



Effects of litter, soil surface conditions, and microhabitat on *Cercocarpus ledifolius* Nutt. Seedling emergence and establishment

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(Received 7 July 2001, accepted 26 January 2002)

We assessed the effects of the litter layer, soil surface conditions, and microhabitat on emergence of the tree *Cercocarpus ledifolius*, and how litter affected establishment and survival of first year seedlings of this species. Natural seedling emergence was similar in three microhabitats: open interspaces (0.12 kg litter m⁻²), beneath *Artemisia tridentata* canopies (0.27 kg litter m⁻²), and beneath *C. ledifolius* canopies (2.5 kg litter m⁻²). However, because seed dispersal is highest under trees, and lowest in the open, seedling emergence seemed to vary and have highest values in open interspaces. Emergence rates did not vary between soil surface treatments, but were lower in experimental litter treatments than in treatments, without litter, independent of microhabitat. In contrast, litter beneath trees favored subsequent seedling establishment and survival. This study shows that the role of the litter layer varies during the first year of the life of this species, with litter inhibiting initial emergence but enhancing early seedling survival.

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Keywords: *Cercocarpus ledifolius*; litter; microhabitat; seedling emergence; seedling survival; seed–seedling conflict

Introduction

Environmental conditions encountered by seedlings during germination and early growth, are crucial for long-term survival of plant populations (Harper, 1977; Golberg & Werner, 1983). The term ‘safe site’ refers to the biotic and abiotic conditions that promote emergence and survival of seedlings of a given species (Harper *et al.*, 1965). Population size, therefore, is expected to be influenced by the presence and abundance of species-specific safe sites (Harper, 1977; Chambers *et al.*, 1990).

Plant litter, by modifying the chemical and physical environment, can play a major role in determining the abundance and distribution of safe sites. Litter can have both positive and negative effects on plant recruitment. These effects vary enormously among species in the community and across microhabitats in the landscape (Carson & Peterson, 1990; Páez & Marco, 2000). Positive effects arise through the ameliorating

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action of litter on biotic and abiotic stresses. Biotically, litter can reduce the density and biomass of herbs (Facelli & Pickett, 1991a), and thus reduce competition (Grime, 1979), and hide seeds from predators (Myser & Pickett, 1993). Litter can also facilitate seedling growth by providing nutrients through mycorrhizal fungus (Pérez Moreno & Read, 2000). Abiotically, litter can reduce temperature and evapotranspiration, release leachates that can be a source of mineral nutrients (Facelli & Pickett, 1991b), and can influence germination cues such as moisture, temperature, and light fluctuations (Carson & Peterson, 1990).

Negative effects of litter on plant establishment are also numerous. In some environments, litter may increase seed and seedling predation by promoting the activity of herbivorous arthropods (Facelli, 1994). Seedling establishment may further be negatively affected by litter as a result of shading, of physical obstruction of seed movement down to the soil surface and seedling emergence through the litter, of reduced thermal amplitude, or of release of phytotoxins (Facelli & Pickett, 1991b).

In addition to litter, soil surface characteristics can influence the suitability of specific sites for particular species. The heterogeneity of the soil surface is characterized by a wide variety of microsites that provide different conditions for germination (Harper *et al.*, 1965). Treatments with more microtopographical relief (soil covered with clods or rocks) had greater germination and root growth of chicory plants, *Cichorium intybus*, than sites with smooth surfaces or with a litter layer (Smith & Capelle, 1992). Furthermore, sufficient water in the soil is essential for seed germination (Oomes & Elberse, 1976), especially in arid environments, and texture of the soil surface may affect both water infiltration and retention (Gutterman, 1993; Kigel, 1995).

The distribution and abundance of safe sites also depends on the array of different microhabitats created by adult plants within a community. Besides competing with establishing seedlings, existing plants have the capacity to modify temperature, humidity, and light beneath their canopies, and to alter biological, physical, and chemical soil properties (Hunter & Aarssen, 1988; Callaway, 1995). Such changes in environmental conditions can become crucial for seedling recruitment in arid and semi-arid ecosystems where the availability of water is a major limiting factor.

The main objective of this work was to determine the role of seedbed conditions on seedling emergence and establishment of curleaf mountain mahogany (*Cercocarpus ledifolius* Nutt., Rosaceae). This tree species produces abundant seed (Russell & Schupp, 1998) yet has little recruitment throughout most of its range (Scheldt & Tisdale, 1970). We address the following specific questions: (1) What is the natural pattern of emergence of *C. ledifolius* seedlings across different microhabitats, and is this pattern related to the pattern of seed dispersal and accumulation? (2) How do litter, soil surface conditions, and microhabitat affect emergence of *C. ledifolius* seedlings? And, (3) how does litter affect seedling establishment and survival over the first summer? Answers to these questions will add to our basic understanding of the ecology of seedling recruitment of *C. ledifolius* in natural systems, as well as potentially provide critical information for managing this important species.

Methods

Study species and site

Cercocarpus ledifolius is a 2–9-m-tall evergreen, montane xerophyte that is widespread in the mountain brush zone of the Intermountain West of North America, where it occurs on warm, dry, rocky ridges and slopes of southern to western exposure (Brotherson, 1990). Seeds are dispersed by wind and redistributed on the soil surface

by wind, gravity, and snowmelt (Russell & Schupp, 1988). *C. ledifolius* is an important species in the Intermountain West; it provides winter browse and cover for wildlife (Davis, 1990), and because it has actinorrhizal root associates that fix atmospheric nitrogen, this tree increases nitrogen levels in the nutrient poor soils where it grows (Lepper & Fleschner, 1977).

Our study was conducted at a site referred to as Swan Flat in northeastern Utah, Cache County, U.S.A., in the Cache National Forest at approximately 41°57'N and 111°28'W. The elevation varies between 2350 and 2500 m, and the slope of the southwest-facing experimental area is about 35%. The study area is 15 km east of the closest climate station. At the station (our site is warmer and drier) temperature varies between 6 and 18°C in summer and -11 and -1°C during winter, with a mean annual temperature of 2.8°C (Utah Climate Center, unpubl. data). Annual precipitation is 1260 mm. The fact that precipitation falls mostly as winter snow make south and south-western slopes of this area particularly arid during the summer.

Curleaf mountain mahogany is the dominant tree species at this time, although isolated Douglas-firs (*Pseudotsuga menziesii*) are present. Big sagebrush (*Artemisia tridentata* ssp. *Vaseyana*) and snowberry (*Symphoricarpos* spp.) are the most common shrubs in the area. Mainly current-year seedlings and mature individuals of *C. ledifolius* are present through the stand; older established seedlings, juveniles, or immature trees are rare.

Natural emergence

Natural patterns of seedling emergence were determined at five locations regularly spaced 30 m apart in the study area. At each location, 10 points were randomly selected in each of three main microhabitats: 'tree', beneath canopies of *C. ledifolius*, 'shrub', beneath canopies of *A. tridentata* and 'open', in open interspaces between woody vegetation. At each point, seedlings per 30 × 30 cm plot were counted once at the end of the germination period (late spring-early summer 1997). We compared seedling numbers across microhabitats of the square root-transformed counts (to meet assumptions of normality and homoscedasticity) in an ANOVA using SAS (1990) MIXED procedure with location as a random effect and microhabitat as a fixed effect and with a Tukey-Kramer adjustment to control for Type I error. These results were qualitatively compared with previously collected seed accumulation data from the same site (Russell & Schupp, 1988). After the counts, the litter from each plot was collected, air-dried, and weighed in order to compare litter mass differences among the microhabitats. We used square root transformed masses in an ANOVA using SAS (1990) GLM procedure.

Field experiment — emergence

To better evaluate the roles of litter, soil surface condition, and microhabitat on seedling emergence, we conducted a field experiment with four seedbed treatments (non-factorial combination of litter and soil surface treatments) in five microhabitats. The four seedbed treatments were as follows: (1) undisturbed soil without litter, (2) undisturbed soil with seeds sown over litter, (3) undisturbed soil with seeds sown under litter, and (4) manually disturbed soil surface without litter. The five microhabitats were: (1) beneath patches of several *C. ledifolius* trees, (2) beneath isolated *C. ledifolius* trees, (3) beneath *A. tridentata* canopies, (4) beneath *Symphoricarpos* spp. canopies, and (5) open interspaces. For each replicate, we sowed 200 seeds into a 30 × 30 cm plot protected during the whole extent of the experiment by a 1.2-cm mesh hardware-cloth cage placed 3 cm into the ground, with a strip of nylon window screening at the base to prevent predation by mammals and crawling

insects. Seeds were laid equally distributed on the surface of each plot. Additionally, in order to exclude naturally dispersing seeds, we placed a screen over each cage in the fall when sowing took place and removed it in the spring. We did not attempt to remove the upper part of the soil surface containing the soil seed bank.

First, all plots were cleared of existing litter and surface seeds before sowing. Then experimental litter was placed in cages according to the treatments, and the soil surface was disturbed to a depth of about 2 cm with a hand cultivator in cages under the disturbed soil surface treatment. The amount of litter used was determined separately for each microhabitat and was the mean dry mass of ten 30×30 cm representative litter collections from each microhabitat. Values, $g\ 900\ cm^{-2}$ (the cage area), for each microhabitat were: 249.2 g for groups of *C. ledifolius*, 103.7 g for isolated *C. ledifolius*, 36.0 g for *A. tridentata*, 45.6 g for *Symphoricarpos* spp., and 14.3 g for open. Litter was collected from representative points in respective microhabitats and was carefully cleaned of mountain mahogany seeds before use.

Plots were set up during fall 1995 before snowfall. The experiment was replicated at five locations regularly spaced 100 m apart on a line through the study site perpendicular to the slope. The total sample was 100 plots with 20,000 seeds (five sites \times five microhabitats \times four treatments \times 200 seeds). During late spring 1996, seedling emergence was recorded weekly for a month, and seedling were marked with toothpicks to avoid recounting. Seedling counts were transformed (square root) to meet assumptions of normality and homoscedasticity. Data were analysed with ANOVA using the SAS (1990) GLM procedure to assess effects of seedbed condition and microhabitat on seedling emergence. We then made three planned contrasts to address specific questions. First, we assessed the importance of litter by contrasting the two litter treatments (2 and 3) as a group with undisturbed soil without litter treatment (1). We assessed the effects of seed location within the litter layer by contrasting the treatment with seeds sown over the litter layer (2) with the treatment with seeds sown under the litter layer (3). The role of soil surface conditions was evaluated by contrasting the two treatments without litter, disturbed (1) *vs.* undisturbed soil (2).

Field experiment — survival

We conducted an additional experiment on the effect of litter on seedling survival following initial emergence by transplanting seedlings into different amounts of litter under *C. ledifolius* trees in a randomized complete block design. Beneath the canopy of 10 trees we set up three 30×30 cm plots, each with different levels of litter: bare soil, mean amount of litter ($249\ g\ 900\ cm^{-2}$) for this microhabitat, and double the mean amount of litter ($498\ g\ 900\ cm^{-2}$). We planted 10 seedlings in each plot for a total $n = 300$ (10 trees \times 3 treatments \times 10 seedlings). We cleared each plot of litter, planted seedlings, and then added back the proper amount of *C. ledifolius* litter collected from the site.

We obtained seedlings by germinating seeds, collected from several trees at the study site, following the method of Kitchen & Meyer (1990). After cold moist stratification on filter paper in a cold room at 1–4°C for 10–12 weeks, we incubated seeds in a growth chamber at 15°C for 10 days and transplanted seedlings into Lännen PaperpotsTM (2.8 cm diameter \times 10 cm length) filled with soil from the study site. After about 5 weeks, when the first pair of true leaves had emerged, we transplanted them to the field. At the planting date our seedlings had reached a size similar to naturally emerged seedlings in the field (3–4 cm). Survival was recorded weekly through the summer until snowfall, for a total of 12 weeks. We performed a survival analysis (SAS LIFEREG procedure, likelihood ratio test, Weibull distribution) of the failure-time data to test for differences among treatments by comparing

predicted median survival values (phat) in weeks for each treatment, that is, time until half the population is expected to have died. Median values were used due to the right-censored nature of some observations whose failure times were greater than the last recorded survival time at the end of the experiment.

Greenhouse experiments

To examine seedling survival and growth when emerging from different depths within a moderately thick litter layer, we planted germinated seeds (emerged radicle = 1 cm long) at different levels in a uniformly thick litter layer (first experiment), and on the soil surface under different depths of litter in the greenhouse (second experiment). We used trays (33 × 46 × 20 cm) filled with 10 cm of commercial potting soil. Each tray was separated into three sections (11 × 46 cm) with dividers, and each section was planted with 15 seeds. For the first experiment, the soil was covered with 7 cm of *C. ledifolius* litter. This quantity was approximately twice the average amount of litter under the tree canopies, and was frequently observed in the study area. Seeds within a section were planted at one of three litter levels: next to the soil (bottom), 4 cm above the soil (middle), and on the surface of the litter (top). Treatments were randomly assigned to a tray sector. We used seven replicate trays ($n = 315$ seeds). In the second experiment, seeds were planted in contact with the soil under three litter depths: no litter, 3 cm of litter (average amount of litter), and 7 cm of litter (twice the average). In this case, we used five replicates ($n = 225$ seeds). In both experiments, plants were watered daily during the experiments. After 12 weeks, established seedlings were counted and harvested in both experiments.

For the first experiment only, we measured stem length and separated seedlings into leaves, stems, and roots. After oven-drying (48 h at 90°C), seedlings were weighed by component parts on an analytical balance (0.0001 g). To assess whether treatments differed in the proportion of planted seeds that produced an established seedling, we lumped replicates and used log-linear models of 2 × 3 contingency tables (SAS 1990, FREQ procedure). To compare stem length and dry weight of leaves, stems, and roots, we used the SAS (1990) MIXED procedure with tray as a random effect and treatment as a fixed effect.

Results

Natural emergence

The three selected microhabitats open, shrub, and tree did not differ in numbers of seedlings naturally emerging [$F = 0.48$, $df. = 2, 125$, $p = 0.661$; Fig. 1(a)]. The quantity of litter varied significantly among the three microhabitats ($F = 209.83$, $df. = 2, 125$, $p = 0.0001$), with shrub ($270 \pm 49 \text{ g m}^{-2}$, back-transformed mean + 1 S.E.) having slightly more litter than open ($118 \pm 37 \text{ g m}^{-2}$) and tree ($2503 \pm 144 \text{ g m}^{-2}$) having substantially more litter than the other two microhabitats.

Field experiment — emergence

In the analysis of variance of seedlings emerging, microhabitat was not significant (Table 1, Fig. 2), whereas seedbed treatment was marginally insignificant ($p = 0.062$) in the full analysis, probably due to small number of replicates. The non-significant microhabitat × seedbed interaction demonstrates the treatment effect was consistent across microhabitats. Planned contrasts showed that the undisturbed soil surface without litter treatment (1) had greater emergence than the two treatments with litter

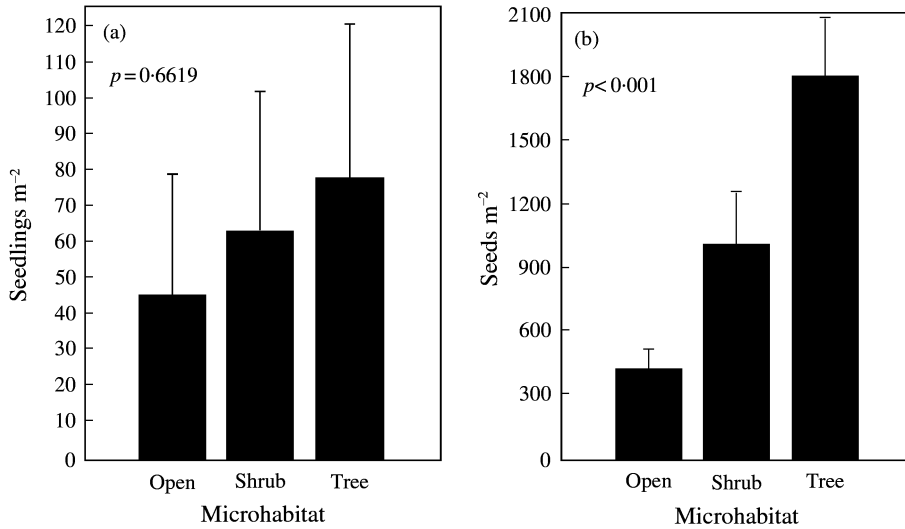


Figure 1. Microhabitat distribution of emerging seedlings and of accumulated seeds: (a) back-transformed mean (+1 S.E.) number of *C. ledifolius* seedlings emerging in the three microhabitats; (b) mean (+1 S.E.) number of seeds accumulated on the ground, in the litter, and in the top 5 cm of soil in the three microhabitats. (b) Modified from Russell & Schupp (1998).

as a group (2 and 3) (Table 1, Fig. 3). Neither the contrast between the two treatments with litter, seeds over (2) *vs.* seeds under litter (3), nor the contrast between the two treatments without litter, undisturbed (1) *vs.* disturbed soil (2), were significant (Table 1, Fig. 3).

Field experiment — survival

Seedling survival under the tree canopies was significantly greater with litter than without litter (Table 2, Fig. 4). The two litter treatments, however, did not differ from each other (Table 2, Fig. 4).

Table 1. ANOVA (GLM procedure) results from experimental seedling emergence data, including the three planned contrasts. Seedbed treatment abbreviations as in Fig. 3

Source	df.	SS	F	p
Model	23	118.27	1.16	0.309
Location	4	12.13	0.68	0.606
Microhabitat	4	14.65	0.83	0.513
Seedbed treatment (1, 2, 3, 4)	3	34.04	2.56	0.062
No litter (1) <i>vs.</i> litter (2, 3)	1	24.75	5.50	0.025
Over litter (2) <i>vs.</i> under litter (3)	1	0.02	0.01	0.944
Undisturbed soil (1) <i>vs.</i> disturbed soil (4)	1	0.02	0.00	0.945
Microhabitat*Seedbed	12	57.45	1.08	0.390
Error	71	314.88		

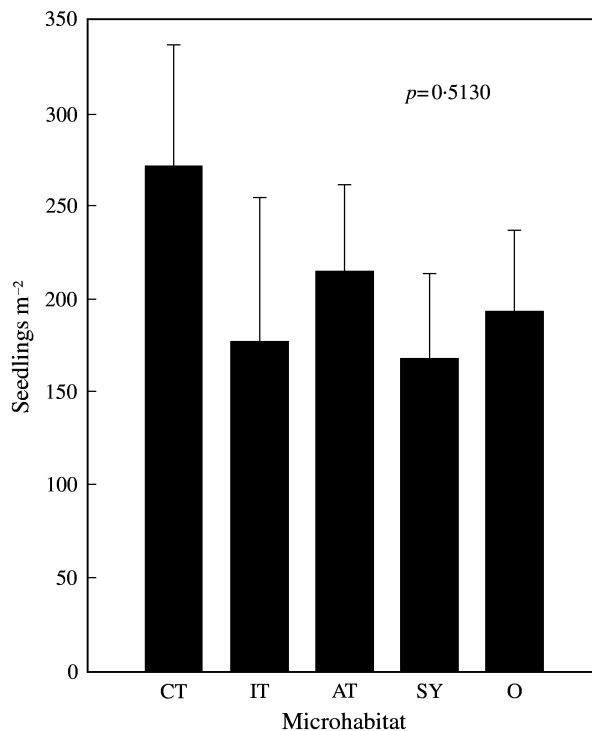


Figure 2. Back-transformed mean (+1 S.E.) number of seedlings emerging in the seedbed experiment by microhabitat. CT = clump of *C. ledifolius* trees; IT = isolated *C. ledifolius* trees; AT = *A. tridentata* shrubs; SY = *Symphoricarpos* spp. Shrubs; and O = open interspaces ($n = 5$).

Greenhouse experiments

In the first experiment with seeds planted at different levels in the litter layer, establishment varied significantly among treatments (likelihood ratio chi-square = 60.88, df. = 2, $p < 0.001$). No emergence occurred for seeds planted at the bottom, while 32 (30%) established when planted in the middle and 33 (31%) established when planted at the top of the litter layer. Stem length was the only growth variable that differed among treatments, with seedlings from the top of the litter having shorter stems than seedlings from the middle of the litter (Table 3).

In the second experiment, with seeds planted on the soil under different litter layers, emergence also varied significantly among treatments (likelihood ratio chi-square = 57.182, df. = 2, $p < 0.001$), with 12 (16%), 48 (64%), and 53 seedlings (71%) established beneath 7, 3, and 0 cm of litter, respectively. The difference was due to low establishment in the deepest layer; establishment did not differ between 3 cm of litter and no litter (likelihood ratio chi-square = 0.76, df. = 1, $p = 0.384$).

Discussion

Natural emergence

In the field, emergence of naturally dispersed *C. ledifolius* seedlings did not differ among the three major microhabitats we identified. This is in stark contrast to the

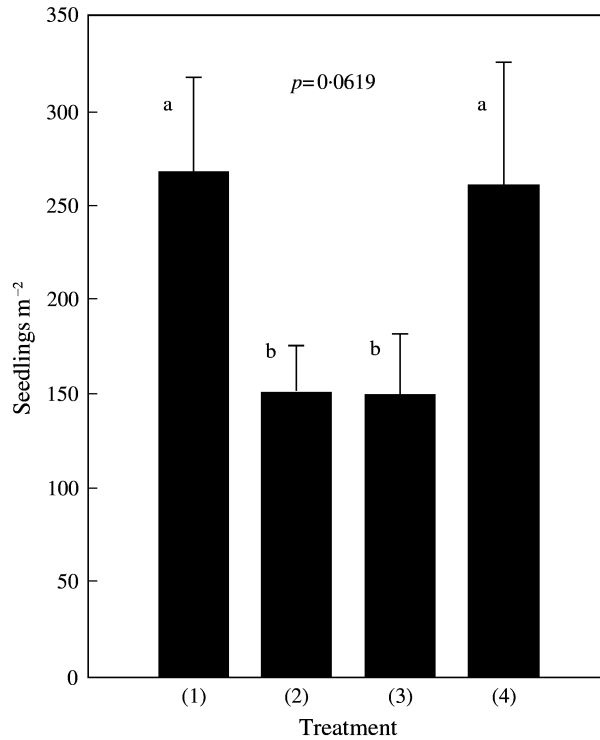


Figure 3. Back-transformed mean (+1 S.E.) number of seedlings emerging in the seedbed experiment by litter and soil surface treatments. (1) no litter, undisturbed soil; (2) seeds planted over the litter layer, undisturbed soil; (3) seeds planted under the litter layer, undisturbed soil; and (4) no litter, disturbed soil. Bars with the same letter do not differ significantly ($\alpha = 0.05$).

pattern of seed accumulation at the same site (Russell & Schupp, 1998), where seed densities were highest beneath *C. ledifolius* tree canopies, intermediate beneath shrubs, and lowest in open interspaces [Fig. 1(b)]. Differential seed predation among microhabitats did not explain the variability on emergence rates (Russell & Schupp, 1998). These contrasting observations suggest that percentage emergence is highest in open interspaces and lowest beneath *C. ledifolius*, conditions under *C. ledifolius* would

Table 2. Analysis of failure-time data for seedling survival (LIFEREG procedure) under three litter treatments

Variable	df.	Estimate	SS	Chi-square	<i>p</i>
Intercept	1	0.84	0.36	26.23	<0.001
Site	9			23.85	0.004
Treatment	2			11.11	0.004
No litter <i>vs.</i> mean litter	1	0.84	0.68	7.27	0.007
No litter <i>vs.</i> double litter	1	2.29	0.89	6.57	0.010
Mean litter <i>vs.</i> double litter	1	0.45	0.98	0.21	0.647
Site*treatment	18			34.23	0.012
Scale parameter	1	0.80	0.07		

Log likelihood = -215.22.

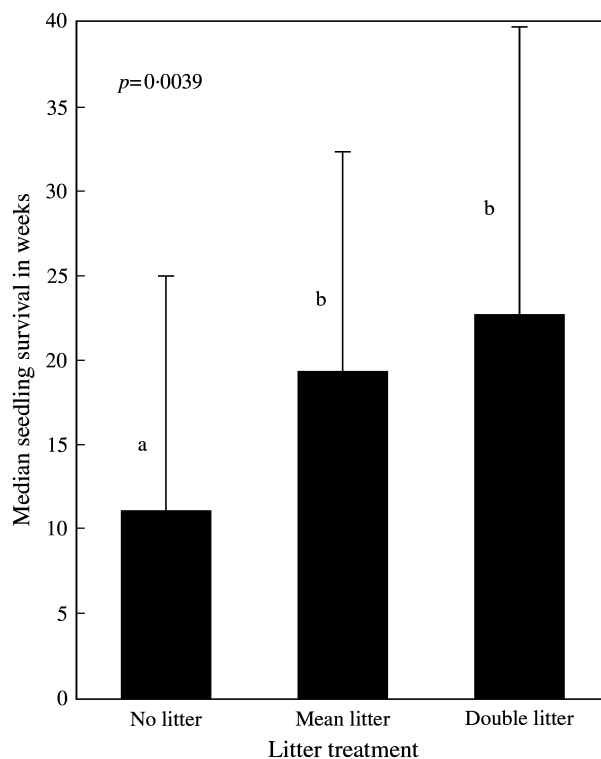


Figure 4. Median seedling survival (± 1 S.E.) in weeks under the three different litter treatments: no litter, mean amount of litter, and double the mean amount of litter. Bars with the same letter do not differ significantly ($\alpha = 0.05$).

inhibit or reduce germination. In the cool spring following snowmelt, when seeds are germinating, diurnal temperatures may be more suitable for seedling emergence in open interspaces than in the shade of other microsites, yet water availability is still sufficient. Chambers (2001) also observed greater *Pinus monophylla* emergence speed and quantity in warmer temperatures of open microhabitats.

Litter effects — emergence

Litter effects on individual species can range from facilitation to interference (Monk & Grabelson, 1985; Facelli & Pickett, 1991b). In particular, in arid and semi-arid

Table 3. Stem length and stem, leaf, and root dry mass for seedlings established from seeds planted in the middle and top layers of litter and *p* values for the depth effect from ANOVA (MIXED procedure). Values in table are back-transformed means (1 S.E.)

Variable	Position in litter		<i>p</i>
	Middle	Top	
Stem length (cm)	7.6 (0.006)	4.8 (0.006)	0.001
Stem dry mass (mg)	57.27 (0.27)	41.25 (0.29)	0.122
Leaf dry mass (mg)	106.09 (0.70)	77.79 (0.77)	0.250
Root dry mass (mg)	32.83 (0.24)	32.26 (0.26)	0.933

environments the litter layer can play a crucial role on species regeneration (Pugnaire *et al.*, 1996). In our study, litter significantly reduced emergence of *C. ledifolius* in the field and in the greenhouse.

A number of mechanisms have been proposed to explain negative effects of litter. Litter may constitute a physical barrier for seedling emergence and/or for seeds reaching the soil surface (Facelli & Pickett, 1991*b*; Caccia & Ballare, 1998; Wilby & Brown, 2001). It may also promote activity of herbivorous arthropods (Facelli, 1994), release allelopathic leachates (Rice, 1979), etc. Field and greenhouse results of this study suggest that litter reduces *C. ledifolius* emergence at least partly because deep layers are a barrier to emergence. Similarly, Facelli *et al.* (1999) observed an increase in seedling establishment under a moderate litter layer but reduced emergence when seeds were planted under a thick litter layer.

As in this study, negative effects of litter on seedling emergence and establishment have been frequently reported in a variety of ecosystems (Williams *et al.*, 1990; Vázquez-Yanes & Orozco-Segovia, 1992; Prach *et al.*, 1996; Yager & Smeins, 1999). However, in contrast to many studies (Hamrick & Lee, 1987; Molofsky & Augspurger, 1992; Hoffman, 1996), our field results are surprisingly consistent, with litter negatively affecting emergence more or less equivalently across a range of microhabitats varying greatly in shade and in type and quantity of litter. The sample ($n = 5$) could have been too small to detect an interaction between microhabitat and litter treatment; however, the power of the test (0.920) supports these results (Table 1).

Soil surface effects — emergence

Unlike the litter effect, the two no-litter treatments with undisturbed soil and disturbed soil surface did not differ in emergence. This suggests soil surface disturbance does not improve seed-soil contact or microenvironmental conditions around the seeds (Hadas, 1982). Although contrary to results of a number of studies showing that soil surface texture can have a large impact on emergence (Eckert *et al.*, 1986; Hamrick & Lee, 1987; Young *et al.*, 1990; Kobayashi & Kamitani, 2000), this is perhaps not surprising. A winter beneath several meters of snow probably promotes sufficient contact, and, because germination takes place during snowmelt, water availability is probably not the problem as it would be later in the season (Guterman, 1993; Kigel, 1995).

Microhabitat effects — emergence

Emergence rates did not differ among the five microhabitats. This is inconsistent with our interpretation of the natural emergence pattern, which suggested higher emergence rates in open interspaces. A possible explanation might involve the seedbank. If there is a viable seedbank, it should be greater beneath *C. ledifolius* trees where higher densities of seeds are accumulating (Russell & Schupp, 1998). Because only the litter and soil surface were cleared of seeds for the experiment, and not the soil, the estimate of emergence beneath *C. ledifolius* may be an overestimate. If true, equal numbers emerging would again suggest higher percent emergence in open interspaces.

The field experiments were such that although litter and soil surface conditions results are robust, the microhabitat results must be considered preliminary. The lack of a microhabitat effect on emergence contradicts results from other studies (Breshears *et al.*, 1998; Rousset & Lepart, 1999; Chambers, 2001). We covered the cages with screen cloth in the fall to prevent seed additions shortly after the first snow storm. We could not remove the screens until the following spring, when most of the

emergence had already occurred. Thus, all treatments had additional shading, which might have affected the results diminishing the differences among microhabitat.

Litter effects — survival

Although the most favorable microsites for *C. ledifolius* emergence seem to be those without litter, the most suitable sites for seedling survival and establishment appear to be those with a moderate litter layer, perhaps because litter provides cooler and moister conditions. This mechanism is supported by greenhouse results where trays were well watered throughout the study and virtually all seedlings that emerged survived. Interestingly, Facelli & Ladd (1996) found opposite results for two species of mesic *Eucalyptus* in Australia, where litter enhanced emergence but reduced seedling survival. These results are examples of seed–seedling conflicts, or discordances between conditions that are best for seeds and those that are best for seedlings (Sork, 1985; Kitajima & Augspurger, 1989; Barret & Silander, 1992; Schupp, 1995). In the case of *C. ledifolius*, the discrepancy seems to also continue into later life stages of the plant. Schultz *et al.* (1996) found that although most current-year seedlings were located beneath tree canopies, where the litter layer was thicker, established seedlings, juveniles, and immature trees were preferentially located in the adjacent *Artemisia* community with little litter. The canopy of trees and their associated litter may protect seedlings from desiccation and temperature extremes, but these seedlings are also in a low-light environment possibly facing competition from the established trees for water and nutrients. The intensity of this competition might increase as the plant matures (Callaway, 1995); over the longer term, the negative effects appear to outweigh the positive effects of growing beneath *C. ledifolius*.

Summary

The role of the litter layer in *C. ledifolius* recruitment seems to vary during the early stages of the life of this species. For *C. ledifolius*, tree inhibits seedling emergence; seeds outside the canopy and in patches without litter have the highest opportunity to emerge (Dealy, 1975). Following emergence, the litter layer beneath *C. ledifolius* appears to supply a favorable microsite for current-year seedlings. Ultimately, competition from established vegetation with which the litter layer is associated might reduce survival of juvenile *C. ledifolius* beneath trees. The balance between inhibition and facilitation within a microhabitat determines the spatial patterns of seedling emergence and early survival (Berkowitz *et al.*, 1995; Callaway & Walker, 1997). Additionally, this balance may shift across sequential stages in a plant's life as well, and such shifts may be critical for determining the overall extent and the spatial distribution of recruitment in the community (Schupp, 1995). From the perspective of the plant life cycle, inhibition and facilitation are dynamic, not static concepts.

We thank S. Russell, T. Milleron, R. Walkenhorst, and B. Bugbee for assistance in the field and in the greenhouse; S. Durham for help with statistical analyses; Utah Climate Center for providing climate data; and W. Thompson of the U.S. forest Service for permission to work at the site. The research was supported by a Fulbright-Central Hispano grant (I. Ibáñez), and by the USU Ecology Center and Utah Agricultural Experiment Station (UAES), USU (E.W. Schupp). Approved as UAES journal paper no. 7027.

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