

## Colonization dynamics and facilitative impacts of a nitrogen-fixing shrub in primary succession

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**Abstract.** Whether nitrogen-fixing plants facilitate or inhibit species change in primary succession is best resolved by examining their impacts throughout the plant's entire life cycle from arrival to senescence. We experimentally examined two aspects of the successional impacts of a nitrogen-fixing shrub, *Coriaria arborea*, on Mt. Tarawera, a volcano in New Zealand: factors limiting *Coriaria* colonization and impacts of *Coriaria*-induced soil changes on a later successional tree, *Griselinia littoralis*. *Coriaria* germination was promoted by artificial wind protection and by the presence of heath shrubs. Transplanted *Coriaria* seedlings survived only if nodulated with *Frankia*, and the addition of *Coriaria*-enriched soils slowed *Coriaria* seedling growth and did not improve seedling survival. This explained why *Coriaria* seedlings were found mostly in protected habitats away from adult *Coriaria*, and suggested that *Coriaria* thickets are not self-replacing. *Coriaria* increased soil fertility by developing a 4 cm thick organic soil horizon that was richer in nitrogen (tenfold) and phosphorus (threefold) than pre-*Coriaria* stages. These soil changes resulted in three- to sixfold increases in growth of *Griselinia* when it was grown in *Coriaria*-enriched soils in a glasshouse. *Coriaria*'s net effect on primary succession is facilitative, but the establishment of *Coriaria* is itself facilitated by the amelioration of the physical habitat by earlier colonists, suggesting facilitation is important throughout the life cycle of *Coriaria*. Sequential facilitative events determine the order of species replacements in this study but inhibition, linked to the developmental stages of *Coriaria*, may determine the rate of species change.

**Keywords:** *Coriaria arborea*; Facilitation; *Griselinia littoralis*; New Zealand; Nitrogen-fixation; Post-volcanic succession; Seed bank; Soil organic matter.

**Nomenclature:** Allan (1961); Webb et al. (1988); Fife (1995), Edgar & Connor (2000).

### Introduction

There is a widely held yet rarely tested assumption that facilitation is essential for the development of plant communities on sites with no 'biological legacy' (primary succession; Clements 1916; Connell & Slatyer 1977). The importance of facilitative interactions is generally expected to increase (and the importance of competition decline) along environmental gradients of increasing stress (Bertness & Callaway 1994; Callaway & Walker 1997). However, several reviews (Matthews 1992; Walker 1993) provide little experimental support for that assumption in primary succession, suggesting that in severe environments, competitive interactions may dominate (Walker & Chapin 1986). Resolution of this apparent contradiction can be found in the complexity of the concept of facilitation and in careful analyses of the temporal context of species interactions during primary succession (Berkowitz et al. 1995; Tielbörger & Kadmon 2000). Factors that control the initial establishment of a potential facilitator (Chapin 1993) and the longer-term consequences of its subsequent presence, even after it dies, are important determinants of the balance between facilitation and competition, the net effects of the facilitator on succession and possibly the trajectory of succession (McCook 1994). Conclusions about species effects on succession are most robust when they incorporate the complexity of species interactions (Levine 2000) throughout the life histories of the interacting species (Grubb 1977; Walker & Chapin 1987; Glenn-Lewin et al. 1992; Brooker & Callaghan 1998; Bruno 2000) yet experimental approaches of this type are uncommon (Walker & del Moral 2003).

In primary succession, vascular species with N (nitrogen)-fixing symbionts (N-fixers) are often the principal facilitators of successional change (Marrs et al. 1983). N-fixers may be essential (obligatory facilitation) or merely improve (facultative facilitation) the dispersal, establishment and/or growth of later successional species. The facilitative process may be considered direct (as when an N-fixer provides critical shade or N) or

indirect (general habitat amelioration), with an immediate or a delayed impact. N-fixers may also inhibit species change in succession (Davis et al. 1985; Walker & Chapin 1987; Wood & del Moral 1987; Blundon et al. 1993; Chapin et al. 1994) by dominating soil and light resources and thereby at least temporarily excluding other species. Volcanic substrates represent an extreme environment where low soil-N levels may inhibit the establishment of N-fixers because of the initial costs of building functioning root nodules (Grubb 1986). Experiments with N-fixers in primary succession on volcanic substrates can help clarify establishment dynamics and the impact of dominant species on ecosystem dynamics (Vitousek & Walker 1989; del Moral & Grishin 1999). Such studies are needed to test successional models and provide managers with tools for ecosystem restoration or acceleration of natural succession.

We experimentally examined the colonization dynamics and successional role of a native thicket-forming actinorhizal shrub, *Coriaria arborea* (Coriariaceae), on primary succession on the volcanic substrates of Mt. Tarawera, North Island, New Zealand. Several species of *Coriaria* are widespread colonists of open habitats throughout New Zealand. Because *Coriaria* is still invading the N-poor volcanic substrates on Mt. Tarawera, we could study several life history phases of *Coriaria*, including its establishment and its potential longer-term impacts on ecosystem properties. Clarkson & Clarkson (1983, 1995) documented the pivotal role of *Coriaria* in the colonization of the upper slopes of Mt. Tarawera and argued that its presence is a necessary precursor for the establishment of forests. They also speculated that the initial colonization of *Coriaria* is limited by dispersal of its N-fixing symbiont, *Frankia*, or by marginal habitat conditions including infertile soils, frosts, or low water availability and noted that experimental tests were required to determine the relative importance of each. Silvester (1976) found that *Coriaria* added up to 150 kg-N $\cdot$ ha $^{-1}$  yr $^{-1}$  over a 20-yr period to a floodplain in New Zealand and, in another situation on pumice soils, *Pinus radiata* tree growth was significantly stimulated by adjacent *Coriaria* (W.B. Silvester pers. obs.). Therefore, we expect *Coriaria* to both contribute N and influence plant succession on Mt. Tarawera, although its influence will probably vary during its various life stages.

In order to test the assumptions of Clarkson & Clarkson (1983, 1995), we addressed two questions relevant to the successional impacts of *Coriaria*, an early successional N-fixing shrub on Mt. Tarawera:

1. Are its germination and seedling establishment limited by soil nutrients, its symbiont *Frankia*, vegetation type or lack of shelter?

2. Do its impacts on soil properties facilitate growth of later successional tree species?

## Methods

### Site description and study design

Field studies were conducted near the summit of Mt. Tarawera, on a plateau of the Kanakana Dome, North Island, New Zealand (38°15' S, 176°30' E; 950 m a.s.l.). Mt. Tarawera is composed of a group of rhyolitic domes that were formed in an eruption ca. 1324 A.D. ( $\pm$  54 yr; Lawlor 1980). The most recent eruption in 1886 deposited 0.5 km $^3$  of volcanic material over the existing domes and surrounding landscape (Timmins 1983), which completely denuded the upper slopes (our study site, Pond & Smith 1886; Timmins 1983). In contrast, on lower slopes some trees survived the eruption and were able to re-sprout (Aston 1916). Our study area is covered with basaltic ash and lapilli weakly bonded by fine rhyolitic ash to a depth of 61 m, with little soil development (Clarkson & Clarkson 1995) and is within the potential natural forest zone, as evidenced by the *Podocarpus hallii*-*Weinmannia racemosa*-*Griselinia littoralis* forest on nearby Makatiti Dome (from 750 m a.s.l. to its summit at 930 m) and the volcano Mt. Taranaki/Egmont at the west coast of North Island (760 m - 1100 m a.s.l.) (Clarkson 1986; Nicholls 1991). At Waiotapu Forest (ca. 10 km southwest of Mt. Tarawera) the average annual precipitation is 1421 mm, and the average annual temperature is 11.1°C (Anon. 1973).

Observations of vegetation change have been nearly continuous since the eruption of Mt. Tarawera (Thomas 1888; Aston 1916; Turner 1928). Detailed vegetation measurements began in 1964 (Burke 1964; Dickinson 1980; Timmins 1983; Clarkson & Clarkson 1983, 1995). These studies documented several successional sequences, most involving changes from a lichen/herb-dominated stage that colonizes open scoria, to a heath shrubland, then to *Coriaria*, and finally to a forest dominated by the trees *Griselinia littoralis* and *Weinmannia racemosa* that persist for > 300 yr. Normally, the gradual invasion of plants from the lower slopes onto the upper portions of the mountain gives rise to progressively younger stands of vegetation with increasing elevation. However, successional vegetation is now restricted to the plateau-like dome tops and we chose five sites representing putative successional stages (Table 1) at the same elevation (950  $\pm$  5 m a.s.l.). All of our study plots were within 1 km $^2$ , with < 10° slope and a southeast aspect. Our 'open' stage was characterized by volcanic cinder with no vegetation cover and approximated the initial condition following the eruption. At our 'herb' stage we selected approximately circular colonies of the herb *Raoulia albo-sericea* (< 5 cm tall, > 30 cm diameter, > 2 m from any shrubs; 80% cover). The dwarf shrub *Dracophyllum subulatum* (40% cover)

**Table 1.** Characteristics of five successional stages on Mt. Tarawera. Age is based on the estimated time to appearance of the characteristic vegetation following the 1886 eruption. Only the Shrub, New *Coriaria* and Old *Coriaria* stages had a developed organic (A<sub>0</sub>) soil horizon.

Stage	Age	Vegetation and habitat	Soils collected
Open	0	None; Volcanic cinder	PM = open mineral
Herb	50	<i>Raoulia</i> ; Herb patches on cinder, < 5cm tall	HM = herb mineral: top 10 cm, A <sub>1</sub> horizon
Shrub	80	<i>Racomitrium</i> <i>Dracophyllum</i> ; Heath shrub-land, 30-70 cm tall	SM = shrub mineral: top 10 cm A <sub>1</sub> horizon SF = shrub full profile: litter, mosses, A <sub>0</sub> horizon, top 10 cm A <sub>1</sub> horizon
New <i>Coriaria</i>	95	<i>Coriaria</i> ; 50-125 cm tall	NM = new mineral: top 10 cm A <sub>1</sub> horizon
Old <i>Coriaria</i>	110	<i>Coriaria</i> ; 100-200 cm tall	OM = old mineral: top 10 cm A <sub>1</sub> horizon OF = old full profile: litter, mosses, A <sub>0</sub> horizon, top 10 cm A <sub>1</sub> horizon OO = old organic: litter, mosses, A <sub>0</sub> horizon

and the moss *Racomitrium lanuginosum* (30% cover) dominated our 'shrub' stage. Our 'new *Coriaria*' stage, the first with *Coriaria* present, was colonizing the margin of the shrub stage (Clarkson & Clarkson 1983, 1995) and was dominated by newly invaded individuals of *Coriaria* (40% cover) with some *Dracophyllum* (20% cover) and *Racomitrium* (10% cover) remaining. Our 'old *Coriaria*' stage was in established stands with > 80% cover of *Coriaria*. The sequential colonization of the mountain summit from below and the limited spatial extent of our stages (ca. 0.5 ha each except the old *Coriaria* stage that covered ca. 4 ha) made it impossible to avoid pseudoreplication (Hurlbert 1984). However, we randomly located multiple plots within the entire area available for each stage. Our conclusions are thus limited to comparisons between the sampled areas and we cannot confirm that differences between our sites are due to time, particularly because successional development on slopes at lower elevations may differ from succession on the summit plateau. Yet on the strength of over a century of observations of vegetation development on Mt. Tarawera, including a photographic record of the summit plateau, we are confident that our sites represent successional stages.

#### Establishment of *Coriaria*

##### Germination in potted soils

We examined the effects of both soils collected from each of the five successional stages on Mt. Tarawera and three nutrient additions on germination of *Coriaria* and subsequent nodulation by *Frankia* (Table 2). *Coriaria* seeds were collected in late October 1998 from a roadside population near the base of Mt. Tarawera (400 m a.s.l.; seeds were not available in quantity at higher elevations but we have found no altitudinal variation in germination or growth characteristics of *Coriaria*; W.B. Silvester pers. obs.).

About 100 seeds (number determined by mass) were sown in early November 1998 into each of 150 0.2-L pots filled with soils collected from the mineral soil layer (top 10 cm) from five stages (PM, HM, SM, NM and OM soils as described in Table 1) and treated with one of three nutrient solutions (complete, minus N or tap water) modified from Middleton & Toxopeus (1973). The solutions were adjusted to a pH of 6.5 and 20 mL were added to the pots thrice weekly. The complete solution included 300 ppm N, an amount sufficient to support maximum growth of *Coriaria* (W.B. Silvester pers. obs.). All pots were randomly located on benches in a glasshouse in Hamilton, New Zealand (40 m a.s.l., 20-25°C), watered with tap water as needed, and rotated every 2 wk. Germination of *Coriaria* was monitored for 6 wk. Emergent seedlings were not marked so maximum seedling numbers were used as an index of germination (Walker et al. 1986) for each pot. After 18 wk, we recorded seedling shoot length and number of *Frankia* nodules on each of four seedlings that were randomly selected from four different pots from each of the 15 nutrient and soil combinations (240 seedlings total).

##### Field germination

Field germination and seedling transplant experiments (Table 2) were conducted in open and shrub stages on Mt. Tarawera to determine the effect of soil fertility, presence of *Frankia*-containing soil, and wind protection on *Coriaria* establishment. Ca. 200 seeds of *Coriaria* (number determined by mass) were sown in mid November 1998 into 12 treatments in the open stage and six treatments in the shrub stage, each with ten replicates (total of 36 000 seeds).

*1. Open stage.* Within a 10 m × 500 m area, we randomly located ten replicate blocks (each 2.5 × 2.5 m) that were at least 20 m apart. Each block contained 12 plots, 20 cm × 20 cm, located 50 cm from any other plot and ran-

domly assigned to treatments representing three soil types (PM, OM, OF), two nutrient levels (fertilized or not) and two microhabitats (windbreak or not) (Table 2). We chose these three soil types because they represented the extremes of low fertility (PM) and high fertility (OF) or provided an addition of *Frankia* without an appreciable increase in nutrients (OM). At each plot, ca. 1 L of soil (from an 8 cm × 8 cm × 15 cm deep hole) was either removed and replaced with 1 L of OF soil (see Table 1), removed and returned to the plot with the addition of 30 ml of OM soil (to add *Frankia*), or removed and returned without amendment (PM soil). This final treatment served as a control for the disruption caused by replacing some of the soils and for any possible addition of seeds from the OM or OF soils. One half of the plots within each block was fertilized with a slow release fertilizer (ca. 10 pellets or 0.2 g, 17% N, 1.6% P, 8.7% K, no micronutrients) mixed into the surface soil prior to seed addition. The fertilizer provided much higher levels of N, P and K than were found in the *Coriaria* soils (0.39% total Kjeldahl N, 0.00066% Olsen P, 0.001% K). One half of the plots was modified such that the *Coriaria* seeds were sown within the centres of windbreaks that consisted of 7 cm tall tephra craters with a basal diameter of 20 cm, resulting in a slightly smaller plot than the unprotected plots.

**2. Shrub stage.** The soil and nutrient addition treatments were similar in the open and shrub stages but we did not use windbreaks in the shrub environment because the dense shrubs (> 4 per m<sup>2</sup>) made windbreaks unnecessary. *Coriaria* seeds were sown in randomly located 20 cm × 20 cm plots within the 50 m × 100 m shrub habitat below the dripline of 25–75 cm tall *Dracophyllum* shrubs. We sowed the seeds on the surface of the overturned mineral soil horizon (SM), after removal of overlying moss, litter and organic soil.

The plots in both the open and shrub stages were watered with 200 ml of tap water from Hamilton immediately after sowing and 3 wk and 6 wk later. Germination and subsequent seedling growth were monitored 2, 3, 6, 15 and 23 wk after sowing. Maximum seedling numbers were again used as an index of germination.

#### Seedling transplants

We transplanted *Coriaria* seedlings to determine which environmental factors limit seedling establishment in open and *Dracophyllum* shrub stages. Nodulation of seedling roots by *Frankia* is presumed critical for seedling survival. Given the extremely limited quantity of available *Coriaria* seedlings that were not nodulated, we chose to compare the effects of the lack of nodulation in the shrub environment where the chance for transplant survival was highest.

**1. Nodulated transplants in the open stage.** We examined the effects of two soil types (PM, OF) representing the local nutrient-poor soil and the soil of maximum fertility, two nutrient levels (fertilized or not), and two microhabitats (windbreak or not) on *Coriaria* seedling growth and survival (eight treatments; Table 2). Nodulated *Coriaria* seedlings were collected from the open stage in late October 1998, trimmed to a similar size and transplanted into moist sand in 0.2-L pots in the glasshouse where they were watered three times a week with a full nutrient solution (Middleton & Toxopeus 1973) minus N (to keep them healthy without inhibiting *Frankia* development and N-fixation). After several weeks, with new shoots beginning to grow, the nodulated seedlings were transplanted into six treatments in the open stage. Ca. 1 L of soil was turned over in each of eight 20 cm × 20 cm plots (50 cm apart) in each of ten replicate blocks located adjacent to the seed plots in the open habitat. The soil in one half of the plots was replaced by 1 L of

**Table 2.** Summary of experiments on Mt. Tarawera (field) and in Hamilton, New Zealand (glasshouse).

Experiment	Treatments
Germination of <i>Coriaria</i>	
Glasshouse	5 soil types × 3 nutrient additions × 10 replicates = 150 pots
Field	
Open stage	3 soil types × 2 nutrient additions × 2 microhabitats × 10 replicates = 120 plots
Shrub stage	3 soil types × 2 nutrient additions × 10 replicates = 60 plots
Establishment of <i>Coriaria</i> (field seedling transplants)	
Nodulated	
Open stage	2 soil types × 2 nutrient additions × 2 microhabitats × 10 replicates = 80 plots
Shrub stage	2 soil types × 2 nutrient additions × 10 replicates = 40 plots
Not nodulated	
Shrub stage	3 soil types × 2 nutrient additions × 10 replicates = 60 plots
Impacts on <i>Griselinia</i> seedlings (glasshouse seedlings)	
Shaded	5 soil types × 2 litter additions × 7 replicates = 70 pots
Unshaded	5 soil types × 2 litter additions × 7 replicates = 70 pots

the OF soil (Table 1); the remainder (PM soil) served as a control for the soil disturbance. One half of the plots received the same amount and type of NPK fertilizer that the field germination plots received, and the surface in one half of the plots was modified to form windbreaks as described for the germination plots. This experiment addressed the questions of whether nutrients and exposure to winds limited *Coriaria* seedling establishment in the earliest successional stage.

*2. Nodulated transplants in the shrub stage.* Additional nodulated *Coriaria* were transplanted in mid November 1998 into two soil types (SM, OF) representing the local soil and the soil of maximum fertility and two nutrient levels (fertilized and not) in the shrub stage (four treatments; Table 2). Again, ten replicate blocks, each containing one of each of the four randomly located treatments, were located near the seed plots, and seedlings were planted in the dripline of *Dracophyllum* shrubs. This experiment explored the possibility that nutrients limit the establishment of *Coriaria* seedlings.

*3. Not-nodulated transplants in the shrub stage.* We examined the effects of three soil types (SM, OF, SM plus *Frankia* addition from 30 mL of OM soil – see field germination experiment) on *Coriaria* seedlings uninfected by *Frankia*. Again, these seedlings were subjected to two nutrient levels (fertilized or not) for a total of six treatments (Table 2). The *Coriaria* seedlings, purchased from a nearby nursery in early October 1998, were trimmed and transplanted into sand and fertilized regularly as described for the nodulated seedlings. We transplanted the seedlings into the *Dracophyllum* shrub habitat in mid November 1998. This experiment addressed whether nodulation was critical to *Coriaria* establishment on Mt. Tarawera and whether artificial or soil-based nutrients could substitute for nodulation.

All transplanted seedlings were watered and seedling survivorship and height growth were monitored for 23 wk. Surviving seedlings were harvested in late April 1999, dried at 60°C, and compared among treatments (root and shoot biomass, percent N; Kjeldahl analysis, Bradstreet 1965) and with initial biomass of ten nodulated and ten not nodulated seedlings.

#### *The effects of Coriaria on soil and light*

By characterizing soils in each of our five successional stages, we measured the effects of *Coriaria* and other successional vegetation on soil depth, bulk density, particle size, pH, C, N, P, cation exchange capacity and base concentrations. Ten measurements of the depth of each soil horizon were averaged. Volumes and mass of three size fractions (gravel, > 16 mm diameter; cin-

der, 2-16 mm; and fines, < 2 mm) were determined for mineral soils in the field from one 20 cm × 20 cm wide pit in each successional stage. Following sieving, the mass and volume (estimated by flotation) of gravel and cinder were determined. The volume of the fines was determined by subtracting the gravel and cinder volumes from the total pit volume (thereby including the volume of air pockets as part of the fines). The mass of the organic horizon and the fines were determined after air-drying for 10-14 d in a 20-25°C glasshouse. We estimated mineral bulk density ( $A_1$  horizon; g/cm<sup>3</sup>) in two ways: the dry mass of the fines per volume of fines (fine bulk density) and the dry mass of gravel, cinder and fines combined per pit volume (total bulk density). Soil N, C and P were estimated on an areal basis by multiplying the concentration of each element × fine bulk density × the volume of soil in 1 m<sup>2</sup> to either a depth of 10 cm (mineral soil) or the depth of the  $A_0$  horizon (organic soil). Field capacity was determined by dividing the weights of saturated minus dry mineral soils over the weights of dry soils (saturated soils were drained for 10 min before weighing; soils were air-dried for 10-14 d). In addition, from each of the five stages, five replicate samples of the mineral soil horizon (to 10 cm depth; composited from two subsamples per collection site) were dried and sieved through a 2-mm mesh. We then analysed sand (60-200  $\mu$ ), silt (2-60  $\mu$ ) and clay (<2  $\mu$ ) fractions using a Malvern Laser Sizer; Singer et al. 1988), pH (Blakemore et al. 1987), organic C (Walkley & Black 1943), total Kjeldahl N (Bradstreet 1965), Olsen extractable P (Olsen et al. 1954), cation exchange capacity and exchangeable bases (Ca, K, Mg and Na; Searle 1986).

Ambient light (photosynthetically active radiation or PAR in microeinstein.m<sup>-2</sup>.s<sup>-1</sup>) was measured from point sensors at noon on a sunny day (12 December 1998) under ten old *Coriaria* shrubs and in adjacent open areas to document light reduction under *Coriaria*.

#### *Impacts of Coriaria soils on Griselinia growth*

To determine the effects of *Coriaria* soils on *Griselinia littoralis* (a tree that follows *Coriaria* shrubs in succession on Mt. Tarawera), 5-mo old stem cuttings of *Griselinia* from a nearby nursery were grown in five soil types with and without additions of *Coriaria* litter and at two light levels (Table 2). The cuttings were trimmed to a similar shoot size and placed in pots containing 1 L of soil from five different sources (HM, SF, OM, OO, OF; see Table 1) in the glasshouse in October 1998. These soils differed from those used in the *Coriaria* germination and transplant experiments because we wanted to provide enough nutrients for *Griselinia* to survive while still trying to determine the relative importance of mineral versus organic soil layers

in the old *Coriaria* stage. Soils were collected from seven different locations at each stage (not pooled) to improve representation of any within-stage variation in soil characteristics. One half of the pots received approximately three layers of *Coriaria* leaf litter (collected from senescing but still connected green leaves on *Coriaria* shrubs in the vicinity of Mt. Tarawera; mean  $\pm$  S.E.:  $7.1 \pm 0.3$  g dry mass;  $2.09 \pm 0.02\%$  N). This amount of leaves approximated the amount of leaf litter normally found under *Coriaria* shrubs. One half of the seedlings was placed on a bench where light was an average of 40% of ambient and one half of the seedlings was placed under shade cloth to reduce incoming light to 15% of ambient, imitating light under *Coriaria* canopies on Mt. Tarawera. Because all shaded plants were on one bench, there was no replication of shade and results from the two light levels were not statistically compared. The pot locations were randomized and the pots rotated every two weeks within each light level. The seedlings were watered with tap water and weeds and leaf-eating insects were removed as needed. All seedlings were harvested in late April 1999 after 25 wk in each treatment. For each seedling we measured maximum number of leaves, stem length (along the longest stem) and leaf area, then dried the seedling to a constant mass at 60°C before determining shoot and root mass, and N content. We also measured initial root and shoot biomass of seven plants.

#### Statistical analyses

Glasshouse germination, nodulation by *Frankia*, and stem lengths of *Coriaria* were compared among treatments with two-way ANOVA to examine nutrient and soil type effects and interactions. Field germination of *Coriaria* was compared with  $\chi^2$  analysis of contingency tables of the maximum number of seeds that germinated in each treatment. Biomass and N content of *Coriaria* seedlings transplanted into the field were analysed by two- and three-way ANOVAs to examine the effects of fertilizer addition, wind protection, and soil type. Root/shoot ratios of field transplants were compared with a Mann-Whitney rank sum test and survivorship was compared by  $\chi^2$  analysis. Soil variables were compared with one-way ANOVAs or Kruskal-Wallis one-way ANOVAs on ranks (Anon. 1995) when normality assumptions were violated. *Griselinia* variables were compared using two-way ANOVA to examine light and soil effects. All significant ANOVAs were followed by Tukey multiple comparison tests. Percentages were arc-sine transformed prior to analyses and significance was determined at the  $P < 0.05$  level. Means are presented with  $\pm$  S.E.

## Results

### *Coriaria* establishment

#### Germination

Complete nutrient fertilization significantly depressed glasshouse germination of *Coriaria* seeds in Mt. Tarawera soils ( $P < 0.001$ ;  $F = 46.1$ ;  $df = 2$ ; as measured by maximum seedling number: mean  $\pm$  S.E. =  $35.1 \pm 1.2$  for all stages combined) compared with no fertilization ( $48.8 \pm 1.1$ ) or fertilization without N ( $49.8 \pm 0.9$ ). There were no differences in germination in response to different soil types ( $P > 0.05$ ). There was a significant fertilization by soil interaction ( $P = 0.002$ ;  $F = 3.3$ ;  $df = 8$ ) because maximum germination was obtained in the treatment without fertilization in the mineral soils of the open (PM) and shrub (SM) stages, but in the  $-N$  treatment in the other soil types (data not presented). Every *Coriaria* seedling that we examined was nodulated with *Frankia* in all three treatments and all five soil types, although there were significantly more *Frankia* nodules per plant ( $P < 0.001$ ;  $F = 21.8$ ;  $df = 2$ ) in pots with complete ( $55.85 \pm 5.2$ ) or  $-N$  fertilizer pots ( $51.7 \pm 4.6$ ) than in unfertilized pots ( $11.9 \pm 1.1$ ). There was no significant soil effect ( $P > 0.05$ ) on nodule number and only a minor fertilizer by soil interaction ( $P = 0.050$ ;  $F = 2.1$ ;  $df = 8$ ) because the PM soils that received a complete fertilizer had fewer nodules than the other fertilized soils.

Field germination (as estimated by maximum seedling density) of *Coriaria* seeds was low in all treatments. However, successional stage, windbreaks, fertilizer and *Coriaria* soil each had significant effects on germination ( $P < 0.001$ ;  $\chi^2 = 26.6$ ;  $df = 2$ ). Germination was highest in the shrub habitat (3.9%;  $N = 466$  seedlings), lowest in the open habitat without windbreaks (0.3%;  $N = 36$ ), and intermediate in the open habitat with windbreaks (1.3%;  $N = 157$ ; Table 3). These results suggest the importance of shelter for seed germination in the open habitat; 12 of the 36 seedlings that germinated in the open habitat without windbreaks were found in a single 2 cm deep crack. Fertilizer treatments only altered germination in the open habitat with windbreaks, where fertilized soils with *Frankia* addition and control soils without fertilizer had the highest germination. In the shrub habitat, where germination was two to 20 times greater than in the open habitats, the addition of *Coriaria* soil had a negative effect on *Coriaria* germination (Table 3). Seeds germinated within 2 wk in the shrub habitat but took 6 wk to begin germinating in the open. Germination clearly limits *Coriaria* establishment on Mt. Tarawera. In the field, only 0.3–3.9% (659) of the 36 000 sown seeds germinated whereas in the glasshouse experiment 30–60% of the 15 000 sown seeds germinated.

### Seedling survivorship and growth

Survivorship of *Coriaria* seedlings transplanted into the shrub habitat was higher for those that were pre-nodulated with *Frankia* (60 - 70%) than for those that were not (0 - 30%; Table 4). Survivorship of nodulated seedlings was approximately equal in the shrub and open habitats and neither fertilization nor *Coriaria* soil addition improved survivorship. Some seedlings still survived at the end of the germination study, and a few in the shrub habitat had grown several sets of leaves, were nodulated with *Frankia*, and were > 2 cm tall.

Windbreaks, fertilization and *Frankia* addition did not affect seedling biomass or N content in either habitat (where applicable; all  $P > 0.05$ ), but *Coriaria* soil addition had a slight negative impact on total biomass ( $P = 0.049$ ;  $F = 4.0$ ;  $df = 1$ ) in the open (Table 4). Seedlings with *Frankia* nodules had several-fold higher biomass than seedlings without nodules ( $P = 0.023$ ;  $F = 8$ ;  $df = 1$ ) despite initial biomass values that were identical ( $0.40 \pm 0.05$  g;  $N = 10$ ). Root/shoot ratios tended ( $P = 0.09$ ;  $U = 50.0$ ) to be higher in the *Coriaria* soil addition treatment for nodulated seedlings (Table 4). When all nodulated treatments were combined, percent N content was higher for *Coriaria* seedlings in the shrub habitat for both shoots ( $P < 0.001$ ;  $F = 69.9$ ;  $df = 1$ ;  $2.03 \pm 0.04$  %N;  $N = 26$ ) and roots ( $P = 0.003$ ;  $F = 9.3$ ;  $df = 1$ ;  $1.49 \pm 0.03$ ) than in the open habitat (shoots:  $1.69 \pm 0.02$ ; roots:  $1.35 \pm 0.02$ ;  $N = 60$ ).

### Impacts of *Coriaria* on soils

Most soil variables were higher in the organic soils from the *Coriaria*-dominated stages than in the open and herb stages (Table 5). The depth of leaf litter layers increased threefold from the herb to the old *Coriaria*

stage and both organic and mineral soil layers also generally increased in depth. Bulk densities of the organic soil layers were lowest in the shrub and old *Coriaria* stages and bulk densities of the mineral soil (fines and total) declined in later stages. Cinder constituted the largest percentage ( $53.9 \pm 4.5\%$ ) of total mass of mineral soil from the pit samples, with fines next ( $30.7 \pm 3.3\%$ ) and gravel last ( $15.3 \pm 5.5\%$ ) when values were pooled across all stages. Fines from the shrub and *Coriaria* stages had significantly lower sand ( $P < 0.001$ ;  $F = 20.1$ ;  $df = 4$ ) and higher silt ( $P < 0.001$ ;  $F = 14.7$ ;  $df = 4$ ) and clay ( $P < 0.001$ ;  $F = 28.1$ ;  $df = 4$ ) content than the open and herb stages. The organic soils of the old *Coriaria* stage had threefold higher field capacity than soils from all other stages.

Soil pH (Table 5) did not vary among the successional stages ( $P > 0.05$ ) but values for soil organic carbon ( $P < 0.001$ ;  $H = 25.5$ ;  $df = 5$ ), total N (both concentrations:  $P < 0.001$ ;  $H = 26.9$ ;  $df = 5$  and areal estimates:  $P < 0.001$ ;  $H = 24.9$ ;  $df = 5$ ), Olsen extractable P (concentration only:  $P < 0.001$ ;  $H = 22.0$ ;  $df = 5$ ) and cation exchange capacity ( $P < 0.001$ ;  $H = 24.8$ ;  $df = 5$ ) were all significantly higher in the organic soils of the old *Coriaria* stage than in earlier stages. Ca ( $P < 0.001$ ;  $H = 24.7$ ;  $df = 5$ ), K ( $P < 0.001$ ;  $F = 25.7$ ;  $df = 5$ ) and Mg ( $P < 0.001$ ;  $H = 24.1$ ;  $df = 5$ ) followed the same pattern as C, N and P but Na ( $P < 0.001$ ;  $H = 19.7$ ;  $df = 5$ ) was highest in the shrub and new *Coriaria* stages, and then declined. Many of these increases were also found in the mineral soils of the new and old *Coriaria* stages. The shrub stage was generally intermediate in soil chemical properties between the pre-*Coriaria* open and herb stages and the later stages dominated by *Coriaria*; however, the shrub stage had lower P concentrations than the herb stage.

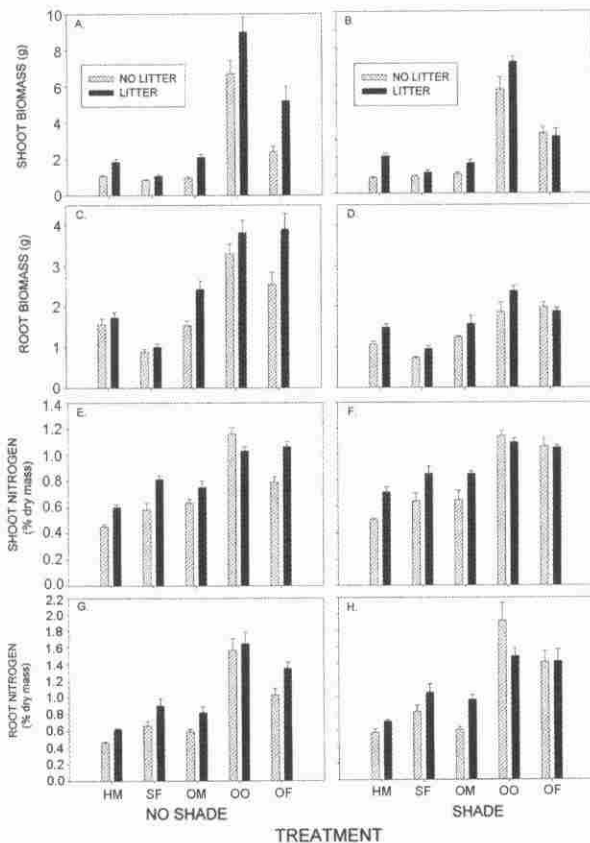
**Table 3.** Maximum seedling number (an index of germination) from *Coriaria* seeds sown on Mt. Tarawera, New Zealand ( $N = 2000$  seeds per treatment) in the open (age 0 yr) and shrub (age 80 yr) stages of succession. Seedlings from all ten plots per treatment were pooled due to high plot by plot variation. The number of plots (out of ten) that had seedlings is shown in parentheses. The totals followed by letters represent overall germination of 12 000 seeds (1.3%: open with windbreak; 0.3%: open without windbreak; 3.9%: shrub). Total values followed by different letters were significantly different ( $P < 0.001$ ;  $\chi^2 = 26.6$ ;  $df = 2$ ). Soil types (in brackets; see Table 1) included a nutrient-rich soil (OF), the local soil at each site (PM or SM) and the local soil plus 30 ml of OM (mineral soil from the oldest stage) to add *Frankia* without nutrient addition. See text for details.

Stage	Treatments				Total	
	Windbreak	Fertilizer	<i>Coriaria</i> soil	<i>Frankia</i>		
<b>Open</b>	Windbreak	Fertilized	[OF] 16 (5)	[PM+OM] 50 (6)	[PM] 21 (2)	87
		Not fertilized	16 (4)	13 (3)	41 (5)	70
	Total		32	63	62	157 a
<b>Shrub</b>	No Windbreak	Fertilized	5 (1)	3 (1)	15 (2)	23
		Not fertilized	1 (1)	5 (2)	7 (2)	13
	Total		6	8	22	36 b
<b>Shrub</b>	No Windbreak	Fertilized	[OF] 35 (7)	[SM+OM] 89 (7)	[SM] 92 (6)	216
		Not fertilized	25 (9)	105 (7)	120 (8)	250
	Total		60	194	212	466 c

### Impacts of *Coriaria* soils on *Griselinia* growth

*Griselinia* root and shoot mass and N content were higher in the organic (OO) and full (OF) profiles of the old *Coriaria* stage ( $P < 0.001$ ; Fig. 1) than soils from the mineral layer of the old *Coriaria* stage (OM), herb stage (HM) or the full profile of the shrub stage (SF), regardless of shade treatment. *Griselinia* stem length, leaf number and leaf area followed identical patterns (data not shown). Further, values for all variables except shaded or unshaded root biomass and shaded root and shoot N were higher ( $P < 0.001$ ) in the organic soils (OO) than the full profile (OF) from the old *Coriaria* stage. Addition of *Coriaria* litter also had an overall positive influence ( $P < 0.001$ ) on all variables (except shoot N of shaded *Griselinia*), although this effect was most pronounced in soils from the herb (HM) and old *Coriaria* (OM, OO, and unshaded OF). Final mass

of shoots and roots varied from 10-100 fold greater than initial shoot ( $0.11 \pm 0.02$  g) or root ( $0.12 \pm 0.01$  g) mass. Significant soil by litter interactions were found for several variables: unshaded root ( $P = 0.048$ ;  $F = 2.5$ ;  $df = 4$ ) and shoot mass ( $P = 0.036$ ;  $F = 2.7$ ;  $df = 4$ ); shaded shoot ( $P = 0.017$ ;  $F = 3.2$ ;  $df = 4$ ); shaded root ( $P = 0.013$ ;  $F = 3.4$ ;  $df = 4$ ) and unshaded shoot ( $P < 0.001$ ;  $F = 6.7$ ;  $df = 4$ ) N; shaded leaf number ( $P = 0.018$ ;  $F = 3.2$ ;  $df = 4$ ); and shaded leaf area ( $P = 0.062$ ;  $F = 2.3$ ;  $df = 4$ ). These interactions emphasize the decoupling of the responses of various seedling parameters to soil and litter treatments within each shade experiment. Yet there was a general similarity between responses of seedlings from the shaded and unshaded experiments (Fig. 1), with a frequent but not consistent increase in root and shoot biomass in seedlings grown in unshaded compared to shaded OO and OF soils.



**Fig. 1.** Characteristics of *Griselinia* seedlings grown for 25 wk at two light levels in a glasshouse (shade = 15% ambient; no shade = 40% ambient) with and without the addition of 7 g of *Coriaria* litter to five soil types from three successional stages (see Tables 1 and 2). **A, B:** shoot mass; **C, D:** root mass; **E, F:** shoot-N content; **G, H:** root-N content. Mean  $\pm$  S.E.;  $N = 7$  seedlings. Soil types: HM = herb stage mineral; SF = shrub stage full profile (organic and mineral); OM = Old *Coriaria* stage mineral; OO = Old *Coriaria* organic; OF = Old *Coriaria* full profile.

**Table 4.** *Coriaria* seedling survivorship (max. = 10), total biomass (root plus shoot in g; mean  $\pm$  S.E.,  $N = 10$ ) and root/shoot ratio for transplanted seedlings that survived 23 wk on Mt. Tarawera, New Zealand. Initial seedling biomass =  $0.40 \pm 0.05$  g,  $N = 10$ . Soil types (see Table 1) are shown in brackets.

Treatment	Nr of survivors	Total biomass (g)	Root/shoot ratio
<b>Open stage - nodulated</b>			
Windbreak			
Fertilized			
<i>Coriaria</i> soil [OF]	9	6.47 $\pm$ 1.89	0.40 $\pm$ 0.03
Without			
<i>Coriaria</i> soil [PM]	6	8.73 $\pm$ 1.67	0.27 $\pm$ 0.02
Not Fertilized			
<i>Coriaria</i> soil [OF]	7	3.25 $\pm$ 0.61	0.37 $\pm$ 0.02
Without			
<i>Coriaria</i> soil [PM]	9	7.03 $\pm$ 1.29	0.31 $\pm$ 0.02
Without Windbreak			
Fertilized			
<i>Coriaria</i> soil [OF]	8	6.25 $\pm$ 0.82	0.34 $\pm$ 0.03
Without			
<i>Coriaria</i> soil [PM]	6	6.06 $\pm$ 1.04	0.32 $\pm$ 0.02
Not Fertilized			
<i>Coriaria</i> soil [OF]	5	4.03 $\pm$ 1.41	0.42 $\pm$ 0.07
Without			
<i>Coriaria</i> soil [PM]	10	6.90 $\pm$ 1.78	0.37 $\pm$ 0.02
<b>Shrub stage - nodulated</b>			
Fertilized			
<i>Coriaria</i> soil [OF]	6	4.58 $\pm$ 1.36	0.29 $\pm$ 0.03
Without			
<i>Coriaria</i> soil [SM]	7	4.17 $\pm$ 1.19	0.29 $\pm$ 0.02
Not Fertilized			
<i>Coriaria</i> soil [OF]	6	4.37 $\pm$ 1.16	0.34 $\pm$ 0.08
Without			
<i>Coriaria</i> soil [SM]	7	3.72 $\pm$ 0.78	0.31 $\pm$ 0.03
<b>Shrub stage - not nodulated</b>			
Fertilized			
<i>Coriaria</i> soil [OF]	1	4.33	0.25
Without			
<i>Coriaria</i> soil [SM]	3	2.73 $\pm$ 0.81	0.32 $\pm$ 0.05
<i>Frankia</i> [SM+OM]	2	2.53 $\pm$ 0.02	0.29 $\pm$ 0.03
Not Fertilized			
<i>Coriaria</i> soil [OF]	2	1.26 $\pm$ 0.20	0.65 $\pm$ 0.11
Without			
<i>Coriaria</i> soil [SM]	0		
<i>Frankia</i> [SM+OM]	2	1.00 $\pm$ 0.44	0.42 $\pm$ 0.07



**Discussion**

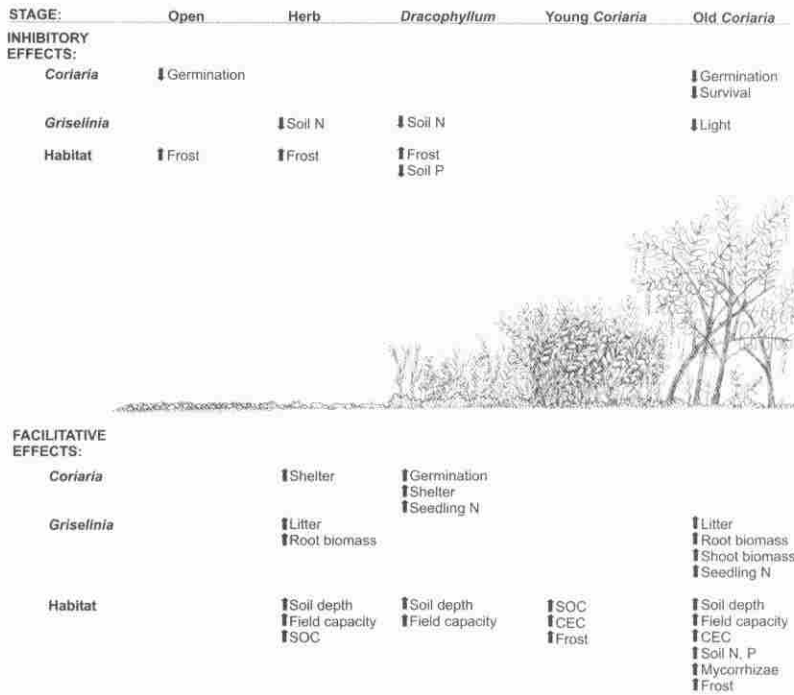
The net effects of a pivotal species on succession result from a complex and dynamic interplay between the species as it develops through its various life stages and the changing successional environment (McCook 1994; Callaway & Walker 1997; Bruno 2000). In this study we determined that the successional role of *Coriaria arborea*, an N-fixing shrub colonizing volcanic substrates, is both facilitative and inhibitory (Fig. 2). *Coriaria* establishment occurred only after the arrival of small herbs and shrubs that ameliorated a harsh physical environment. As *Coriaria* stands developed, the dramatic increases in soil fertility and, to a lesser degree, additions of *Coriaria* leaf litter, promoted the growth of the later successional tree, *Griselinia*. Shade, simulating mature *Coriaria* stands, did not markedly depress *Griselinia* growth in glasshouse experiments, but soils from mature *Coriaria* stands inhibited *Coriaria* regeneration, suggesting a mechanism for its eventual replacement by *Griselinia*. Sequential facilitative events appear to determine the order of species replacements in this primary succession but inhibitory mechanisms, linked to the developmental stages of *Coriaria*, may determine the rate of species turnover.

*Controls over the establishment of Coriaria*

The first life history stages of *Coriaria* (dispersal, germination and seedling survival) determine the degree and timing of *Coriaria*'s influence on succession. We did not directly examine dispersal, but what is known about seed mass, dispersal mode and seed banks can partially explain *Coriaria* colonization dynamics. On the uppermost slopes, the earliest colonists are dispersed by wind (e.g. *Raoulia* spp., *Rytidosperma gracile*, ferns and mosses; Aston 1916). Woody plants such as *Coriaria* (seed mass = 0.4 mg; Wardle 1991) and *Griselinia* (26.0 mg) are primarily bird-dispersed, so we postulate that their dispersal is facilitated by prior vegetative growth (*Raoulia* for *Coriaria*, *Coriaria* for *Griselinia*) that provides perches, protective cover and perhaps alternative foods for the birds (McDonnell & Stiles 1983; Willson & Traveset 2000). However, the later successional tree *Weinmannia* has light (0.1 mg), wind-dispersed seeds, so clearly variables other than seed mass (e.g. drought tolerance) affect colonization success. The presence of more seeds in soils under *Coriaria* than in earlier successional environments (Clarkson et al. 2002) supports our suggestion that the *Coriaria* shrubs trap seeds (facilitate dispersal) of other species, perhaps from both wind and animal dispersal.

**Table 5.** Soil characteristics from study sites on Mt. Tarawera, New Zealand. Depths ( $N = 10$ ), particle size ( $N = 5$ ) and chemical properties ( $N = 5$ ) are means  $\pm$  S.E. Values in the same row followed by the same letter are not significantly different ( $P > 0.05$ ). All data shown are for the  $A_1$  mineral soil horizon (sampled to a depth of 10 cm) unless otherwise noted. NA = not applicable.

Parameter	Open	Herb	Successional stage		Old <i>Coriaria</i>	
			Shrub	New <i>Coriaria</i>	Mineral	Organic
<b>Depth (cm)</b>						
Litter/Moss	0	2.58 $\pm$ 0.21 a	3.85 $\pm$ 0.23 b	3.88 $\pm$ 0.49 b	NA	7.30 $\pm$ 0.38 c
Organic ( $A_0$ )	0	0	4.50 $\pm$ 0.27 a	0.71 $\pm$ 0.10 b	NA	4.41 $\pm$ 0.35 a
Mineral ( $A_1$ only)	0	<1	1.10 $\pm$ 0.50 a	3.30 $\pm$ 0.50 b	3.46 $\pm$ 0.35 b	NA
<b>Bulk density (g.cm<sup>-3</sup>)</b>						
Organic	NA	0.42	0.25	0.46	NA	0.34
Fines	1.04	0.85	0.37	0.34	0.43	NA
Total	1.46	1.31	0.88	0.97		1.04
<b>Particle size (% volume)</b>						
Sand	49.2 $\pm$ 2.9 a	46.8 $\pm$ 2.4 a	35.3 $\pm$ 1.8 b	33.0 $\pm$ 1.1 bc	24.7 $\pm$ 1.1 c	NA
Silt	44.0 $\pm$ 2.4 a	45.9 $\pm$ 1.9 ab	53.0 $\pm$ 1.1 bc	55.0 $\pm$ 0.5 c	59.8 $\pm$ 0.6 c	NA
Clay	6.8 $\pm$ 0.6 a	7.3 $\pm$ 0.7 a	11.7 $\pm$ 0.7 b	12.0 $\pm$ 0.5 b	15.5 $\pm$ 0.5 c	NA
<b>Field capacity (% dry mass)</b>	26	35	39	38	37	122
<b>pH</b>	6.20 $\pm$ 0.04 a	6.05 $\pm$ 0.04 a	5.99 $\pm$ 0.03 a	6.09 $\pm$ 0.03 a	6.00 $\pm$ 0.05 a	5.98 $\pm$ 0.11 a
<b>Organic Carbon (%)</b>	0.0 a	0.16 $\pm$ 0.07 a	0.58 $\pm$ 0.09 b	0.84 $\pm$ 0.08 b	0.82 $\pm$ 0.12 b	6.48 $\pm$ 0.88 c
(g.m <sup>-2</sup> )	0.0 a	82.69 $\pm$ 34.57 b	148.07 $\pm$ 22.14 bc	168.50 $\pm$ 16.64 c	215.09 $\pm$ 30.90 c	648.00 $\pm$ 62.29 d
<b>Total Kjeldahl nitrogen (%)</b>	0.01 $\pm$ 0.03 a	0.02 $\pm$ 0.02 ab	0.03 $\pm$ 0.02 bc	0.06 $\pm$ 0.03 c	0.07 $\pm$ 0.09 c	0.39 $\pm$ 0.31 d
(g.m <sup>-2</sup> )	8.38 $\pm$ 1.79 a	10.85 $\pm$ 3.00 a	9.19 $\pm$ 0.60 a	11.63 $\pm$ 0.61 a	18.46 $\pm$ 2.45 b	39.20 $\pm$ 2.48 c
<b>C/N Ratio</b>	0.0	7.6	16.1	14.5	11.6	16.5
<b>Olsen Phosphorus (<math>\mu</math>g.g<sup>-1</sup>)</b>	2.4 $\pm$ 0.2 ab	3.5 $\pm$ 0.2 a	1.9 $\pm$ 0.2 b	2.4 $\pm$ 0.2 ab	2.2 $\pm$ 0.3 ab	6.6 $\pm$ 0.3 c
(g m <sup>-2</sup> )	0.132 $\pm$ 0.011 a	0.180 $\pm$ 0.090 a	0.054 $\pm$ 0.005 b	0.044 $\pm$ 0.003 b	0.080 $\pm$ 0.003 c	0.130 $\pm$ 0.004 a
<b>Cation exchange capacity (me 100.g<sup>-1</sup>)</b>	2.62 $\pm$ 0.22 ab	2.66 $\pm$ 0.29 ab	3.98 $\pm$ 0.37 a	6.04 $\pm$ 0.32 c	2.00 $\pm$ 0.13 b	11.40 $\pm$ 1.62 d
<b>Bases (me.100g<sup>-1</sup>)</b>						
Ca	0.86 $\pm$ 0.12 a	1.09 $\pm$ 0.11 ac	1.18 $\pm$ 0.18 ac	3.34 $\pm$ 0.15 b	1.91 $\pm$ 0.21 c	9.05 $\pm$ 1.02 d
K	0.11 $\pm$ 0.05 a	0.14 $\pm$ 0.01 a	0.12 $\pm$ 0.02 a	0.30 $\pm$ 0.02 b	0.30 $\pm$ 0.05 b	0.50 $\pm$ 0.02 c
Mg	0.38 $\pm$ 0.07 a	0.46 $\pm$ 0.05 ab	0.67 $\pm$ 0.10 b	2.34 $\pm$ 0.08 c	0.82 $\pm$ 0.04 b	2.58 $\pm$ 0.24 d
Na	0.11 $\pm$ 0.01 a	0.11 $\pm$ 0.01 a	0.22 $\pm$ 0.02 b	0.27 $\pm$ 0.01 b	0.13 $\pm$ 0.02 a	0.14 $\pm$ 0.01 a



**Fig. 2.** Summary of inhibitory and facilitative effects of each of five successional stages on the germination and growth of *Coriaria arborea* and *Griselinia littoralis* seedlings from observations and field and glasshouse experiments. Stage impacts on general habitat variables (mostly soil parameters) also have variable indirect and direct inhibitory or facilitative effects on seedling germination and growth.

Suggested limits to germination and establishment of *Coriaria* include low-nutrient soils, lack of the symbiont (*Frankia*), microhabitat variables and water availability (Clarkson & Clarkson 1983, 1995; Clarkson 1990). We did not find support for the hypothesis that nutrient limitation inhibited germination. Instead, germination was inhibited in the glasshouse by N but not by other nutrients (provided artificially or by addition of soils collected from under *Coriaria*) and field germination was inhibited by additions of *Coriaria* soil (but not artificial fertilizer) in both the open and *Dracophyllum*-dominated shrub stages. Similarly, fertilization and *Coriaria* soil additions did not improve survival or growth of transplanted *Coriaria* seedlings. Possible explanations for the inhibitory effects of *Coriaria* soil on *Coriaria* germination and seedling growth include a build up of soil pathogens or some form of auto-toxicity (Mahall & Callaway 1992).

*Frankia* is essential to *Coriaria* seedling survival and growth, as demonstrated by the high mortality of transplants that were not nodulated. However, *Frankia*, dispersed to Mt. Tarawera via wind and water dispersal of organic fragments, does not limit *Coriaria* establishment as previously suggested (Clarkson & Clarkson 1995) because it is apparently already widespread (cf. Young et al. 1992). Soils with *Frankia* amendments did not alter field germination; all seedlings that germinated in the glasshouse were infected with *Frankia* nodules and all established seedlings in the field were infected. *Frankia* was also widespread on recent volcanic surfaces in Hawaii despite a lack of native actinorhizal N-fixers (Vitousek & Walker 1989). *Frankia* and seeds of *Coriaria*

apparently disperse separately but mutual contact and sufficient water and organic matter are needed to support the formation of nodules (Sprent & Sprent 1990). How fast nodulation occurs is not known, but we never found naturally occurring seedlings that were not nodulated on Mt. Tarawera.

Microhabitat had a greater influence than fertilization or *Frankia* on field germination of *Coriaria*, with 4–5 × better germination in our windbreaks than outside in the earliest (open) stage and 2–20 × better germination in the shrub than the open stage. These results suggest soil moisture (higher in the shrub than open stage and presumably higher in our windbreaks than outside them) may be an important factor limiting *Coriaria* establishment.

The establishment of *Coriaria* on Mt. Tarawera is limited to sites with previous colonists (e.g. *Raoulia* patches, *Dracophyllum* shrubs) or protected gullies, such as experimentally demonstrated with our windbreaks. Early colonists may not only facilitate *Coriaria* by providing shelter, but also by accumulating organic matter that increases soil water retention and nutrients such as N and P necessary for activation of the nitrogenase enzyme complex (Grubb 1986; Sprent & Thomas 1984; Sprent & Sprent 1990). The inhibitory influence of soils from under *Coriaria* further suggests that most *Coriaria* regeneration will occur in habitats not currently occupied by *Coriaria* shrubs. This aspect of *Coriaria* regeneration fits the classic idea of a facilitator altering the environment such that the establishment of other species is promoted (see below), but its own regeneration inhibited (Clements 1916).

### Facilitation

The old *Coriaria* stage had dramatically higher soil fertility compared with earlier stages, suggesting indirect facilitation of succession from soil development. Most of the increases in organic matter, cation exchange capacity, and soil nutrients were in the organic rather than mineral layers of soil. Similar increases have been found in other primary seres (Walker 1993) and form the basis for the idea that N-fixers facilitate soil development and perhaps increase the rate of vegetation change in primary succession (Crocker & Major 1955; Lawrence et al. 1967; Marrs et al. 1983). Typical rates of N accumulation range from 12–360 kg-N.ha<sup>-1</sup>.yr<sup>-1</sup> on floodplains (Van Cleve et al. 1971; Luken & Fonda 1983; Walker 1989), mine tailings (Bradshaw 1983, Marrs et al. 1983), and glacial moraines (Crocker & Major 1955; Chapin et al. 1994). Volcanic seres are generally at the lower end of this range of accumulation rates (Walker 1993) and our study is no exception. Soil N accumulated on our sites at ca. 10 kg-N.ha<sup>-1</sup>.yr<sup>-1</sup> when averaged over the 110 yr chronosequence but at ca. 45 kg-N.ha<sup>-1</sup>.yr<sup>-1</sup> during the 20 yr since the arrival of *Coriaria*.

Soils from under *Coriaria* shrubs in the old *Coriaria* stage had a strong positive influence on all measured variables of growth and nutrient status of *Griselinia*. A similar response was found when both *Griselinia* and *Weinmannia* seedlings were grown in soils from successional stands of *Carmichaelia*, an N-fixing shrub on New Zealand floodplains (Bellingham et al. 2001). Another source of N on Mt. Tarawera is an expanding gull colony (*Larus dominicanus*). It will be interesting to see if the initial invasion of non-native grasses into these N-rich patches (Clarkson & Clarkson 1995) will lead to an entirely different successional sequence dominated by high-nutrient adapted invasive species, or to invasion by *Griselinia*.

The addition of *Coriaria* litter increased *Griselinia* growth in soils from each successional stage, suggesting direct facilitation through biotic interactions. The mostly parallel responses of shaded and unshaded *Griselinia* seedlings suggest that *Griselinia* plants are not strongly inhibited by the shade found under *Coriaria* shrubs (<15% of ambient light). In contrast, *Coriaria* does not tolerate low light levels (Silvester 1976). These results suggest that the net effect of increased nutrient levels and different shade tolerances will lead to successional replacement from *Coriaria* to *Griselinia* and *Weinmannia*, followed by more shade-tolerant species (Tilman 1985), as is occurring at lower elevations on Mt. Tarawera (Clarkson & Clarkson 1983, 1995).

### Successional implications

Facilitation appears to be an important mechanism affecting all life history stages of *Coriaria* and perhaps driving succession on Mt. Tarawera. However, due to our sample design, our results can only be extrapolated with caution beyond our plots to larger landscape processes. We suggest (but do not show) that early successional shrubs facilitate *Coriaria* arrival. We demonstrated that *Dracophyllum* shrubs facilitated *Coriaria* germination. Each of these processes occurred before *Coriaria* began its purported facilitative impacts on succession, as suggested by increases in soil nutrients and organic matter that improved growth of the later successional *Griselinia* in glasshouse experiments. We suggest that without *Coriaria*, succession on Mt. Tarawera would be delayed at the *Dracophyllum* stage (dominated by ericaceous shrubs adapted to low nutrients) because *Griselinia* performed poorly in soils from that stage. Yet growth responses in a glasshouse may not represent field performance. For example, Walker & Chapin (1987) found that although soils altered by the N-fixing *Alnus* from an Alaskan floodplain facilitated growth of late successional *Picea* in a glasshouse, the net effect of *Alnus* on *Picea* under field conditions was negative. Nevertheless, the facilitative link between *Coriaria* and *Griselinia* seems strong. In our study area, *Coriaria* colonized ca. 95 yr after the eruption and *Griselinia* is just now beginning to colonize (ca. 20 yr later). Further, during several decades of our observations on Mt. Tarawera, > 95% of all *Griselinia* seedlings have established in *Coriaria* thickets. Finally, by inhibiting shade intolerant species (species richness declined with the development of *Coriaria* thickets; Clarkson 1990), *Coriaria* increases the rate of succession. We have established long-term exclusion plots to examine soil and vegetation development in the absence of *Coriaria*. The net facilitative impact of *Coriaria* on succession on Mt. Tarawera may be due to its inputs as an N-fixer, combined with its relative shade intolerance or short life span relative to later successional species, or the occasional break-up of its canopy by frost.

Thicket-forming species can simultaneously inhibit later successional understorey species through light reduction or root competition and facilitate their establishment by additions of organic matter or increased soil stability or shade (Wood & del Moral 1987; Guariguata 1990; Walker 1999). Isolated individuals or open-canopies of N-fixers do not usually have as strong an influence (positive or negative) on establishment of late successional seedlings as do dense thickets (Walker & Chapin 1987; Chapin et al. 1994). At our study sites, periodic dieback of the *Coriaria* canopy due to frost may open the thicket and release understorey seedlings of late successional species. On 17 April 1999, all surviving *Coriaria*

seedlings transplanted into the shrub habitat had severe damage from an isolated frost (recorded as  $-1^{\circ}\text{C}$  at the Waitapu Forest climatological station at the base of Mt. Tarawera). Frost damage to adult *Coriaria* has been documented several times in recent decades but shrubs that are not too severely damaged are able to re-sprout from the base (Clarkson & Clarkson 1995). Where frost impedes initial establishment of *Coriaria*, the *Dracophyllum* shrub stage is prolonged, in contrast to the acceleration of succession when established *Coriaria* are damaged by frost (Fig. 2).

Mt. Tarawera is a heterogeneous area where multiple successional pathways are occurring simultaneously due to differential damage to the pre-eruption vegetation, different substrate textures and slopes, different microclimates, and different human land use histories (Timmins 1983; Clarkson & Clarkson 1983, 1995; Clarkson 1990). Our study is near the upper elevational limit of *Coriaria*, on a very exposed yet flat and stable plateau, and it is subject to increasing tourism and the impacts of non-native plants (including a few small herbaceous N-fixers such as *Lotus pedunculatus* and *Ornithopus perpusillus*) and animals that include possums (*Trichosurus vulpecula*), deer (*Cervus unicolor* and *C. elaphus scoticus*), rabbits (*Oryctolagus cuniculus*), gulls (*Larus dominicanus*) and wallabies (*Macropus eugenii*) (Clarkson & Clarkson 1995). Each variable potentially affects succession through changes in soil nutrients, herbivory loads, competition or direct damage and may alter the influence of *Coriaria* on the basic pattern of succession that we have described here.

### Conclusion

Our study of the early stages of invasion by an N-fixer on a New Zealand volcano supports the traditional facilitative role that has long been assumed for N-fixers in primary succession. However, we also demonstrate that *Coriaria* establishment is facilitated by the presence of earlier colonists through physical amelioration of the habitat. Our results suggest that *Coriaria*'s dramatic impact on soil fertility favours the establishment of later successional *Griselinia* and does not promote the regeneration of *Coriaria* under itself. Although this conforms to the relay floristics or facilitation model of succession, it is only part of a complex of species interactions (cf. Pickett et al. 1987; Walker & Chapin 1987; Glenn-Lewin et al. 1992) that includes inhibitory interactions, abiotic disturbances such as frosts, herbivory, and invasions by non-native species (some of which are also altering soil-N). The influence of a critical species on succession, its interactions with other species and its environmental impacts are best examined at each life history and successional stage from arrival to senescence.

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