Available online at www.sciencedirect.com
ScienceDirect
Forest Ecology and Management 234 (2006) 333–343
Forest Ecology and Management
www.elsevier.com/locate/foreco

Direct seeding to restore rainforest species: Microsite effects on the early establishment and growth of rainforest tree seedlings on degraded land in the wet tropics of Australia

Susan J. Doust *, Peter D. Erskine, David Lamb *

Rainforest Co-operative Research Centre, School of Integrative Biology, The University of Queensland, Brisbane, Qld 4072, Australia

Received 4 April 2006; received in revised form 18 July 2006; accepted 18 July 2006

Abstract

Reforestation in tropical areas is usually attempted by planting seedlings but, direct seeding (the artificial addition or sowing of seed) may be an alternative way of accelerating forest recovery and successional processes. This study investigated the effects of various sowing treatments (designed to create different microsite conditions for seed germination) and seed sizes on the early establishment and growth of directly sown rainforest tree species in a variety of experimental plots at three sites in the wet tropical region of north-east Queensland, Australia. The different sowing treatments were found to have significant effects on seedling establishment. Broadcast sowing treatments were ineffective and resulted in very poor seedling establishment and high seed wastage. Higher establishment rates occurred when seeds were buried. Seed size was found to be an important factor affecting establishment in relation to micro-site condition. In general, larger seeded species had higher establishment rates at all three sites than species of small and intermediate seed size, but only in sowing treatments where seeds were buried. Overall these results suggest that direct sowing of seed can be used as a tool to accelerate recolonisation of certain rainforest tree species on degraded tropical lands, but initial success will be dependent on the choice of sowing method and its suitability for the seed types selected. The results also indicate that the recruitment of naturally dispersed tree species at degraded sites is likely to be severely limited by the availability of suitable microsites for seed germination. Consequently the natural recovery of degraded sites via seed rain can be expected to be slow and unpredictable, particularly in areas where soil compaction has occurred.

Keywords: Direct seeding; Reforestation; Restoration; Humid tropical forests; Seed size

1. Introduction

Dispersal has been noted as a key factor affecting species distributions (Primack and Miao, 1992) and dispersal limitation has been suggested to be the most fundamental factor likely to impede recruitment of plant species to disturbed sites (Guariguata and Ostertag, 2001; Uhl, 1988; Wijdeven and Kuzee, 2000). This limitation is normally overcome by planting seedlings of preferred species. However, this can be expensive and, under certain conditions, direct seeding might be an attractive and much cheaper alternative (Engel and Parrotta, 2001; Lamb and Gilmour, 2003; Lamb et al., 2005). In this case, factors limiting the germination of seeds and seedling growth and survival will be the primary bottlenecks limiting ecosystem recovery.

The post-dispersal barriers at degraded sites potentially able to limit plant recruitment include micro-environmental conditions which affect moisture availability (including soil topography), soil structure and low levels of nutrient availability (Guariguata and Ostertag, 2001; Nussbaum et al., 1995). Other important limits include root and shoot competition from herbaceous vegetation (Nepstad et al., 1991; Putz and Canham, 1992; Holl, 1998) and damage from seed predators and seedling herbivores (Nepstad et al., 1990; Holl et al., 2000; Chapman and Chapman, 1998). These factors, in conjunction with the life history traits of seed size and germination phenology, influence species' recruitment patterns by determining the availability of 'safe sites' for their establishment (Foster and Janson, 1985; Eriksson and Ehrlen, 1992).

Favourable micro-sites that enable tree seeds to germinate successfully may be relatively uncommon in the harsh

* Corresponding authors. Tel.: +61 7 3365 2045; fax: +61 7 3365 1699.
E-mail addresses: sdoust@hotmail.com, susan.doust@aad.gov.au (S.J. Doust), d.lamb@uq.edu.au (D. Lamb).

0378-1127/$ – see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2006.07.014

conditions typically experienced at degraded sites (De Steven, 1991). These sites often have compacted soils and are subject to wide fluctuations in temperature and moisture. Micro-climatic or micro-topographic conditions at a site may need to be altered or ameliorated in some manner to facilitate species re-establishment. Eriksson and Ehrlen (1992) suggest that if micro-site limitation is the critical factor regulating recruitment of a population then a managed or induced increase in micro-site availability should lead to an increase in seedling recruitment.

Investigations into how direct seeding might be applied to degraded land in tropical and sub-tropical rainforest regions are limited, even though the technique may have some significant cost advantages (Engel and Parrotta, 2001; Camargo et al., 2002; Sun and Dickinson, 1995; Vanderwoude et al., 1996). Some studies have identified weed competition as a major factor increasing seedling mortality in direct sowing in comparison to higher cost methods of tree establishment (Engel and Parrotta, 2001; Sun and Dickinson, 1996). In previous direct seeding research in north-east Australia, Bell (1998) and Snell and Brooks (1998) have suggested this weed competition might be overcome by sowing seeds onto dense mulch layers formed from dead weeds after site preparation prior to sowing. This type of site preparation could inhibit the growth of new weeds and facilitate the establishment of tree seedlings during the stage of early growth.

Contrary to these studies, work in other regions has demonstrated that the excessive accumulation of litter cover can either prevent the penetration of seedling radicles or prevent germination through shading and thus retard the emergence of desired species (De Steven, 1991; Grime, 1991; Harper, 1977). The deep burial of small seed under soil or litter layers has also been found to rapidly exhaust seed stored energy reserves before emergence is complete causing increased rates of mortality (Kitajima and Fenner, 2000). These different experiences suggest direct seeding into mulch might be a high risk method to use when restoring tropical forests at degraded sites.

In order for direct seeding to become a viable rehabilitation method suitable methodologies must incorporate techniques that regularly promote, or at least do not inhibit, the successful establishment of a wide range of species. Such species are likely to have varying seed sizes and life history traits.

Many of the studies to date of direct seeding with rainforest species have focussed on the use of pioneer tree species (or those found to naturally occur at the early stages of succession) (see for example Vanderwoude et al., 1996; Sun et al., 1995; Engel and Parrotta, 2001). Pioneer species are often characterised by the prolific production of small sized seeds, and typically dominate natural tree regeneration in open sites and large forest gaps (Turner, 2001). Small seed size enables greater dispersal to open habitats by a wide variety of bird species, some of which forage extensively across the landscape and roost outside forest areas in early secondary growth and grassland habitats (e.g. in north Queensland brown cuckoo doves and currawongs) (Jones and Crome, 1990). Large seeded species may be more poorly dispersed because of the reluctance of many larger vertebrate seed dispersers to utilise or move through degraded or cleared habitats (due to removal or decrease in the structural complexity of the vegetation) (Crome and Moore, 1990; Nepstad et al., 1990; Harrington et al., 1997; Laurance, 1997; Wunderle, 1997). Such observations bring into question whether the paucity of later successional or larger seed species in such environments is primarily a result of dispersal limitation, or a result of the incapacity of these plant species to establish in these areas due to other post dispersal establishment barriers, such as the lack of suitable microsites for seed germination. The exclusive use of small seeded pioneer species in direct seeding may have limited application for forest restoration practitioners whose primary objective is to introduce a broader range of species to a site in order to accelerate succession and regain previous biodiversity.

The aims of the present study were, therefore, to determine how different sowing treatments (microsites) affected the

Table 1
Characteristics of study sites

Site	Latitude, longitude	Elevation (m a.s.l.)	Aspect	Annual Rainfall (mm)[a]	Land use after clearing	Predominant weed species present
Wadda Plantation	S17°32′16.8″, E145°50′39.5″	121 (lowland foothills)	SSW	3393	Cattle grazing/banana plantation	*Megathyrus maximus*
Palmerston	S17°36′54″, E145°47′15″	365 (mid elevation)	North	3168	Powerline corridor	*Megathyrsus maximus* *Melinus minutiflora* *Lantana camara* *Rubus alceifolius* *Ageratum houstonianum*
Massey Creek	S17°36′42.69″, E45°33′3.89″	1027 (higher elevation)	North	2643	Cattle grazing	*Sporobolus pyramidalis*/*Sporobolus natalensis* *Brachiaria decumbens* *Ageratum houstonianum*

[a] Annual rainfall is mean annual total precipitation from meteorological stations within 5 km distance from field sites.

establishment and growth of various tree species with different seed sizes, and how these sowing treatments also affected the re-establishment and growth of weeds.

2. Methods

2.1. Study sites

Direct seeding trials were established in the wet season of 2000/2001 (December) in north east Queensland, Australia. Three sites, Wadda, Palmerston and Massey Creek, were selected along an altitudinal gradient running from the lowland foothills of the Innisfail area (Wadda), to elevated areas towards the southern end of the Atherton Tableland (Massey Creek; see Table 1). Along this gradient, mean maximum and minimum temperatures decreased with increasing elevation (Malcolm et al., 1999). High altitude areas of the tablelands receive extended periods of low cloud and drizzle during the winter (dry season months) and frosts are a seasonal feature of the environment on many sites above 700 m altitude (Duff and Stocker, 1989). Much variation is seen to occur in local conditions due to small changes in topography across the landscape (Malcolm et al., 1999). The upland site at Massey Creek received substantial exposure to prevailing winds, evidenced by its close proximity to a renewable energy wind farm.

All sites had been cleared of forest for more than 40 years previously and were generally dominated by non-native grasses (see Table 1). Previous forest types were Complex Mesophyll Vine Forest (at Palmerston and Wadda) and Complex Notophyll Vine Forest (at Massey Creek) (Tracey, 1982). The soils at all the sites were classified as basaltic krasnozem (red podsolic) (Bultitude et al., 1999). Soils at Massey Creek were possibly very leached due to overland or sheet flow of water down-slope during rain periods and were also highly compacted due to the site being used for cattle grazing for several decades prior to establishment of the experiment (personal communication, Queensland Parks and Wildlife Service, 2001).

2.2. Tree species selection

Species selection was primarily determined by seasonality and seed availability in the period prior to trial establishment. Only tree species were used as the study was primarily concerned with establishing species for initial site capture and accelerating tree recolonisation. Eighteen species from 16 families were used. These have a diversity of ecological attributes, including a range of seed sizes, dispersal mechanisms and are representative of a variety of successional stages including early pioneers as well as late stage (or climax) species (Table 2).

Table 2
Characteristics of species used in direct seeding trials

Species[a]	Family	Sites[b]	Seed size[c]	Seral stage[d]	Dispersal vector[e]
Acacia celsa Tindale	Mimosaceae	W, P, M	S	1	I B
Alphitonia petriei C.T White & Braid	Rhamnaceae	W, P, M	S	1	B M
Athertonia diversifolia (C.T. White) L.A.S. Johnson & B.G. Briggs	Proteaceae	M	L	5	M G
Barringtonia calyptrata (R.Br. ex Meirs) R.Br. ex F. M. Bailey	Lecythidaceae	W	L	5	M C Bt Wt
Castanospermum australe A.Cunn. & Fraser ex Hook.	Fabaceae	W, P	L	4	M G Wt
Corynocarpus cribbianus (F.M. Bailey) L.S.Sm.	Corynocarpaceae	W, P, M	L	5	M C G
Cryptocarya oblata F.M. Bailey	Lauraceae	W, P, M	L	5	M C Bt G
Diploglottis smithii S.T. Reynolds	Sapindaceae	W, P	I	5	M B C Bt
Elaeocarpus grandis F.Muell	Elaeocarpaceae	W, P, M	I	6	M B C
Euodia xanthoxyloides F.Muell	Rutaceae	W, P, M	S	2	B I
Ficus pleurocarpa F.Muell	Moraceae	W, P, M	S	5	Bt B M C
Flindersia brayleyana F.Muell	Rutaceae	W, P, M	I	6	Wd
Geissios biagiana (F.Muell) F.Muell. ex Engl.	Cunoniaceae	P, M	S	5	Wd
Nauclea orientalis (L.) L.	Rubiaceae	W, P	S	2	M C Bt B
Prumnopitys amara (Blume) de Laub	Podocarpaceae	M	L	4	M C
Prunus turneriana (F.M. Bailey) Kalkman	Rosaceae	W, P, M	L	5	M C Bt
Syzigium cormiflorum (F.Muell.) B.Hyland Waterh.	Myrtaceae	P	L	5	M C G
Xanthostemon whitei Gugerli	Myrtaceae	M	S	4	Wd Wt

[a] Nomenclature follows that of Hyland et al. (1999).
[b] Sites where sown: W, Wadda; P, Palmerston; M, Massey Creek.
[c] Seed size category based on seed weight, S, small (<0.01–0.099 g); I, intermediate (0.1–4.99 g); L, large (>5.0 g) (seed size category determined from mean of a random sample of no less than 20 seeds per species).
[d] Seral stage: early (1), early–intermediate (2), intermediate (3), intermediate–late (4), late (5), generalist (6) (Osunkoya et al., 1994; Tucker personal communication, 1999; Olsen personal communication, 2002; personal observation).
[e] Dispersal vector: B, bird (except Cassowary); Bt, bat; M, mammal (ground dwelling/arboreal); C, cassowary; I, insect; Wt, water; Wd, wind; G, gravity (Tucker personal communication, 1999; Irvine personal communication, 2002).

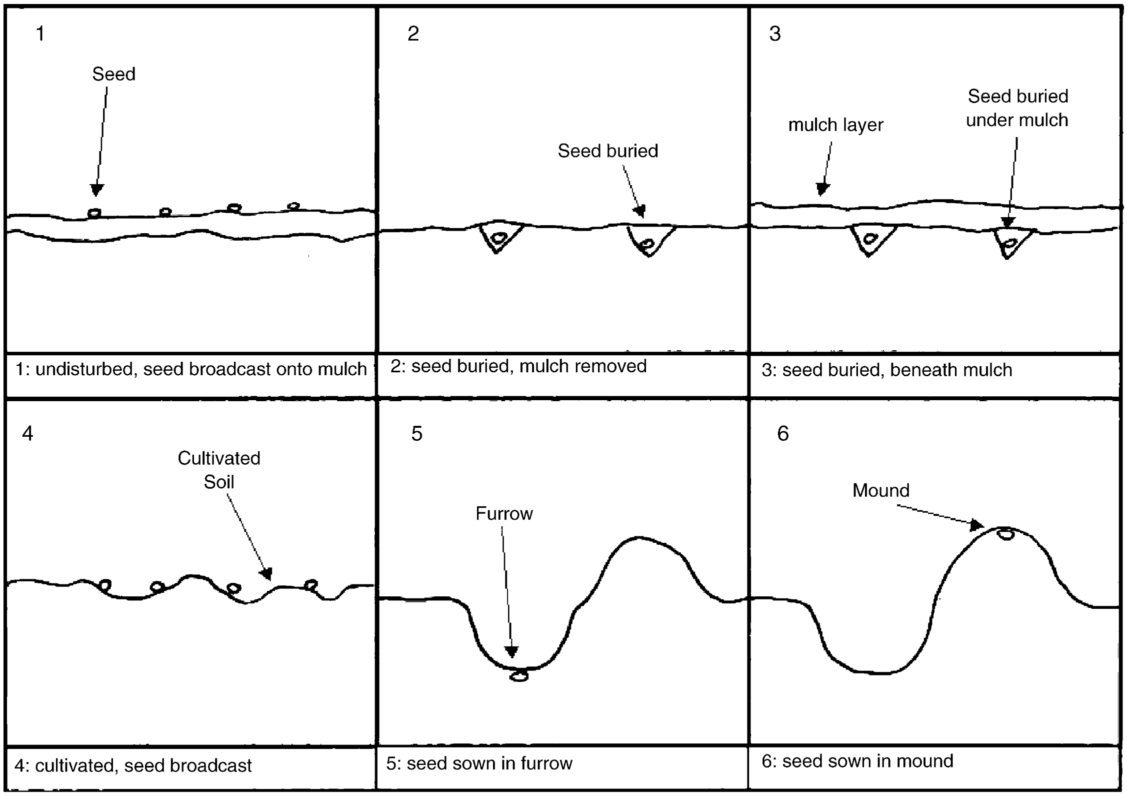

Fig. 1. Sowing treatments. Numbers (1–6) correspond to treatment numbers.

2.3. Seed collection, storage, viability and pre-germination treatments

Seeds were collected from parent trees (a minimum of three) in close proximity to the experimental sites to ensure seed stocks were local provenance and adapted to local climate and soil types. After collection, seed was cleaned to remove dehiscent capsules and fleshy parts. Storage periods did not exceed 3 weeks for any fleshy fruited species. For seeds of *Barringtonia calyptrata*, *Corynocarpus cribbianus* and *Prunus turneriana*, fleshy parts were left intact during the period of storage to minimise moisture loss and to reduce the effects of storage on seed survival. Seeds of these species were cleaned (flesh removed) immediately prior to sowing.

Estimates of seed quality of small seeded species were determined through germination trials conducted in a glasshouse. Germination percentages were used as a baseline for calculations of species establishment rates in the field experiments. The viability of larger seeded and recalcitrant species was determined through visual examination and not by germination trials as many have slow or erratic germination rates. Large hard coated seeds were also tested for viability by flotation tests in water. Pre-germination treatments for particular species were carried out immediately prior to sowing. Pre-treatments were scarification in boiling water and soaking for 48 h (as of Sun and Dickinson, 1995) for *Alphitonia petriei* and also *Acacia celsa*. Suitable pre-treatments to enhance germination rates were not known for any of the other species tested at the time of the experiments (personal communication, Centre for Tropical Restoration, 1999).

2.4. Site preparation, maintenance and experimental design

Existing weed growth at each of the study sites was cleared via mechanical and chemical treatments prior to trial establishment. Chemical treatment consisted of two applications of post-emergent non-residual herbicide (Nufarm Glyphosate 360® 100 mL/15 L of water) with approximately 1 month between applications.

The experimental trials at each site were established according to a split-plot design with whole plots in a randomised complete block design (RCBD). At each site five blocks (6 m × 8 m) were established. Blocks were spaced at a minimum of 5 m apart. Each block was then subdivided into six 2 m × 2 m experimental plots to which one of six different sowing treatments was randomly allocated (Fig. 1).

Experimental plots were then further segregated into three split-plots (2 m × 66 cm) to accommodate three seed size category treatments (randomly allocated to split-plots). Seeds were classified according to mean seed weight as small (<0.01–0.099 g), intermediate (0.1–4.99 g) or large (>5 g). Hence the sowing method was the whole plot factor (5 replications) and seed size was the split-plot factor (5 replications).

2.5. Treatments

The sowing treatments (applied to 2 m × 2 m plots) were designed to create different micro-site conditions for germination and to create conditions that could be easily replicated using conventional farming implements for broad-scale application, e.g. mound ploughing, cultivation or shallow ripping (Fig. 1). These treatments were applied manually. In treatment 1, seeds were broadcast onto a mulch layer consisting of dead organic weed matter residual from site preparation. This treatment involved no soil disturbance. In treatment 2 the dead weed mulch was removed and seeds were buried in the topsoil. The sowing depth was approximately 5–20 mm depending on seed size (larger seeds required more soil coverage). In treatment 3 seeds were buried in topsoil and the mulch was replaced. Treatments 4–6 involved more soil disturbance than the first three treatments. In treatment 4 mulch was removed, the site was cultivated and seeds were broadcast over the area. Treatments 5 and 6 were a furrow and mound treatment respectively and were oriented east–west to reduce shading effects on seedling germination. In treatment 5 seeds were sown in the bottom of the furrows while in treatment 6 seeds were sown in the top of the mound.

The species used in the seed mixtures for the split-plots varied slightly between the three experimental sites (Table 2). Seed mixtures were determined by the composition of species in natural forest types near the experimental areas. Sowing density in the seed size treatments (split-plots) varied depending on the seed size. Smaller seeded species were usually sown in higher densities than the larger seeded species because of limits on the availability of larger seeded species. Seed were sown 2 weeks after the final herbicide application for site preparation at the commencement of the wet season period in December.

Grass weed control was carried out using the grass-specific herbicide Fusilade® (Fluazifop-p) which was applied to all sown plots at the label rate of 50 mL/10 L or 2 L/ha. This was applied 2 months after seeds were sown in the field.

2.6. Data collection and analyses

Mulch consisted of dead weed matter residual after initial spraying and slashing preparation. Prior to seeding, three vertical measures of mulch depth above the soil layer were taken at random locations within each whole plot after sowing treatments had been applied. Mean mulch depths at the sites were: 3.2 cm (±0.49) at Massey Creek in the uplands; 7.2 cm (±0.70) at Palmerston and 8.3 cm (±0.97) at Wadda in the lowlands.

Assessments of seedlings and weeds were carried out at 2 months and 8 months after seeds were applied. Tree seedlings surviving at the site at the time of monitoring were identified and stem lengths were measured from soil level to the apical tip. Heights were then grouped according to species and a mean height per species per treatment at each assessment period was obtained. The percentage cover, and cover composition of weed species (to the nearest %) was assessed by a visual estimate from 1 randomly selected 50 cm × 50 cm quadrat placed flat on the ground within each whole plot. Maximum weed height was also recorded within quadrats.

The production of live root biomass by weed species was assessed by the extraction of 1 soil core from a randomly selected location in each whole plot in August 2001. Samples were collected using a hand soil auger (7 cm diameter) which enabled sampling to be carried out without incurring damage to the tree seedlings and extracted to a depth of 25 cm. Live root matter was separated by elutriation and sieving (using 0.5 mm and 1 mm sieves) and then extracted using forceps. It was then dried in an oven at 75 °C for 24 h (Bohm, 1979) and weighed.

2.7. Statistical analyses

Treatment effects on seedling establishment rates and weed cover, height and composition were assessed by analysis of variance (ANOVA) according to a split-plot model on a randomised complete block design (RCBD). Sowing treatments were analysed as a whole plot factor with 6 levels (error term: block × whole plot) and seed size category analysed as a sub plot factor with three levels (error term: block × sub plot). Interaction between the levels of whole plot treatments and sub-plot treatment were analysed by the error term: block × whole plot × sub-plot, being within block comparisons (Milliken and Johnson, 1984). Percentage data were transformed using an arc-sine square root transformation as of Zar (1996) prior to statistical analyses, while descriptive statistics presented are of original untransformed data. Post hoc analyses for pair-wise comparisons of means were undertaken using Tukey's HSD test ($\alpha = 0.05$). Repeated measures analysis of variance were used to compare seedling survival, weed height, cover and composition between assessment periods (with month of assessment as the repeated measures factor). Results of tests were considered significant at α level 0.05. All analyses were performed using Statistica 6.0 (Stat-Soft Inc., 2002, Tulsa, USA).

3. Results

3.1. Glasshouse viabilities and germination patterns

Elaeocarpus grandis and *Prumnopitys amara* both failed to germinate in glasshouse and field trials and were therefore excluded from further analyses. Three small seeded species (*Euodia xanthoxyloides*, *Ficus pleurocarpa* and *Xanthostemon whitei*) showed very low germination rates (<5%) in the glasshouse trials and poor establishment in the field and, because of this, could not be statistically analysed. All other species in the trial had viabilities of 20–100%.

3.2. Climatic conditions over the study period

Growing conditions were favourable during the period of the trial. Mean monthly temperatures varied between 15 °C (minimum) and 33 °C (maximum) in the lowlands and between 8 °C (minimum) and 33 °C (maximum) in the uplands. The rainfall received was similar at all three sites. In the first month (December) it ranged from 60 mm to 110 mm. Rainfall increased over the next 2 months peaking in February (750–835 mm) but declined from then on with only 7–10 mm received in July.

Table 3
Seedling establishment in sowing treatments after 8 months

Sowing treatment	Site					
	Massey Creek (1027 m)		Palmerston (365 m)		Wadda (121 m)	
	Establishment rate (%)*	No./10 m^2	Establishment rate (%)*	No./10 m^2	Establishment rate (%)*	No./10 m^2
1	1.8 (0.9)a	3.6 (0.9)	2.1 (1.0)a	5.2 (1.4)	3.3 (1.4)a	3.4 (0.8)
2	24.3 (3.0)b	23.4 (2.9)	33.4 (0.9)b	45.0 (4.8)	25.5 (1.8)b	17.0 (0.5)
3	22.6 (3.5)b	19.6 (2.6)	31.3 (3.5)b	36.0 (6.4)	26.4 (1.9)b	17.4 (1.4)
4	2.7 (1.4)a	3.0 (0.4)	1.4 (0.6)a	6.6 (2.5)	3.2 (1.9)a	4.0 (1.0)
5	25.9 (2.5)b	34.0 (1.1)	15.8 (0.8)c	29.0 (3.5)	19.7 (1.6)bc	14.0 (0.9)
6	22.9 (4.3)b	19.6 (2.5)	13.4 (1.4)c	17.6 (2.9)	10.9 (1.4)ac	12.6 (0.9)

Values are replicate block means ± S.E. ($n = 5$).
[*] Means with the same letter following are not significantly different ($\alpha = 0.05$).

3.3. Overall seedling establishment success

Establishment rates (shown in Table 3) were determined by calculating the number of seedlings present as a percentage of the number of viable seeds sown per plot. At 8 months there was a significant difference in seedling establishment between sowing treatments at all three sites (Massey Creek, $F_{5,20} = 17.6$, $p < 0.0001$; Palmerston, $F_{5,20} = 46.46$, $p < 0.0001$; Wadda, $F_{5,20} = 25.43$, $p < 0.0001$). Higher establishment rates were observed for all species when seed were buried, particularly for large seeded species. The two broadcast sowing treatments (1 and 4) consistently showed the lowest overall establishment rates (less than 4% at all sites). These results were significantly lower than all other treatments at Massey Creek and Palmerston and all other treatments except for the mound treatment (6) at Wadda.

At Massey Creek (the higher elevation site) site there was no difference in seedling establishment between treatments 2 (buried, mulch removed), 3 (buried under mulch), 5 (furrow) and 6 (mound). At Palmerston (the mid elevation site) levels of seedling establishment in treatments 2 and 3 were significantly higher than treatments 5 and 6. Similarly, at Wadda (the low elevation site) treatments 2 and 3 showed the highest establishment, followed by treatment 5.

3.4. Influence of seed size on seedling establishment in sowing treatments

Results are presented in Table 4. Seedling establishment varied significantly between seed size categories in relation to sowing treatments at all three sites (Massey Creek: 2 months—$F_{10,40} = 3.6$, $p = 0.001$, 8 months—$F_{10,40} = 6.29$, $p = 0.0001$; Palmerston: 2 months—$F_{10,40} = 6.86$, $p < 0.0001$, 8 months—$F_{10,40} = 15.96$, $p < 0.0001$; Wadda: 2 months—$F_{10,40} = 3.33$, $p = 0.003$, 8 months—$F_{10,40} = 14.69$, $p < 0.0001$). Overall differences in establishment between treatments tended to become more significant over time as the survival of species with small and intermediate seed size declined and germination rates of large seeded species increased.

At Massey Creek (the higher elevation site) the treatment fostering the highest establishment rates of small seeded

Table 4
Seedling establishment (% ± S.E.) of small (S), intermediate (I) and large (L) seed size categories in the six sowing treatments

	Site								
	Massey Creek			Palmerston			Wadda		
	S[a]	I[a]	L[a]	S[a]	I[a]	L[a]	S[a]	I[a]	L[a]
2 months									
1	0.9 (0.3)a	0a	0a	1.6 (0.7)a	3.3 (3.3)a	1.6 (1.0)ac	1.8 (0.6)a	0a	0.8 (0.8)a
2	7.6 (2.0)ab	6.7 (6.7)a	19.9 (6.0)b	12.4 (3.6)a	29.0 (7.0)a	37.2 (2.8)b	6.7 (2.1)a	14.3 (6.0)a	22.2 (5.2)b
3	6.8 (3.0)ab	0a	13.8 (6.0)ab	8.5 (1.5)a	15.7 (5.2)a	38.2 (4.9)b	3.5 (0.4)a	7.1 (2.3)a	16.9 (1.0)ab
4	0.8 (0.3)a	0a	0a	2.1 (0.8)a	0a	0.8 (0.8)a	4.2 (1.1)a	1.4 (1.4)a	9.7 (3.0)ab
5	20.9 (6.8)b	0a	9.7 (6.5)ab	8.8 (1.5)a	4.3 (1.8)a	25.2 (3.4)b	10.1 (1.6)a	15.7 (1.4)a	22.1 (4.9)b
6	7.9 (1.7)ab	13.3 (13.3)a	8.1 (4.0)ab	6.5 (1.5)a	14.8 (5.9)a	24.0 (2.5)bc	9.0 (1.1)a	10.0 (1.8)a	7.6 (1.6)ab
8 months									
1	2.2 (0.9)a	0a	2.0 (2.0)a	1.5 (0.7)a	1.4 (1.4)a	2.8 (2.0)a	1.0 (0.5)a	0a	6.0 (3.0)a
2	9.0 (1.8)a	0a	41.9 (5.6)b	10.2 (2.1)a	18.6 (3.6)a	58.0 (2.8)b	1.0 (0.3)a	4.3 (1.8)a	48.7 (3.6)b
3	6.0 (3.0)a	0a	41.0 (7.2)b	7.0 (1.9)a	20.0 (4.2)a	55.2 (5.6)b	1.1 (0.2)a	4.3 (2.9)a	50.5 (3.5)b
4	1.7 (0.3)a	0a	4.0 (2.9)a	2.2 (0.9)a	1.4 (1.4)a	0.8 (0.8)a	1.3 (0.7)a	0a	5.7 (3.9)a
5	17.7 (4.4)a	0a	38.7 (6.2)b	7.7 (1.5)a	9.1 (5.7)a	25.1 (3.5)c	1.6 (0.4)a	8.6 (5.7)a	34.9 (2.7)bc
6	7.3 (1.5)a	13.3 (13.3)a	35.3 (6.7)b	3.9 (0.9)a	8.6 (4.2)a	22.8 (2.2)c	3.2 (0.7)a	4.3 (2.9)a	18.3 (3.3)ac

Sowing treatments: 1, seed broadcast onto mulch; 2, seed buried, mulch removed; 3, seed buried beneath mulch; 4, soil cultivated, seed broadcast; 5, seed sown in furrow; 6, seed sown in raised bed. Values are replicate block means ± S.E. ($n = 5$).
[a] Means with the same letter following are not significantly different ($\alpha = 0.05$). Separation of means determined using Tukeys HSD ($\alpha = 0.05$).

Table 5
Seedling heights (cm ± S.E.) according to seed size categories in the six sowing treatments at 8 months after direct sowing[a]

	Site								
	Massey Creek			Palmerston			Wadda		
	S[a]	I[a]	L[a]	S[a]	I[a]	L[a]	S[a]	I[a]	L[a]
1	11.9 (1.4)	–	17.8 (0)	16.5 (3.8)	10 (0)	26.1 (2.1)	21 (2.5)	–	34.3 (7.1)
2	13.4 (1.3)	–	22.6 (1.7)	8.4 (1.6)	6.6 (0.8)	27.3 (0.7)	7.1 (1)	6.4 (3)	31.5 (1.2)
3	13.8 (2.4)	–	21.7 (1.7)	16 (1.7)	6.2 (1.1)	26.9 (2.1)	9.6 (1.4)	6.4 (0.9)	29.7 (1.6)
4	17.8 (3.6)	–	19.1 (0.1)	14.2 (5)	4 (0)	32 (0)	10 (3.9)	–	36.5 (3.1)
5	15.3 (1.9)	–	23.9 (1.4)	14.9 (2)	8.3 (2)	24.2 (2.3)	9.2 (1.5)	5.2 (0.7)	33.1 (2.4)
6	9 (0.4)	8 (0)	22.7 (2.8)	12.5 (1.3)	5.8 (0.5)	22.4 (1.6)	8.8 (0.9)	8 (1.5)	24.1 (1.5)

Sowing treatments: 1, seed broadcast onto mulch; 2, seed buried, mulch removed; 3, seed buried beneath mulch; 4, soil cultivated, seed broadcast; 5, seed sown in furrow; 6, seed sown in raised bed.

[a] Values are replicate block means ± S.E. ($n = 5$).

species was treatment 5 (furrow), and establishment was significantly higher at 2 months compared to treatments where seed was broadcast (1 and 4). This effect had diminished by 8 months due to the decline in survival of small seeded species. Species with intermediate seed size exhibited the highest establishment rates at 2 months in treatments 2 (buried, mulch removed) and 6 (mound) (with no survival recorded in other treatments), but by 8 months seedlings only survived in treatment 6. Establishment rates of large seeded species at 2 months remained low due to slow or erratic germination, but by 8 months large seeded species exhibited high rates of establishment in all treatments except the two broadcast sowing treatments (1 and 4).

At Palmerston (the mid elevation site), treatments 2, 3 and 5 appeared to be the most conducive to the establishment of species with small and intermediate seed sizes, with the lowest rates of recruitment evident in the broadcast treatments (1 and 4), although differences were not significant. Large seeded species again established more successfully in treatments 2 (buried, mulch removed) and 3 (buried under mulch) and showed poor establishment in broadcast treatments (1 and 4) at 8 months.

At Wadda (the low elevation site) treatments 2, 5 and 6 showed the higher rates of seedling establishment of species with small and intermediate seed sizes, but differences were not statistically significant at either 2 or 8 months. Large seeded species were most successful in sowing treatments 2 and 3, followed by treatment 5. Establishment rates in these treatments were significantly higher than in treatments 1 and 4 which showed poor success.

In general higher establishment rates were observed for species with large seeds, although species composition in split-plots varied over time due to differential survival patterns of individual species. Large seeded species tended to have higher establishment when seeds were buried (treatments 2, 3 and 5) and much poorer establishment rates where the broadcast sowing methods were used (treatments 1 and 4). Species with small seeded and intermediate seed size often showed better

Table 6
Weed cover (dicotyledon and monocotyledon)[1], weed height[2] and monocotyledon weed cover[3] in the six sowing treatments

	Site								
	Massey Creek			Palmerston			Wadda		
	Cover[1], % (±S.E.)	Height[2], cm (±S.E.)	Mono[3], % (±S.E.)	Cover, % (±S.E.)	Height, cm (±S.E.)	Mono, % (±S.E.)	Cover, % (±S.E.)	Height, cm (±S.E.)	Mono, % (±S.E.)
2 months									
1	74 (6.2)b	31.4 (4.8)a	27 (7.2)a	68.4 (7.1)ab	44.6 (2.5)a	11.2 (7)a	67 (4.6)c	112 (13.3)ab	41 (10.7)b
2	76 (3.3)b	36.8 (4.4)a	27.6 (9)a	85.6 (4)a	39 (14.1)a	5.6 (2.5)a	79.4 (3.6)bc	93 (14.5)ab	31 (9.7)ab
3	72 (2.5)ba	29 (9.2)a	15.8 (5.9)a	64 (6.4)b	28.8 (6.9)a	3.8 (1.7)a	45.8 (4.2)a	75 (7.7)a	8 (3.9)a
4	70 (5.7)ba	25.6 (4.3)a	15.8 (7.2)a	79 (6.6)ab	39.2 (7.8)a	0a	86 (4.3)b	115 (8.9)b	58 (11.9)b
5	49 (3.3)a	31 (4.1)a	14.2 (4.9)a	75 (3.2)ab	51 (6.6)a	2.2 (1)a	78 (3.7)bc	102 (7.2)ab	25 (5.7)ab
6	64 (7.9)ba	34 (2.5)a	10.6 (4.2)a	71.4 (3.1)ab	50.6 (10.4)a	4 (4)a	70 (2.2)c	92 (9)ab	33 (6.8)b
8 months									
1	83 (4.9)b	32 (5.6)a	40.9 (8.9)a	76 (1.9)a	120 (19.2)a	7 (3.7)a	73 (5.4)ab	160 (17.9)a	48.1 (11.2)a
2	88 (1.2)b	30 (3.2)a	45.9 (13.5)a	73 (3.4)a	71 (19)a	16 (3.6)a	83 (3.4)b	176 (12.9)a	53.1 (8.2)a
3	88 (1.2)b	28.4 (2.2)a	47.4 (9.4)a	63 (6.8)a	109 (18.9)a	10.4 (3.8)a	61 (6)a	150 (13.8)a	35.8 (9.8)a
4	90 (3.9)b	34 (6.6)a	40.8 (12.1)a	76 (3.3)a	82 (24.8)a	6 (1.9)a	76.6 (3)ab	160 (8.9)a	34.5 (6.2)a
5	70 (2.2)a	39 (3.3)a	24.9 (5.9)a	68 (4.9)a	117 (15.5)a	8.8 (4.8)a	67 (3.4)ab	154 (6.8)a	31.9 (6.1)a
6	70 (0)a	26 (3.7)a	21.7 (4.7)a	70 (5.9)a	106 (25.4)a	14.7 (4.7)a	72 (6)ab	166 (5.1)a	48.4 (8.3)a

Means with the same letter following are not significantly different ($\alpha = 0.05$). Separation of means determined using Tukeys HSD ($\alpha = 0.05$). Values are replicate block means ± S.E. ($n = 5$). *Sowing treatments:* 1, seed broadcast onto mulch; 2, seed buried, mulch removed; 3, seed buried beneath mulch; 4, soil cultivated, seed broadcast; 5, seed sown in furrow; 6, seed sown in raised bed.

establishment rates when seeds were buried than when broadcast, but these differences tended to decrease over time due to seedling mortality. It must be noted that the soils at the three sites were well textured, well drained and moderately fertile. An altered result may occur on soils that do not exhibit similar qualities.

3.5. Seedling height in relation to sowing treatments and seed size

Sowing treatments had no effect on seedling growth, irrespective of seed size at 8 months. Large seeded species generally showed higher growth rates than small and intermediate seed size species (Table 5).

3.6. Effect of sowing treatments on weed cover, composition and height growth

The various sowing treatments had limited effect on weed recolonisation. No single sowing treatment consistently limited the reoccurrence of weed growth at all three sites (Table 6). Despite this, treatment 3 (buried under mulch) was more effective relative to the other treatments at Wadda and Palmerston, and treatment 5 (furrow) was more effective at Massey Creek.

Weed height did not vary significantly between the sowing treatments at Massey Creek or Palmerston. At the lowland site at Wadda, weed height was significantly lower in treatment 3 (buried under mulch) than in treatment 4 (no mulch, cultivated, broadcast) at 2 months, but this was likely a result of the comparatively very low percentage of monocot weed cover in treatment 3 (primarily *Megathyrsus maximus* (Guinea grass)).

The six sowing treatments did not affect below-ground root competition, except at Massey Creek where treatment 5 (furrow) was seen to have the lowest weed root biomass in the soil (0.8 g $\pm$ 0.12 dry weight/962.1 cm^3 of soil), which was significantly lower than the highest value of weed root biomass found in treatment 1 (undisturbed soil and mulch layer) (3.1 g $\pm$ 0.64) ($F_{5,20} = 2.79$, $p = 0.046$).

4. Discussion

4.1. Effect of sowing treatments on seedling establishment

The microsite differences created by the various sowing treatments were found to have significant effects on the numbers of seedlings established at all sites. The two broadcast sowing methods (treatments 1 and 4) consistently showed the lowest overall seedling establishment of all treatments. In contrast, treatments 2 and 3 where the seed was buried with minimal soil disturbance, proved to be the most successful treatments with the highest levels of seedling establishment recorded. Treatments 5 (furrow) and 6 (mound), were generally less successful but achieved higher establishment rates than treatments 1 and 4. These differences in seedling establishment were probably largely due to difference in moisture and light as a result of various levels of soil disturbance and soil coverage of sown seed. Modification of seed–water relationships through changing contact with soil layers or exposure to the atmosphere has been long established in the literature as a major factor affecting plant recruitment from seed (Harper et al., 1964), and the micro-topography of the surface of the soil has been known to determine the density of safe-sites available for germination (Fenner, 1985). Woods and Elliott (2004) have also found that burial significantly increased germination percentage of direct sown seeds in experiments conducted at forest restoration sites in Northern Thailand.

The generally lower seedling establishment recorded in the furrow treatment (5) in comparison to treatments 2 (buried, mulch removed) and 3 (buried under mulch) may have been a result of the removal of the topsoil layer resulting in a depleted nutrient base for seedling establishment. However, in a similar direct seeding trial conducted in the late wet season (April) (Doust, 2005), significantly higher establishment was observed in the furrow treatment (5) at Massey Creek than in other treatments at this site. This suggests furrowing may have provided an advantage to seedling establishment during periods of lower rainfall at this site, by reducing wind exposure of seedlings (subsequently lowering rates of leaf desiccation), and moisture loss from the soil surface in the furrow. Higher moisture levels in the furrow would also act to buffer soils from severe falls in temperature during seasonal frost events. Either wind and/or frost injury (recorded as curled leaves with dead brown tips or edges) was seen to affect over 20% of seedlings at Massey Creek at the August 2001 assessment with overall lower levels of damage recorded in the furrow treatment (5).

The lower seedling establishment in the mound treatment (6) in comparison to treatments 2 (buried, mulch removed) and 3 (buried under mulch) at the lower altitude sites can most likely be attributed to the increased exposure of the soil and seedlings and poor soil water retention. The mound treatment showed even lower seedling establishment in similar direct sowing trials conducted in the late wet season (April) (Doust, 2005). Poor establishment in mounds may have also been a result of increased susceptibility of the sown seeds to predation. Soil disturbance of mounds was recorded at both the lower altitude sites (Palmerston and Wadda) and was most likely a result of feral pig (*Sus scrofa*) activity. Upturning of soil is usually a reliable indicator of feral pig activity and feral pigs have been known to opportunistically predate seeds and fruits in the study region (Laurance and Harrington, 1997), particularly in areas where soil has already been disturbed (personal communication, Queensland Parks and Wildlife Service, 1999).

The broadcast sowing treatments (1 and 4) proved to be the least successful. In similar sowing trials conducted in the late wet season (April) (Doust, 2005) when rainfall levels had declined, treatments 1 and 4 showed even lower establishment rates at all three sites (less than 2% at Massey Creek). Seed mortality as a result of exposure to desiccation or to seed predation on the soil or mulch surface was the most likely reason for failure of these treatments. Under natural circumstances seed burial probably occurs only infrequently, especially for larger seeded species, but may be important in degraded habitats where seeds are vulnerable to predation or where the risk of seed mortality is increased due to extreme conditions experienced at the soil surface (e.g. high soil temperatures (Zimmerman et al., 2000)). Seed loss to predation has been found to be higher for seed exposed on the soil surface than for buried seed (Crawley, 2000). Seed predation rates in the region may also increase in dry season periods in response to seasonal variation in the availability of food resources. Fruit and seed availability starts to become more limiting during the 'lean time' (March to June) when the number of cloudy days is at its peak and fruit production is at its lowest (Goosem and Tucker, 1995).

4.2. Effects of seed size on seedling establishment in sowing treatments

Although differences between the sowing methods were seen to affect the success of seedling establishment, it is also clear that seed size was very influential. Large seeded species established in higher proportions at all three sites than species of small and intermediate seed size, but this was only the case in treatments where seeds were buried. Subsequently establishment of large seeded species was greater in treatments 2 (buried, mulch removed), 3 (buried under mulch), 5 (furrow) and 6 (mound) than in the two broadcast sowing treatments (1 and 4) at all sites. This result suggests that soil coverage was a major determinant of the success of germination of the species tested. Species that are likely to be highly dependent on soil moisture during the germination phase of establishment are those that are soft coated and thus particularly prone to desiccation, as is common in many large seeded rainforest species due to increased water retention of the storage tissue (e.g. *Castanospermum australe*, *Cryptocarya oblata*, *Syzigium cormiflorum*) (Turner, 2001). Species that are hard coated (e.g. *Athertonia diversifolia*, *Prunus turneriana*) may also require sufficient permeation of water through the seed coat for imbibition before germination will occur (Murdoch and Ellis, 2000).

Treatments where seeds were buried (2, 3, 5 and 6) also proved to be more successful than the broadcast sowing treatments (1 and 4) for species with small and intermediate seed size, suggesting that even for small seeds availability of suitable safe-sites was a limiting factor at the establishment stage. Despite there being no significant variation in establishment of small seeded species between treatments 2 (buried, mulch removed) and 3 (buried under mulch), treatment 2 consistently showed marginally higher recruitment at all sites suggesting that the mulch layer may have afforded a partial barrier to the establishment of small seeded species. Litter layers derived from trees and herbaceous vegetation have been found to act as physical barriers to the germination of small seeded species in several previous studies (see for example Carson and Peterson, 1990; Vazquez-Yanes and Orozco-Segovia, 1992; Woods and Elliott, 2004).

There was little variation between the two broadcast sowing methods (1 and 4) in the establishment of small and intermediate sized species despite the varied micro-topographical conditions between the two treatments (the cultivation of the topsoil layer in treatment 4 provided a more heterogenous micro-topography than the undisturbed soil and mulch layer in treatment 1).

Several of the more successful small seeded species sown in these trials were early successional species (e.g. *Acacia celsa*, *Alphitonia petriei*), characterised with high juvenile mortality after germination (Turner, 2001). Subsequently the poor seedling establishment in the broadcast treatments which predominantly consisted of these early phase small seeded species, was further depleted over time in contrast to treatments that fostered the establishment of larger seeded species. Thus, in consideration of these results, broadcast treatments utilised in this study can be considered ineffective and unsuitable for direct sowing at degraded sites in the region, particularly when aiming to minimise seed wastage.

As broadcast sowing essentially simulates natural seed dispersal in many instances (e.g. from seed rain), these results suggest that the likelihood of successful seedling establishment occurring after a natural dispersal event is relatively low. In the absence of artificial intervention, large seed inputs and numerous chance events resulting in seed burial would be necessary to initiate tree recolonisation at these sites. This is particularly the case for larger seeded species where the availability of suitable microsites is likely to be even more restricted than for smaller seeded species. Only in situations where seeds are dispersed by a large vertebrate or frugivore (e.g. a cassowary) and deposited in dung will they likely experience a similar environment to burial in soil and benefit from sufficient moisture retention around the seed. Subsequently germination of seeds dispersed in dung may be higher than of seeds deposited by other dispersal mechanisms at degraded sites, though a paucity of larger fauna entering successional habitats will limit the chances of this occurring.

Micro-site limitation has also been noted as a factor impeding tree establishment in several previous studies (see for example Eriksson and Ehrlen, 1992; Hulme, 1996; Mazia et al., 2001). As micro-site limitation essentially acts to restrict the degree of seedling establishment it could also be considered a factor limiting the diversity of species colonising a site. The diversity of species recruitment is most likely to be affected by micro-site condition where seed size varies between species by several magnitudes, thus dramatically altering species requirements for establishment.

4.3. Effect of sowing treatments on weed recolonisation

Variation in the degree of soil disturbance and the presence of mulch layers in the sowing treatments had limited effect on the re-establishment of weed species. This indicates that at these sites (and at similar degraded sites) where weeds have been growing and reproducing for long periods of time, more severe weed control measures will be required prior to direct sowing to limit weed regrowth. An increased commitment to weed control prior to direct seeding of the tree species (such as successive herbicide treatments on new weed growth following the initial herbicide and slashing treatments) would possibly increase the effectiveness of more subtle weed suppression techniques (such as the minimisation of soil disturbance) and would assist in exhausting the weed seed store. Any weed suppressant effect that mulch layers may have is likely to be transient and may only be effective within the first few weeks after site preparation (depending on mulch thickness and decomposition rates).

The lower weed cover and below ground root competition in treatment 5 (furrow) at Massey Creek was caused by the removal of the upper part of the soil profile (to a depth of approximately 20 cm) which contained the greatest proportion of root matter and material available for vegetative reproduction by the pasture grasses that dominated the weed component at this site. Use of furrowing as a worthwhile means of reducing weed regrowth will be dependent on the rooting depth of weed species present as well as soil depth and must be considered in relation to any negative or positive impacts on tree seedling growth (such as reduced nutrient availability from topsoil removal, or reduced exposure and increased soil moisture levels).

5. Conclusions

The micro-site effects on species establishment observed in this study suggest the best results from direct seeding will come when there is an opportunity to manipulate the soil environment to create appropriate microsites. Even so, it will be difficult to restore species rich communities by direct seeding alone since many species are likely to be unsuited to this regeneration method. Optimal results may come from a combination of low-cost direct seeding and the higher-cost but more reliable planting of seedlings.

The success of seedling establishment recorded in these trials essentially displays the minimum success achievable using direct sowing. Maintenance in these trials was very minimal, suggesting that improved survival and growth of tree seedlings is likely to have been attained with an increased commitment to weed control at the sites.

Acknowledgements

The authors would like to thank Dr. Amanda Snell, Simon Brooks and staff from the Queensland Forestry Research Institute (Queensland Department of Primary Industries and Fisheries) and Nigel Tucker and staff from the Centre for Tropical Restoration (Queensland Parks and Wildlife Service). Thanks to James Walle for comments on the manuscript. Susan Doust was supported by a University of Queensland postgraduate scholarship and research support from the Rainforest-CRC.

References

Bell, R., 1998. Establishment of broad scale direct seeding trials in riparian areas in the Johnstone River Catchment: completion report. Johnstone River Catchment Management Association.

Bohm, W., 1979. Methods of Studying Root Systems. Springer-Verlag, Heidelberg.

Bultitude, R.J., Garrad, P.D., Wegner, S., Donchak, P.J.T., Fanning, C.M., 1999. Innisfail, Sheet SE 55-6, Explanatory Notes, second ed. Department of Mines and Energy, Brisbane.

Camargo, J.L.C., Ferraz, I.D.K., Imakawa, A.M., 2002. Rehabilitation of degraded areas of central amazonia using direct sowing of forest tree seeds. Restor. Ecol. 10, 636–644.

Carson, W.P., Peterson, C.J., 1990. The role of litter in an old-field community: impact of litter quantity in different seasons on plant species richness and abundance. Oecologia 85, 8–13.

Chapman, C.A., Chapman, L.J., 1998. Forest restoration in abandoned agricultural land: a case study from East Africa. Conserv. Biol. 13, 1301–1311.

Crawley, M.J., 2000. Seed predators and plant population dynamics. In: Fenner, M. (Ed.), Seeds: The Ecology of Regeneration in Plant Communities. second ed. CABI Publishing, UK, pp. 167–182.

Crome, F.H.J., Moore, L.A., 1990. Cassowaries in north-eastern Queensland: a report of a survey and a review and assessment of their status and conservation and management needs. Aust. Wildl. Res. 17, 369–385.

De Steven, D., 1991. Experiments on mechanisms of tree establishment in old-field succession: seedling emergence. Ecology 72, 1066–1075.

Doust, S.J., 2005. Seed and seedling ecology in the early stages of rainforest restoration. Ph.D. Thesis. The University of Queensland, Australia.

Duff, G.A., Stocker, G.C., 1989. The effects of frosts on rainforest/open forest ecotones in the highlands of North Queensland. Proc. R. Soc. Queensl. 100, 49–54.

Engel, V.L., Parrotta, J.A., 2001. An evaluation of direct seeding for reforestation of degraded lands in central Sao Paulo state, Brazil. For. Ecol. Manage. 152, 169–181.

Eriksson, O., Ehrlen, J., 1992. Seed and microsite limitation of recruitment in plant populations. Oecologia Heidelberg 91, 360–364.

Fenner, M., 1985. Seed Ecology. Chapman and Hall Ltd., London.

Foster, S.A., Janson, C.H., 1985. The relationship between seed size and establishment conditions in tropical woody plants. Ecology 66, 773–780.

Goosem, S., Tucker, N.I.J., 1995. Repairing the Rainforest: Theory and Practice of Rainforest Re-establishment in North Queensland's Wet Tropics. The Wet Tropics Management Authority, Queensland, Australia.

Grime, J.P., 1991. Plant Strategies and Vegetation Processes. John Wiley & Sons, Avon, UK.

Guariguata, M.R., Ostertag, R., 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. For. Ecol. Manage. 148, 185–206.

Harper, J.L., 1977. Population Biology of Plants. Academic Press, London.

Harper, J.L., Williams, J.T., Sagar, G.R., 1964. The behaviour of seeds in soil. 1: The heterogeneity of soil surfaces and its role in determining the establishment of plants from seed. J. Ecol. 53, 273–286.

Harrington, G.N., Irvine, A.K., Crome, F.H.J., Moore, L.A., 1997. Regeneration of large-seeded trees in Australian rainforest fragments: A study of higher-order interactions. In: Laurance, W.F., Bierregaard, R.O.J. (Eds.), Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities. University of Chicago Press.

Holl, K.D., 1998. Effects of above- and below-ground competition of shrubs and grass on *Calophyllum brasiliense* (Camb.) seedling growth in abandoned tropical pasture. For. Ecol. Manage. 10, 187–195.

Holl, K.D., Loik, M.E., Lin, E.H.V., Samuels, I.A., 2000. Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. Restor. Ecol. 8, 339–349.

Hulme, P.E., 1996. Natural regeneration of yew (*Taxus baccata* L.): microsite, seed or herbivore limitation? J. Ecol. 84, 853–861.

Hyland, B.P.M., Whiffin, T., Christophel, D.C., Gray, B., Elick, R.W., Ford, A.J., 1999. Australian Tropical Rain Forest Trees and Shrubs. CSIRO Publishing, Collingwood, Victoria.

Jones, R.E., Crome, F.H.J., 1990. The biological web—plant/animal interactions in the rainforest. In: Webb, L.J., Kikkawa, J. (Eds.), Australian Tropical Rainforests: Science, Values, Meaning. CSIRO Publications, Australia.

Kitajima, K., Fenner, M., 2000. Ecology of seedling regeneration. In: Fenner, M. (Ed.), Seeds: The Ecology of Regeneration in Plant Communities. second ed. CABI Publishing, United Kingdom, pp. 331–359.

Lamb, D., Gilmour, D.A., 2003. Rehabilitation and Restoration of Degraded Forests. IUCN, Gland, Switzerland and Cambridge, UK and WWF, Gland, Switzerland.

Lamb, D., Erskine, P.D., Parrotta, J.A., 2005. Restoration of degraded tropical forest landscapes. Science 310, 1628–1632.

Laurance, W.F., 1997. Hyper-disturbed parks: Edge effects and the ecology of isolated rainforest reserves in tropical Australia. In: Laurance, W.F., Bierregaard, R.O. (Eds.), Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities. University of Chicago Press, Chicago, pp. 71–83.

Laurance, W.F., Harrington, G.N., 1997. Ecological Associations of Feeding Sites of Feral Pigs in the Queensland Wet Tropics. Wildl. Res. 24, 579–590.

Malcolm, D.T., Nagel, B.K.A., Sinclair, I., Heiner, I.J., 1999. Soils and Agricultural Land Suitability of the Atherton Tablelands, North Queensland. Department of Natural Resources, Brisbane.

Mazia, C.N., Chaneton, E.J., Ghersa, C.M., Leon, R.J.C., 2001. Limits to tree species invasion in pampean grassland and forest plant communities. Oecologia 128, 594–602.

Milliken, G.A., Johnson, D.E., 1984. Analysis of Messy Data. Lifetime Learning Publications, Belmont, USA.

Murdoch, A.J., Ellis, R.H., 2000. Dormancy, viability and longevity. In: Fenner, M. (Ed.), Seeds: The Ecology of Regeneration in Plant Communities. second ed. CABI Publishing, UK, pp. 183–214.

Nepstad, D.C., Uhl, C., Adilson Serrao, E., 1991. Recuperation of a degraded Amazonian landscape: Forest recovery and agricultural restoration. Ambio 20, 248–255.

Nepstad, D., Uhl, C., Adilson Serrao, E., 1990. Surmounting barriers to forest regeneration in abandoned, highly degraded pastures: a case study from Paragominas, Para, Brazil. In: Anderson, A.B. (Ed.), Alternatives to Deforestation: Steps toward Sustainable Use of the Amazon Rain Forest. Columbia University Press, New York.

Nussbaum, R., Anderson, J., Spencer, T., 1995. Factors limiting the growth of indigenous tree seedlings planted on degraded rainforest soils in Sabah, Malaysia. For. Ecol. Manage. 74, 149–159.

Osunkoya, O.O., Ash, J.E., Hopkins, M.S., Graham, A.W., 1994. Influence of seed size and seedling ecological attributes on shade tolerance of rainforest tree species in Northern Queensland. J. Ecol. 82, 149–163.

Primack, R.B., Miao, S.L., 1992. Dispersal can limit local plant-distribution. Conserv. Biol. 6, 513–519.

Putz, F.E., Canham, C.D., 1992. Mechanisms of arrested succession in shrublands: Root and shoot competition between shrubs and tree seedlings. For. Ecol. Manage. 49, 267–275.

Snell, A.J., Brooks, S.J., 1998. Direct seeding as a method of revegetating degraded land. In: Proceedings of the 6th International Workshop of Bio-Refor, Brisbane, Australia, December 2–5.

Sun, D., Dickinson, G., 1995. Direct seeding for rehabilitation of degraded lands in north-east Queensland. Aust. J. Soil Water Conserv. 8, 37–40.

Sun, D., Dickinson, G.R., Bragg, A.L., 1995. Direct seeding of *Alphitonia petriei* (Rhamnaceae) for gully revegetation in tropical northern Australia. For. Ecol. Manage. 73, 249–257.

Sun, D., Dickinson, G.R., 1996. The competition effect of *Brachiaria decumbens* on the early growth of direct-seeded trees of *Alphitonia petriei* in tropical north Australia. Biotropica 28, 272–276.

Tracey, J.G., 1982. The Vegetation of the Humid Tropical Region of North Queensland. CSIRO, Melbourne.

Turner, I.M., 2001. The Ecology of Trees in the Tropical Rain Forest. Cambridge University Press, Cambridge.

Uhl, C., 1988. Restoration of degraded lands in the Amazon Basin. In: Wilson, E.O., Peter, F.M. (Eds.), Biodiversity. National Academy Press, Washington, DC.

Vanderwoude, C., Pickersgill, G., Dickinson, G., 1996. The efficacy of direct-seeding as a revegetation strategy for humid and sub-humid areas of Queensland. In: Managing and Growing Trees Training Conference, Bundaberg, Australia, pp. 227–235.

Vazquez-Yanes, C., Orozco-Segovia, A., 1992. Effects of litter from a tropical rainforest on tree seed germination and establishment under controlled conditions. Tree Physiol. 11, 391–400.

Wijdeven, S.M.J., Kuzee, M.E., 2000. Seed availability as a limiting factor in forest recovery processes in Costa Rica. Restor. Ecol. 8, 414–424.

Woods, K., Elliott, S., 2004. Direct seeding for forest restoration on abandoned agricultural land in northern Thailand. J. Trop. For. Sci. 16 (2), 248–259.

Wunderle, J.M., 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. For. Ecol. Manage. 99, 223–235.

Zar, J.H., 1996. Biostatistical Analysis, third ed. Prentice Hall International, Inc..

Zimmerman, J.K., Pascarella, J.B., Aide, T.M., 2000. Barriers to forest regeneration in an abandoned pasture in Puerto Rico. Restor. Ecol. 8, 350–360.