphate has been reported to produce a growth response (Richardson & Hill 1998). Augusto et al. (2005) found that the response of vegetation in pine forest understorey to increasing doses of P fertiliser was an increase in both gorse density (plants m⁻²) and biomass. In high P fertiliser treatments, the understorey was almost completely composed of gorse, and the mean total biomass reached 31 000 kg ha⁻¹ after six growing seasons.

Egunjobi (1969) reported the superiority of gorse over other legume species in its ability to accumulate N. During the period of rapid dry-matter accumulation, N accumulated at an annual rate of 100–200 kg ha⁻¹ in gorse sites (Egunjobi 1969). Watt et al. (2003) assessed N fixation by broom, another common weed in New Zealand. They reported that broom was an effective fixer, deriving 81% of N in above-ground tissues from the atmosphere, which was equivalent to 111 kg ha⁻¹ N per year, and returned 17 kg ha⁻¹ N to the soil as leaf litterfall from mid- to late autumn. Watt et al. (2003) also suggested that there was some transfer of fixed N from the broom to radiata pine (*Pinus radiata*).

Litter accumulation and decomposition

Most of the annual production of biomass, with its high N content, ends up in litter (Hackwell 1980; Ganjegunte et al. 2005). Litterfall includes all plant organs and tissues that fall to the ground, together with decomposing roots. Egunjobi (1971a,b) reported that litterfall accounts for nearly 50% of total annual dry matter production in gorse sites. It is the principal source of organic matter for the biochemical cycling of nutrients in terrestrial ecosystems (Meentemeyer et al. 1982).

Gorse produced more litter than other shrubs and shrubtree stands at Taita (Egunjobi 1969). For example, Egunjobi (1969) reported an annual litterfall for a 7- to 8-year-old gorse site was approximately 9000 kg ha⁻¹. Also, the litter mass and its N content changed with the age of the gorse stand (Table 2). Lee et al. (1986) recorded gorse densities of 60 000 stems ha and a mean litter depth of 55 mm on mature sites in Dunedin, New Zealand. In large gorse thickets, large amounts of dead material can collect both in the branches and on the ground. Gorse material collected above the ground generally has a lower density and is in a more aerated state (Egunjobi 1969). Large amounts of litter produced by gorse can modify the substrate, and make it acidic (Lee et al. 1986). Accumulation of such an acidic litter layer at gorse sites may impact on soil health and could inhibit establishment of other species (Lee et al. 1986).

Decomposition of litter is an important process in most terrestrial ecosystems because of its role in regulating build-up of soil organic matter, releasing of nutrients for plant growth, and influencing C flux from soil (Ganjegunte et al. 2005). Rates of litter decomposition are influenced by both the quantity and quality of litter as well as by environmental parameters such as temperature, humidity, moisture content and readily available sources of C (Prescott et al. 1993; Forrester et al. 2006).

Nitrogen-fixing species often have high tissue N concentrations and low C:N ratios. The litter decomposes more rapidly and can provide substantial amounts of N to the soil through litter decomposition (Forrester et al. 2006; Goergen et al. 2009). In New Zealand, Egunjobi (1969) showed that N concentrations are generally higher in gorse litter than in litter collected under other shrubs and trees. Nitrogen can be transferred from N-fixing species to non-N-fixing species via the decomposition of litter and the subsequent mineralisation of organic N including root exudates (Forrester et al. 2006).

Table 2. Quantity of litter and its N content on the floor of gorse sites* at Taita, Lower Hutt (adapted from Egunjobi 1969).

Age of gorse	Litter (kg ha ⁻¹)	N content of litter	
(years)		(%)	(kg ha ⁻¹)
4	9 130	1.50	137
7	8 800	1.47	129
10	11 810	1.93	228

^{*} Note this does not include seeds as they probably were excluded by sieve.

However, we have little knowledge of whether such transfer happens in gorse-dominated ecosystems.

The mixing of litters (from radiata pine and understorey litters) can reduce the overall nutrient turnover rates in the mixed litter materials (Ganjegunte et al. 2005). The consequences of mixing litter from different species on the long-term dynamics and quality of soil organic matter has not been sufficiently researched (Prescott 2005). As gorse sites can produce large amounts of litter material with a relatively high concentration of N (Egunjobi 1969), it is important to investigate the fate of the gorse-derived N in the receiving environment and its ecological impact, particularly in a sensitive environment. Studies on gorse litter quality and decomposition, and the mineralisation rates of N in litter and soil, are essential to quantify the potential N input to the lakes catchments from gorse ecosystems.

Nitrogen mineralisation

Mineralisation is a process where organic N is converted into inorganic or mineral N in two stages: ammonification and nitrification (Bolan & Hedley 2003). The amounts of C and N in litter and in decomposing microbial biomass are important factors controlling the occurrence of net N mineralisation or net N immobilisation. In an incubation study, O'Toole et al. (1984) observed that although there was a lengthy delay prior to onset of active N mineralisation in fresh gorse litter, this material released significantly more mineral N during 80 days' incubation than either senescent gorse or non-gorse litter. Ammonium-N comprised >90% of the N released by each material (O'Toole et al. 1984).

Despite many studies on litter decomposition, there is little information on decomposition and N mineralisation of litter and soil under gorse sites. O'Toole et al. (1984) observed that the patterns and quantities of N mineralisation differed markedly in 'high' and 'low' gorse soils. Release of soil N commenced without delay in the high-gorse soil and increased considerably up to c. 96 days of incubation. In contrast, N mineralisation rates in the low-gorse soil remained very low throughout incubation and were very much inferior to rates in the high-gorse soil. Wardle and Greenfield (1991) studied mineral N release from root nodules of a range of nodulated leguminous and non-leguminous plants; in the short term (< 2 months) much of the nodule N is not mineralised when incorporated into soil systems. The component that is released as mineral N appears to be significantly influenced by the forms of N present in the nodules, but not by the total concentrations of N or the C:N ratios of the tissues investigated (Wardle & Greenfield 1991). On average, invasive leguminous species can increase soil N mineralisation and nitrification by at least 50% (Rout & Callaway 2009).

Denitrification and nitrous oxide (N₂O) emissions

Denitrification is a complex biological process responsible for returning fixed N to the atmosphere (Philippot et al. 2009). Some field experiments have shown that there can be some loss of fixed N from soils by denitrification carried out by rhizobia (O'Hara & Daniel 1985). However, we are not aware of any research on soil processes within gorse ecosystems

and the influence of gorse on denitrification. The contribution of actively N-fixing plants to N_2O has been rarely reported and the relationship between N_2O emissions and biological N fixation by legumes is not well understood (Zhong et al. 2009). There is a clear knowledge gap regarding how emissions of N_2O are affected by gorse, despite its importance from a climate-change point of view.

Nitrogen content in soil

During and after litter decomposition, N in plants is released to soil. In general, soils under N-fixing plants often have greater amounts of available N than soils from areas lacking N-fixers. The N concentration was higher in the soils under gorse sites than under older stands dominated by non-N-fixing shrubs and trees (Egunjobi 1969). Over 65% of the N taken up by gorse is returned annually to the soil from measurements of the N concentration of plant contents, litterfall, and rain throughfall (Egunjobi 1971a,b). The N content of the soil and of the soil plus total vegetation tends to increase with increasing gorse cover (O'Toole et al. 1984). Sparling et al. (1994) reported that organic C and N were higher under gorse than under other vegetation. Sites with gorse accumulated more N because of its N-fixing ability and the large quantities of litter it produced. However, the exact mechanisms responsible for this increase in available soil N have not been characterised for many systems, gorse included. Two potential mechanisms could be decomposition of N-rich litter and rhizodeposition of amino acids (Jones et al. 2004).

Although decomposition as a mechanism is well known, rhizodeposition has received little attention as a source of N to total ecosystem N budgets (Goergen et al. 2009). This suggests that invasive woody legumes may contribute substantial amount of N to ecosystems via this mechanism, but information on N rhizodeposition from gorse is lacking and more research is needed in this area.

Extent of N leaching under gorse

The loss of N from the root zone has environmental implications such as nitrate pollution of groundwater, eutrophication of surface waters and emissions of the greenhouse gas N_2O (Philippot et al. 2009). In addition to 'fixing' N, gorse can produce N-rich biomass and residues (Egunjobi 1969). Fixed N and N from mineralisation of the N-rich litter have the potential to become nitrified and subsequently leach nitrate into soil—water systems (Goldstein et al. 2010), although this issue remains unexplored for gorse.

Dyck et al. (1983) studied nitrate losses from various undisturbed and disturbed (by spraying, crushing and burning) gorse and forest ecosystems. Soil water was periodically collected from 10 suction-cup samplers for up to 2 years after disturbance in each treated area as well as in undisturbed controls, and analysed for nitrate N as an indicator of nutrient loss. They found that in undisturbed areas more nitrate was leached from sites under gorse than from sites under the tree species. For example, nitrate-N concentrations from the gorse area averaged 5.1 g m⁻³ whereas nitrate concentrations from radiata pine stands averaged 0.006 g m⁻³. In the same study, Dyck et al. (1983) suggested that decomposing gorse tissue released fairly large amounts of nitrate to groundwater.

Nitrate levels in soil water under the control plot in the gorse area averaged 5.1 g m⁻³ and showed a peak in the first winter of monitoring and another peak the following autumn. While nitrate-N concentrations in the treated sites (crushed and burned) were high one week after burning, a maximum recorded value (23.3 g m⁻³) occurred in week 10. Nitrate in soil water increased immediately in response to the second burn and peaked at 22 g m⁻³. Concentrations then rapidly declined to background levels in the control plots. Spraying had no effect on nitrate levels in soil water.

Egunjobi (1969) suggested that the level of soil N will decrease as gorse is replaced by non-N-fixing species. This decline will be due to lower uptake of N from non-N-fixing species, leaching, and runoff losses. According to Egunjobi (1969) this should continue as gorse is replaced by other species, leading to a decline in soil N content.

Care must be taken when estimating leaching losses under gorse because of low throughfall at gorse sites (i.e. not all the rainfall is available to leach N). Throughfall is generally defined as that portion of the gross rainfall that reaches the soil directly through spaces in the canopy and as drip from leaves, twigs, and stems (Aldridge 1968). Aldridge (1968) reported that throughfall levels were 20–30% of the gross rainfall reaching the ground for the same period on a similar gorse site.

In most areas of New Zealand, nitrate leaching mainly occurs in late autumn, winter, and early spring, when there is an excess of rainfall over evapotranspiration and the soil is at or near field capacity (Magesan et al. 1996). At these times of the year, plant uptake of N is low and therefore nitrate may be present in considerable quantities in the soil solution. Recently some studies have looked into N leaching under gorse stands. However, more research is needed to see how soil type, climatic conditions, distribution and age of gorse will impact on water quality.

Conclusions and suggestions for future research

Despite the widespread occurrence of gorse in plantation forests in New Zealand, little research has been undertaken to investigate N cycling under gorse-dominated ecosystems. With water quality and climate change becoming important issues, research on amounts and rates of N fixation by gorse is crucial because of the potentially large amounts of N fixed, cycled and possibly leached. Also, because of its ability to rapidly accumulate dry matter, gorse may be effective at sequestering atmospheric carbon. But we found no published research on this topic.

As rates of N fixation depend on a number of factors such as the density, age and growth of the host plants and the degree of nodulation, research on these factors is also important. Since the amount of N fixation in the nodule depends on soil temperature, moisture, pH, and nutrient availability, both laboratory and field studies are needed in this area of research.

Gorse can produce large quantities of litter and the gorse sites generally accumulate more N than other shrubs. Studies on gorse litter decomposition (and rhizodeposition) and the mineralisation rate of N in litter and soil are essential to quantify potential N inputs to lake catchments from gorse-dominated ecosystems.

Under the scenario of global warming, research is needed to see how N fixation in gorse responds to atmospheric CO₂, and

N accumulation in soil. The influence of biological N fixation on denitrification and N_2O emissions in gorse ecosystems has not been reported and the relationship between biological N fixation and denitrification and/or N_2O emissions in gorse ecosystems is not well understood.

Until recently, few studies have looked into N leaching under gorse stands. However, more research is strongly recommended to see how soil type, climatic conditions, distribution and age of gorse, land-use change and land-use history will contribute to the potential leaching loss of N from soils and have impacts on water quality and eutrophication of water bodies.

Finally, a mechanistic understanding of plant—microbe—soil N cycling is missing for gorse ecosystems. The time is ripe to place greater emphasis on linking microbially mediated soil N transformations, plant—microbe interactions, and plant N uptake and utilisation (Jackson et al. 2008).

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References

- Adams MA, Simon J, Pfautsch S 2010. Woody legumes: a (re)view from the South. Tree Physiology 30: 1072–1082.
- Aldridge R 1968. Throughfall under gorse (*Ulex europaeus*) at Taita, New Zealand. New Zealand Journal of Science 11: 447–451.
- Anderson SAJ, Anderson WR 2009. Predicting the elevated dead fine fuel moisture content in gorse (*Ulex europaeus* L.) shrub fuels. Canadian Journal of Forest Research 39: 2355–2368.
- Arianoutsou M, Thanos CA 1996. Legumes in the fireprone Mediterranean regions: an example from Greece. International Journal of Wildland Fire 6: 77–82.
- Augusto L, Crampon N, Saur E, Bakker MR, Pellerin S, de Lavaissière C, Trichet P 2005. High rates of N fixation of *Ulex* species in the understory of maritime pine stands and the potential effect of phosphorus fertilization. Canadian Journal of Forest Research 35: 1183–1192.
- Azcón R, Rubio R, Barea JM 1991. Selective interactions between different species of mycorrhizal fungi and *Rhizobium meliloti* strains, and their effects on growth, N₂-fixation (¹⁵N) and nutrition of *Medicago sativa* L. New Phytologist 117: 399–404.
- Bao IM, Rodriguez RJL, Dominguez GMJ, Crespo RI, De Vega A 1998. *Ulex europaeus* as a protein source for the agrifood industry in Galicia, Spain. In: El Bassam N, Behl RK, Prochnow B eds Sustainable agriculture for food, energy and industry: strategies towards achievement. London, James & James. Pp. 716–721.
- Bellingham PJ, Peltzer DA, Walker LR 2005. Contrasting impacts of a native and an invasive exotic shrub on flood-plain succession. Journal of Vegetation Science 16: 135–142.
- Bolan NS, Hedley MJ 2003. The role of carbon, nitrogen and sulfur cycles in soil acidification. In: Rengel Z ed. Hand

- book of soil acidification. New York, Marcel Dekker. Pp. 29–56.
- Cheaïb A, Mollier A, Thunot S, Lambrot C, Pellerin S, Loustau D 2005. Interactive effects of phosphorus and light availability on early growth of maritime pine seedlings, Annals of Forest Science 62: 575–583.
- Clements DR, Peterson DJ, Prasad R 2001. The biology of Canadian weeds. 112. *Ulex europaeus* L. Canadian Journal of Plant Science 81: 325–337.
- Colebatch G, Trevaskis B, Udvardi M 2002. Symbiotic nitrogen fixation research in the postgenomics era. New Phytologist 153: 37–42.
- Dixon ROD, Wheeler CT 1983. Biochemical, physiological and environmental aspects of symbiotic nitrogen fixation. In: Gordon JC, Wheeler CT eds Biological nitrogen fixation in forest ecosystems: foundations and applications. The Hague, Martinus Nijhoff / Dr W. Junk. Pp. 107–171.
- Druce AP 1957. Botanical survey of an experimental catchment, Taita, New Zealand: the central catchment at Taita Experimental Station. DSIR Bulletin 124. Wellington, Department of Scientific and Industrial Research. 81 p.
- Dyck WJ, Gosz JR, Hodgkiss PD 1983. Nitrate losses from disturbed ecosystems in New Zealand A comparative analysis. New Zealand Journal of Forestry Science 13: 14–24.
- Egunjobi JK 1969. Dry matter and nitrogen accumulation in secondary successions involving gorse (*Ulex Europaeus* L.) and associated shrubs and trees. New Zealand Journal of Science 12: 175–193.
- Egunjobi JK 1971a. Ecosystem processes in a stand of *Ulex Europaeus* L. I. Dry matter production, litter fall and efficiency of solar energy utilization. Journal of Ecology 59: 31–38.
- Egunjobi JK 1971b. Ecosystem processes in a stand of *Ulex Europaeus* L. II. The cycling of chemical elements in the ecosystem. Journal of Ecology 59: 669–678.
- Ehrenfeld JG 2003. Effects of exotic plant invasions on soil nutrient cycling processes. Ecosystems 6: 503–523.
- Fageria NK, Stone LF 2006. Physical, chemical, and biological changes in the rhizosphere and nutrient availability. Journal of Plant Nutrition 29: 1327–1356.
- Forrester DI, Bauhus J, Cowie AL, Vanclay JK 2006. Mixedspecies plantations of *Eucalyptus* with nitrogen-fixing trees: A review. Forest Ecology and Management 233: 211–230.
- Franche C, Lindström, K, Elmerich C 2009. Nitrogen-fixing bacteria associated with leguminous and non-leguminous plants. Plant and Soil 321: 35–59.
- Fustec J, Lesuffleur F, Mahieu S, Cliquet J-B 2010. Nitrogen rhizodeposition of legumes. A review. Agronomy for Sustainable Development 30: 57–66.
- Gadgil RL 1982. Biological nitrogen inputs to exotic forests. In: Gandar PW ed. Nitrogen balances in New Zealand ecosystems. Palmerston North, Department of Scientific and Industrial Research. Pp. 123–129.
- Gage DJ 2004. Infection and invasion of roots by symbiotic, nitrogen-fixing rhizobia during nodulation of temperate legumes. Microbiology and Molecular Biology Reviews 68: 280–300.
- Galloway JN 1998. The global nitrogen cycle: changes and consequences. Environmental Pollution 102: 15–24.
- Ganjegunte GK, Condron LM, Clinton PW, Davis MR 2005. Effects of mixing radiata pine needles and understory litters on decomposition and nutrients release. Biology

- and Fertility of Soils 41: 310-319.
- Gaynor DL, MacCarter LE 1981. Biology, ecology, and control of gorse (*Ulex Europaeus* L.): a bibliography. New Zealand Journal of Agricultural Research 24: 123–137.
- Goergen E, Chambers JC, Blank R 2009. Effects of water and nitrogen availability on nitrogen contribution by the legume, *Lupinus argenteus* Pursh. Applied Soil Ecology, 42: 200–208.
- Goldstein CL, Williard KWJ, Schoonover JE, Baer SG, Groninger JW, Snyder JM 2010. Soil and groundwater nitrogen response to invasion by an exotic nitrogenfixing shrub. Journal of Environmental Quality 39: 1077–1084.
- Gonzalez M, Mathieu A, Augusto L, Gire C, Bakker MR Budynek A. 2010. Gorse seed bank variability in maritime pine stands. Seed Science Research 20: 31–38.
- Goulding KWT, Bailey NJ, Bradbury NJ, Hargreaves P, Howe M, Murphy DV, Poulton PR, Willison TW 1998. Nitrogen deposition and its contribution to nitrogen cycling and associated soil processes. New Phytologist 139: 49–58.
- Graham PH Vance CP 2003. Legumes: Importance and constraints to greater use. Plant Physiology 131: 872–877
- Hackwell K 1980. Gorse: a helpful nurse plant for regenerating native forest. Forest and Bird 13(5): 25–28.
- Harris RJ, Toft RJ, Dugdale JS, Williams PA, Rees JS 2004. Insect assemblages in a native (kanuka–*Kunzea ericoides*) and an invasive (gorse–*Ulex europaeus*) shrubland. New Zealand Journal of Ecology 28: 35–47.
- Healy AJ 1961. The interaction of native and adventive plant species in New Zealand. Proceedings of the New Zealand Ecological Society 8: 39–43.
- Hill RL, Gourlay AH, Barker RJ 2001. Survival of *Ulex europaeus* seeds in the soil at three sites in New Zealand. New Zealand Journal of Botany 39: 235–244.
- Isern TD 2007. A good servant but a tyrannous master: Gorse in New Zealand. The Social Science Journal 44: 179–186.
- Jackson LE, Burger M, Cavagnaro TR 2008. Roots, nitrogen transformations, and ecosystem services. Annual Review of Plant Biology 59: 341–363.
- Jensen ES, Hauggaard-Nielsen H 2003. How can increased use of biological N₂ fixation in agriculture benefit the environment? Plant and Soil 252: 177–186.
- Jones DL, Hodge A, Kuzyakov Y 2004. Plant and mycorrhizal regulation of rhizodeposition. New Phytologist 163: 459–480.
- Krause MA, Beck AC, Dent JB 1988. Control of gorse in hill country: an economic assessment of chemical and biological methods. Agricultural Systems 26: 35–49.
- Lambert MG, Jung GA, Costall DA 1989. Forage shrubs in North Island (New Zealand) hill country: 1. Forage Production. New Zealand Journal of Agricultural Research 32: 477–483.
- Lee WG, Allen RB, Johnson PN 1986. Succession and dynamics of gorse (*Ulex europaeus* L.) communities in the Dunedin Ecological District, South Island, New Zealand. New Zealand Journal of Botany 24: 279–292.
- Ligero P, de Vega A, van der Kolk JC, van Dam JEG 2011. Gorse (*Ulex europaeus*) as a possible source of xylans by hydrothermal treatment. Industrial Crops and Products 33: 205–210.
- MacCarter LE, Gaynor DL 1980. Gorse: a subject for biological control in New Zealand. New Zealand Journal of Experimental Agriculture 8: 321–330.

- MacConnell JT, Bond G 1957. A comparison of the effect of combined nitrogen on nodulation in non-legumes and legumes. Plant and Soil 8: 378–388.
- Magesan GN, White RE, Scotter DR 1996. Nitrate leaching from a drained, sheep-grazed pasture. I. Experimental results and environmental implications. Australian Journal of Soil Research 34: 55–67.
- Matthews LJ 1982. Pasture weeds of New Zealand. In: Holzner W, Numata N eds Biology and ecology of weeds. The Hague, The Netherlands, Dr W. Junk. Pp. 387–393.
- McAlpine KG, Timmins SM, Westbrooke I 2009. Bone-seed (*Chrysanthemoides monilifera* ssp. *monilifera*) invasion effects on native regeneration in New Zealand coastal plant communities. New Zealand Journal of Ecology 33: 72–82.
- McQueen JC, Tozer WC, Clarkson BD 2006. Consequences of alien N₂-fixers on vegetation succession in New Zealand. In: Allen RB, Lee WG eds Biological invasions in New Zealand. Ecological Studies 186. Berlin, Springer. Pp. 295–306.
- Meentemeyer V, Box EO, Thompson R 1982. World patterns and amounts of terrestrial plant litter production. BioScience 32: 125–128.
- Miller D 1970. Gorse (*Ulex europaeus* L.). In: Miller D.
 Biological control of weeds in New Zealand, 1927-48.
 DSIR Information Series 74. Wellington, Department of Scientific and Industrial Research. Pp. 27–58.
- Moss GR 1960. Gorse, a weed problem of thousands of acres of farm land. New Zealand Journal of Agriculture 100: 561–567.
- O'Hara GW, Daniel RM 1985. Rhizobial denitrification: a review. Soil Biology and Biochemistry 17: 1–9.
- O'Toole P, Dowds J, Farrell EP 1984. Nitrogen accumulation by *Ulex gallii* (Planch.) in a forest ecosystem. Irish Forestry 41: 14–29.
- Partridge TR 1989. Soil seed banks of secondary vegetation on the Port Hill and Banks Peninsula, Canterbury, New Zealand, and their role in succession. New Zealand Journal of Botany 27: 421–436.
- Philippot L, Hallin S, Börjesson G, Baggs EM 2009. Biochemical cycling in the rhizosphere having an impact on global change. Plant and Soil 321: 61–81.
- Prescott CE 2005. Do rates of litter decomposition tell us anything we really need to know? Forest Ecology and Management 220: 66–74.
- Prescott CE, Taylor BR, Parsons WFJ, Durall DM, Parkinson D 1993. Nutrient release from decomposing litter in Rocky Mountain coniferous forest: influence of nutrient availability. Canadian Journal of Forest Research 23: 1576–1586.
- Quinn JM, Stroud MJ 2002. Water quality and sediment and nutrient export from New Zealand hill-land catchments of contrasting land use. New Zealand Journal of Marine and Freshwater Research 36: 409–429.
- Rees M, Hill RL 2001. Large-scale disturbances, biological control and the dynamics of gorse populations. Journal of Applied Ecology 38: 364–377.
- Resh SC, Binkley D, Parrotta JA 2002. Greater soil carbon sequestration under nitrogen-fixing trees compared with *Eucalyptus* species. Ecosystems 5: 217–231.
- Richardson B, Vanner A, Ray J, Davenhill N, Coker G 1996. Mechanisms of *Pinus radiata* growth suppression by some common forest weed species. New Zealand Journal of Forestry Science 26: 421–437.

- Richardson RG, Hill RL 1998. The biology of Australian weeds. 34. *Ulex europaeus* L. Plant Protection Quarterly 13: 46–58.
- Rout ME, Callaway RM 2009. An invasive plant paradox. Science 324: 734–735.
- Sandrey RA 1985. Biological control of gorse: an ex-ante evaluation. Agricultural Economics Research Report 172. Lincoln College, Canterbury, New Zealand. 96 p.
- Schortemeyer M, Atkin OK, McFarlane N, Evans JR 2002. N₂ fixation by *Acacia* species increases under elevated atmospheric CO₂. Plant, Cell & Environment 25: 567–579.
- Silvester WB 1976. Ecological and economic significance of the non-legume symbioses. In: Newton WE, Nyman CJ eds Proceedings of the 1st International Symposium on Nitrogen-fixation. Pullman, WA, Washington State University Press. Pp. 489–507.
- Sixtus CR, Hill GD, Scott RR 2003. The effect of temperature and scarification method on gorse (*Ulex europaeus* L.) seed germination. New Zealand Plant Protection 56: 201–205.
- Sparling GP, Hart PBS, August JA, Leslie DM 1994. A comparison of soil and microbial carbon, nitrogen and phosphorus contents, and macro-aggregate stability of a soil under native forest and after clearance for pastures and plantation forest. Biology and Fertility of Soils 17: 91–100.
- Streeter JG 1985. Nitrate inhibition of legume nodule growth and activity. I. Long term studies with a continuous supply of nitrate. Plant Physiology 77: 321–324.
- Sullivan JJ, Williams PA, Timmins SM 2007. Secondary forest succession differs through naturalised gorse and native kānuka near Wellington and Nelson. New Zealand Journal of Ecology 31: 22–38.
- Sullivan JJ, Williams PA, Timmins SM, Smale MC 2009. Distribution and spread of environmental weeds along New Zealand roadsides. New Zealand Journal of Ecology 33: 190–204.

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- Tarayre M, Bowman G, Schermann-Legionnet A, Barat M, Atlan A 2007. Flowering phenology of *Ulex europaeus*: ecological consequences of variation within and among populations. Evolutionary Ecology 21: 395–409.
- Thornton B, Millard P, Tyler MR 1995. Effects of nitrogen supply on the seasonal re-mobilization of nitrogen in *Ulex europaeus*. New Phytologist 130: 557–563.
- Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG 1997. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications 7: 737–750.
- Wardle DA, Greenfield LG 1991. Release of mineral nitrogen from plant root nodules. Soil Biology and Biochemistry 23: 827–832.
- Watt MS, Clinton PW, Whitehead D, Richardson B, Mason EG, Leckie AC 2003. Above-ground biomass accumulation and nitrogen fixation of broom (*Cytisus scoparius* L.) growing with juvenile *Pinus radiata* on a dryland site, Forest Ecology and Management 184: 93–104.
- Weir BS, Turner SJ, Silvester WB, Park D-C, Young JM 2004. Unexpectedly diverse *Mesorhizobium* strains and *Rhizobium leguminosarum* nodulate native legume genera of New Zealand, while introduced legume weeds are nodulated by *Bradyrhizobium* species. Applied and Environmental Microbiology 70: 5980–5987.
- Wilson HD 1994. Regeneration of native forest on Hinewai Reserve, Banks Peninsula. New Zealand Journal of Botany 32: 373–383.
- Yelenik SG, Stock WD, Richardson DM 2007. Functional group identity does not predict invader impacts: differential effects of nitrogen-fixing exotic plants on ecosystem function. Biological Invasions 9: 117–125.
- Zabkiewicz JA, Gaskin RE 1978. Effect of fire on gorse seeds. Proceedings of the New Zealand Weed and Pest Control Conference 31: 47–52.
- Zahran HH 2001. Rhizobia from wild legumes: diversity, taxonomy, ecology, nitrogen fixation and biotechnology. Journal of Biotechnology 91: 143–153.
- Zhong Z, Lemke RL, Nelson LM 2009. Nitrous oxide emissions associated with nitrogen fixation by grain legumes. Soil Biology and Biochemistry 41: 2283–2291.