# SEEDS STORED IN THE FOREST FLOOR IN A NATURAL STAND OF *Pinus montezumae* Lamb.

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## *ABSTRACT*

Seed banks have been studied to a greater extent in agriculture than in forestry due to long-standing concerns about the threat to agricultural crops posed by weed species. However, in forest areas seed banks have an important influence on plant succession since the vegetation that colonizes a space after a major disturbance will arise at least partly from them. Knowledge about this condition can help land managers to prescribe site treatments that produce desired vegetation from the perspectives of wildlife habitat, reduced plant competition with crop tree species, and related management concerns. The variability of the soil seed bank of a *Pinus montezumae* forest was assessed using seedling-emergence method for soil samples. The number of species and seedling abundance were evaluated by sampling four plots in a natural regeneration area. A total of 43 species were recorded in the seed bank (2 trees, 17 shrubs, 1 grass and 23 herbs). Viable seeds of most species were contained in similar abundance in the humus and mineral soil layers. Dominant species in the stand (*P. montezumae)* and codominant species *(P. ayacahuite*, *Abies religiosa,* and *Alnus firmifolia*) were poorly represented in the soil seed bank which was dominated by seeds of an array of annual and perennial herbs. Regeneration of commercial species under any silvicultural method must come from current seed production, or seed produced off site, but not from the soil seed bank.

***Key words***: *Abies religiosa, Alnus firmifolia*, natural regeneration, *Pinus montezumae* Lamb., seedling, soil seed bank.

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## RESUMEN

Los bancos de semillas han sido estudiados más en la agricultura que en el área forestal debido a la preocupación sobre el peligro de que los cultivos sean dominados por malas hierbas. Tienen una gran influencia en la sucesión vegetal que coloniza un área después de un disturbio. El conocimiento sobre bancos de semillas en el suelo puede ayudar a prescribir los tratamientos que propicien condiciones de vegetación deseadas desde la perspectiva de hábitat de fauna silvestre, reducción de competencia con especies de importancia y otros problemas relacionados con el manejo forestal. La variación del banco de semillas en el suelo de un bosque de *Pinus montezumae* fue evaluado por medio del método de emergencia en muestras de suelo; se determinó la abundancia y el número de taxa mediante el muestreo en cuatro parcelas en un área de regeneración natural. Los resultados indican 43 especies (dos de árboles, 17 de arbustos, una de pasto y 23 de hierbas). La abundancia de semillas viables fue similar para la mayoría de ellas en la capa de humus y suelo mineral; en tanto que las dominantes del rodal (*P. montezumae)* y codominantes *(P. ayacahuite*, *Abies religiosa* y *Alnus firmifolia*), no estuvieron presentes en el banco, en el cual dominaron herbáceas anuales y perennes. La regeneración de las especies comerciales para este tipo de bosque, bajo cualquier método silvícola, debe provenir de semilla producida en el año *in situ* o de áreas aledañas, pero no del banco de semillas.


**Palabras clave:** *Abies religiosa, Alnus firmifolia*, regeneración natural, *Pinus montezumae* Lamb., plántula, banco de semillas en el suelo.

## INTRODUCTION

The soil seed bank is defined as all viable seed present under and on the surface of the soil (Simpson *et al.*, 1989). Seed banks have been studied to a greater extent in agriculture than in forest lands due to long-standing concerns about the threat to agricultural crops posed by weed species. However, seed banks in forests areas have a great influence on plant succession as the vegetation that colonizes an area following a major disturbance will arise at least partly from them. Some plant species emerging in disturbed forest areas are not found in the mature forest, suggesting an origin from migrant or buried seeds (Strickler and Edgerton, 1976). In fact, some studies suggest that germination of the seed bank is the most important process in contributing to the initial composition of plant communities following a disturbance in forested areas (McGee and Feller, 1993).

Unfortunately, long-term storage of seeds in the forest floor is more characteristic of less desirable pioneer trees, annual plants, and shrubs than of commercial tree species. Many of these species have seeds with hard, nearly impermeable coats that allow the embryos to survive for the many decades that may elapse between major fires or similar disturbances. Examples of such species include representatives from the genera *Rubus*, *Ribes* and *Ceanothus* as well as the short-lived pin cherry (*Prunus pensylvanica* L.f.) (Marks, 1974).

Seeds of a few forests species may remain viable in the humus layers beneath uncut stands for periods longer than one year. One example is Atlantic white-cedar (*Chamaecyparis thyoides* (L.) Britton, Stern & Poggenb.), whose seeds are stored in large quantities in the poorly aerated peats in which this species grows (Little, 1950). Another example is yellow-poplar (*Liriodendron tulipifera* L.) (Clark and Boyce, 1964) which seems to require high temperatures or exposure to light to germinate. The seeds of various ash species (*Fraxinus* spp.) also remain stored in the forest floor for one or two years because it takes them that long after dispersal to mature. With such species it is often possible to expect a seemingly miraculous regeneration after harvesting the entire seed source (Smith, 1986).

Seeds buried in the soil may be exposed to conditions suitable for germination following logging or other site disturbances. To determine species composition of the stand following such a change, it must be considered that composition, depth distribution and density of seeds buried in the litter and soil, all interact with the environmental factors, especially light and temperature. Pre-disturbance and post-disturbance stand composition may differ dramatically. Such differences emphasize the importance of buried viable seeds and seed dispersal from adjacent stands in the successional dynamics on the disturbed site. To understand the contribution of seed propagules to forest stand dynamics, it is important to know the composition and spatial distribution of seed banks and their responses to environmental conditions (Pratt *et al.,* 1984).

Two contrasting techniques are used to estimate soil seed bank composition (Simpson *et al.*, 1989; Brown, 1992). In the first one, physical extraction of the seeds from the soil by a combination of sieving, flotation, or air flow separation, is followed by manual identification of species using seed characteristics. However, this gives no information about viability, which, subsequently, must be established through the tetrazolium or germination tests. It also requires a ‘library’ of seeds of known identity in order to compare those removed from soil samples. This method probably over-estimates the soil seed bank, as it detects many unviable seeds.

In contrast, seedling emergence techniques provide an estimate of viable seeds in the soil based on germination of seeds maintained under conditions favorable for germination. These requirements are seldom completely met, as germination patterns are very sensitive to fluctuating temperatures, oxygen availability, soil texture and other factors. Thus, these techniques probably under-estimate viable buried seed abundances. Despite this limitation, for community level studies, especially where the potential number of species is high, it is a useful measure because direct counting is extremely tedious and time-consuming, and also requires that the viability be tested.

A combination of seedling emergence and direct counting methods provides a more precise estimate of the seed bank size than either technique alone (Conn *et al.,* 1984), but this is only practical for small samples and where a seed 'library' exists.

In the coniferous forest, the severity of the environment and disturbance events determine plant regeneration strategies (Archibold, 1989). Knowledge of forest soil seed banks and their response to changes can help to understand plant succession. It will also help land managers prescribe site treatments that produce desired vegetation conditions from the perspectives of wildlife habitat, reduced plant competition with crop tree species, and related management concerns (McGee and Feller, 1993).

The viability of naturally dispersed seeds of spruces (*Picea*) and many pines (*Pinus*) normally extends into the next growing season and rarely into the second growing season (Stein *et al.,* 1974). The well known failure of conifer seeds to persist beyond one year in seed banks has been reported for a variety of forest communities in North America, as seed bank composition studies from The United States and Canada have all documented very short resident times for major conifers (Table 1).

Table 1. Summary of studies on conifer forest soil seed banks in North America.

| Region | Species | Seed longevity (years) | Reference |
|---|---|---|---|
| Central Idaho | *Abies grandis* (Douglas ex D. Don) Lindl. | 1 | Kramer and Johnson, 1987 |
| | *Picea engelmanii* Parry | 1 | |
| | *Pinus contorta* Douglas ex Loudon | 1 | |
| | *Pinus ponderosa* Douglas ex C. Lawson | 1 | |

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| Region | Species | Seed longevity (years) | Reference |
|---|---|---|---|
| California | *Pinus lambertiana* Douglas<br>*Pinus ponderosa*<br>*Pinus jeffreyi* Balf.<br>*Abies concolor* (Gordon) Lindl. ex Hildebr.<br>*Abies magnifica* A. Murr. | No seeds of conifers reported in samples collected in September | Quick, 1956 |
| Pacific Northwest | *Pinus monticola* Douglas ex D. Don | 1 | Haig, 1932 |
| Washington | *Pseudotsuga menziesii* (Mirb.) Franco | 1 | Isaac, 1935 |
| Ontario, Canada | *Picea mariana* (P.Mill.) B.S.P. | 1.3 | Fraser, 1976 |
| Alaska | *Picea mariana* | 1.3 | Zasada *et al.,*1983 |
| Eastern Canada | *Pinus banksiana* Lamb.<br>*Pinus strobus* L.<br>*Picea mariana*<br>*Abies balsamea* (L.) Mill. | 2<br>1<br>2<br>1 | Thomas and Wein, 1985 |
| Maine | *Picea rubens* Sarg.<br>*Picea glauca* (Moench) Voss<br>*Picea mariana*<br>*Abies balsamea*<br>*Pinus strobus*<br>*Tsuga canadensis* (L.) Carrière | 1<br>1<br>1<br>1<br>1<br>1 | Frank and Safford, 1970 |
| Washington | *Pinus ponderosa* | 1 | Pratt *et al.*, 1984 |
| Species natural distribution | *Pinus monticola* | 3 | Haig *et al.*, 1941; Hofmann, 1917 |

Mercado and Arriaga (1995) report the soil seed bank composition for a Mexican pine-oak ecosystem (*Pinus lagunae* (Rob.-Pass.) Passini*, Quercus devia* Goldman and *Arbutus peninsularis* Rose & Goldman). Other studies have been developed in lower montane forest (transition zone between neartic and neotropical floristic regions) of Mexico (Williams-Linera, 1993). Many studies on soil seed banks exist for tropical regions in Mexico (Guevara and Gómez-Pompa, 1972; Castro-Acuña and Guevara-Sada, 1976; Álvarez-Buylla and Martínez-Ramos, 1990; Vázquez-Yánes and Orozco-Segovia, 1990; Rico-Gray and García-Franco, 1992; Quintana-Ascencio *et al.,* 1996; Vázquez-Yánes *et al.*, 1996).

Flores and Pérez (1990) sampled the forest floor in stands of *P. montezumae* at San Juan Tetla, Puebla, Mexico, before the seed dispersal season. They found an average of 60 seeds/m$^2$ of *P. montezumae* with 0% viable seed, which indicates the short period of time that seeds of this species remain viable.

Several questions about the role of the soil seed bank in stands of this species were identified: What is the abundance and diversity of the soil seed bank? Does one or a few species dominate? Are many species represented? Are species predominantly herbaceous or woody?

In order to provide answers to these questions, the purpose of this study was to characterize the soil seed bank of a *Pinus montezumae* forest. The specific objectives were:

1. To identify species and estimate seedling abundance that can be expected in a regenerating stand from buried seeds using the seedling-emergence method for soil samples from stands of *Pinus montezumae* at San Juan Tetla.

2. To determine the depth distribution of buried seeds within the soil profile beneath *P. montezumae* stands.

3. To assess the degree to which seed bank populations reflect the species composition of current stands.

## MATERIALS AND METHODS

San Juan Tetla Experimental Station lied on the east slope of the Iztaccíhuatl volcano (19° 10'N, 98° 36'W), in the Municipio of Chiautzingo, State of Puebla, Mexico. The station has 15,80 ha approximately and its altitude range goes from 3,000 to 3,600 m; it includes mainly mixed stands of *P. montezumae*, *P. hartwegii* Lindl., *Abies religiosa*, *P. ayacahuite* var. *veitchii* (Roezl) Shaw and various hardwood species (Boyás, 1993).

The average annual precipitation is 1,169 mm, maximum rainfall occurs in summer (June-August), decreases to very low levels in winter (December-February), and remains low until May.

The stands used in this study were located about 1.5 km east of the station headquarters and were dominated by *P. montezumae*, with minor and varying proportions of three other conifers: white pine (*P. ayacahuite* var. *veitchii*), yellow pine (*P. teocote* Schiede ex Schltdl. & Cham.) and fir (*Abies religiosa*).In addition, several species of hardwoods are present, including alder (*Alnus firmifolia*), willows (*Salix oxylepis* Schn. and *Salix* sp.) and an oak (*Quercus laurina* Humb. *et* Bonpl.). The understory is dense enough to make it difficult to walk through the stand; it was dominated by small *Alnus* sp., *Quercus* sp., *Salix* sp. and a lush growth of perennial and malodorous *Senecio* sp. and other herbaceous vegetation. The understory is sufficiently dense to make it difficult walking through the stand.

The inventory indicates that this stand averages 156.1 trees/ha with a basal area of 37.61 $m^2$/ha, of which 110.9 trees/ha and 32.75 $m^2$/ha were montezuma pine, which made up 70 per cent of the stems $ha^{-1}$ and 87 per cent of the basal area $ha^{-1}$.

Soil samples were collected from four blocks in a natural regeneration study area. Soil and litter samples were collected on July from rectangular plots of 0.16 $m^2$, after *P. montezumae* seed dispersion (Acosta and Musálem, 1986). Six systematically distributed samples were taken from each block, and all of them were separated into three layers: litter, organic matter (humus) and mineral soil (horizon $A_1$). The litter layer at San Juan Tetla can be deep, as much as 40-50 cm at some sites, but none of the samples in this study had this depth (Table 2). A fixed mineral soil depth of 10 cm was also assessed. The samples for each litter, organic matter (humus) and mineral soil depth interval from the 6 plots were kept separate within each block, placed in plastic bags and thoroughly mixed. The six samples were divided into three subsamples (litter, organic matter and mineral soil) from each block (3 soil subsamples x 6 plot/block x 4 blocks = 72 subsamples total). The total surface area sampled was 3.84 $m^2$.

The seedling-emergence method was chosen because it has the advantage over physical separation techniques of being less labor intensive, and does not need additional viability tests (Roberts, 1981). As forest soil contains large amounts of organic material, the seedling-emergence method is the only practical method available, and hence it has been used by most researchers (Kjellson, 1992). Finally, no ‘library’ of seed samples was available for species likely to be contained in the soil seed bank of San Juan Tetla.

Table 2. Mean soil depth (cm) of soil samples at San Juan Tetla.

| Soil layers | Block | | | |
|---|---|---|---|---|
| | 1 | 2 | 3 | 4 |
| Litter | 4.17 | 3.33 | 6.50 | 5.25 |
| Organic matter | 5.00 | 5.33 | 6.83 | 4.83 |
| Mineral soil | 10.00 | 10.00 | 10.00 | 10.00 |
| Total depth | 19.17 | 18.67 | 23.33 | 20.08 |

All soil and litter samples were placed in 50 x 70 cm wooden flats in a greenhouse. Samples were watered as needed. Number and emergence time of seedlings were recorded weekly for a nine months period. Annual seedlings were removed after species identification to eliminate crowding of new emergents and to prevent seed production from mature plants.

## Data analysis

Plant identification was based on the checklists made specifically for San Juan Tetla (May-Nah, 1971; Boyás, 1993). and the flora of the Valle de México, according to the similarity of ecosystems (Sánchez, 1979; Rzedowski and Rzedowski, 1985).

Comparisons between soil samples for different blocks *(e.g.* 1 *vs* 2, 1 *vs* 3, etc.) were tested in order to find differences in species composition among the four blocks. These similarity was calculated through Sorensen's index of similarity (Jonsson, 1993):

$$Cs = 2j / (a+b)$$

Where:

$j$ = number of species common to both samples and

$a$ = number of species in the sample a

$b$ = number of species in the sample b

The index varies from 0 when both samples have no species in common, to 1 when all species occur in common in both samples.

## RESULTS

The relationship between soil depth and species density is summarized for all plants in Table 3. From the soil samples, a total of 1,797 germinants representing 43 species (2 trees, 17 shrubs, 1 grass and 23 herbs) emerged. Sixteen species occurred in all four blocks (9 herbs and 7 shrubs). The estimated total seed densities varied from 307 $m^{-2}$ in block 1 to 595 $m^{-2}$ in block 4; the highest densities were found in blocks 3 and 4 and the lowest in blocks 1 and 2. The observed differences in density among blocks were caused primarily by the variable distribution of *Senecio cinerarioides* Kunth, with large seed banks of 274 seed $m^{-2}$ in plot 4. Only one species of grass (*Brachypodium mexicanum* (Roem. & Schult.) Link) was found in blocks 1 and 2.

Seeds of woody species occurred in low densities. The most abundant tree was *Buddleia cordata* subsp. *cordata* Kunth, which germinated in three of the four blocks. *Dicotyledonous* seedlings were much more numerous than monocotyledons in all blocks. Nine herbs and three shrubs found in this study were not reported in the checklist for San Juan Tetla (May-Nah, 1971; Boyás, 1993). Seeds of canopy and shrub layer dominants (*Pinus montezumae*, *P. ayacahuite* var. *veitchii*, *Salix* sp. and *Alnus firmifolia*) were completely absent in the buried seed bank.

The qualitative difference between humus and mineral soil is high. Almost all species were present in the humus layer, but only 27 of the 43 species were present in the mineral soil. The most abundant species (*Senecio cinerarioides*, *Trifolium repens* and an unidentified Compositae) were most abundant in the mineral soil layer. The second most abundant group of species (*Gnaphalium brachypterum*, *Taraxacum officinale* and *Chenopodium album*) were more abundant in the humus layer.

Table 3. Number of seedlings present by soil layer over all plots at San Juan Tetla.

| Species | Soil layer | | | Total |
|---|---|---|---|---|
| | Litter | Humus | Mineral Soil | |
| Trees | | | | |
| *Buddleia parviflora* Kunth | | 2 | | 2 |
| *Buddleia cordata* subsp. *cordata* Kunth | | 8 | 6 | 14 |
| Shrubs | | | | |
| *Baccharis conferta* Kunth | | 6 | 4 | 10 |

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| Species | Soil layer | | | Total |
|---|---|---|---|---|
| | Litter | Humus | Mineral Soil | |
| *Eupatorium glabratum* Kunth | | 27 | 12 | 39 |
| *Ageratina pazcuarensis* (Kunth) R.M.King & H.Rob. | | 5 | | 5 |
| *Fuchsia thymifolia* Kunth | | 1 | 1 | 2 |
| *Gnaphalium americanum* P. Mill. (*) | | 5 | 2 | 7 |
| *Gnaphalium brachypterum* DC. (*) | 1 | 107 | 14 | 122 |
| *Gnaphalium* sp. | | 22 | 6 | 28 |
| *Penstemon campanulatus* (Cav.) Willd. | | 3 | 13 | 16 |
| *Phytolacca octandra* L. (*) | | 3 | | 3 |
| *Ribes ciliatum* Humb. & Bonpl. ex Schult. | | 4 | | 4 |
| *Rubus pringlei* Focke | | 2 | | 2 |
| *Senecio argutus* A. Rich. | | 1 | | 1 |
| *Senecio cinerarioides* Kunth | 12 | 202 | 236 | 450 |
| Shrubs | | | | |
| *Senecio salignus* DC. | 1 | 34 | 21 | 56 |
| *Senecio sinuatus* HBK. | | 36 | 47 | 83 |
| *Stevia rhombifolia* Kunth | | 13 | 8 | 21 |
| *Symphoricarpos microphyllus* Kunth | | 8 | 2 | 10 |
| Grasses | | | | |
| *Brachypodium mexicanum* (Roem. & Schult.) Link | 3 | 2 | | 5 |
| Herbs | | | | |
| *Alchemilla procumbens* Rose | | 7 | 9 | 16 |
| *Archibaccharis hieraciifolia* Heering | | 4 | 2 | 6 |
| *Arenaria repens* Sessé & Moc. (*) | | 1 | 4 | 5 |

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| Species | Soil layer | | | Total |
|---|---|---|---|---|
| | Litter | Humus | Mineral Soil | |
| *Arenaria* sp. | 1 | 31 | 12 | 44 |
| *Brassica campestris* L. | 16 | 6 | 2 | 24 |
| *Chenopodium album* L. | 26 | 51 | 18 | 95 |
| *Chenopodium ambrosioides* L. | 1 | 1 | | 2 |
| *Fragaria mexicana* Schltdl. | | 16 | 7 | 23 |
| *Geranium potentillifolium* DC. | | 72 | 23 | 95 |
| *Herbs* | | | | |
| *Geranium seemannii* Peyr. (*) | | 3 | | 3 |
| *Hieracium abscissum* Less. | | | 1 | 1 |
| *Licopersicum esculentum* L. (*) | | 2 | | 2 |
| *Lopezia racemosa* Cav. | | 1 | | 1 |
| *Physalis acuminata* Greenm. (*) | | 10 | | 10 |
| *Physalis stapelioides* Bitter | | 3 | | 3 |
| *Salvia polystachya* Ortega (*) | | 1 | | 1 |
| *Siegesbeckia orientalis* L. (*) | | 5 | 2 | 5 |
| *Solanum demissum* Lindley | 1 | | 5 | 2 |
| *Solanum nigrum* L. (*) | 8 | 34 | 29 | 40 |
| *Taraxacum officinale* G.H. Weber ex Wiggers (*) | 8 | 54 | 249 | 91 |
| *Trifolium repens* L. (*) | 17 | 37 | 103 | 294 |
| *Valeriana procera* Kunth | 95 | 1 | 838 | 1 |
| Unidentified Compositae (*) | | 33 | | 153 |
| Total | | 864 | | 1797 |

(*) Not reported in the checklist for San Juan Tetla.

The number of germinants was significantly higher (p<0.0001) in humus and mineral soil than litter, but no significant differences between humus and mineral soil or between blocks or samples within plots were found when seed densities were compared (Table 4).

Table 4. Analysis of variance summaries for seedling density at three soil depths and four plots at San Juan Tetla.

| Source | DF | Sum of Squares | Mean Square | F Value | Pr > F |
|---|---|---|---|---|---|
| Model | 41 | 34124.23 | 832.29 | 1.73 | 0.0606 |
| Error | 30 | 14446.41 | 481.54 | | |
| Corrected Total | 71 | 48570.64 | | | |

| R-Square | C.V. | Root MSE | Mean |
|---|---|---|---|
| 0.702569 | 95.12229 | 21.94418 | 23.06944 |

| Source | DF (n-1) | Type III SS | Mean Square | F Value | Pr > F |
|---|---|---|---|---|---|
| Block | 3 | 2247.37500 | 749.12500 | 1.56 | 0.2206 ns |
| Sample(block) | 15 | 9774.37500 | 651.62500 | 1.35 | 0.2331 ns |
| Sample | 5 | 2155.56944 | 431.11389 | 0.90 | 0.4968 ns |
| Sample*layer | 10 | 2851.13889 | 285.11389 | 0.59 | 0.8075 ns |
| Layer | 2 | 13695.19440 | 6847.59720 | 14.22 | 0.0001 ** |
| Plot*layer | 6 | 3400.58333 | 566.76389 | 1.18 | 0.3448 ns |

T tests (LSD) for variable: No. of seedlings; Alpha = 0.01 df = 30 MSE = 481.5472
Means with the same letter are not significantly different.

| T Grouping | Mean | N | Layer |
|---|---|---|---|
| A | 36.000 | 24 | Humus |
| A | 29.250 | 24 | Mineral Soil |
| B | 3.958 | 24 | Litter |

A comparison of the relative abundance of species in seed banks, performed using Sorensen's similarity index, indicated a relatively close correspondence between the four blocks (0.65 to 0.83). The highest similarity was scored for the comparison of blocks 3 and 4, which shared 22 species.

## DISCUSSION

Seed bank density.- The densities of buried seeds found in the plots of San Juan Tetla (mean for the four plots = 468 seeds $m^{-2}$) were intermediately relative to densities reported for conifer forests by other authors (Ahlgren, 1979; Granström, 1981; Fyles, 1989). Seed densities reported in other studies have been highly variable, where some conifer forests had less than a hundred (Higo *et al.,* 1995) to several hundreds of buried seeds $m^{-2}$ (Ingersoll and Wilson, 1990; Williams-Linera, 1993; Zobel *et al.,* 2007). Pratt *et al.* (1984) quantified over 14,000 seeds $m^{-2}$ in the seed bank in an autumn collection in a coniferous forest in central Washington. Kjellsson (1992) described densities over 15,000 seeds $m^{-2}$ in Danish deciduous forests. In contrast, Schiffman and Johnson (1992) found an average of 0.43 viable seeds $m^{-2}$ at Jefferson National Forest, Virginia, while only 0.23 seeds $m^{-2}$ were viable in the mature oak-dominated forest. Clearly, many factors influence soil seed bank densities and generalities about forest soil seed banks are impossible to make.

Seed distribution in relation to soil depth.- Most studies about seed banks in forests soils have reported a decrease of seed density with depth (Pratt *et al.,* 1984; Archibold, 1989; McGee and Feller, 1993; Moscoso and Diez, 2005). The vertical distribution of seeds in the soil examined in the present case showed no such general trend, but distinctive distribution patterns were observed for some species. Diverse herb species (*Licopersicum esculetum*, *Lopezia racemosa*, *Physalis acuminata*, *Physalis stapelioides*, *Salvia polystachya* and *Siegesbeckia orientalis*), and several shrubs (*Phytolacca octandra*, *Ribes ciliatum*, *Rubus pringlei* and *Senecio argutus*) were totally confined to the organic matter (humus) layer, while the most abundant (*Senecio cinerarioides*, *Trifolium repens* and one unidentified Compositae) were found, mainly, in the mineral soil layer.

Species recorded deep in the soil generally have seeds with capability for long-term survival. Observations on the longevity of seeds of other *Senecio* species (22-100 years) (Harrington, 1972; Thompson and Grime, 1979), together with the data presented here, suggest that *Senecio cinerarioides* may possess a persistent seed bank. The abundance of *S. cinerarioides* in the soil plots reflects the high production of those plants that do become established.

The depth distributions of the seeds of different species suggest that most of the seeds of *S. cinerarioides* and *Trifolium repens* may be quite old. The actual age of even the deepest situated seeds is unknown. Continuous accumulation of plant litter, activities of soil animals, and progressive decomposition of the humus layer may all assist in moving newly produced seeds downwards from the soil surface at an unknown rate (Granström, 1981).

Small animals have been considered an important factor in herbaceous plant seed dispersal (Mladenoff, 1990; Kjellsson, 1992). Some authors (Granström, 1981; Turnbull *et al.,* 1983) suggest that species with small seeds may have been moved downwards to the mineral soil by the activities of ants or other animals. McRill and Sagar (1973) have demonstrated that earthworms are able to ingest and relocate seeds of many small-seeded species in the soil. Earthworm activity is very low in these *Pinus montezumae* forests and is probably unimportant in terms of the vertical distribution of seeds. An alternative explanation for the presence of seeds in the mineral soil is that all the seeds registered in this soil layer could be located in the upper part of the mineral soil layer. No partitioning of the mineral soil samples was done, so possible seed stratification at different depths is unknown.

Seed bank composition.- With 43 species, the *P. montezumae* seed bank community is more diverse than most conifer forest seed banks (Pratt *et al.,* 1984). Buried seed reserves are not extensive in coniferous forests where seeds quickly lose viability, and many other seeds are lost to predators. Studies elsewhere, reviewed by Archibold (1989) and Hills and Morris (1992) suggest that early successional plant species are better represented in soil seed banks than later successional species, as such representation allows earlier successional species to be maintained in a region that is prone to periodic disturbance.

No germinants of conifer tree species were found in this study. Dominant tree species are rarely characterized by abundant buried seed reserves, but the early successional species are well represented. Pratt *et al.* (1984) discovered in a seed bank of a *P. ponderosa-Symphoricarpos albus* (L.) Blake habitat a reversal of dominance between the study-area vegetation and the seed bank. Annual forb species, which account for relatively little cover in the stand, comprised most of the seed bank. In contrast, tree and shrub species, which dominated the vegetation, accounted for less than 1% of the seed bank. They estimated the *P. ponderosa* seed density in spring as 17 seeds $m^{-2}$, and zero seeds $m^{-2}$ in autumn prior to seed fall down. Also, in South Africa, De Villiers *et al.* (2003) concluded that the seed bank site would be a good source of future annual plants, but not of perennial vegetation.

Several other studies of conifer-dominated ecosystems (Kellman, 1970 and 1974; Johnson, 1975; Strickler and Edgerton, 1976; Whipple, 1978; Hill and Stevens, 1981; Mercado and Arriaga-Cabrera, 1995) have reported uncommon germination of conifer seeds. In a *Pinus-Quercus* forest in the state of Baja California Sur, México, Mercado and Arriaga (1995) found that the primary species of this forest (*Pinus lagunae* M.-F. Passini, *Quercus devia* Goldman and *Arbutus peninsularis* Rose & Goldman) were not present in the soil seed bank. Zobel *et al.* (2007) studied a mesophyte mixed spruce forest and found a poor correspondence between the vegetation and the seed bank. *P. montezumae*, the dominant conifer in the study area, generally produces good seed year crops at 3-5 year intervals (Acosta and Musálem, 1986), and its seeds remain viable for 7-12 months (Flores and Pérez, 1990). *P. ayacahuite* produces good seed crops annually, and they remain viable for about the same period mentioned above (Serrano, 1986).

Species of *Alnus* have been reported to retain their viability for only a short period of time (McGee and Feller, 1993), which could explain why no germinants of alder were found in the study.

The presence of *Solanum* spp., *Fuchsia thymofila* and *Senecio* spp. in the soil seed bank suggest a persistency of these species, while others with low density and in few samples comprise the transient ones.

Sampling was carried out a few years after a good seed crop of *P. montezumae*, and several months after seeds of *P. ayacahuite* were dispersed. One important feature of some plants is large seeds, which however makes them susceptible to seed predation (Eriksson, 1995). In a comparative study of small and large seeded species, Reader (1993) found that only species with seeds larger than 0.3 mg were negatively affected by seed predators. Seeds of *P. montezumae* and *P. ayacahuite* are well above this limit, suggesting that they may suffer from heavy predation.

Increasing seed size makes species more likely to succeed in recruitment under litter, but less likely to be preserved in persistent seed banks. Seed predators are more likely to affect large seeded species, so decreasing seed size enhances development of seed banks, but makes species dependent on factors which temporarily remove the limiting effects of litter.

The results of the experiment suggest that for all species examined here, mineral soil was equal to forest floor (litter and humus) as a germination substrate. Removal of the forest litter and organic matter would remove about one-half of the soil seed bank. If exposure of mineral soil provides a generally superior substrate for seed germination, loss of half of the seed bank might not necessarily lead to a reduction in vegetation cover in the early successional plant community. Only a few species were restricted to just litter and organic matter, so species diversity would not be changed dramatically.

Caution must be applied in extrapolating seed bank studies to potential seedling populations in the field, partly because of problems in determining soil seed banks and because species establishment from a seed bank is a function of the depth to which the soil is disturbed. Burning, removal, or redistribution of the forest floor will result in different impacts on the seed bank and different potential plant populations (McGee and Feller, 1993). Burning alone can remove different amounts of forest floor depending on the severity of the fire, as has been found in southwestern British Columbia and elsewhere (Feller, 1989).

## CONCLUSIONS

Seed density and species diversity of the seed bank in *Pinus montezumae* stands sampled for this study compared with literature reports were average, facts that are attributed to the high density of shrubs and herbs.

Dominant species (*P. montezumae*) and codominant species (*P. ayacahuite* var. *veitchii*, *Abies religiosa* and *Alnus firmifolia*) in the stand were not comparable with species dominance in the seed bank.

Viable seeds of most species were contained in similar abundance in the humus and mineral soil layers.

Regeneration of desirable (commercial) species under any regeneration cutting method will be expected from seed production in the current or future years, or few seeds produced off site, but none will be expected from the soil seed bank.

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