

**Soil Seed Banks in Coniferous, Fire-Adapted, and Southwestern U.S. Ecosystems:
An Annotated Bibliography**

**Judy Springer and Rob Hastings
Ecological Restoration Institute
Northern Arizona University
Flagstaff, AZ**

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1. Abrams, M. D., and D. I. Dickmann. 1984. Apparent heat stimulation of buried seeds of *Geranium bicknellii* on jack pine sites in northern lower Michigan. *The Michigan Botanist* **23**:81-88.

Geranium bicknellii dominates vegetative cover the first year after fire on many jack pine sites in northern lower Michigan, but in subsequent years it disappears. To test whether heat from fire was responsible for this behavior, experiments using seed buried in the soil of different aged jack pine sites were initiated. Germination of buried geranium seed only occurred in heated treatments from 3- and 35-year-old sites; unheated controls produced no germinants. The apparent heat requirements for germination of buried geranium seed from sites in northern lower Michigan contrasts with other Lake States studies and suggests ecotypic differences in germination behavior. Unheated soil from the 35- and 55-year-old sites produced significantly greater numbers of grass germinants than did heated treatments. Many important members of the plant community recorded on each site did not produce germinants in this experiment, and several species that germinated from buried seed were not surveyed on the site.

Jack pine, Geranium bicknellii, Michigan, heat

2. Amezaga, I., and M. Onaindia. 1997. The effect of evergreen and deciduous coniferous plantations on the field layer and seed bank of native woodlands. *Ecography* **20**:308-318.

Vegetation and seed bank changes due to the replacement of a native woodland 29 yr ago by coniferous plantations (evergreen coniferous *Pinus radiata* and deciduous coniferous *Larix kaempferi*) were studied in a replicated experiment in the Basque Country, northern Spain. In the vegetation the species richness was lower in both coniferous plantations than in the native woodland but there was no significant difference in species richness between the two coniferous plantations. The highest similarity between the vegetation and the seed bank was in the *P. radiata* plantations (0.51). There was higher vegetation similarity between the native woodland and the larch plantation (0.65) than that with the pine plantation (0.58). Seed bank species richness was higher in the larch plantation than in the native woodland but species richness in the seed bank did not differ between the coniferous plantations. The seed bank showed no difference in the species similarity between the plantations and the native woodland. This was mainly due to the similarity between the broad ranged species. In the coniferous plantations the vegetation diversity was lower than in the native woodland; however, in the seed bank the diversity was higher. Coniferous plantations affected mainly the shade-tolerant and shade-intolerant vernal (*Caltha palustris*, *Galium odoratum*, *Heleborus viridis* and

Saxifraga hirsuta), which disappeared from the field layer of plantations while the shade-intolerant not vernal species were favoured by the plantations (*Blackstonia perfoliata*, *Danthonia decumbens*, *Deschampsia flexuosa*, *Hypericum androsaemum*, *Holcus lanatus*, *Lotus corniculatus* and *Plantago lanceolata*). There was no significant difference in vegetation or seed bank between the two types of coniferous plantations.

Pinus radiata, *Larix kaempferi*, *Spain*, *pine plantations*, *shade tolerance*

3. Anderson, C. J., and J. A. MacMahon. 2001. Granivores, exclosures, and seed banks: harvester ants and rodents in sagebrush-steppe. *Journal of Arid Environments* **49**:343-355.

Experiments were conducted to assess the influences of granivores on the seed bank in sagebrush-steppe. Rodent and/or ant exclosures were established at two distances from five harvester ant mounds. Monthly soil samples were collected from the exclosures, and from open access areas at two distances to ascertain changes in the seed bank. Seed dish experiments were conducted monthly to establish a maximum seed removal rate. Rodents were trapped monthly. More seeds were recovered from rodent exclosures than from ant exclosures. Seed banks changed temporally and spatially, with more seeds recovered in September and at 6 m from mounds. Rodents removed seeds more rapidly from seed dishes than did ants. Ants removed more seeds from dishes closest to the nests. Rodents may have a larger impact on the local seed bank than harvester ants. Ant activities, other than seed consumption, may have more influence on vegetation.

Granivory, *harvester ants*, *rodents*, *sagebrush steppe*, *exclosures*

4. Archibold, O.W. 1979. Buried viable propagules as a factor in postfire regeneration in northern Saskatchewan. *Canadian Journal of Botany* **57**:54-58.

Soils collected from seven sample plots in a burned mixed-wood area in northern Saskatchewan were held at optimum laboratory conditions to determine the number of viable seeds and latent underground buds. A total of 270 plants developed, representing a rate of emergence of 426 plants/m² of which 372 plants (87%) originated from seed and 54 (13%) came from remnant roots or rhizomes. In addition, 19 birch seeds were extracted from the soil following the germination tests giving a total count of 456 propagules/m². Tree species accounted for 42.9% of this total.

Saskatchewan, *rhizomes*, *fire*, *propagules*, *birch*, *natural regeneration*

5. Archibold, O.W. 1980. Seed input into a postfire forest site in northern Saskatchewan. *Canadian Journal of Forest Research* **10**:129-134.

Seed traps were installed at seven sites along a transect in a burned mixedwood forest site in northern Saskatchewan to determine annual seed inputs. The seeds were returned to the laboratory for germination and identification. A total of 1698 seeds was collected in the 1977-1978 season, representing a seeding rate of 8.98 million seeds/ha. *Epilobium angustifolium* L. was most abundant representing 63% of the total. *Betula papyrifera* Marsh. accounted for 27.6% and *Picea glauca* (Moench) Voss 6.1%. The seed count for 1978-1978 was 651 (3.44 million/ha) and represented a significant decline in herb and tree seeds.

Saskatchewan, *fire*, *Betula papyrifera*, *Picea glauca*

6. Archibold, O.W. 1989. Seed banks and vegetation processes in coniferous forests. Pages 107-122 in M. A. Leck, V. T. Parker and R. L. Simpson, editors. Ecology of soil seed banks. Academic Press, San Diego, California, USA.

Persistent seed banks represent a mechanism of survival for species growing in regions subject to periodic disturbance. Throughout coniferous forests, fire is the major natural hazard, but the plants are well adapted and recovery even on the most intensely burned sites starts rapidly. Often the first plants to establish are opportunistic species which produce numerous, readily transported seeds. Many plants will develop vegetatively. Few species are dependent on seed reserves that have accumulated in the soil between disturbances, and the seed bank is characteristically small in these regions. The size of the buried seed pool reflects the type, intensity, and frequency of disturbance. The manner in which these factors influence seed production, storage, and subsequent plant establishment is discussed.

Coniferous forest, fire, persistent seeds, succession, disturbance

7. Arkle, P.J., D.C. Malcolm and C.J. Nixon. 2002. Role of the soil seed bank in the restoration of a native pinewood at Glen Garry, Inverness-shire. Botanical Journal of Scotland **54**(2):221-236.

The potential recovery of ground vegetation in a pinewood at Glen Garry, from which introduced tree species had been removed, was studied by sampling the upper soil seed bank and comparing the species composition of germinating seedlings with extant vegetation. Mean numbers and species of seedlings emerging differed between a control site (not under-planted) and two formerly under-planted sites cleared at different times. Germinating seedling numbers also differed with depth (0-10 cm). *Calluna vulgaris* and *Juncus* spp. dominated fifteen species germinating from the seed bank, while some other pinewood species were not found. Although seedling pine occurred, their survival will be affected by competition from *Betula* spp. and *Deschampsia flexuosa*. Other elements of the vegetation will recover from the seedbank or by migration, their distribution being influenced by topographic variations and the nature of the developing tree stand. Timing of clearance of exotics in relation to pine seed production and soil scarification might accelerate recovery of the pinewood flora generally.

Scotland, Betula, pine forest, soil scarification, exotic species

8. Arriaga, L., and C. Mercado. 2004. Seed bank dynamics and tree-fall gaps in a northwestern Mexican *Quercus-Pinus* forest. Journal of Vegetation Science **15**:661-668.

21 species, 20 genera and 14 families constitute the seed bank of this forest community. Fabaceae, Asteraceae, Euphorbiaceae, and Lamiaceae were the most frequently represented families in the seed bank. Floristic composition and species richness varied according to the different modes of tree death. Species composition of seed banks and standing vegetation had very low similarity coefficients and were statistically different. Seed bank sizes varied between 164 and 362 ind.m⁻² in the mature forest plot for the dry and rainy seasons, respectively, while soil seed bank sizes for gaps ranged between 23–208 ind.m⁻² for the dry season and between 81–282 ind.m⁻² for the rainy season. Seed bank sizes and germination response were always higher in the rainy season under all the environmental conditions analysed. Results suggest that timing

responses to gap formation of the soil seed bank could be more delayed in this temperate forest than expected.

Baja California Sur, Mexico, disturbance, gap creation mode, seasonal response, seedling emergence, Sierra de la Laguna, temperate forest

9. Artigas, F. J., and R. E. J. Boerner. 1989. Advance regeneration and seed banking of woody plants in Ohio pine plantations: implications for landscape change. *Landscape Ecology* **2**:139-150.

Silviculturally-managed pine plantations within southern Ohio are chronically disturbed patches of introduced vegetation distinct from the surrounding matrix of hardwood forest. To determine the successional pathways by which such pine stands might blend back into the hardwood forest matrix under different types of silvicultural management, we determined the current status of hardwood regeneration under 24 pine stands. Stands of *Pinus virginiana* (Virginia pine) had the highest density of hardwood seedlings and samplings (20,560 stems ha⁻¹) whereas *P. strobus* (white pine) stands averaged only 7090 hardwood stems ha⁻¹; *P. resinosa* (red pine) stands were intermediate. The most abundant hardwood seedling and sapling species under pine canopies were *Acer rubrum* and *Cornus florida*. DCA ordination of the seedling + sapling assemblages clustered most of the *P. resinosa* and *P. strobus* stands in the center of the ordination along with a group of species which are common in second-growth forests of the area. *P. virginiana* stands, in contrast, were scattered throughout the ordination space. Most of the woody species common in second-growth forests of the region were also common in the pine understory. Multiple regression indicated that large plantations with deeper litter, higher soil pH and lower total hardwood density had the greatest abundance of mesic-site species in the understory. This relationship did not hold for *P. resinosa* stands, however, due to more frequent and intense silvicultural intervention. The seed bank was not an important source of woody seedlings to the understory assemblage under intact pine plantations. The vegetation of 1-4 yr old clear-cut sites was dominated by wind and bird dispersed species which were generally absent from the understory of intact plantations. The authors conclude these chronically disturbed planted patches will revert to matrix vegetation faster if the disturbance is allowed to end in a gradual manner through stand senescence than if it is abruptly ended by clear-cutting.

Landscape ecology, pine, succession, seed regeneration, Ohio, hardwood forest, succession, pine plantations, seed dispersal

10. Ashton, P. M. S., P. G. Harris, and R. Thadani. 1998. Soil seed bank dynamics in relation to topographic position of a mixed-deciduous forest in southern New England, USA. *Forest Ecology and Management* **111**:15-22.

The authors examined the floristic significance of soil seed banks in relation to valley, midslope and ridge sites in a 70–90-year old forest in northeastern Connecticut. A-horizon mineral soils were collected to 5 cm depth in the early spring from forest understory sites across the topography. Samples from each of the sites were exposed to full sun within a greenhouse. Records of germination were made at regular intervals over a 60-day period. These showed significant differences among sites in number of species and total number of germinants. Greatest numbers of species and germinants were

recorded from valley sites and these progressively declined from midslope to ridgetop. Twenty-five different species were identified. Species were grouped into growth habits – graminoids, herbs, shrubs, trees, and vines. Over 61% of all germinants across all sites were graminoids. Seventy-four percent of all germinants in the valley sites were graminoids, with over 93% of them represented by two sedge species, *Carex glaucoidea* and *C. lupulina*. On the ridgetop sites graminoids were more evenly distributed among six different species. The percentage in each growth habit changed rank across topographic position with germinants of graminoids and trees most abundant on valley sites; herbs, on midslopes, and shrubs, on ridgetops. All germinants, except for those of the trees, *Carex* spp., and two herb species were weedy species that were not characteristic of the existing vegetation. Germinants of the trees, *Carex* spp., and herbs that were characteristic of the existing vegetation were mostly confined to soils from the valley sites. Two weedy herbs, *Plantago major* and *Verbascum thapsus*, are exotic introductions that originally came from Europe. Only one vine, *Vitis aestivalis*, from a midslope site germinated. Species diversity is higher on midslope sites than valleys and ridgetops. The significance of these findings in relation to site productivity and disturbance history is discussed.

Buried seed, Carex spp., Connecticut, forest understory, land use, slope position, regeneration, disturbance, graminoids

11. Augusto, L., J.-L. Dupouey, J.-F. Picard, and J. Ranger. 2001. Potential contribution of the seed bank in coniferous plantations to the restoration of native deciduous forest vegetation. *Acta Oecologica* **22**:87-98.

In this study from north-eastern France, the authors compared the soil seed bank and current vegetation under coniferous plantations and adjacent native deciduous forests. The objective was to assess how much of the initial plant diversity is retained in such plantations, and the potential to restore this initial plant community from the seed bank in case of reversion to broadleaf stands. Four stands growing side by side and with different dominant species were selected at two locations (site of Haye: *Quercus petraea*, *Pseudotsuga menziesii*, *Pinus sylvestris* and *Picea abies*; site of La Petite-Pierre: *Quercus petraea*, *Fagus sylvatica*, *Pinus sylvestris* and *Picea abies*). In each stand, ground vegetation was surveyed and the soil seed bank was sampled. Composition of ground flora and seed bank of stands were quite different: only 11 to 30 % of the species were in both the ground flora and the seed bank. Composition of the seed bank was mainly influenced by site location and silvicultural practices such as the type of afforestation or the tree cover. Species richness of seed banks and vegetation were higher in the site of Haye than in the site of La Petite-Pierre. Seedling density strongly decreased with stand age. Whereas between 65 and 86 % of species found in the ground vegetation of native deciduous stand were also present in the understory or the seed bank of mature coniferous stands, this was only about 50 % in young coniferous stands. Species of deciduous stands which were absent from coniferous stands were typical of old forests. In contrast, species mainly found in the coniferous stands were often ruderal. In the studied areas, it would be possible to restore up to 86 % of the native deciduous forest vegetation, but some plant species typical of ancient forests may have disappeared during the coniferous stage.

Native forest, pine plantation, France, ruderal species

12. Auld, T. D. and R.A. Bradstock. 1996. Soil temperatures after the passage of a fire: Do they influence the germination of buried seeds? *Australian Journal of Ecology* **21**:106-109.

Soil temperatures down to a depth of 5 cm were measured in the days following one fire in summer, one fire in winter and in unburnt vegetation during summer. Soil temperatures did not rise above 40°C after the winter fire or in unburnt vegetation during summer. Consequently, no impact on seed dormancy in the soil seed bank was expected. After a summer fire, soil temperatures above 40°C were found up to 4.5 cm depth, while temperatures above 60°C were found only in the top 0.5 cm of soil. These temperatures are sufficient to break seed dormancy in some legume species in the seedbank. Hence, the season of burn may influence the number of seeds in the soil that have their dormancy broken and subsequent germination levels.

Fire season, legumes, seed dormancy, germination, soil temperatures, seasonality, dormancy

13. Auld, T.D., D.A. Keith and R. A. Bradstock. 2000. Patterns in longevity of soil seedbanks in fire-prone communities of south-eastern Australia. *Australian Journal of Botany* **48**(4):539-548.

Seed burial in nylon mesh bags over a 2-year period was used to examine seed longevity patterns in 12 shrub and two graminoid species in fire-prone habitats around Sydney, south-eastern Australia. Most species released a large fraction of their annual seed-crop in a dormant state and all species showed evidence for some form of persistent seedbank. However, regressions of seed persistence over time were in most cases poor predictors of seed decay (9 of 14 study species). Considerable variation in the degree and pattern of seed longevity was apparent in the study species. Three functional groupings of species are suggested. (1) Seed half-lives in the soil predicted to be greater than 2 years and evidence of imposed secondary dormancy (continuous, *Kunzea spp.* or seasonal, *Grevillea caleyi*). Only *Kunzea capitata* and *G. caleyi* showed significant seed decay in this group. (2) Seed half-lives in the soil predicted to be greater than 2 years and no evidence of secondary dormancy (nine species). Six species had high seed dormancy at release (only two of which showed significant seed decay). Three species had initial seed dormancy of 40-57% - two (*Asterolasia elegans* and *Zieria involucreta*) with significant decay only for the non-dormant seed fraction, and one (*Comesperma ericinum*) with significant decay of both the dormant and non-dormant seed fractions. (3) Two species (*Darwinia biflora* and *Persoonia pinifolia*) showed evidence of very short mean half-lives of seeds in the soil (0.4-1.0 years). The threatened species, *D. biflora*, had a rapid initial seed decay over 6 months followed by little decay for 18 months, and the half-life of seeds is likely to be a poor predictor of seed longevity. For *P. pinifolia*, maintenance of a soil seedbank is predicted to be dependent on continual inputs of seeds locally or dispersal of seeds from other sites.

Australia, longevity, graminoid species, fire, seed persistence, dormancy

14. Bai, Y., and J. T. Romo. 1997. Seed production, seed rain, and the seedbank of fringed sagebrush. *Journal of Range Management* **50**:151-155.

Increases in fringed sagebrush (*Artemisia frigida* Willd.) following disturbance on Northern Mixed Prairie are due to enhanced growth of established plants and seedling

recruitment. The roles of seed production and the soil seedbank in population dynamics of fringed sagebrush following disturbance are, however, unknown. Furthermore, seed rain has not been documented for this species. The objectives of this study were to determine: 1) the effect of disturbances in the sward on seed production; 2) relationships between the soil seedbank and current seed production; and 3) seed rain over time for fringed sagebrush. Disturbances of clipping, litter removal, tillage, and a combination of clipping and litter removal were imposed on a sandy range site in central Saskatchewan. Following disturbance seed production per plant either increased or was unchanged compared to the undisturbed control. Greater seed production resulted from increased production of seeds per head, heads per inflorescence and inflorescences per plant. The timing of seed rain varied considerably among individual plants. Five temporal patterns of seed rain were identified for individual fringed sagebrush plants: 1) 5.2% of the plants began and completed dispersing seeds within 6 to 8 weeks of flowering; 2) 20.8% began dispersing within 6 to 8 weeks of flowering and completed dispersal before snow was received in autumn; 3) 37.7% began dispersing seeds within 6 to 8 weeks of flowering and continued over the winter; 4) 29.9% delayed dispersal of seeds more than 8 weeks after flowering and continued over the winter; and 5) 6.5% began and completed seed dispersal during the winter. The number of fringed sagebrush seeds in the soil was correlated with seed production only when many seeds were produced ($r=0.76$), indicating that annual seed production is of limited importance for maintaining a seedbank. A persistent seedbank is important in maintaining fringed sagebrush populations when seed production is limited. Diverse rates and times of seed rain along with a persistent seedbank may enable fringed sagebrush to occupy safe sites that develop in time.

Artemisia frigida, seeds, seed output, seed dispersal, environmental factors, disturbed land, Saskatchewan

15. Bakker, J. P., E. S. Bakker, E. Rosen, G. L. Verweij, and R. M. Bekker. 1996. Soil seed bank composition along a gradient from dry alvar grassland to *Juniperus* shrubland. *Journal of Vegetation Science* 7:165-176.

Dry alvar grasslands on limestone on the Baltic island of Öland, SE Sweden, are very species-rich as long as the traditional agricultural exploitation of grazing and fire wood collection continues. After abandonment, encroachment of *Juniperus communis* starts and a closed woodland can develop within 100 yr. A chronosequence representing a successional series, was used for the comparison of sites still grazed, and sites ungrazed for about 20, 55 and 80 yr. respectively. Out of the 58 characteristically dry alvar grassland species 55% disappeared from the established vegetation after 80 yr of abandoning, and 80% also vanished from the seed bank. *Arenaria serpyllifolia*, *Trifolium repens*, *Agrostis vinealis*, *Linum catharticum*, *Polygala vulgaris*, *Cerastium fontanum*, *Luzula campestris*, *Achillea millefolium* and *Potentilla tabernaemontani* were the only species left in the seed bank. More than 75% of the dry alvar grassland species were classified as having a transient or short-term persistent seed bank. It is concluded that restoration management, by cutting junipers, of overgrown dry alvar grasslands cannot rely on the longevity of seeds in the soil. Seeds have to be dispersed by wind or grazing animals.

Juniperus communis, seedling, seed longevity, species richness, restoration management, succession, encroachment, regeneration, alvar grassland, Sweden

16. Bartolome, J. W. 1979. Germination and seedling establishment in California annual grassland. *Journal of Ecology* **67**:273-281.

Data for plant density, germinable seed in the soil, and seed production in annual grassland were obtained at Hopland Field Station, California, USA, in 1973 and 1974. The study combined indirect estimates of numbers of seed in the soil, germination in soil samples containing natural seed, and estimation of plant density. Autumn patterns of establishment differed significantly between the two study years. Plant density increased through the autumn, reaching peaks of 261.8 and 345.3 plants per dm² in the seventh week after germination began, in 1973 and 1974 respectively. The numbers of germinable seed in the top 6.4 cm of the soil prior to the start of the growing season were 670.5 per dm² in 1973 and 610.2 per dm² in 1974, and thus showed little difference between years. Comparison of depletion of the seed-bank in the soil and increase of plant density showed that seeds germinating in the first week of the growing season produced fewer established seedlings than seeds germinating in the second or third weeks. The few seeds remaining in the fifth and sixth weeks had a high probability for successful establishment. Six species-groups exhibiting contrasting strategies for germination and establishment are discussed in detail.

California, annual grassland, germination, seasonality

17. Baxter, B. J. M., J. Van Staden; J. E. Granger, and N. A. C. Brown. 1994. Plant-derived smoke and smoke extracts stimulate seed germination of the fire-climax grass *Themeda triandra*. *Environmental and Experimental Botany* **34**(2):217-223.

Plant-derived smoke and aqueous extracts of smoke stimulate germination of dormant seed of the important fire-climax grass *Themeda triandra* (redgrass). The positive germination response to smoke increased as the state of seed imbibition increased. Furthermore, aqueous smoke extracts significantly increased seed germination at optimum and sub-optimum germination temperatures. Ethrel and ethylene, at a wide range of concentrations, failed to increase *T. triandra* seed germination, indicating that ethylene is not the active component of plant-derived smoke. Similarly, ash or aqueous ash extracts failed to stimulate germination. In contrast, aqueous smoke extracts prepared from burning fynbos vegetation and grass leaf material stimulated *T. triandra* seed germination. The bioactive component of plant-derived smoke may originate from a commonly occurring source, possibly being a thermal breakdown product of hemicellulose or cellulose.

Themeda triandra, plant-derived smoke, aqueous extracts, seed germination, ethylene, South Africa, fynbos, fire

18. Bond, W. J., K. Maze and P. Desmet. 1995. Fire life histories and the seeds of chaos. *Ecoscience* **2**(3):252-260.

Changes in plant population size are usually attributed to exogenous factors such as drought or herbivore outbreaks. However, in theory, populations may oscillate from endogenous density-dependent causes alone. Under some conditions these oscillations are very irregular and are called chaos. There are very few examples of endogenous

oscillations in plants and these are controversial. Large fluctuations in population size occur after fires in many species of Proteaceae in South African and Australian shrublands. These non-sprouting species form single-aged cohorts with recruitment dating from the last fire. Variation in cohort size has usually been attributed to exogenous factors, especially the length of the fire interval, fire season, and post-burn weather conditions. The authors studied the importance of endogenous density-dependence in generating population oscillations in these proteoid shrubs. Using a variety of approaches, they show that density-dependent reduction in fecundity may lead to endogenous oscillations in some species. They explore the “seeds of chaos” by defining attributes of species and populations most likely to generate endogenous oscillations. Finally, the authors note the implications of the phenomenon for research in, and management of, these systems.

Seed biology, plant demography, chaos, fynbos, Proteaceae, fire ecology, South Africa, Australia

19. Brown, D. 1992. Estimating the composition of a forest seed bank: A comparison of the seed extraction and seedling emergence methods. *Canadian Journal of Botany* **70**:1603-1612.

The composition of a forest seed bank was estimated using two methods: (i) seed extraction, i.e., the physical separation of the seeds from the soil via flotation in a salt solution, and (ii) seedling emergence, i.e., the germination of seedlings from soil samples incubated under greenhouse conditions for 5 months. The extraction method predicted a density of 12,5000 seeds/m², while the emergence method detected 3800 emergents/m². There was considerable disparity in species composition derived from the two methods. The extraction method identified 102 different taxa, with 22 species making up 99% of the seeds and 5.6 ± 0.2 species per sample. In contrast, the emergence technique identified fewer species (60) but had more species per sample (7.6 ± 0.21). Eleven species made up 99% of the emergents. *Verbascum thapsus* represented 34% of the seedlings in the emergence study but only 1% of the extracted seeds. Members of the Polygonaceae represented 19% of the extracted seeds but less than 1% of the seedling emergents. No tree or shrub species were found with the emergence method, although they represented 8% of the extracted seeds. There was a poor correlation between the estimates of species number, seed density, and diversity obtained from the two methods. The seed extraction method had considerably higher variability for these parameters. It is apparent from this study that the seedling emergence and seed extraction methodologies do not produce similar estimates of the seed bank composition. The differences are such that comparisons should not be drawn between studies using the different methods. Careful considerations should be given to both the objectives of the seed bank study and the relevant literature prior to the selection of an appropriate method.

Methodology, species composition, diversity, density, sample number, Verbascum thapsus, seed extraction, seed emergence

20. Cabin, R. J. 1996. Genetic comparisons of seed bank and seedling populations of a perennial desert mustard, *Lesquerella fendleri*. *Evolution* **50**:1830-1841.

The genetic relationship between seeds that successfully germinate and those that remain dormant in the soil was analyzed in a perennial desert mustard, *Lesquerella*

fendleri. By comparing allele frequencies and heterozygosity of *Lesquerella* soil seeds and seedlings, assessing the differentiation among and between their populations and examining the genetic structure of the two populations, it was found that *Lesquerella* soil seeds and seedlings are genetically unidentical. Findings suggest that *Lesquerella* seedlings in this system represent a nonrandom genetic subset of the *Lesquerella* seed bank.

Desert, Lesquerella fendleri, genetics, dormancy

21. Cabin, R. J., and D. L. Marshall. 2000. The demographic role of soil seed banks. I. Spatial and temporal comparisons of below-and above-ground populations of the desert mustard *Lesquerella fendleri*. *Journal of Ecology* **88**:283-292.

Although seed banks may often affect the colonization, succession and structure of surface plant communities, few studies have investigated the demographic relationship between seeds in the soil and above-ground plant populations over space and time. The authors examined this relationship in the perennial mustard *Lesquerella fendleri* between 1991 and 1994 within a New Mexico desert ecosystem characterized by open patches of soil (intershrub areas) interspersed with dominant creosote (*Larrea tridentata*) shrubs (subshrub areas). For the first 2 years of the study, *Lesquerella* soil seed, surface plant and seed production densities were greater in subshrub vs. intershrub areas. Within the subshrub areas, there were more *Lesquerella* soil seeds and surface plants in the northern and central microsites, compared with the southern and perimeter microsites, respectively. The mean density of the subshrub seed bank did not increase following large inputs of new seeds (2400 seeds m²) in the summer of 1992. In contrast, virtually all of the relatively modest *Lesquerella* intershrub seed production at this time (169 seeds m²) appeared to survive, so that for the remainder of the study most soil seeds were found in the intershrub sites. This spatial reversal of seed bank densities preceded a similar switch in the relative densities of the *Lesquerella* sub- and intershrub surface plant populations in the last 2 years of the study. This study supports the hypothesis that desert seed bank patchiness contributes to surface plant patchiness, but does not support the idea that seed banks are comprised primarily of seeds produced during favourable reproductive periods. Because there was a closer spatial match between *Lesquerella* soil seeds and surface plants than between soil seeds and seed production, the above-ground population may be limited to sites favourable for soil seed persistence.

Seed persistence, desert, Lesquerella fendleri, New Mexico, shrubs, patchiness

22. Cabin, R. J., R. J. Mitchell, and D. L. Marshall. 1998. Do surface plant and soil seed bank populations differ genetically? A multipopulation study of the desert mustard *Lesquerella fendleri* (Brassicaceae). *American Journal of Botany* **85**:1098-1109.

Seed banks are an important component of many plant populations, but few empirical studies have investigated the genetic relationship between soil seeds and surface plants. The authors compared the genetic structure of soil seeds and surface plants of the desert mustard *Lesquerella fendleri* within and among five ecologically diverse populations at the Sevilleta National Wildlife Refuge in Central New Mexico. At each site, 40 *Lesquerella* surface plants and 40 samples of soil seeds were mapped and genetically analyzed using starch gel electrophoresis. Overall allele frequencies of soil seeds and surface plants showed significant differences across the five populations and

within three of the five individual populations. Surface plants had significantly greater amounts of single and multilocus heterozygosity, and mean surface plant heterozygosity was also greater at the total population level and in four of the five individual populations. Overall soil seed (but not surface plant) homozygosity was significantly greater than predicted by Hardy-Weinberg expectations at the total and individual population levels. Although F_{st} estimates revealed similarly small but significant genetic divergence within each life-history stage, estimates of coancestry showed that fine-scale (0.5-2m) genetic correlations among the surface plant genotypes were roughly twice those of soil seed genotypes. An unweighted pair group method with arithmetic mean cluster analysis indicated that in the two geographically closest sites, the surface plants were slightly more genetically similar to each other than to their own respective seed banks. The authors also found weak and/or negative demographic associations between *Lesquerella* soil seed and surface plant densities within each of the five sites. They discuss the difficulties involved with sampling and genetically comparing these two life-history stages.

Allele frequencies, Brassicaceae, coefficient of coancestry, ecological genetics, heterozygosity, Lesquerella fendleri, population genetic structure, seed banks, Wright's F statistics, New Mexico

23. Carrington, M.E. 1999. Post-fire seedling establishment in Florida sand pine scrub. *Journal of Vegetation Science* **10**(3):403-412.

This study deals with a quantification of pre- and post-fire seedling establishment and microsite characteristics in two Florida sand pine scrub sites burned in May 1993. In addition, life history characteristics related to seedling establishment are described for five perennial species - *Calamintha ashei*, *Chapmannia floridana*, *Eriogonum floridanum*, *Garberia heterophylla* and *Palafoxia feayi*. Post-fire seedling establishment in sand pine scrub was sparse (median = 1, 12 seedling/m²), with 17 of 35 species establishing seedlings. *Chapmannia*, *Eriogonum*, *Garberia* and *Palafoxia* resprouted and flowered after fire; *Eriogonum* and *Garberia* had strong post-fire seedling establishment responses within 19 months post-fire. *Calamintha* individuals were killed by fire, but this species had a strong post-fire seedling establishment response, presumably from seeds in a soil seed bank. *Eriogonum* and *Calamintha* seedlings established preferentially in plots centered on conspecific adults. For these species with poor seed dispersal, spatial patterns of seedling establishment may be influenced more by pre-fire adult plant location than by post-fire microsite conditions. Post-fire seedling density in sand pine scrub was much lower than in California chaparral and South African sand plain lowland fynbos.

Fire, Florida, sand pine scrub, fynbos, chaparral, seed dispersal

24. Chambers, J. C., S. B. Vander Wall, and E. W. Schupp. 1999. Seed and seedling ecology of pinon and juniper species in the pygmy woodlands of western North America. *Botanical Review* **65**:1-28.

Knowledge of the seed and seedling ecology of the pinon and juniper woodlands of western North America is essential for understanding both the northward migration and expansion of the woodlands during the Holocene ([less than]11,500 B.P.), and the accelerated expansion of the woodlands since settlement of the West by Anglo-Americans around 200 years ago. The authors follow the fates of seeds and seedlings of

the different pinon and juniper species within the woodlands from seed development to seedling establishment, and discuss the implications of this information for the past and present expansion of the woodlands. Substantial seed losses can occur during seed development due to developmental constraints, and before or after seed maturation as a result of insects, pathogens, or predatory animals. In pinon pines, the primary seed dispersers are scatter-hoarding birds (corvids) and rodents that harvest seeds from the trees or after seed fall and cache them in the soil. In contrast, most junipers appear to be dispersed primarily by frugivorous birds and mammals that ingest the seeds and defecate them onto the soil surface. The authors have recently documented that scatter-hoarding rodents also disperse juniper seeds. Disperser effectiveness, or the contribution a disperser makes to the future reproduction of a plant population, may vary among species of pinons and especially junipers. Pinon seeds are short-lived and exhibit little dormancy, and they probably only germinate the spring following dispersal. Juniper seeds are long-lived and seed dispersal can occur over one or more years. Seedling establishment of pinon pines is facilitated by nurse plants but, while junipers often establish beneath nurse plants, they are capable of establishing in open environments. In the southwestern United States, higher establishment of juniper occurs in open environments due to more favorable precipitation, and competition may be more important than facilitation in determining establishment. Because ecotones form the interface between the woodlands and adjacent communities, they can provide valuable information on both the seed dispersal and seedling establishment processes responsible for tree expansion. Before Anglo-American settlement, fires occurred as frequently as every 50-100 years throughout much of the woodlands. During this century, fire frequencies have been reduced due to the indirect effects of livestock grazing and the direct effects of removing Native Americans from the ecosystem and implementing active fire-prevention programs. The result has been an increase in tree-dominated successional stages at the expense of grass-dominated stages.

Pinon, juniper, pygmy woodlands, southwestern United States, seed dispersal, fire, birds, rodents

25. Cheplick, G. P. and J. A. Quinn 1988. Subterranean seed production and population responses to fire in *Amphicarpum purshii* (Gramineae). *Journal of Ecology* **76**:263-273.

Early in the summer growing season, annual peanutgrass (*Amphicarpum purshii*) rapidly forms a seed bank by producing large, subterranean seeds. This study tests the hypothesis that since this species grows mostly in the fire-prone Pine Barrens of New Jersey, this adaptive trait might enhance population survival after a fire. At two sites in southern New Jersey plots containing either *Andropogon* litter (site A) or perennial herbs (site B) were burned on 28 October 1983, and subsequent performance of *Amphicarpum* plants monitored during the 1984 growing season. At both sites, only seedlings from the subterranean seeds were found. At site B where the burn removed perennial herbs, plants had significantly greater biomass and reproductive output than those in paired unburned plots. In an *Amphicarpum* population at Atsion, New Jersey, where a pitch pine forest had burned in the previous season, plants in the burned area were over 1 m tall and produced 50 times as many aerial spikelets as those in an adjacent unburned forest. Dry heat treatments of subterranean seeds significantly reduced germinability at temperatures as low as 60°C. The temperature in experimental burns was 85°C at the soil surface, but

high temperatures did not penetrate deeper than the top 1 cm of the soil. The subterranean seed placement of *Amphicarpum* occurs at an average depth of 3.5 cm, protected from the potentially detrimental effects of high temperature at and above the soil surface.

New Jersey, pine barrens, fire, pitch pine, grasses, germination, heat, soil temperatures

26. Clark, D. L., and M. V. Wilson. 1994. Heat-treatment effects on seed bank species of an old-growth Douglas-fir forest. *Northwest Science* **68**:1-5.

Although many studies have investigated the density and species composition of soil seed banks, few studies have investigated the effect of disturbance on seed banks. An earlier field study (Clark 1991) showed that the density of buried seeds of an old-growth Douglas-fir forest after logging and slash-burning was significantly less than the seed bank density of an adjacent, undisturbed old-growth Douglas-fir forest. The purpose of the present study was to investigate the mechanisms for this seed bank reduction. Six species found in the old-growth seed bank received experimental heat treatments that included six combinations of temperature, duration and soil moisture. Generally, germination percentages were not significantly affected when seeds were heated at 50C for one hour in either the wet or dry soil, but were significantly reduced at 100C for 15 min in both the wet and dry soils. When the seeds were heated at 75C for 15 min, germination was significantly reduced in the wet soil only. Because of the seeds' sensitivity to heat, few of these seed bank species are likely to be available for establishment after fire, even one of low intensity. This experimental study supports the hypothesis that seed mortality from elevated temperature during fire reduced seed bank densities of the old-growth forest and does not support the hypothesis that the reduction was due to stimulation of germination by heat. Although this study tested species with different growth forms and longevities, germination responses were generally the same for all species.

Douglas-fir, Pacific Northwest, heat, fire, old-growth forest, germination

27. Cushwa, C., R. E. Martin, and R. L. Miller. 1968. The effects of fire on seed germination. *Journal of Range Management* **21**:250-254.

Fire is characteristically used in the pineywoods of the Southeast to produce repetitive abundant stands of native legumes. However, results are frequently erratic and unpredictable. Seed germination results following simulated fire conditions are presented. Results show dry heat ineffective in increasing germination, whereas moist heat greatly increased both germination rate and total germination of some species of seed.

Pine, heat, germination, soil moisture, southeastern United States, legumes, fire

28. Dwyer, D. D., and E. V. Aquirre. 1978. Plants emerging from soils under three range condition classes of desert grassland. *Journal of Range Management* **31**:209-212.

This research was conducted to determine emergence of seedlings from surface soil collected on black grama (*Bouteloua eriopoda*) grassland sites in good, fair, and poor condition classes. The species that emerged and their numbers were compared to the species actually found on the field locations. The following conclusions were drawn: (1) The fair condition site had more seedlings emerge than the other two and of these seedlings by far the most were grasses; (2) Mesa dropseed (*Sporobolus flexuosus*) was

the most abundant grass species emerging from collected soil for all three condition classes, but it was much more abundant from fair condition soil; (3) Though black grama dominated the good condition range, emergence of black grama seedlings in the greenhouse from collected soil was much below expectations; (4) More plant species occurred in the field than emerged from collected soils; (5) Secondary successional patterns cannot be predicted accurately from techniques used in this study; (6) Mesa dropseed appears to be a key mid-successional species, filling a broad niche from low good to low fair range condition.

Grasslands, black grama, Bouteloua eriopoda, succession

29. Dyer, A. R. 2002. Burning and grazing management in a California grassland: seed longevity and maternal effects. *Restoration Ecology* **10**:107-111.

Prescribed fire is an important management tool for reducing the dominance of non-native species in annual grasslands; both annual and perennial native species show strong vegetative responses in the subsequent growing season. However, although the post-fire contribution of native species to the seed bank is assumed to be larger than in pretreatment years, the effects on seed quality, particularly viability and longevity, are not well understood. In this study, the author germinated *Nassella pulchra* (purple needlegrass) seed that had been stored for 10 years after collection from target plants receiving treatment combinations of summer burning and grazing by sheep. Seeds from burned plants were larger and had higher germinability than seed from unburned plants. Seeds from plants that were both burned and grazed had the highest germination. The strong relationship between long-term viability and seed size suggests greater maternal provisioning and increased seed quality subsequent to burning and grazing. The author concludes that managing for seed quality may be a useful approach for conservation of native species in California's critically endangered grassland habitats.

Annual grassland, prescribed fire, germination, grazing, maternal effects, Nassella pulchra, purple needlegrass, soil seed bank, seed viability, California

30. Ferrandis, P., J. M. Herranz and J.J. Martínez-Sánchez. 1996. The role of soil seed bank in the early stages of plant recovery after fire in a *Pinus pinaster* forest in SE Spain. *International Journal of Wildland Fire* **6**(1):31-35.

The implication of the viable soil seed bank in the early stages of the plant recovery after fire was studied in a recently burnt Mediterranean pine forest of *Pinus pinaster*. Seed number contained in soil samples taken immediately after fire and emergent seedling number recorded in the field during the subsequent year were compared. Although the fire effect was important, available seed density in the soil after fire was relatively high (around 2,200 seeds/m²). A small group of species containing the main shrub species in the unburnt community predominated both in the viable seed bank and field germination after fire. However, these species showed low germination rates in the field, as opposed to species with the lowest presence in the seed bank. The predominance of woody obligate seeders in the seed bank after fires and the high specific correspondence between seed bank and germination in the field, emphasize the important role of the seed bank contained in the soil before fire in the postfire species establishment.

Pinus pinaster, Spain, fire, germination,

31. Ferrandis, P., J.M. Herranz and J.J. Martínez-Sánchez. 1999. Effect of fire on hard-coated Cistaceae seed banks & its influence on techniques for quantifying seed banks. *Plant Ecology* **144**(1):103-114.

The impact of fire on hard-coated Cistaceae (*Halimium ocymoides*, *Cistus ladanifer* and *C. salvifolius*) soil seed banks in a Mediterranean 'maquis' shrubland, and its effect on seed germinability were studied. The study also contrasts the effectiveness of two widely used techniques for quantifying seed banks, the seedling emergence and the physical separation methods, in relation to fire. The null hypothesis that a massive enhancement of physically-dormant Cistaceae seed germination by fire would make use of the time-consuming physical separation technique unnecessary was tested. Fire reduced Cistaceae seed banks in the 0–2 cm deep soil layer by both fire-consumption and lethal temperatures, revealed by the significant decreasing of the seed bank density and by the increase of apparently-intact but soft-unviable seeds, respectively. In contrast, no damage was recorded in the 2–5 cm soil layer. A dramatic seed bank depletion (> 90%) in both soil layers was recorded one year after fire in the burnt area, coinciding with a significant increase of seedling density confined to the first post-fire year. The ecological consequences of this massive post-fire seed bank input are discussed. A germinability test revealed that germination of surviving Cistaceae seeds was significantly enhanced in all cases except for the *C. salvifolius* seed bank in the deeper soil layer. However, final germination levels (60–75%) did not correspond to the magnitude of seed bank depletion, especially for *C. salvifolius*, which suggests that other environmental factors not exclusively associated with fire may also be important in softening Cistaceae seeds. Germination enhancement by fire soil-heating was not high enough to reject the physical separation technique, at least in the deeper soil layer. The simultaneous use of both seedling emergence and physical separation is recommended for reliable seed bank estimates when a physically-dormant hard-seeded component can be expected in the soil, as in many Mediterranean ecosystems, regardless of fire occurrence.

Cistus, *germinability*, *Halimium*, *physical dormancy*, *physical separation method*, *seedling emergence method*, *maquis shrubland*, *heat*, *soil temperature*, *germination*

32. Ferrandis, P., J.M.Herranz and J.J. Martínez-Sánchez. 1999. Fire impact on a maquis soil seed bank in Cabañeros National Park (Central Spain). *Israel Journal of Plant Sciences* **47**: 17-26.

The direct impact of fire on the soil seed bank and the changes observed one year later were studied by analysis of seed content in sample layers at depths of 0-2 cm and 2-5 cm. Fire had a severe but selective impact on the soil seed bank: species with transient seed reserves accumulating on the soil surface were eliminated, whereas species with persistent buried seed reserves tended to remain in the soil after the passage of fire. Thick seed coats were shown to be an efficient mechanical protection barrier to fire. One year after fire, trade-off between input and output into seed bank produced a conspicuous recovery of seed density and species richness on the soil surface, and a pronounced impoverishment in the 2-5-cm-depth soil layer. In general, seed banks of woody species were severely depleted due to the lack of replacement following fire, with the exception of *Erica*, which maintained a high seed bank density in the upper soil layer. The post-fire recovery of soil seed populations was mainly due to two clearly differentiated groups of

annuals. The first group was of species whose seeds survived fire, germinated, and completed their phenological cycle. They were mainly fire-ephemerals. The second group consisted of wind-dispersed species whose soil seed banks had suffered a very severe (even total) depletion by fire. They were mainly Gramineae and Compositae species which behaved as opportunistic fire-sensitive invaders.

Maquis shrubland, fire, seed dispersal, Erica, fire ephemerals

33. Flinn, M.A. and R.W. Wein. 1977. Depth of underground plant organs and theoretical survival during fire. *Canadian Journal of Botany* **55**:2550-2554.

For 21 study sites in the Acadia Forest Experiment Station, near Fredericton, New Brunswick, 34 commonly occurring understory species were studied to determine the depth of underground plant organs capable of growing shoots. Depth of these plant parts tended to be species specific. These depth data, together with a knowledge of the sprouting ability of the underground organs, were used to postulate which species would survive fires of varying intensities. Most species found in the litter layer or in the F and H layer of the forested study sites would be susceptible to fires of low intensity. *Rubus canadensis*, *Kalmia angustifolia*, *Vaccinium myrtilloides*, *Pteridium aquilinum*, and *Viburnum cassinoides* would probably survive severe fires because the subterranean plant organs capable of reproduction were found in the mineral soil. In the bog study sites, *Vaccinium oxycoccos*, *Andromeda glaucophylla*, *Kalmia angustifolia*, *Chamaedaphne calyculata*, *Ledum groenlandicum*, and *Rhododendron canadense* would likely survive severe fires because the plant organs capable of vegetative reproduction were found 25 cm below the surface of the bog.

New Brunswick, Canada, bog, underground organs, rhizomes, sprouting, fire

34. Fyles, J. W. 1989. Seed bank populations in upland coniferous forests in central Alberta. *Canadian Journal of Botany* **67**:274-278.

The species composition and abundance of viable seed in organic forest floor and surface mineral soil from two high-latitude jack pine dominated and two white spruce dominated stands were determined by enumerating germinants from samples placed on moist peat-moss beds. Estimated seed density ranged from 500 to 2600 seeds/m², representing 13 species of trees, shrubs, and forbs. About half of the species in the seed bank were present as mature plants in each stand. The high seed densities recorded are inconsistent with the previously proposed poleward decline in the abundance of buried seed. The role of buried viable seed differed among species in relation to inherent seed dispersal capabilities and seed longevity. Several species were recorded that are considered to have a very short period of viability in the soil. It is suggested that even a short residence in the seed bank may be adaptive in areas where spring burning accounts for a large proportion of the total area burned annually.

Alberta, Canada, jack pine, white spruce, seed dispersal, longevity, seasonal burning

35. Granström, A. 1982. Seed banks in five boreal forests stands originating between 1810 and 1963. *Canadian Journal of Botany* **60**:1815-1821.

The viable seed content of soil samples from five coniferous forest stands in northern Sweden, aged 16-169 years, was determined by means of germination trials. The

soil samples were separated into five fractions: three organic horizons and two mineral soil horizons. Seedlings of 15 phanerogam species emerged, representing densities of 239-763 seeds/m² in the soils from the different stands. The depth distributions of the seeds varied with both plant species and forest stand. Most seeds were found at various depths in the humus layer, but in one stand an appreciable seed density of *Luzula pilosa* was present in the mineral soil. Most of the seedlings belonged to plant species present in the vegetation or with good means of dispersal. The depth distribution data, however, suggest that *Luzula pilosa* in particular may have a persistent seed bank. The role of persistent seeds in the vegetational composition of the boreal forest is discussed.

Coniferous forests, boreal forests, Sweden, seed persistence

36. Greenberg, C. H., D. G. Neary, L. D. Harris, and S. P. Linda. 1995. Vegetation recovery following high-intensity wildfire and silvicultural treatments in sand pine scrub. *American Midland Naturalist* **133**:149-163.

The authors hypothesized that clear-cutting mimics natural high-intensity disturbance by wildfire followed by salvage logging in sand pine scrub, and tested whether vegetation adapted to recovery from fire would respond similarly to another type of biomass removal. They measured plant community composition and structural characteristics in three replicated disturbance treatments and in mature sand pine forest (MF). Treatments were: (1) high-intensity burn, salvage logged and naturally regenerated (HIBS); (2) clear-cut, roller-chopped, and broadcast-seeded (RC); and (3) clear-cut and bracke-seeded (BK). All treatments were sampled 5-7 yr postdisturbance. Nonwoody plant species richness and diversity were significantly lower in MF than in disturbance treatments. Ruderal species were more abundant in HIBS and RC, but not to the exclusion of the characteristic suite of native scrub species. Shrub richness and diversity did not differ, but some species responded differently among treatments. Differences may be due to season of disturbance or rhizome depth [e.g., *Serenoa repens* (Bartr.) Small vs. *Sabal etonia* Swingle ex Nash.]. Oak stem density was significantly lower in HIBS and RC. Most structural characteristics were similar in HIBS, RC and BK but differed from ME. Results suggest that many scrub species responded similarly to aboveground biomass removal and the consequent structural and microclimatic conditions across these disturbance types. The authors suggest that plant resiliency traits, which evolved in response to the selective pressures of high-intensity disturbance and harsh environmental conditions, confer resiliency to human-caused disturbance as well. Mechanical biomass removal may be a suitable ecosystem management practice where burning is impractical. Due to the absence of a "virgin" (unsalvaged) burn treatment or pretreatment data and the short-term scope of this study, interpretation of results should be made with caution.

Sand pine scrub, Florida, ruderal species, oak, mechanical treatments, fire, salvage logging

37. Guo, Q. F., P. W. Rundel, and D. W. Goodall. 1998. Horizontal and vertical distribution of desert seed banks: patterns, causes, and implications. *Journal of Arid Environments* **38**:465-478.

This study examined small-scale seed distribution using published data collected using the same techniques and the same group of observers in four locations in North American deserts (Curlew Valley, Utah in the Great Basin Desert; Rock Valley, Nevada

in the Mojave Desert; Silverbell, Arizona in the Sonoran Desert; and Jornada, New Mexico in the Chihuahuan Desert). The distribution patterns were examined horizontally (under shrub canopy to open areas) and vertically (measured at the soil surface and at four depth intervals) in relation to seed morphology. At all four sites, seed distribution of individual species was positively related to seed abundance. Horizontally, total number of seeds per unit area decreased from under the shrub canopy to intershrub areas. Vertically, total number of seeds declined as soil depth increased. Most species were only present in a small proportion of samples. Small seeds were either abundant and broadly distributed or rare and found in a few samples, but larger seeds were always low in abundance and restricted to a small proportion of samples. For annual species, significantly higher proportions of larger seeds than smaller seeds were found deeper in the soil. However, when much larger-seeded species, i.e. herbaceous perennials and shrubs, were included in the analyses, most very small or very large seeds were found in the upper-most layers of soils and intermediate to large-sized seeds deeper in the soils. Such seed distribution related to seed morphology and soil factors may have significant ecological implications in plant population dynamics and community structure in desert ecosystems.

North American deserts, seed horizontal distribution, seed morphology, seed vertical distribution, shrub canopy

38. Guo, Q. F., P. W. Rundel, and D.W. Goodall. 1999. Structure of desert seed banks: comparisons across four North American desert sites. *Journal of Arid Environments* **42**:1-14.

The similarities and differences in seed bank structure across four locations in the North American deserts (Curlew Valley, Utah in the Great Basin; Rock Valley, Nevada in the Mojave Desert; Silverbell, Arizona in the Sonoran Desert; and Jornada, New Mexico in the Chihuahuan Desert) were compared using published data. Species composition at Curlew Valley was most distinctive among the four study sites. In all four sites, average seed size decreased in this order: shrub, herbaceous perennial, and annual species. Mean seed sizes were similar across the Curlew Valley, Rock Valley and Silverbell sites but much smaller at the Jornada site. Most species have small seeds, but the number of seeds varied greatly among these small-seeded species; i.e. seeds of these species could be highly abundant or very rare in the seed banks. In contrast, very few species have large seeds and the seeds of these species were always rare. The possible roles of underlying soil and climatic factors in structuring desert seed bank structure are discussed.

Comparison, growth forms, North American deserts, seed size

39. Halpern, C. B., S. A. Evans, and S. Nielson. 1999. Soil seed banks in young, closed-canopy forests of the Olympic Peninsula, Washington: potential contributions to understory reinitiation. *Canadian Journal of Botany* **77**:922-935.

During early stand development, coniferous forests of the coastal Pacific Northwest commonly pass through a period of dense shade and intense competition during which the abundance and diversity of understory plants decline dramatically. In young, managed forests, silvicultural thinning has been proposed to enhance the structural and floristic diversity of the understory. Although germination of buried seeds is likely to be stimulated by thinning, little is known about the composition of the soil

seed bank in these forests. The authors used the greenhouse emergence method to assess the potential contribution of the seed bank to understory reinitiation in 40- to 60-year-old, closed-canopy forests on the Olympic Peninsula, Washington. Seed banks were well developed (610-7009 germinants/m²), containing 46 native and exotic species representing a diversity of life forms. However, many common forest understory species were absent; only 11 species were typical understory plants and these comprised <10% of all germinants. In contrast, 30% of all species and 50% of all germinants were exotic, ruderal forbs. Wind-dispersed annuals and perennials dominated litter samples, whereas ruderal forbs and graminoids with limited dispersal dominated soil samples. Their results suggest that silvicultural thinning will enhance the establishment of ruderal, exotic species but will contribute little to the regeneration from buried seed of the vast majority of forest understory plants.

Pacific Northwest, tree thinning, shade tolerance, ruderal species, graminoids, seed dispersal, seed emergence method, succession, exotic species

40. Hardegree, S. P., and W. E. Emmerich. 1992. Seed germination response of four southwestern range grasses to equilibration at subgermination matric-potentials. *Agronomy Journal* **84**:994-998.

Seed priming at subgermination water potential has been shown to enhance the germination response of a wide number of plant species. Optimal priming conditions for germination enhancement are usually found to be at the least negative water potential that prevents radicle emergence. Equilibration of seeds at more negative water potentials may have detrimental effects on germination relative to control treatments. Seeds of *Bouteloua curtipendula* (Michx.) Torr., *Cenchrus ciliaris* L., *Eragrostis lehmanniana* Nees, and *Panicum coloratum* L. were equilibrated over the matric potential range of -1.6 to -17.5 MPa and germinated over the matric potential range of 0 to -1.6 MPa. Matric-priming at -1.6 MPa frequently increased germination percentage and rate at reduced water potential. Matric-priming at water potentials more negative than -1.6 MPa had a less positive and sometimes detrimental effect on germination relative to control treatments. Germination response of primed seeds showed a tendency toward, but not necessarily achievement of, control levels at the most negative priming-water potentials.

Matric priming, germination, southwestern United States, graminoids

41. Harrington, G. N. and M. A. Driver. 1995. The effect of fire and ants on the seed-bank of a shrub in a semi-arid grassland. *Australian Journal of Ecology* **20**:538-547.

Invasion of grasslands by woody plants following the introduction of domestic stock is a worldwide phenomenon. Burning is frequently recommended as a remedial measure but for a pastoral enterprise it is costly and the frequency of the fires required is of critical economic importance. The size and longevity of the soil seed-bank is an essential part of the response of shrub populations to prescribed fire regimes. In this study the seed-bank of the semi-arid zone shrub *Dodonaea attenuata* in *Eragrostis eriopoda* tussock grassland was examined in relation to harvesting by ants and the burning history of the sites. On unburnt sites, more than 3500 seeds per m² entered the seed-bank in the summer 1984-85 but sites burnt 5 years previously produced less than one-third of that number. Burnt shrubs did not flower for 5 years and no seeds survived in the soil through to 1985. Burning immediately prior to seed ripening destroyed the seed crop but burning

after seed-fall stimulated a greater germination in the following spring than on unburnt treatments. Ants rapidly harvested most of the seeds produced and after 20 months the combined effects of ant harvesting and germination had reduced the seed-bank at unburnt sites to 8-21 seeds per m² and at sites burnt 7 years previously to less than two seeds per m². Seeds were initially harvested in summer by *Pheidole* spp. of ants for their elaiosome and then discarded in middens outside the entrance to the ant nest. During the subsequent cool season the seeds were taken back into the nest and stored at depths ranging from 2 to 30 cm. It was concluded that ants provided short-range dispersal (<10m) and promoted the contagious distribution of *D. attenuata*, which is advantageous for a fire-susceptible, arid-zone shrub invading a grassland liable to be burnt: seedlings derived from seeds in ant storage chambers near the soil surface and in sparse grass situations caused by competition from shrubs may obtain some survival advantage. Prescribed fire has potential as a management tool for controlling population density of *D. attenuata* because, depending upon season and frequency, it reduces seed rain by killing shrubs, suppresses flowering activity and destroys seed crops on the plant. Under the influence of a regime of regular burning, such as prevailed prior to the European pastoral industry, the limited soil seed-bank would have been a major constraint on *D. attenuata* populations.

Grasslands, fire, ants, seed dispersal, grazing, Australia, Dodonaea attenuata, Eragrostis eriopoda

42. Hartnett, D.C. and D.R. Richardson. 1989. Population Biology of *Bonamia grandiflora* (Convolvulaceae): Effects of fire on plant and seed bank dynamics. *American Journal of Botany* **76**(3): 361-369.

The effects of disturbance on reproduction and plant and seed bank dynamics in the perennial herb *Bonamia grandiflora* were studied by comparing populations in recently burned, mechanically disturbed, and undisturbed habitats in central Florida over a 3-year period. Plant densities, seed production, and the occurrence of herbivory and predispersal seed predation varied considerably between sites and between years, with recently disturbed sites supporting the densest and most dynamic populations. Death of established plants was rare in all sites. In each site, the soil seed bank was several-fold larger than single season seed rains suggesting that *B. grandiflora* seeds are long-lived and accumulate in the soil. There was no evidence that postdispersal predation or pathogens have any significant influence on the seed bank dynamics. Fire resulted in large increases in stem densities due to both increased clonal stem production and new genet recruitment from seed. Burning also caused significant increases in the percentage of flowers producing seed and the numbers of capsules and seeds per plant. The seed rain was ten to thirty times greater in the burned site relative to adjacent unburned sites during the 3 years after burning. However, additions to the seed bank from the postfire seed rain were balanced by equivalent losses due primarily to seed mortality during fire, and to a much lesser extent due to germination and new genet establishment. As a result, the subsequent densities of seeds stored in the soil in these two sites are similar, indicating that fire results in a significant turnover in the seed bank population but no immediate change in its size. These effects on seed bank dynamics, in addition to new genet recruitment, suggest that periodic fires may play an important role in the maintenance of genetic variability as well as the size of these populations.

Florida, Bonamia grandiflora, disturbance, fire, genetic variability

43. Hassan, M. A., and N. E. West. 1986. Dynamics of soil seed pools in burned and unburned sagebrush semi-deserts. *Ecology* **67**:269-272.

Soil seed pools are rarely monitored in different seasons at the same site. This study site had a modicum of *Bromus tectorum* and much native perennial bunchgrass in the aboveground vegetation. The area had not been burned for at least 100 years prior to the study. Vegetation was sampled before and after a wildfire and soil seed bank samples were collected at 4 times over a year-long period. Viable seed pools were dominated by *Bromus tectorum*, even though it was not widely abundant in above ground vegetation, while bunchgrass and *Artemisia* seeds were few. The lowest numbers of viable seeds in the seed pool were observed in March and June in both burned and unburned plots; highest numbers were observed in fall-collected samples. The lack of seeds in the spring is presumably linked to a lack of seed rain and depletion of the seed bank due to germination, decomposition, and granivory during that part of the year. The authors also observed that the greatest concentration of viable seeds from major taxa were under shrub canopies rather than in the interspaces. Seed pools were well stocked with *B. tectorum* seeds, even on remnants of unburned, late seral vegetation. Although fire reduced it by half, the seed pool of *B. tectorum* increased within 1 yr to almost twice the level observed on unburned areas.

Bromus tectorum, *Artemisia*, fire, seasonality, sagebrush, shrub interspaces

44. Henderson, C. B., K.E. Petersen, and R. A. Redak. 1988. Spatial and temporal patterns in seed bank and vegetation of a desert grassland community. *Journal of Ecology* **76**:717-728.

Plant and seed temporal and spatial patterns and the correlation between vegetation and seed bank were examined from 150 samples collected from an 8-ha site in a desert grassland community in north-central New Mexico USA. Total plant cover increased through the growing season but relative cover of all species except three annuals remained constant. Spatial pattern of the vegetation was patchy, but species associations within the vegetation patches were weak. Species composition of the seed bank was similar to the vegetation (88.9% concordance) and like the vegetation, seeds were patchily distributed with little evidence of pattern at the species level. Relative seed densities varied little through the growing season and were positively correlated with cover for the same species. High correlation between the seed bank and vegetation are postulated to be a consequence of frequent and unpredictable disturbance but may further be promoted by the effects of seed predation on seed bank turnover rates.

Desert grassland, patchy distribution, temporal patterns, spatial patterns, disturbance, New Mexico

45. Honnay, O., B. Bossuyt, K. Verheyen, J. Butaye, H. Jacquemyn and M. Hermy. 2002. Ecological perspectives for the restoration of plant communities in European temperate forests. *Biodiversity and Conservation* **11**:213-242.

Simultaneously with increasing afforestation efforts in western Europe, among conservationists the consciousness is growing that protecting areas to conserve biodiversity will not be sufficient in the long term, and that also the ecological restoration of more or less severely altered areas will be necessary. The probability that recently

established forest stands develop towards their ecological reference (i.e. ancient forest) depends largely on the possibility of the target species to colonize them. The authors focused on the colonization ability of forest plant species and particularly on so-called ancient forest plant species. Major constraints for ecological forest restoration are the spatial characteristics of the target site (isolation, shape and area), imposing dispersal limitations, and in the duration and intensity of the historical land use, leading to changes in habitat characteristics influencing recruitment probability. They reviewed the ecological literature with respect to these constraints and conclude that it takes at least a century to restore the understorey layer of recent forests, even when the target stand is adjacent to a well-developed ancient forest. Both recruitment and dispersal limitation of the target species are responsible for this. Newly established forests should therefore be situated at a minimal distance of the ancient forest source. In other cases, forest plant species will not be able to colonize the newly established forest on a measurable time scale and artificial introduction of forest plant species can be taken into consideration. The negative effects of habitat characteristics, and mainly high soil nutrient values in the recent forest stand can be mitigated by soil nutrient lowering measures. Disturbances in the recent forest should be minimized to maintain a high canopy closure level, preventing light demanding, highly competitive species from establishing a stable population. An additional negative consequence of soil disturbances is that it stimulates germination of species from the soil seed bank, which is mainly composed of highly competitive or ruderal species.

Ancient forest species, dispersal limitation, ecological restoration, edge effects, recruitment limitation, reforestation, seed bank, SLOSS, soil chemistry, Europe

46. Ingersoll, C. A., and M. V. Wilson. 1990. Buried propagules in an old-growth forest and their response to experimental disturbances. *Canadian Journal of Botany* **68**:1156-1162.

Soil blocks collected from an old-growth *Pseudotsuga menziesii* forest were subjected to three types of disturbances (shade removal, surface burning, and soil churning) in a factorial experiment. Most emergents (88%) were vegetative sprouts. Total emergence and emergence of vegetative sprouts were significantly higher in the undisturbed (control) treatment than in any other treatment. As intensity of disturbance (measured by the number of disturbance factors applied) increased, the number of emergents declined. Exposure to sun caused a significant decline in emergence of each of the six most abundant species; the effects of burning and churning varied by species. Burning decreased the emergence of species with shallow regenerating structures. None of the experimental treatments significantly affected seedling emergence. Density of emergents (both seedlings and vegetative sprouts) was higher under greenhouse condition (411.7/m²) than in the experimental treatments (94.6/m²) indicating that greenhouse emergence is more suitable for quantifying the buried propagule bank.

Propagules, old-growth forest, disturbance, fire, Pseudotsuga menziesii

47. Ingersoll, C. A., and M. V. Wilson. 1993. Buried propagule bank of a high subalpine site: microsite variation and comparisons with aboveground vegetation. *Canadian Journal of Botany* **71**:712-717.

The authors assessed the composition and spatial pattern of the persistent buried propagule bank (seeds and vegetative structures) of a treeline site in the Oregon Cascade Mountains. They monitored emergence from soil cores removed from four microsite types and recorded vegetation cover and seedling abundance on the site. Over 3100 seedlings/m² emerged from the greenhouse soil cores; the seed bank was dominated by *Juncus* species. Few vegetative sprouts emerged. Vegetated microsites produced significantly more emergents than did bare soils, but even bare soils contained abundant seeds. Overall site cover was low and few seedlings occurred on the site. Discrepancies between aboveground and belowground abundance were common. *Phyllodoce empetriformis* and *Luetkea pectinata* were abundant in the vegetation and produced many seeds but were poorly represented in the seed bank and as seedlings on the site. Other species were abundant in the seed bank, but rare in the vegetation. The results indicate that despite the abundance of seeds in bare soil, colonization is likely to be extremely slow.

Subalpine, seedlings, microsite, spatial pattern, Oregon, Juncus

48. Inouye, R. S. 1980. Density-dependent germination response by seeds of desert annuals. *Oecologia* **46**:235-238.

Field observations and experiments indicate that the presence of seedlings at high densities inhibits subsequent germination of desert annuals. Since plants growing at high densities face severe competition for limited resources, this response by seeds is interpreted as an adaptation to avoid an unfavorable competitive climate where growth and survivorship are likely to be low.

Desert, annuals, germination, seedling density

49. Izhaki, I., N. Henig-Sever, N. and G. Ne'eman, G. 2000. Soil seed banks in Mediterranean Aleppo pine forests: the effect of heat, cover & ash on seedling emergence. *Journal of Ecology* **88**(4): 667-675.

East Mediterranean Aleppo pine (*Pinus halepensis*) forests are subjected to periodic stand-replacing fires. The authors simulated two of the effects of fire on the germinable soil seed bank in four pine stands on Mt. Carmel, Israel, that differed in their post-fire ages. Soil samples were heated to 100 °C, or covered by pine ash. Vermiculite was used to simulate litter cover. Heat exposure increased overall seedling density, richness and taxon diversity in all stands, but density of annual taxa (e.g. grasses and legumes) were not clearly affected. Ash cover dramatically decreased germination of all taxa and highest germination was achieved with heating and no cover. Vermiculite cover resulted in intermediate germination levels. The combined effect of heat exposure and ash cover, simulating a post-fire situation under a canopy of pine, reduced the germination level of all taxa in the soil seed bank. However, it also creates conditions that facilitate the establishment of pine seedlings from the canopy stored seed bank.

Ash cover, Cistus, fire, heat exposure, Pinus halepensis, seed bank, Aleppo pine forests

50. Johnson, T. K., and C. D. Jorgensen. 1981. Ability of desert rodents to find buried seeds. *Journal of Range Management* **34**:312-314.

There were significant variations in how many caches of buried Indian rice grass (*Oryzopsis hymenoides*) seeds were found by *Dipodomys microps*, *Dipodomys ordii*, *Microdipodops megacephalus*, *Perognathus formosus*, *Perognathus longimembris*, *Perognathus parvus*, *Peromyscus maniculatus*, and *Reithrodonotomys megalotis*. Success ranged from that of *P. maniculatus* and *R. megalotis*, that failed to find any buried seeds in dry sand, to *P. formosus*, that found 57.5% of the seeds buried at 0.6 cm, to *M. megacephalus* that found 50% buried 1.3 cm deep. *Peromyscus maniculatus* and *P. parvus* found more buried seeds as the soil moisture was increased.

Rodents, deserts, Oryzopsis hymenoides, soil moisture

51. Keeley, J. E. 1987. Role of fire in seed germination of woody taxa in California chaparral. *Ecology* **68**:434-443.

Germination behavior of 45 tree, shrub, subshrub, and liana taxa from fire-prone coastal sage scrub and chaparral was investigated. Seeds were sown on filter paper or potting soil, in the light or dark, with or without powdered charred wood (charate), and after heating treatments of 1 h at 70°, 5 min at 100°, 5 min at 120°C, or no heat. Germination medium had a significant effect on >70% of the species, although the pattern of response to other treatments remained the same on both media. Germination of over half of the species was inhibited in the dark, but two species were light inhibited. Charate significantly enhanced the germination of approximately one quarter of the species. A similar proportion of species exhibited heat-stimulated germination. In only a few species did both heat and charate play a role in stimulating germination. Nearly a third of the species had seeds that germinated readily upon wetting, and germination was not further stimulated by any fire-related cue. These different germination syndromes are correlated with different life history syndromes. Most coastal sage subshrubs germinate readily in the absence of fire-related stimuli and thus are capable of colonizing other forms of disturbance. For many of these species, germination was inhibited in the dark. This may result in a portion of the seed pool remaining dormant until fire since, in the case of several species, dark inhibition is overcome by charate. Chaparral shrubs and trees that germinate readily upon wetting seldom establish seedlings after fire. Their persistence in these fire-prone environments is due to resprouting after fire. Seedling establishment and population expansion for such species is dependent upon extended fire-free periods. In contrast, woody species that fail to germinate without some fire-related cue have seedling establishment and potential population expansion that are restricted to postfire conditions. The present mixture in species composition may be maintained by variable burning regimes.

Chaparral, charred wood, coastal sage, germination, heat, life history, light

52. Keeley, J. E. 1991. Seed germination and life history syndromes in the California Chaparral. *Botanical Review* **57**:81-116.

Syndromes are life history responses that are correlated to environmental regimes and are shared by a group of species. In the California chaparral there are two syndromes contrasted by the timing of seedling recruitment relative to wildfires. One syndrome, here called the fire-recruiter or refractory seed syndrome, includes species (both resprouting and non-resprouting) which share the feature that the timing of seedling establishment is specialized to the first rainy season after fire. These species are linked by the

characteristic that their seeds have a dormancy which is readily broken by environmental stimuli such as intense heat shock or chemicals leached from charred wood. Seeds of some may require cold stratification and/or light in addition to fire related stimuli. In the absence of fire related cues, a portion or all of a species' seed pool remains dormant. Most have locally dispersed seeds that persist in the soil seed bank until the site burns. In the absence of fire, or other disturbance, opportunities for population expansion are largely lacking for species with this syndrome. The other syndrome, here called the fire-resister or non-refractory seed syndrome, includes species that are resilient to frequent fires (mostly by vegetative resprouting), but require fire-free periods for recruiting new seedlings. All are linked by the characteristic that their seeds germinate in the absence of cues related to wildfires. In many cases no form of seed dormancy is present and the seeds germinate soon after dispersal; consequently these species do not accumulate a persistent seed bank. Germination and seedling establishment is independent of fire and thus opportunities for population expansion are also independent of fire. Recruitment appears to require relatively mesic conditions and this may account for the patchy distribution of these species within the matrix of relatively arid sites. Finding such sites has selected for propagules specialized for wind or animal dispersal; the majority are bird dispersed.

California, chaparral, seed dispersal, fire, germination, heat, germination cues

53. Keeley, J. E. 1977. Seed production, seed populations in soil and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparral shrubs. *Ecology* **58**:820-829.

A study of seed production, seed storage in the soil, and seedling production after fire was undertaken for a sprouting and a nonsprouting congeneric pair of species of *Ceanothus* and *Arctostaphylos*. All species exhibited large fluctuations in annual seed production. There was a significant correlation between fruit production and precipitation in the previous year. It is hypothesized that high carbon gain in years of high precipitation results in high numbers of floral primordia which, in these species, remain dormant until the following year. It was also noted that high fruit production was not dependent upon high precipitation the same year; suggesting that the fruits were utilizing carbon stored from the previous year. All 4 species were capable of producing more seeds in a single season than were stored in the soil. Apparently the soil seed pools do not represent a steady accumulation of seeds in the soil but rather are the result of dynamic fluctuations in seed inputs and outputs. Each species also had more seeds in the soil, by several orders of magnitude, than seedlings after fire in an adjacent burned stand. The sprouting and seedling reproductive strategies are quite different in the two genera. The information from this study coupled with that from other studies indicate 4 reproductive modes: sprouting and seedling production (*C. leucodermis*), abundant seedling production (*C. greggii*), low seedling production but better "equipped" seedlings (*A. glauca*), and predominantly sprouting (*A. glandulosa*).

Arctostaphylos, California, Ceanothus, chaparral, reproductive strategies, seed production, soil-seed pools

54. Keeley, J. E. 1987. Ten years of change in seed banks of the chaparral shrubs, *Arctostaphylos glauca* and *A. glandulosa*. *The American Midland Naturalist* **117**:446-448.

In 1 decade, more than 107 seeds/ha were dispersed by two species of *Arctostaphylos* in a stand of chaparral. At the end of this decade no significant change in the size of the soil seed bank was detected for either species. Previous studies suggest that predation by ground-dwelling rodents limits the accumulation of seeds in the soil.

Rodents, chaparral, predation, Arctostaphylos

55. Keeley, J. E., and C. J. Fotheringham. 1997. Trace gas emissions and smoke-induced seed germination. *Science* **276**:1248-1251.

Dormant seeds of a California chaparral annual were induced to germinate by smoke or vapors emitted from smoke-treated sand or paper. Nitrogen oxides induced 100 percent germination in a manner similar to smoke. Smoke-treated water samples inducing germination were comparable in acidity and concentration of nitrate and nitrite to nitrogen dioxide (NO₂)-treated samples. Vapors from smoke-treated and NO₂-treated filter paper had comparable NO₂ flux rates. Chaparral wildfires generate sufficient nitrogen oxides from combustion of organic matter or from postfire biogenic nitrification to trigger germination of *Emmenanthe penduliflora*. Nitrogen oxide-triggered germination is not the result of changes in imbibition, as is the case with heat-stimulated seeds. Fire-prone mediterranean-climate regions are noted for their abundance of plant species whose germination and recruitment are restricted to postfire environments. For seeds of many species (such as Fabaceae, Convolvulaceae, and Rhamnaceae), heat shock during fire weakens the cuticle and loosens cells in localized regions, such as the hilum or strophiole, allowing imbibition and germination. However, many species that restrict germination to postfire environments lack an impervious external cuticle and are not heat stimulated; instead, germination can be induced by chemicals released from the combustion of natural fuels. Incubation in the presence of charred wood has been shown to induce the germination of the Californian chaparral annual *Emmenanthe penduliflora*, as well as that of other species. Smoke triggers the germination of South African fynbos and savanna, western Australian heath, and Great Basin (Utah) scrub. Although 71 compounds have been identified from active fractions of smoke, none of these compounds were highly stimulatory in pure form, and other studies have also failed to identify the active components of smoke. Here the authors show that certain trace gases from smoke are sufficient to trigger germination and discuss mechanisms of how these gases may induce germination.

California, chaparral, germination cues, smoke, nitrate, nitrite, fire, *Emmenanthe penduliflora*

56. Keeley, J. E., C. J. Fotheringham, and M. Fenner. 2000. Role of fire in regeneration from seed. Pages 311-330 in M. Fenner, editor. *Seeds: the ecology of regeneration in plant communities*. CABI Publishing, Wallingford, UK.

57. Keeley, J. E. 1986. Seed germination patterns of *Salvia mellifera* in fire-prone environments. *Oecologia* **71**:1-5.

Salvia mellifera seeds from coastal sage, chaparral and desert scrub in southern California failed to germinate in the dark unless exposed to powdered charred wood. This

pattern was observed for seeds given a one month stratification at 5 C and for ones not stratified and also for seeds incubated under continuous 23 C or a diurnal alternation of 13 C/23 C. Dark inhibition of germination was also overcome, but only in seeds from chaparral populations, if seeds were incubated on commercial potting soil under alternating 13 C/23 C. Seeds in the light germinated readily in all but one population from desert scrub vegetation. Germination of seeds from this population was markedly stimulated by dry heating of the seeds at either 70 C for 5 h or 115 C for 5 min. For all populations there were numerous significant interactions between incubation temperature, pre-chilling stratification, light, and heating/charred wood treatments. Timing of germination was remarkably consistent between populations; the vast majority of seeds germinated within the first week at 23 C (or 13 C/23 C) regardless of whether or not they had received a pre-chilling treatment.

Chaparral, ecotypes, fire, germination, Salvia mellifera, heat, charred wood, germination cues

58. Kellman, M. C. 1970. The viable seed content of some forest soil in coastal British Columbia. *Canadian Journal of Botany* **48**:1383-1385.

The upper 10 cm of surface soil and litter beneath a coniferous forest in coastal British Columbia was found to contain over 1000 viable seeds per square meter. *Alnus rubra* Bong. made up 68.9% of all viable seed, although 18 other species, mainly weedy and secondary types, were recorded.

Ruderals, British Columbia, Alnus rubra, coniferous forest

59. Kellman, M. C. 1974. Preliminary seed budgets for two plant communities in coastal British Columbia. *Journal of Biogeography* **1**:123-133.

Production, movement and storage of seed in an old growth coniferous forest and adjacent secondary community in British Columbia, Canada, were monitored for 3 years. The old growth forest possessed a small seed budget that included some seed of secondary species, characteristic of disturbed situations. The secondary community possessed a far larger seed budget, dominated by locally-growing secondary species. Small quantities of seed of secondary species were able to infiltrate appreciable distances into the old growth forest. However, the store of seed of these species within the forest was insufficient to account for the large populations that soon appear at logged sites, unless initial populations deriving from this source had undergone very rapid expansion thereafter. The development of rotational tree harvesting in the area is likely to promote an expanding seed budget for secondary species, and a diminishing one for the primary species, characteristic of old growth forests.

Old-growth coniferous forest, British Columbia, disturbance, ruderal species

60. Kelly, V. R., and T. V. Parker. 1990. Seed bank survival and dynamics in sprouting and nonsprouting *Arctostaphylos* species: seed bank dynamics. *American Midland Naturalist* **124**:114-123.

Members of the chaparral genus *Arctostaphylos* regenerate after fires either by obligate seeding or facultative sprouting. To test the hypothesis that sprouting species differ from nonsprouting species, the authors compared flower, fruit and seed production and changes in soil seed densities between sprouting (S) and nonsprouting (NS)

Arctostaphylos species during 18 months. They estimated postdispersal seed predation experimentally by comparing seed banks that excluded vertebrate predators with seed banks that excluded no predators. They also determined changes in unmanipulated, naturally occurring seed banks during the same time period. Production of inflorescences, infructescences and fruit did not differ significantly between *A. canescens* (NS) and *A. glandulosa* (S). Densities of whole and damaged seeds were consistently higher in seed banks of *A. glandulosa* than in *A. canescens* seed banks, but densities of viable seeds were lower in *A. glandulosa* seed banks. In two additional pairs of *Arctostaphylos* species examined, total and viable seed bank densities were higher for nonsprouting species than sprouting species. Densities of experimentally enclosed seed banks did not change during 18 mo, whereas unenclosed, experimental seed banks decreased by 60% (*A. canescens*) and 53% (*A. glandulosa*) in 5 mo. Similarly, densities of naturally occurring seed banks decreased by 29% (*A. canescens*) and 14% (*A. glandulosa*) in 11 mo. Postdispersal seed predation was important in reducing the survival of seeds in soil seed banks, whereas senescence and decay were not. However, there was no consistent relationship between sprouting and nonsprouting in these *Arctostaphylos* species.

Chaparral, fire, sprouting, Arctostaphylos, predation, germination, seed dispersal

61. Kemp, P. R. 1989. Seed banks and vegetation processes in deserts. Pages 257-282 in M. A. Leck, V. T. Parker, and R. L. Simpson, editors. Ecology of Soil Seed Banks. Academic Press, San Diego, California, USA.

Seeds are a crucial and integral part of desert ecosystems. For annual (ephemeral) species, which may constitute 40% or more of the desert flora, seeds can be the most prevalent form of the species, and, during long droughts, the only form for several years. Seeds of most desert plant species represent the only means of dispersal and access to new regions. They constitute an important available food resource for some animal species. Finally, seeds are the source of variation for genetic differentiation and evolution in some of North America's most recent, and perhaps rapidly changing, ecosystems. In view of the importance of seeds to the structure and function of desert plant communities, it is surprising that so little is known about desert seed banks and about their relationship to plant population dynamics. Our knowledge of desert vegetation is derived largely from studies of physiological and morphological adaptations of plants and studies of community structure and floristic composition. Much less is known about population dynamics and population processes, such as growth, recruitment, dispersal, and dormancy, that depend on the distribution and behavior of seeds. Knowledge of seed banks and their relationship to the desert vegetation is a fundamental part of understanding the processes by which desert plants have become adapted to their harsh and uncertain environment. This chapter discusses the size and variation of seed banks in desert soils and the importance of annual species and offers preliminary ideas about how seed banks are related to plant population dynamics and ultimately to community structure.

Deserts, seed dispersal, population dynamics, dormancy, annual species, community structure

62. Kinucan, R.J. and F.E. Smeins. 1992. Soil seed bank of a semiarid Texas grassland under three long-term (36-years) grazing regimes. *American Midland Naturalist* **128**:11-21.

Species composition and density of the readily germinable soil seed bank of three long-term (36-year) grazing treatments (heavy continuous, moderate deferred rotation and ungrazed enclosure) were determined for a summer and spring period for a semiarid grassland of the western Edwards Plateau, Texas. Total seed densities (2552 to 4409 seeds/m²) did not differ among grazing treatments, but did vary seasonally. Species composition varied among treatments. Heavy continuous grazing had a high proportion of early-seral, annual-dicot taxa. Seeds of late-successional midgrass species (e.g., *Bouteloua curtipendula*, *Eriochloa sericea*) were not stored in the soil of any treatment and appeared to be transient. Many other species appeared to maintain persistent seed banks, including seeds of the current mid-successional dominant shortgrass, *Hilaria belangeri*. Similarity of composition between germinable seeds in the soil and existing plant communities was low. Soil seed bank is a primary control of secondary succession in these grasslands, and absence of late-successional species in the seed bank impairs the rate of succession.

Texas, grazing, grasslands, species composition, succession, seed persistence

63. Komarova, T. A. 1985. Role of forest fires in germination of seeds dormant in the soil. *Soviet Journal of Ecology* **16**:311-315.

The authors investigated the reserve of viable seeds in the litter and upper layers of soil at four sites that experienced fires about 200, 70 and 9 years ago and a one-year-old burn, which successively characterize late, middle and early stages of the postfire succession of a broad-leaved Siberian stone pine forest. The species composition and abundance of sprouts were established on the fresh burn. Factors preventing and promoting seed germination are analyzed. Forest fires are examined as a peculiar signal for activation of seeds dormant in the soil.

Siberia, stone pine, sprouting, fire, succession, dormancy

64. Koniak, S., and E. L. Richard. 1982. Seed reserves in soil of successional stages of pinyon woodlands. *The American Midland Naturalist* **108**:295-303.

Seedlings emerging from soil, duff and litter samples from four microsites (duff, transition, interspace, shrub) and four successional stages (grass-forb, shrub-tree, tree-shrub, tree) were recorded for 6 weeks. Seed reserves in soils decreased in number and species diversity from early to late successional stages. Of seedlings emerging, 89% were annuals. The shrub microsite from the shrub-tree stage had the highest total and perennial seed reserves. As shrub cover decreased, the transition microsite between the duff and interspace became the most important source of total seed reserves, and the duff microsite became the most important source of perennial seed reserves.

Succession, species diversity, pinyon woodlands, duff, litter, interspaces

65. Korb, J. E., N. C. Johnson, and W. W. Covington. 2004. Slash pile burning significantly reduces arbuscular mycorrhizal propagule densities and the soil seed bank. *Restoration Ecology* **12**:52-62.

Ponderosa pine forest restoration consists of thinning trees and reintroducing prescribed fire to reduce unnaturally high tree densities and fuel loads to restore ecosystem structure and function. A current issue in ponderosa pine restoration is what to do with the large quantity of slash that is created from thinning dense forest stands. Slash pile burning is currently the preferred method of slash removal because it allows land managers to burn large quantities of slash in a more controlled environment in comparison with broadcast burning slash. However, burning slash piles is known to have adverse effects such as soil sterilization and exotic species establishment. This study investigated the effects of slash pile burning on soil biotic and chemical variables and early herbaceous succession on burned slash pile areas. Slash piles were created following tree thinning in two adjacent approximately 20-ha ponderosa pine (*Pinus ponderosa*) restoration treatments in the Coconino National Forest near Flagstaff, Arizona. The authors selected 30 burned slash pile areas and sampled across a gradient of the burned piles for arbuscular mycorrhizal (AM) propagule densities, the soil seed bank, and soil chemical properties. In addition, they established five 1-m² plots in each burned pile to quantify the effect of living soil (AM inoculum) and seeding amendments on early herbaceous succession in burned slash pile areas. The five treatments consisted of a control (no treatment), living soil (AM inoculum) amendment, sterilized soil (no AM inoculum) amendment, seed amendment, and a seed/soil (AM inoculum) amendment. Slash pile burning nearly eliminated populations of viable seeds and AM propagules and altered soil chemical properties. Amending scars with native seeds increased the cover of native forbs and grasses. Furthermore adding both seed and living soil more than doubled total native plant cover and decreased ruderal and exotic plant cover. These results indicate that seed/soil amendments that increase native forbs and grasses may enhance the rate of succession in burned slash pile areas by allowing these species to outcompete exotic and ruderal species also establishing at the site through natural regeneration.

Slash piles, burning, fire, mycorrhizae, ruderal species, ponderosa pine, restoration, Arizona, broadcast burning, soil amendments

66. Kramer, N. B., and F. D. Johnson. 1987. Mature forest seed banks of three habitat types in central Idaho. *Canadian Journal of Botany* **65**:1961-1966.

Soils were sampled in two 5-cm layers under mature forests in *Pseudotsuga menziesii*/*Physocarpus malvaceus*, *Abies grandis*/*Acer glabrum*, and *Abies grandis*/*Vaccinium globulare* habitat types in central Idaho. Seed content of sample soils was determined using a wet sieve seed extraction process followed by greenhouse germination tests. Viable seeds representing more than 80 different species were recorded, with viable seed densities averaging $1065 \pm 727/\text{m}^2$ and ranging as high as $4116/\text{m}^2$. Most viable seeds (67%) were found in the top 0- to 5-cm soil layer. *Ceanothus velutinus*, *Physocarpus malvaceus*, and *Carex* spp. accounted for nearly 50% of all viable seeds encountered. Buried seed constancies are presented to compare buried seed occurrence by habitat type.

Idaho, Pseudotsuga menziesii, Abies grandis, douglas-fir, grand fir, seed extraction method

67. Lamont, B. B.; E. T. Witkowski, and N. J. Enright. 1993. Post-fire litter microsites: safe for seeds, unsafe for seedlings. *Ecology* **74**(3):501-512.

The authors explore the effect of post—fire microsites on seed and seedling distribution and hence their potential role in community restoration. A summer wildfire and control burn in a sclerophyll shrubland in mediterranean Australia produced mosaics of physically and chemically contrasting microsites of litter and sand. Most seeds (>75%) of all species released from the burnt canopies fell, or were redispersed by wind, into the litter patches after both fires. Data on microsite characteristics and wind exposure (fire intensity), height of fruits, time of release, and seed properties were required to interpret relative distribution between the litter and sand patches. Seeds remained equally viable (up to 100%) over summer—autumn in the litter and sand and had equally high rates and levels (up to 100%) of subsequent winter germination. However, seedlings were 2—3 times less likely to survive in the litter and survivors were 35% smaller than those in the sand by the end of the first summer. *Banksia hookeriana* was particularly vulnerable to microsite properties, whereas the needle—leaved *Hakea polyathema* showed only minor responses. Pre—summer thinning of seedlings in the litter increased survival of the remainder by 2 times and size of the survivors by 31%. The fire—sensitive, small—seeded *B. hookeriana* had 17 times more seeds in the backburn litter than the resprouting, larger—seeded *B. attenuata*, which more than compensated for its 3 times greater seedling mortality levels over the dry summer. Recruitment of species prone to density—dependent mortality in the litter was enhanced by the retention of some seeds in the sand where competition for water was minimal, as indicated by the 2.2 times greater stomal conductance of their seedlings in early summer.

Litter, sand, fire, sclerophyll shrubland, Australia, seed dispersal, germination, sprouting, competition

68. Landis, T. D. 2000. Where there's smoke... there's germination. *Native Plants Journal* 1:25-29.

Seeds of many fire-adapted plants are very difficult to germinate, and some species have been impossible to propagate by seed. Recent research has shown that fumigating seeds with smoke or soaking them in smoke solutions improves germination of many species. The exact physiological mechanism for this response is unknown but using smoke as a pre-sowing seed treatment holds considerable promise for propagating plants for restoration of fire-adapted communities. In particular, smoke treatments can be used to germinate seeds of recalcitrant species. This paper reviews the current literature on smoke treatment of seeds with the purpose of encouraging those treatments on other species.

Seed treatment, native plants, nursery, seedlings, restoration, smoke, fire

69. Legg C.J., E. Maltby and M.C.F. Proctor. 1992. The ecology of severe moorland fire on the North York Moors: seed distribution and seedling establishment of *Calluna vulgaris*. *Journal of Ecology* 80: 737-752.

Regeneration of *Calluna vulgaris* following normal heath fires is from surviving stem bases or, where survival is poor, from a seed bank. Severe fires causing ignition of surface organic horizons kill stem bases and cause a serious depletion of the seed bank, most of which (up to 10^6 seeds m^{-2}) lies in the litter and upper 2-3cm of soil or organic material. Germinable seeds were detected in appreciable numbers down to 6cm beneath the boundary of the F/O soil horizons in soil cores from mature heath vegetation on a

blanket peat and peaty stagnopodzol. However, severe fires in which more than 10cm of peat is ignited will destroy all of the viable seed bank. At the site studied, the seed-rain density for *Calluna* was approximately inversely proportional to the dispersal distance: regression equations predicted an annual seed rain of only c. 25 seeds m⁻² at 10 m from source plants. Small numbers of wind-dispersed flowers retaining some seeds may be important in long-distance dispersal. The crustose lichens *Lecidea granulosa* and *L. uliginosa* and several species of algae form a near-ubiquitous film over the surface of exposed organic soil following severe moorland fires. This creates a crust overlying unconsolidated sub-surface peat. The lichen-alga film significantly reduced germination of *Calluna* seeds by about 40%. No evidence was found to link poor germination or growth to low pH, low nutrient levels or soil toxicity. Fertilizer experiments show that addition of potassium increases the root:shoot ratio of *Calluna* seedlings while nitrogen increases shoot growth at the expense of root development. It is suggested that the seedling root:shoot ratio may be important in establishment and in surviving the effects of needle ice formation, surface instability and desiccation. Transplant experiments and observations on naturally occurring seedlings show that summer desiccation of seedlings.

Germination, revegetation, seedlings, seed dispersal, heathlands, Calluna vulgaris, root:shoot ratio, fire, litter, algae, lichen, England

70. Major, J., and W. T. Pyott. 1966. Buried, viable seeds in two California bunchgrass sites and their bearing on the definition of a flora. *Vegetatio* **13**:253-282.

A complete description of a plant community must include the buried viable seeds in the soil. The plants occurring in this form are a part of the flora, which helps to determine the community, even though they are not readily evident. The importance of defining an ecosystem's flora is reviewed. When the soil's buried viable seed population is used to help determine the flora, various problems arise since perennial plants reproduce much less abundantly by seed than do annuals, laboratory germination conditions probably do not suit all species, and seeds are not distributed at random so sampling is made difficult. In an investigation of buried viable seeds in two grazed and ungrazed California bunchgrass sites poor correspondence between vegetation and soil seed populations was found. Numbers were 8000 to 12,000 seeds per m². Figures of this order of magnitude are general in the periodical literature which describes the buried viable seed populations and the factors which influence them qualitatively and quantitatively in various kinds of arable, mesic pastured or mown, steppe, and forest plant communities. Not only are the plants evident above ground in a stand of vegetation part of the ecosystem which includes that vegetation, so also are the plant disseminules in the soil. This paper records a determination of the kinds and numbers of viable seeds in two stands of *Stipa pulchra*, bunchgrass vegetation in the eastern foothills of the central Coast Ranges of California. Such vegetation is variable from year to year, over a climatic cycle of years, and successional (i.e., it is seral and therefore changes with time, other habitat factors being constant). By no means all the species which can occur in this vegetation over a period of several years are evident above ground at one time. The authors have attempted to use the soil content of buried, viable seeds in the two stands as a measure of this potential flora.

California bunchgrass, grazing, Stipa pulchra, species composition

71. Manders, P.T. 1990. Soil seed banks and post-fire seed deposition across a forest-fynbos ecotone in the Cape Province. *Journal of Vegetation Science* **1**(4): 491-498.

The relative sizes and composition of soil seed banks, the influence of fire and the post-fire deposition of seeds were investigated in a riparian forest and adjacent fynbos and transitional vegetation in Swartboskloof. Brief complementary studies of soil seed banks were conducted in poorly-developed forest and scree forest soils. Numbers of species in each vegetation type were very similar, but there were fewer seeds in riparian forest soil than in the transitional and fynbos zones. These patterns were not repeated in poorly-developed forest and scree forest. No effects of fire on soil seed banks were detected. Forest soil had relatively large numbers of seeds stored at 10 to 15 cm deep, with many zoochorous and few myrmecochorous seeds. Anemochorous and ornithochorous seeds of forest species formed a major component of seed deposition within the transitional and fynbos zones in the first year after fire. The numbers of anemochorous forest seeds in the fynbos declined with distance from the forest edge. The deposition of ornithochorous forest seeds was less closely related to distance from the source, and was not exclusively associated with the presence of tall or fruit-bearing shrubs. Regeneration after canopy-destroying disturbance in the forest is likely to emanate from the soil seed banks of pioneer species which now or previously occurred on forest margins. Seed availability does not appear to limit colonization of fynbos by forest species soon after fire.

Disturbance, forest regeneration, ornithochory, seed dispersal, succession, zoochory, ants, South Africa, fynbos, scree forest, fire

72. Marañón, T., and J. W. Bartolome. 1989. Seeds and seedling populations in two contrasted communities: open grassland and oak (*Quercus agrifolia*) understory in California. *Acta Oecologia/Oecologia Plantarum* **10**:147-158.

Seed production, soil seed reserve, and seedling establishment were studied in two annual communities: open grassland and oak woodland understory in California. The soil seed reserve in the open grassland (15,980 to 40,730 seeds per m²) was composed mostly of annual grasses, whereas the smaller reserve in the oak understory (5,760 to 6,850 seeds per m²) was dominated by *Stellaria media*. At bi-weekly censuses the authors recorded timing of emergence, seedling numbers, and survival during a drought period after germination. A variety of species response was found in both communities. The average species seed weight was higher in the shaded understory community (7.80 mg) than in the open grassland (5.01 mg). It is suggested that differences among species in seed size and seedling behaviour would promote coexistence in annual communities.

California, Mediterranean grassland, seed reserve, seed size, seed weight, seedling survival, oaks, annual species

73. Martin, J.L. 1955. Observations on the origin and early development of a plant community following a forest fire. *For. Chron.* **31**:154-161.

The origin of the species on a burned-over area in southwestern Nova Scotia was determined by means of covered plots, and the early stages of succession were followed closely for two years. All of the herbaceous and shrub species which appeared on the area during the first two years were survivors of the fire. Bracken fern showed unquestionable dominance the first year, but its position was severely contested by other herbaceous

species and the heath plants during the second year. Seedlings of grey birch and large-toothed aspen appeared the second year and were restricted to patches of bare mineral soil. Sucker growth of red oak, red maple and grey birch was rapid, but it was pruned heavily by deer feeding.

Fire, Nova Scotia, bracken fern, heath, browsing, deer

74. Martin, S. C. 1970. Longevity of velvet mesquite seed in the soil. *Journal of Range Management* **23**:69-70.

One velvet mesquite seed out of 450 that were buried in 1948 on the Santa Rita Experimental Range was sound and germinated after it was dug up 20 years later. The percentage of apparently sound seeds declined fairly rapidly as seeds germinated or decayed (only 10% were sound after 10 years), but viability of the apparently sound seed remained high to the end of the study. Thus, even if no new seed is produced or introduced, some mesquite seedlings may emerge 20 years or more after clearing.

Velvet mesquite, desert, Arizona, longevity

75. Matlack, G.R., D.J. Gibson and R.E. Good. 1993. Clonal propagation, local disturbance, and the structure of vegetation: ericaceous shrubs in the pine barrens of New Jersey. *Biological Conservation* **63**:1-8.

Ericaceous shrubs dominate the upland plant communities of the New Jersey coastal plain, both in terms of species diversity and abundance of individuals. Niches of these species are most clearly separated in the character and vigor of their responses to disturbance, particularly to fire and tree canopy gaps. *Gaylussacia baccata* resprouts quickly from buried rhizomes after mild ground fires, and is most flexible in taking advantage of canopy gaps. Its co-dominant, *Vaccinium vacillans*, shows superior survival after severe fires by virtue of a deeper rhizome system, and resprouts with greater vigor than *Gaylussacia* at very high fire frequencies. In the sympatric sub-shrub *Gaultheria procumbens* long, infrequently branching rhizomes distribute ramets over large areas, possibly colonizing small gaps in the shrub and herb canopies. Thus, shrub community structure in this high-disturbance ecosystem is maintained by subtle evolutionary variations on a common theme of clonal propagation.

New Jersey, pine barrens, clonal propagation, sprouting, disturbance, fire, rhizomes

76. McLean, A. 1969. Fire resistance of forest species as influenced by root systems. *Journal of Range Management* **22**(2):120-122.

There is a close relationship between root system characteristics and the relative fire resistance of douglas-fir forest zone species in southern interior British Columbia. Susceptible species are usually those that have fibrous root systems or produce stolons or rhizomes which grow above mineral soil. Moderately resistant species usually have fibrous roots with rhizomes which grow less than 5 cm below the mineral soil surface. Resistant species are those that have rhizomes which grow between 5 and 13 cm below the mineral soil surface and those species with taproots which are able to regenerate from below their crowns. Both timber milkvetch and lupine are undesirable range plants and yet both may increase after a fire.

Douglas-fir, roots, rhizomes, taproots, fire resistance, British Columbia, Canada, Pseudotsuga menziesii

77. McGee, A., and M. C. Feller. 1993. Seed banks of forested and disturbed soils in southwestern British Columbia. *Canadian Journal of Botany* **71**:1574-1583.

The species composition and density of seed banks in the forest floors and mineral soils of several undisturbed (immature, midseral forests) and disturbed (transmission line rights-of-way) ecosystems in southwestern British Columbia were estimated using the seedling-emergence method. The total soil surface area sampled was 9.4 m². Germination behaviour of seven dominant species in response to depth of burial and substrate was also studied in a greenhouse experiment. A total of 16,289 seedlings germinated, representing 62 native and naturalized vascular plant species and several unidentified grass species. Most seedlings emerged from the forest floor, and the number of germinants generally decreased with increasing sample depth. Drier ecosystems had the lowest number and density of germinants. Burial depth significantly affected germination of all species tested. Mineral soil was equal, or superior, to forest floor as a germination substrate for all species tested. Depth-substrate interactions for several species indicated that the pattern of influence of burial depth in relation to substrate varied with species. Caution is urged extrapolating greenhouse seed-bank studies to potential weed populations in the field. Establishment of species from the seed bank will be a function of the depth to which the soil is disturbed and the kind of disturbance (burning, scarification) imposed.

British Columbia, coastal western hemlock zone, seed germination, seed diversity, seed density, seed emergence method, litter

78. Meney, K.A., G. M. Nielsen and K.W. Dixon. 1994. Seed bank patterns in *Restionaceae* and *Epacridaceae* after wildfire in kwongan in southwestern Australia. *Journal of Vegetation Science* **5**:5-12.

Post-fire seed germination, seedling mortality and seed banks were investigated in scrub-heath (kwongan) in SW Australia. Study species included herbaceous and woody, obligate seeders and resprouters in two non-bradysporous but significant plant families (*Restionaceae* and *Epacridaceae*). In all species, seedlings were recruited only in the first autumn-spring after fire and occurred in similar densities as the estimated germinable annual seed input. Seedlings were absent from unburnt vegetation. Although most species retained some residual seeds after fire, tests (excised embryo culture) indicated that a negligible number of seeds were germinable. Regardless of fire response or species, there appeared to be a large loss of seeds each year and in most cases, only a small proportion of the annual seed production was used in post-fire recovery of plants. Based on seedling:parent ratios, all species had the capacity to reconstitute parent densities from germinants in the first year after fire, but high seedling mortality and no further recruitment resulted in less seedlings than replacements for four resprouter *Restionaceae* and three *Epacridaceae* (all obligate seeders) at the end of the third year after fire.

Fire, seed germinability, seed viability, seedling mortality, seedling recruitment, kwongan, obligate seeders, annual species

79. Menges, E.S. and N. Kohfeldt. 1995. Life history strategies of Florida scrub plants in relation to fire. *Bulletin of the Torrey Botanical Club* **122**:282-297.

Most species of scrubby flatwoods (59%) and rosemary scrub (53%) had no significant trend in post-fire abundance. About twice as many scrubby flatwoods species increased as decreased in frequency with time since fire; increasers included ground lichens and two of the three dominant oaks. Similar numbers of species increased and decreased in rosemary scrub. Most increasers were ground lichens and most decreasees were herbaceous perennials. In scrubby flatwoods, most plants with vegetative recovery modes tended to increase in frequency with time since fire, mixed recovery mode plants usually had no trend, and obligate seeders decreased. In rosemary scrub, mixed recovery modes were associated with decreasing post-fire trends, while seeders tended to increase in post-fire abundance. Infrequently-burned rosemary scrub provides opportunities for seedling recovery from fire, evident both in its dominant species and in the many endemic and open-space specialist herbs. In contrast, recovery from fire by resprouting and clonal growth is common in the more-frequently burned scrubby flatwoods, promoting rapid post-fire recovery and long-term competitive superiority in this more productive habitat. To promote life history and species diversity, fire management in Florida scrub should avoid overly regular fire regimes, fire suppression or too-frequent burning. Modal intervals will differ between scrubby flatwoods (5-20 years) and rosemary scrub (15-40 years). When to reburn rosemary scrub may depend on the specific responses of its many endemic plant species to fire.

Life history strategy, fire, Florida scrub, rosemary scrub, scrubby flatwoods, resprouter, seeder, post-fire abundance patterns, post-fire recovery guild, shrubs, shrublands, open space, sprouting, lichens, oak, interspaces

80. Miller, G.R. and R.P. Cummins. 2003. Soil seed banks of woodland, heathland, grassland, mire and montane communities, Cairngorm Mountains, Scotland. *Plant Ecology* **168**:255-266.

The size and species composition of soil seed banks were assessed at 111 altitudinally diverse sites in the Cairngorm Mountains. Mean densities of germinable seeds varied from 83 000 m⁻² in Scots pine (*Pinus sylvestris* L.) woodland at 230–490 m to 200 m⁻² in moss (*Racomitrium lanuginosum* (Hedw.) Brid.) heath at 1000–1120 m. Seed banks were dominated by *Calluna vulgaris* (L.) Hull, not only wherever it was prominent in the vegetation, but also at some sites with less than 5% cover of parent plants in the ground vegetation. Many species conspicuous in the vegetation were under-represented in or absent from the seed bank and surface vegetation generally was more species rich than was the underlying seed bank, especially in high montane communities. Multiple regression was used to examine the relationship between the density of buried *Calluna* seeds and the abundance of parent plants in the vegetation, site altitude and the organic matter content of the soil. The model fitted to woodland communities accounted for 95% of the variation in seed density. The heathland model was less predictive but still explained 52% of the variation in seed bank size. In mire communities there was no relationship, collective or individual, between buried seed density and the measured environmental variables, possibly due to variations in the duration and frequency of waterlogging at these sites. The potential role of seed banks for initiating the recolonisation of disturbed ground is discussed. Densities of buried seeds at most

Calluna-dominant sites were probably sufficient to generate successful recolonisation but the prospects for recovery were poor at other sites, particularly in graminaceous communities at 800 m or higher.

Altitude, Calluna vulgaris, recolonisation, soil organic matter, species richness, heathland, Scotland, Scots pine, Pinus sylvestris, Calluna

81. Mladenoff, D. J. 1990. The relationship of the soil seed bank and understory vegetation in old-growth northern hardwood-hemlock treefall gaps. *Canadian Journal of Botany* 68:2714-2721.

In mature northern hardwood forests, small treefall gaps constitute an important mode of compositional and structural change within the long return time of larger catastrophic disturbances. The soil seed bank and patterns in vegetation layers are described in this disturbance regime context. In these small treefall gaps, herbaceous and woody vegetation species present are similar to those of forest understory plots, differing primarily in abundance. Seed bank communities are compositionally more similar among gaps than forest understory plots, but vegetation similarity is equal among forest plots and among gaps. Seed bank-vegetation similarity is greater among forest plots than in gaps. Seed bank strategies differ among the plant species characteristic of the differing forest layers. Dominant canopy tree species (*Acer saccharum*, *Tsuga canadensis*, *Betula alleghaniensis*) are not an important component of the seed bank. Bird-dispersed shrub and herbaceous species and ant-dispersed herbs are important in the seed bank, especially in gaps. In particular, based on gap seed bank response, it appears that understory shrub abundance and pattern within the forest change with the time since large-scale disturbance, in accordance with species adaptations to the size and increase in number of small treefalls in the mature forest. These species patterns may relate to the patchy nature of resource availability that develops, especially that of nitrogen, which is controlled by the canopy species-gap mosaic.

Treefall gaps, soil seed bank, disturbance, northern hardwoods, old growth, succession, shrubs, patchiness, seed dispersal, ants, birds, hemlock

82. Moore, J. M., and R. W. Wein. 1977. Viable seed populations by soil depth and potential site recolonization after disturbance. *Canadian Journal of Botany* 55:2408-2412.

Seedling emergence from organic and mineral soil layers was measured for nine study sites at the Acadia Forest Experiment Station near Fredericton, New Brunswick. The number of viable seeds showed a decrease from deciduous-dominated forest, to conifer-dominated forest, to organic soil study sites. Viable seed number varied from 3400/m² for a deciduous-dominated forest study site to zero for a bog study site. Most seeds germinated from the upper organic soil layers of all study sites and were predominately *Rubus strigosus* Michx. After the germination experiment, ungerminated seeds, which showed no viability by the tetrazolium test, were separated from the soil. These seeds were almost entirely *Betula* spp. and seed numbers were as high as 4200-9400/m² for a deciduous-dominated forest. The applicability of the results to differing types of postdisturbance revegetation is discussed.

Disturbance, recolonization, Rubus, Betula, New Brunswick, Canada, coniferous forest, bogs

83. Morin, H., and S. Payette. 1988. Buried seed populations in the montane, subalpine, and alpine belts of Mont Jacques-Cartier, Quebec. *Canadian Journal of Botany* **66**:101-107.

The analysis of the total buried seed population along an altitudinal gradient in the Mont Jacques-Cartier area, southern Quebec, reveals a close relationship between buried seed flora and aboveground vegetation. Eighty-one percent of the species present in the total buried seed population were present in the aboveground vegetation of the study sites. The total number of seeds in the buried seed population, the number of species in the total buried seed population, and the number of seeds and species in the seed bank did not show any significant linear correlation with altitude. A shift from a boreal to an arctic-alpine buried seed population with increasing altitude was observed, instead of a decrease in seed bank size.

Quebec, Canada, boreal, alpine, arctic, species composition

84. Mull, J. M., and J. A. MacMahon. 1996. Factors determining the spatial availability of seed densities in a shrub-steppe ecosystem: the role of harvester ants. *Journal of Arid Environments* **32**:181-192.

The seed banks of deserts typically show a high degree of spatial variability. The authors examined the influence of the western harvester ant, *Pogonomyrmex occidentalis*, on the spatial heterogeneity of soil seeds in the semi-arid shrub-steppe of south-western Wyoming. Seeds were sampled in the foraging areas of three ant colonies over 2 years, primarily to assess the distribution of seeds with respect to harvester ant nests and foraging trails. In 1989, seed densities varied at the smallest spatial scale sampled — the microhabitat (undershrub vs. interspace). In 1990, seed densities varied at the largest spatial scale sampled — the colony foraging area. Seed abundance varied temporally in both years. Harvester ants affected the patterns of seed density in two ways. First, seed numbers in 1989 were higher in interspace areas away from foraging trails than in interspace areas near them, indicating that trails restrict colony search effort. Second, and contrary to expectations, seed numbers in 1990 were higher near harvester ant nests than in surrounding areas. This difference was attributable to higher densities of the alien annual grass *Bromus tectorum* and suggests that harvester ants indirectly facilitate *B. tectorum* near their nests.

harvester ant, granivory, seed bank, Pogonomyrmex occidentalis, shrub-steppe, Wyoming, shrub interspace, seed abundance, Bromus tectorum

85. Ne'eman, G. and I. Izhaki. 1999. The effect of stand age and microhabitat on soil seed banks in Mediterranean Aleppo pine forests after fire. *Plant Ecology* **144**: 115-125.

Soil samples from three microhabitats (gaps, beneath shrubs and beneath trees) in five stands of various post-fire ages (6–55 years) were collected in an east Mediterranean Aleppo pine *Pinus halepensis* forest. Total germinable seed bank densities varied between 300 and 1300 seeds per m². Herbaceous taxa were the major constituents of the germinable seed bank in gaps, regardless of stand age. Perennials were the major components beneath shrubs in all stands except the youngest stand where herbaceous species were the major components in all microhabitats. Important tree and shrub species (e.g., *Pinus halepensis*, *Quercus calliprinos*, *Pistacia lentiscus*, *Phillyrea latifolia*) of the mature pine forest were not an important component of the soil seed bank and therefore,

little resemblance was observed between the above-ground plant species composition and soil seed bank composition. This is consistent with the fact that these species regenerate by resprouting rather than by germination from the seed bank. Both microhabitats and forest-stands, which were of different ages, contributed to the variation in taxa richness, germinable seed density and diversity among samples. The effect of small-scale spatial heterogeneity (among microhabitats) was much more pronounced. In contrast to other studies, species richness, species diversity, and density of seed banks did not decrease with post-fire age. Moreover, stand age was a poor predictor for these attributes of the soil seed bank in an Aleppo pine forest. The heterogeneity plays an important role in conservation and management of this ecosystem.

Aleppo pine forest, Fire, Germination, Microhabitat, Spatial heterogeneity, Pinus halepensis

86. Nelson, J. F., and R. M. Chew. 1977. Factors affecting seed reserves in the soil of a Mojave Desert ecosystem, Rock Valley, Nye County, Nevada. *The American Midland Naturalist* **97**:300-320.

During 1972, a 2nd year of low herb production, there was a significant variation of seed reserves in the upper 2 cm of soil, with a doubling from February to June and a density-independent halving by October. In October 1972 there were 8×10^6 seeds/ha (5.3 kg/ha). After very high herb production in the spring, seed densities in October 1973 were 10-16 times greater under shrubs and 23-27 times greater in exposed areas (max 187.5×10^6 seeds/ha, 84.3 kg/ha). The increase was principally by the winter annual grass, *Festuca octoflora*. In 1972, where there was a small difference in rodent density between two plots (0.8:1.0) there was no effect of rodents on seed density. In 1973, when there was a 1:17.8 ratio of rodent densities, there was a significant effect on seeds under shrubs. Then from October 1973 to October 1974, seed reserves in exposed areas between shrubs decreased by 20% in the plot with few rodents, and by 40% in the plot with many rodents. Eating of seeds by rodents accounted for 30 to 80% of the seed reserve decreases observed. Germination losses were no more than 25%. There is slight evidence that pocket mice selectively decrease abundance of the heavier species of seeds. Seed density was at least five times greater under shrubs than in exposed areas; density was significantly correlated with the size of shrub canopy. There was also a significant effect of the species of shrub on the density of seeds. During years of low production, under-shrub areas are a refuge for herb seed production, and in such years shrub seeds form a larger portion of the seed crop and new reserves. The difference in response of shrubs and herbs to weather increases the stability of seed reserves. In May 1973 the number of herbs per 100 seeds in the previous October was 16.8 under shrubs and 43.6 in exposed areas; this implies a minimum germination of 24% of seeds over the whole habitat. It takes an exceptional coincidence of events, even in deserts, to cause a severe depletion of seed reserves.

Mojave Desert, Nevada, Festuca octoflora, rodents, shrub interspaces, predation

87. Odgers, B.M. 1996. Fire, buried germinable seed banks and grass species establishment in an urban eucalypt forest reserve. *Australian Journal of Botany* **44**: 413-419.

The buried germinable seed banks of two natural contrasting savanna open-forest sites were investigated before and after a wildfire. It was found that while the number of buried germinable grass and sedge seeds remained the same, the number of buried germinable dicotyledon seeds in both sites increased after the fire. It was also found that there were similar species of grasses present in the buried germinable seed banks before and after the fire. When germinating grass seedlings in the burnt and unburnt sites were compared, similar species of grasses were found in the germinating seedlings at both sites; however, more grass seedlings germinated in the burnt site than in the unburnt site.

88. Odion, D. C., and F. W. Davis. 2000. Fire, soil heating, and the formation of vegetation patterns in chaparral. *Ecological Monographs* **70**:149-169.

The authors documented patterns of surface heating associated with chaparral fire to characterize fundamental scale variation in the intensity of this stand-replacing disturbance. Stands were dominated by chamise (*Adenostoma fasciculatum*), a postfire seeder/sprouter. Nonsprouting *Arctostaphylos* and *Ceanothus* spp. were also present. The amount and distribution of canopy fuel that collapsed during fire and smoldered on the ground caused pronounced spatial variation in total surface heating. The strength of relationships among patterns of soil heating, preburn canopy, surviving seeds, and seedlings and herbaceous resprouts was consistently most pronounced in blocks 3–5 m long. At this scale, postburn patterns were strongly negatively associated with the amount of preburn canopy and the pattern of soil heating this fuel created. Seedlings or herbaceous resprouts of numerous species were abundant where soil heating was relatively low, most notably in natural and created canopy gaps. Conversely, areas where dense canopy occurred before fire, especially gaps displaced by fuel addition, were barren except for occasional *Arctostaphylos* and *Ceanothus* seedlings. These obligate postfire seeders, along with the shrub *Helianthemum scoparium*, had more deeply buried seeds, and some of them were able to survive where soil heating was prolonged. However, *Helianthemum* did not emerge from depth. Seedlings of *Arctostaphylos* and *Ceanothus* nearest *Adenostoma* burls survived significantly better when *Adenostoma* failed to resprout. Seed mortality prevented *Adenostoma* seedling emergence from occurring where its seeds were most abundant prior to fire, which was in proximity to its burls. *Adenostoma* seedlings did emerge in areas of lower soil heating, but their survival was inversely related to the density of *Helianthemum* seedlings. No shrub seedlings emerged after the first year following fire because their seed banks were exhausted by fire-induced mortality and/or germination. After 4–5 yr, few young *Adenostoma* remained. The combination of seedling and resprout regeneration allowed this shrub to maintain dominance, but to a lesser extent in the older stand. The results support a vegetation pattern–process model in which local species distributions after fire in *Adenostoma* chaparral are antecedently linked to the physical and chemical properties of the canopy. These control the nature of combustion, the soil heating that results, and the distribution of seeds and resprout tissues that survive. The vegetation develops entirely from these sources, so fire-induced patterns are manifest in the long-term structure of this vegetation.

Arctostaphylos, *Adenostoma fasciculatum*, *Ceanothus*, *chaparral*, *fire disturbance intensity*, *Helianthemum scoparium*, *obligate seeder*, *seed germination*, *seed distribution*, *seed mortality*, *shrub canopy*, *soil heating*, *vegetation patterns*

89. Odion, D. C. 2000. Seed banks of long-unburned stands of maritime chaparral: composition, germination behavior, and survival with fire. *Madroño* **47**:195-203.

Seed germination requirements in the California chaparral have been described mainly from freshly collected seed. However, uncertainties remain because the behavior of seeds in the soil can differ. The author studied germination of the seed bank in long-unburned stands of maritime chaparral in central coastal California. Seedlings emerging from soil samples were quantified and provided with appropriate temperature and moisture conditions following 1) no other treatment, 2) a heat treatment to optimize germination of heat-stimulated species, 3) the same heat with the addition of charred wood, and 4) the burning of chaparral stands prior to collection of samples. The author compared germination in these treatments with seedling emergence in the field following fire. He also collected and divided samples into 0-2.5 and 2.5-7.5 cm depth fractions to evaluate abundance of seed at the surface and depth before and after fire. Seed of one annual had reduced germination following the heat treatments. Seeds of all other species common enough to evaluate statistically were heat tolerant. However, because seeds were found to be mostly near the surface, there was considerable mortality with fire. Moreover, seedling populations in the field only accounted for a fraction of the seed bank that survived fire, and seventeen species that germinated in samples did not germinate and/or emerge in the field. Most species' germination and emergence was influenced in some way by heat and/or charate. Germination of two *Ceanothus* was dependent on heat. *Adenostoma fasciculatum* Hook. & Arn., *Arctostaphylos purissima* P. Wells, and two annuals had germination that was enhanced by heat and enhanced further when charate was added. Despite the importance of fire effects, there were no short-lived species having entirely fire-dependent germination. Germination and/or emergence of 3 species was negatively affected by charate. These germinated sparingly or not at all after fire.

California, chaparral, fire, germination, Ceanothus, Arctostaphylos, heat, charate, annual species

90. Oosterheld, M., and O. Sala. 1990. Effects of grazing on seedling establishment: the role of seed and safe-site availability. *Journal of Vegetation Science* **1**:353-358.

The first objective of this paper was to assess the effects of grazing on seedling establishment of two species whose relative abundance at the adult stage is affected by grazing in a contrasting fashion. Second, the authors evaluated the relative importance of seed versus safe-site availability in explaining the effect of grazing on seedling establishment. They monitored seedling establishment on a grazed area, on two areas which had not been grazed for two and seven years, and on plots which had been experimentally defoliated. The species compared were *Danthonia montevidensis*, a native perennial grass which dominates both grazed and ungrazed communities, and *Leontodon taraxacoides*, an invading exotic rosette species from the Compositae family. Continuous grazing enhanced seedling establishment of both species through its effect on the availability of safe sites. Seed availability accounted for only one, but very important, grazing effect: the lack of response by *L. taraxacoides* to the defoliation in the seven-year old enclosure. Its seed supply was depleted by exclusion of grazing, and consequently, its short-term regeneration capacity after disturbance was lost.

Grazing, safe sites, disturbance

91. Pake, C. E., and D. L. Venable. 1996. Seed banks in desert annuals: implications for persistence and coexistence in variable environments. *Ecology* 77:1427-1435.

It is widely believed that desert annual plants maintain between-year seed banks, yet few field studies actually have measured the proportion of the viable seed bank that remains dormant through a season. Dormancy and germination fractions were quantified for a guild of winter annuals on a creosote flat in the Sonoran Desert for three years. Predictions from two types of theoretical models applicable to temporally variable environments were examined: (1) the evolution of life history traits promoting persistence in the face of temporal variation and (2) the role of temporal variation in mediating species coexistence. The density of ungerminated seeds was estimated by collecting soil samples after germination, but prior to new seed set. Seedlings were followed in nearby plots to estimate the density of germinated seedlings and their reproductive success. Long-term data collected from permanent plots over a 10-yr period were used to calculate temporal variation in reproductive success for each species. Species with higher temporal variation in reproductive success had lower germination fractions and smaller seeds, consistent with the theory that seed dormancy and large seed size are partially substitutable bet-hedging strategies. The data also suggested that this system possesses traits that are necessary for temporal variation to promote coexistence. First, between-year seed banks, necessary to buffer populations in unfavorable years, were documented for 17 species. Second, there was a strong tendency for year-to-year variation in germination fractions to vary among species. Finally, plants germinated more in years of higher reproductive success. The authors discuss how a correlation between germination and reproductive success enhances the role of temporal variance in success hierarchies in promoting species coexistence.

Sonoran desert, annual species, germination, temporal variation

92. Paniagua, M.R.N. & Calvo, L. 1998. Seed bank in two different areas (burnt & control) in a Scots pine stand (*Pinus sylvestris* L.) in northern Spain In: Proceedings of 14th Conference on Fire & Forest Meteorology vol. 2: 1834-1852.

The authors conducted a seed bank study in a Scots pine (*Pinus sylvestris* L.) stand in León (northern Spain), comparing a burned area with an unburned one. The main species in the burned area was *Halimium* sp. while in the control area the main species was *Erica* sp. They also include a list of the most common species in the aboveground vegetation.

Scots pine, Pinus sylvestris, fire, Erica, Halimium, Spain

93. Parker, V.T., and V. R. Kelly. 1989. Seed banks in California chaparral and other Mediterranean climate shrublands. Pages 231-255 in M. A. Leck, V. T. Parker, and R. L. Simpson, editors. *Ecology of Soil Seed Banks*. Academic Press, San Diego, California, USA.

Mediterranean summer-dry climates are dominated by sclerophyllous evergreen shrub communities. This vegetation type is found in California (chaparral), in central Chile (matorral), around the Mediterranean Sea (e.g., macchia, maquis, and garrique), on the south and west coasts of South Africa (fynbos), and in southern and southwestern Australia (e.g., mallee-heath). Although these ecosystems are diverse and unique in the

plant and animal communities that compose them and in other respects, climatic stress, nutrient limitation and recurrent fires each limit the number and types of species that can survive. This is especially true at the critical stage of seedling establishment. These diverse vegetations share similarities at the seedling establishment stage. Two principal establishment environments exist temporally within chaparral. One, undisturbed chaparral, often in older stands, has several stresses, including low levels of resources, growth-inhibiting compounds, and high levels of predation. This undisturbed chaparral includes the small gaps that may occur following death of individuals. The second environment, disturbed by fire, has resources such as light, water and often nutrients that are temporarily more available. In the former, seedling establishment is spatially and temporally rare, while in the latter, *en masse* germination and establishment can occur for a number of species. The authors' goal in this chapter is to review and synthesize the literature on chaparral seed banks, and to make comparison where possible with seed banks in other Mediterranean shrub communities. Specifically, the authors consider seed bank formation and accumulation based on seed production, dispersal into the seed banks, and seed predation. They also compare germination cues and seedling establishment patterns of species with and without persistent seed banks. Finally, they consider seed bank patterns at the ecosystem level in relation to dominance and biogeographic patterns within chaparral.

California, chaparral, sclerophyll vegetation, fire, Mediterranean vegetation, temporal variation, seed predation, seed dispersal, seed persistence

94. Philip, L. 2004. The impact of burn intensity from wildfires on seed and vegetative banks, and emergent understory in aspen-dominated boreal forests. *Canadian Journal of Botany* **82**(10):1468-1480.

This paper compares seed and vegetative banks, and the emergent understory in unburned, lightly burned, and intensely burned patches within an aspen-dominated boreal forest in northeastern Alberta, Canada. Propagule banks were measured immediately after the fire, while the understory was surveyed 2 years later. Seedling and shoot emergence techniques were used to assess the abundance and assemblage of species within seed and vegetative banks. Median seed density was ordered unburned > lightly burned = intensely burned patches. A cumulative index of vegetative bank abundance was ordered unburned > lightly burned > intensely burned patches. Species assemblages were significantly different amongst burn intensities for seed banks and emergent understory. Vegetative bank assemblages were significantly different between unburned and burned patches but not between lightly and intensely burned patches. Furthermore, seed and vegetative bank assemblages within each burn intensity were also significantly different. Indicator species analysis suggested that all significant differences were due largely to broad assemblage differences rather than a few unique species. Ordination with nonmetric multidimensional scaling correspondence analysis separated seed and vegetative banks, and emergent understory along two axes (88.8% of the total variation). The first axis (50.3% of the total variation) indicated that the unburned and lightly burned species assemblages were more similar to the vegetative bank, while the intensely burned patches were more similar to the seed bank. The second axis (38.5% of the total variation) placed vegetative banks closer to emergent vegetation than seed banks.

Bud bank, vegetative bank, aspen, boreal, fire, Alberta, Canada

95. Pierce, S.M., and R.M.Cowling. 1991. Dynamics of soil-stored seed banks of six shrubs in fire-prone dune fynbos. *Journal of Ecology* **79**:731-747.

Soil-stored seed banks of six non-sprouting dominant shrubs with small seeds (0.4-4.6 mg) were determined in three mature (13-year-old) dune fynbos communities each autumn for 3 successive years. A comparison of methods of estimating seed banks by counting seeds vs. counting germinants showed neither method to be superior, a knowledge of other life-history characteristics, such as seed input and germination cues, was essential in evaluating results. Instead of the large seed banks typical of shrubs from fire-prone vegetation, dune fynbos shrubs had relatively small seed banks – the highest mean seed density recorded was $825 + 1187 \text{ seed m}^{-2}$ (mean + 1 SD, n=50). Shrub and community seed banks showed no significant increments over 3 years. After a fire, seed banks were depleted by more than half. Removal of seeds by ants and rodents from the soil surface was relatively rapid. Almost all seed had been removed from open depots by the sixth day of cafeteria experiments. Removal rates by ants of elaiosome-bearing (myrmecochorous) seeds was not significantly different from non-myrmecochorous species, neither were the intact seeds of a myrmecochorous species removed faster than the seeds from which the elaiosome had been removed. The results indicated that seeds are removed by ants as much for granivory as for myrmecochory. Seed burials showed that seed bank losses due to decay and germination varied widely amongst species and with seed age, with losses ranging from 12% to 93%. There were large differences in seed-bank size between the six species which could be attributed to their life-history attributes such as seed production, dispersal mode and germination requirements. The myrmecochorous species with relatively large and poorly dispersed seeds, small to moderate seed production and seed-bank sizes, and germination and seedling establishment cued to post-fire conditions, were most vulnerable to local extinction.

Dunes, fynbos, fire, seed emergence method, seed extraction method, ants, rodents, myrmecochory, seed size, seed dispersal, germination cues

96. Pratt, D. W., R. A. Black, and B. A. Zamora. 1984. Buried viable seed in a ponderosa pine community. *Canadian Journal of Botany* **62**:44-52.

The seed bank of a *Pinus ponderosa* – *Symphoricarpos albus* stand in east-central Washington was examined with respect to species composition, depth distribution, and termination responses to heat and shade treatments. Seeds of 57 species were present in the seed bank to a depth of 10 cm. Twenty-one of these species were not found in the aboveground vegetation of the study area. Estimated viable seed densities in spring and autumn collections were $13,052 \pm 1481$ and $14,463 \pm 1356 \text{ seeds m}^{-2}$ respectively. *Stellaria media* and *Poa pratensis*, both alien species, accounted for 50% of the buried viable seeds. Seed density was highest in litter samples. Total seed density decreased with soil depth, although seeds of some pioneer species were more abundant in the mineral soil than in the litter. Species dominating the seed bank were generally unimportant in the aboveground vegetation. Woody species, which dominated the aboveground vegetation, accounted for only 1% of the seed bank. Annual forbs dominated the seed bank (45% of total buried viable seed) but were not dominant in the vegetation. Seeds of several species survived prestratification heat treatments.

Poststratification heat treatments inhibited germination or destroyed seed of nearly all species. As shading increased, germination of most species decreased. However, shade did not inhibit germination of species characteristic of mature successional stages.

Pinus ponderosa, *ponderosa pine*, *Washington*, *litter*, *annual species*, *fire*, *heat*, *shade*, *succession*

97. Preston, C. A. and I.T. Baldwin. 1999. Positive and negative signals regulate germination in the post-fire annual, *Nicotiana attenuata*. *Ecology* **80**(2):481-494.

The litter of many plant species is known to inhibit germination, and this phenomenon is commonly interpreted as allelopathic inhibition of one species by another. However, an alternative interpretation is that seeds may be using environmental signals to inform the timing of their germination and thereby use dormancy as a mechanism of habitat choice. *Nicotiana attenuata* Torr ex Wats. (Solanaceae) is typically found for less than three years after fire in the sagebrush, blackbrush, and pinyon-juniper forests of the Great Basin desert of North America. A dormant seed bank is established during this ephemeral post-fire period, and pyrolysis products of [Alpha]-cellulose (containing only C, H, and O) in wood smoke are known to initiate germination in dormant seeds of this species. The authors demonstrated in a glasshouse experiment that germination into burned soils (as compared to unburned) results in a 12-fold increase in lifetime seed production, which reflects a minimum estimate of the fitness benefit of making accurate germination decisions. With seed bioassays, they examined the distribution of this smoke signal in the [A.sub.1] soil layer at several burned areas in southwestern Utah, United States to determine whether the presence of this smoke-derived germination cue predicts the spatial and temporal occurrence of *N. attenuata* populations after fires. Although they found no evidence for the germination signal in areas that had not been burned for 30 yr, the occurrence of the germination signal did not perfectly coincide with the distribution of populations. The authors found evidence for its transport by wind and water into adjacent unburned areas (from 40 m to 1 km away from a burned site) and its persistence over time (for [greater than or equal to] 7 yr), making this signal an unreliable indicator of the plant's habitat. To resolve this discrepancy, they examined the effect of unburned [A.sub.0] soil horizon on smoke-induced germination. The litter-containing [A.sub.0] soil horizon (and aqueous extracts thereof), collected from underneath seven dominant species from later stages of post-fire succession, completely inhibited germination of both dormant and nondormant seeds, even in the presence of a smoke cue in excess of that required to elicit germination. The inhibitory effect was limited to the early stages of germination (48 h after exposure to smoke), and they confirmed these results with natural seed banks. The authors also demonstrated that the [A.sub.0] soil horizons and their aqueous extracts are not toxic to *N. attenuata* seeds or growing plants, and they have no effect on lifetime seed production. Moreover, they do not inhibit the germination of the nondormant, conspecific native tobacco, *N. trigonophylla*, which grows in the same area but is not associated with fire. Hence, these negative factors do not function in allelopathically mediated competitive interactions between *N. attenuata* and later successional species. The authors propose that the occurrence of *N. attenuata* populations after fires can be explained by the combined stimulatory effect of smoke-derived signals on the dormant seed bank and the inhibitory effect of signals from unburned litter, and that both signals are required for *N. attenuata* to identify its germination niche.

Soil horizons, allelopathy, fire, germination signals, litter-inhibited germination, Nicotiana attenuata, positive and negative control, seed dormancy, smoke-induced germination

98. Price, M. V., and J. W. Joyner. 1997. What resources are available to desert granivores: seed rain or soil seed bank? *Ecology* **78**:764-773.

Patterns of resource availability mold many ecological processes, but little is known about the availability of resources to consumers in nature, even for well-studied systems such as the granivorous animals of North American deserts. What is known about seed resources in deserts is based primarily on seeds extracted from soil samples, but this might present a distorted view of resource availability if animals mostly harvest newly produced seeds before they enter the soil seed bank. In order to assess how large the distortion might be, the authors simultaneously monitored the seed bank and "seed rain" over a 19-mo period in the eastern Mojave Desert of California. The seed bank averaged ~ 106000 seeds/m² and 38 g/m², much higher than values reported for other North American desert sites. This corresponds roughly to the seed production of a single year, since daily seed rain averaged 262 seeds/m² and 0.26 g/m². However, input from the seed rain did not accumulate in the soil. Instead, the seed bank decreased by a daily average of 114 seeds/m² and 0.007 g/m² during the study. This suggests that virtually all seeds germinate, die, or are harvested by granivores soon after being dispersed. Large seeds comprised a greater fraction of the seed rain than of the seed bank, suggesting that such seeds are differentially depleted, probably by granivores, before they enter the soil. Because seed drop was seasonal, temporal variation comprised a significant component of among-sample variance in the seed rain. Temporal variance in the seed bank was much smaller, presumably because granivores harvested most of the seed rain. Conversely, spatial variance was a significant component for the seed bank, but not the seed rain, perhaps as a result of spatial patterns of seed harvest or seed caching by granivores. By virtue of these variance patterns, as well as other attributes, seeds in the soil present different challenges to granivores than do newly produced seeds. Our understanding of desert granivore foraging and community ecology, and of granivore–seed interactions, depends critically on choosing the appropriate measure of seed availability to granivores.

Food storage, granivory, rodents, Mojave Desert, resource availability, resource dynamics, seed caching, seed rain, temporal variation, California

99. Price, M. V., and O. J. Reichman. 1987. Distribution of seeds in Sonoran Desert soils: implications for heteromyid rodents foraging. *Ecology* **68**:1797-1811.

The authors used a hierarchical sampling design to investigate temporal and spatial patterns of variation in the topsoil seedbank at a site on the Santa Rita Experimental Range, 50 km south of Tucson, Arizona. Replicate sets of contiguous 4 x 4 cm samples to 2 cm depth ("transects") were collected three times per year, from 1980 to 1983, from four microhabitats that are differentiated by desert heteromyid rodents: large and small open spaces, under canopies of large shrubs, and under canopies of small trees. They also analyzed texture and organic content of soils from the four microhabitats. Seeds from 54 plant taxa were encountered, most of them rare. Average seed mass across species was 1.28 mg/seed, but because tiny seeds were most numerous, the abundance—weighted average was 0.16 mg/seed. Total seed abundance was highly variable, ranging

from 0 to 256 seeds and from 0 to 146 mg per sample. The fourfold temporal variation in mean mass or number of seeds per sample was largely due to between—year rather than between—season effects. Seed standing crops were positively correlated with rainfall during the previous 6—mo rainy period, and were lowest in fall and winter of 1982 after 2 yr of poor winter rains. Mean seed number per sample, which reflects primarily abundance of tiny seeds, did not vary among microhabitats. Mean per—sample seed mass, which reflects abundance of the large seeds eaten by rodents, did vary among microhabitats, however, with values being higher under shrubs and trees than in open spaces. The low mean abundance in open spaces was due more to a high frequency of seedless samples than to low maximum per—sample abundance. Hence, profitable seed patches do occur in open spaces, but are rarer than under shrubs or trees. Within microhabitats there was significant variation among replicate transects and among samples within transects. On a local scale, seeds occurred in patches 12 cm in diameter in all microhabitats and sampling periods. Seed species composition varied seasonally and among microhabitats, and there was an overall correlation between seed and adult microhabitat distribution for spring ephemerals. Soil from open spaces was finer and had lower organic content than that under shrub or tree canopies. The results suggest that the resource upon which desert granivores depend is highly variable in time and space. Microhabitat is one of the most conspicuous sources of variation, and heteromyid rodent species differ in use of those microhabitats (open spaces vs. areas under canopies of perennial plants) that differ most noticeably in seed abundances, species composition, and soil characteristics.

Sonoran Desert, rodents, predation, foraging, granivores, Arizona, interspaces

100. Qi, M., and J. B. Scarratt. 1998. Effect of harvesting method on seed bank dynamics in a boreal mixedwood forest in northwestern Ontario. *Canadian Journal of Botany* **76**:872-883.

The effects of harvesting on seed bank dynamics in a boreal mixedwood forest were studied on replicated 10-ha treatment blocks harvested by different clear-cutting or partial-cutting systems in the fall of 1993. From 1994 to 1995 the authors monitored seed rain, soil seed banks, and seasonal changes in species composition in understory vegetation and seed banks in all harvest blocks plus three uncut controls. No persistent conifers were found in the soil seed banks of any treatment. The number of seeds of other species generally decreased with soil depth in all treatments, with the lower layer of organic soil yielding the highest numbers of seedlings. Many seeds of sedges and some herbs were found in the upper mineral soil horizon, indicating significant longevity. While disturbance by harvesting operations altered the distribution of seeds in the soil profile, harvesting method had little effect on the total number of species present in post-harvest seed banks or understory vegetation. There were no differences in seasonal compositional changes between treatments. Seed rain monitoring indicated that few conifer seeds were added to the seed bank. *Betula papyrifera* Marsh. was the dominant tree species in seed rain in the partial cutting treatments. However, in the second post-harvest year on clear cut sites sedges and grasses increased from less than 1 to 14% of seed rain. The results suggest that predominantly hardwood stands with prolific understory vegetation will initially develop on the treated sites, with a variable, but depleted conifer content.

boreal mixedwood forest, natural regeneration, seed rain, succession, vegetative propagation, conifer forest, Ontario, Canada,

101. Quick, C. R. 1956. Viable seeds from the duff and soil of sugar pine forests. *Forest Science* **2**:36-42.

Duff samples were collected from mature forest in the Sierra Nevada of California to determine if kind and amount of post-logging brush could be approximated from the kind and number of viable seeds found in a relatively few small duff samples. Sixty-four samples of duff down to mineral soil were collected in September 1947 under virgin mixed-conifer timber on the Stanislaus Experimental Forest, Dodge Ridge, Pinecrest, Tuolumne Co., California. Each small sample represented 1/50,000 acre of area. The duff and soil collections were reduced by a variety of methods to seed concentrates of small volume. These seed concentrates were inspected; then cultured in autoclaved sand wet with mineral nutrient solution. Seedlings resulting from germination cultures indicated that the average viable-seed content of duff and soil under virgin, largely over-mature timber on the sampled areas, on a per acre basis, was 1,865,000 seeds of snowbrush and sweetbitch (*Ceanothus cordulatus* Kell. and *C. parvifolius* Trel.); 475,000 seeds of assorted dicot plants (including seeds of the iris and lily families); 16,000 seeds of *Ribes* (largely *Ribes roezli* Regel); 155,000 seeds of deerbrush (*Ceanothus integerrimus* H. & A.); 155,000 seeds of grasses (including seeds of rushes and sedges), and 10,000 seeds of manzanita (largely *Arctostaphylos patula* Greene); a total of about 2,820,000 viable seeds per acre.

Seed emergence method, sugar pine, California

102. Read, T.R., S.M. Bellairs, D.R. Mulligan and D. Lamb. 2000. Smoke and heat effects on soil seed bank germination for the re-establishment of a native forest community in New South Wales. *Austral Ecology* **25**:48-57.

The effects of plant-derived smoke and of heat on the emergence of seedlings from seeds were assessed. Seeds had been stored in forest topsoil used for mine site rehabilitation. The study was carried out in a dry sclerophyll, spotted gum (*Corymbia maculata*), forest community at the Mount Owen open-cut coal mine in the Hunter Valley region of New South Wales. Samples of the surface 2.5 cm of topsoil were either exposed to cool smoke from eucalypt foliage for 60 min, heated to 80°C, or left untreated. Seedling emergence from the seed bank in this soil was then monitored in a glasshouse. Within the first month, smoke alone promoted a 4.3-fold increase in the density of seedlings relative to control. There were 540 emergents per m² in the control and 2309 per m² in the smoke treated topsoil. Many annual and perennial herbs emerged but grasses responded most strongly to smoke. Germination in seven of the 20 grass species was promoted by smoke. Smoke promoted the germination of some introduced species as well as native species, and accelerated the rate at which seedlings emerged, although these differences sometimes declined with time. Heat also stimulated germination but smoke and heat stimuli appeared to be complementary in their promotion of seedling emergence from the topsoil seed bank. Each treatment increased the density of different species, enhanced the species richness of different components of the seed bank, and had different effects on the rate of emergence. The results suggest that increased seed germination in the field immediately following a moderate intensity fire

may sometimes be the result of heat stimulation of the soil seed bank. These findings may have important implications for minesite revegetation programs where topsoils are replaced after mining and rapid germination of seeds stored in these soils is required during short periods when conditions are favourable for germination.

Emergence, germination, heat, mine rehabilitation, sclerophyll, seed dormancy, smoke, Australia,

103. Reichman, O. J. 1979. Desert granivore foraging and its impact on seed densities and distributions. *Ecology* **60**:1085-1092.

Field experiments were conducted to determine the foraging behaviors of granivorous desert ants and rodents and to ascertain the impact of these foraging efforts on the density and distribution of seeds in the soil. Foraging experiments were performed which involved providing seeds within taxon-specific enclosures in scattered and clumped distribution on the soil surface and 1.5 cm below the surface. These experiments indicated that ants only foraged on the surface, whereas rodents were able to garner seeds from below the ground. Ants foraged ~ 85% of the experimental seed distributions on the surface and were able to retrieve ~ 45% of the seeds they detected during any 24-h experimental run. Rodents detected 100% of tall distributions and got ~96% of the seeds from all distributions except scattered/belowground, from which they gathered only 75% of the seeds. Three-year experiments using enclosures which excluded either ants, rodents, both taxa, or neither taxa, indicated that either taxon alone, or both taxa together, have a severe impact on the density of seeds in the soil. When neither is present, seed densities remain high. Furthermore, any combination of granivores greatly reduces the number of samples with either high numbers of seeds or high biomass of seeds, although the ants tend to leave a greater number of large clumps of seeds than the rodents. Clumping indices are also extremely high in the absence of granivores. In opposition to the apparently detrimental effect of seed use by the granivores, surface seed-caching by rodents appears to enhance seed germination.

ants, community structure, consumer impact, desert foraging, rodents, seed densities, seed distributions, granivores, seed caching, ants, deserts

104. Reichman, O. J. 1984. Spatial and temporal variation of seed distributions in Sonoran Desert soils. *Journal of Biogeography* **11**:1-11.

Samples taken in seventeen different microhabitats in the Sonoran Desert, NW of Tucson, Arizona (U.S.A.), revealed large variation in spatial (78-fold) and temporal (28-fold) patterns of seed distribution. Seed densities were lowest in normally dry washes and open areas between shrubs, were intermediate between shrubs, and were highest in artificial and naturally occurring depressions in the soil surface. There were microsites with high seed densities within microhabitats of low overall seed density. Differences between microhabitats were greatest during periods of high seed production and tended to disappear in seasons when rainfall was low. Seed densities were not correlated with shrub canopy volume, but were correlated with the dimensions of microtopographic depressions. Seeds which were small, or round, tended to form higher density patches than large or long seeds.

Sonoran desert, Arizona, seed density, shrub interspaces, depressions, seed size, seed shape

105. Romme, W. H., L. Bohland, C. Persichetty, and T. Caruso. 1995. Germination ecology of some common forest herbs in Yellowstone National Park, Wyoming, U.S.A. *Arctic, Antarctic, and Alpine Research* **27**:407-412.

Seed viability and dormancy mechanisms were investigated in seven herbaceous plant species and one low shrub species common in the first few years of postfire succession in subalpine forests of Yellowstone National Park, Wyoming, U.S.A. Seeds of *Epilobium angustifolium* (fireweed) had rapid and high percent germination in both the fall and spring after seeds were collected. Seeds of *Lupinus argenteus* (lupine) germinated well after several months of warm or cold storage, and the rate of germination but not the final percent germination was increased by scarification. Seeds of *Arnica cordifolia* (heartleaf arnica) were nearly all non-viable; only one seed germinated out of 650 tested, and no seedlings were observed in the field. Small sample sizes limited the scope of testing of the other species, but both *Cirsium arvense* (Canada thistle) and *Epilobium ciliatum* (willow-herb) showed moderate to high germination in the spring after several months of storage, *Hieracium albiflorum* (hawkweed) germinated better in the fall than in the following spring, *Vaccinium scoparium* (dwarf huckleberry) seeds germinated in the fall 1 mo after collection, and seeds of *Antennaria racemosa* (pussytoes) failed to germinate when tested in the fall 1 mo after collection. These results, combined with field studies, indicate that large-scale fires provide opportunities for recruitment of new genetic individuals, increased genetic diversity, and colonization of new patches on the forest floor in several species, including *Epilobium angustifolium*, *Lupinus argenteus*, *Hieracium albiflorum*, and *Cirsium arvense*. These effects are likely to persist for many decades in these long-lived perennial plant species.

Germination, Wyoming, revegetation, succession, scarification, fire

106. Rydgren, K. and G. Hestmark. 1997. The soil propagule bank in a boreal old-growth spruce forest: changes with depth and relationship to aboveground vegetation. *Canadian Journal of Botany* **75**:121-128.

The species composition and the depth distribution of the soil propagule banks of bryophytes and vascular plants from three different soil layers in a boreal old-growth spruce forest in SE Norway were studied using the emergence method. A total of 34 taxa germinated with a predominance of ferns and mosses. The frequency of the different species exhibits a common community pattern with a few common and a large number of low frequency species. The tree *Betula pubescens*, the ferns *Athyrium filix-femina*, *Gymnocarpium dryopteris*, and *Phegopteris connectilis*, and the mosses *Plagiothecium laetum* agg. and *Polytrichum* spp. were the most frequent. There is only a moderate correspondence, decreasing with soil depth, between the propagule bank and the aboveground vegetation in the sampled plots. In the soil profile, the litter layer on average had more taxa than the peaty mor and bleached layer (7.7, 6.0, and 5.5 taxa, respectively). Five of the 17 taxa occurring in more than 10% of the soil samples from the different soil layers were significantly more frequent in the upper soil layer, while two taxa were more frequent in either peaty more and (or) the bleached layer than in the uppermost layer. The propagule bank in the different soil layers represents an in situ potential for regeneration of the vegetation after different degrees of disturbance in the forest floor.

Disturbance, propagules, boreal forest, old-growth forest, Norway, seed emergence method

107. Rydgren, K., G. Hestmark, and R. H. Okland. 1998. Revegetation following experimental disturbance in a boreal old-growth *Picea abies* forest. *Journal of Vegetation Science* **9**:763-776.

The authors studied revegetation patterns after experimental fine-scale disturbance (e.g. uprooting) in an old-growth *Picea abies* forest in southeastern Norway. An experimental severity gradient was established by manipulation of the depth of soil disturbance; two types of disturbed areas were used. Species recovery was recorded in the disturbed patches in three successive years after disturbance. The cover of vascular plants and, even more so the cover of bryophytes and lichens, recovered slowly after disturbance. The least severe treatments (removal of vegetation and removal of vegetation and the litter layer) was followed by the fastest recovery. The mean number of vascular plant species was usually higher three years after disturbance than before disturbance, while the opposite was true for bryophytes. Several vascular plant species that were abundant in intact forest floor vegetation (*Vaccinium myrtillus*, *V. vitis-idaea* and *Deschampsia flexuosa*) recovered during a three-year period primarily by resprouting from intact rhizomes and clonal in-growth. Other important recovery mechanisms included germination from a soil-buried propagule bank (e.g. *Luzula pilosa*, *Plagiothecium laetum* agg., *Pohlia nutans* and *Polytrichum* spp.) and dispersal of propagates into the disturbed patches (e.g. *Betula pubescens* and *Picea abies*). Microsite limitation seemed to occur in several species that were abundant in the soil propagule bank (e.g. the ferns *Athyrium filix-femina*, *Gymnocarpium dryopteris* and *Phegopteris connectilis*) but which did not appear in disturbed patches.

Disturbance severity influenced revegetation patterns, recorded both as trajectories of vegetation composition in a DCA ordination space and as change in floristic dissimilarity. The length of the successional path (compositional change measured in β -diversity units) increased with increasing disturbance severity, and was also influenced by the area of the disturbed patch and the distance to intact vegetation. The rate of succession depended on the method by which it was measured; decreasing year by year in floristic space, while first decreasing and then increasing in ordination space. The reason for this difference is explained.

Boreal forest, disturbance area, disturbance severity, gap, microsite limitation, Norway, recruitment, succession

108. Sabo, D. G., G. V. Johnson, W. C. Martin, and E. F. Aldon. 1979. Germination requirements of 19 species of arid land plants. Research Paper. Rocky Mountain Forest and Range Experiment Station **RM-210**.

Information on the germination requirements of these species can be helpful to seed technologists as well as to land managers. Those faced with revegetating disturbed areas of all kinds, for example, road cuts, severely depleted ranges, or mine spoil areas, can use these data for proper species selection, time of planting, conditions required for successful germination, and as a guide to seed viability standards. Areas of the Southwest with the potential for strip mining, due to the extreme climatic conditions, are poised in a delicate ecological balance. Success in reclaiming devastated land depends on knowledge

of many parameters, including conditions for optimum seed germination. The objectives of this study were to determine: (1) optimum temperatures for germination of seed of the various candidate species of grasses and shrubs; (2) the effects of moisture stress applied to seeds at an optimum temperature for germination; and (3) the effect of light, if any, on germination.

Revegetation, germination, arid lands, southwestern United States, temperature, light

109. Scheiner, S. M. 1988. The seed bank and above-ground vegetation in an upland pine-hardwood succession. *The Michigan Botanist* **27**:99-106.

The author reports here on a survey of the seed bank of an upland pine-hardwood succession sequence in northern lower Michigan. A comparison is made between the species composition of the seed bank and the above-ground vegetation. In particular, the seed bank and vegetation on one site was surveyed for three years following clear-cutting and fire. Thus, this study provides some understanding of the sources for recruitment into this newly disturbed site. This successional sequence is of special importance because it is one of the longest studied with an extensive longitudinal data base. This report updates and expands on previous studies.

Pine forest, hardwood forest, succession, clear cutting, fire, Michigan

110. Smith, M. A., W.A. Loneragan, C. D. Grant, and J. M. Koch. 2000. Effect of fire on the topsoil seed banks of rehabilitated bauxite mine sites in the jarrah forest of Western Australia. *Ecological Management and Restoration* **1**(1):50-60.

Germinable seed stores of 5- and 8-year-old rehabilitated bauxite mine pits in southwest Western Australia were assessed before and after burning. These seed stores were compared to those of adjacent unmined Jarrah (*Eucalyptus marginata*) forest, to identify at what age fire can be reintroduced, in order to measure restoration success and reduce fire hazard. Soils were sampled in early summer (before fire) and late autumn (after fire). Before fire, the mean topsoil seed bank of 5-year-old sites was 2121 seeds per m² while 8-year-old sites had a mean of 1520 seeds per m². Only the 5-year-old sites were significantly different from the forest mean of 1478 seeds per m² for the same season. After summer burns (and possibly due to seasonal effects) topsoil seed banks of rehabilitated areas (sampled in autumn) decreased by an average of 53 per cent. Topsoil seed banks of 5–8-year-old sites were resistant to lower intensity burns, with 362 seeds per m² of native species surviving mild burns and 108 seeds per m² of native species surviving after an intense summer fire. The topsoil seed reserve of 5–8-year-old rehabilitated areas had a high proportion of annual weed species while the forest sites had high levels of subshrubs and native annuals. Low-intensity burns did not alter the composition of life-forms in the soil seed bank, while intense burns favoured annual weed and shrub species. The results indicate that it is not appropriate to introduce fire to rehabilitated areas before 8 years, due to limited fuel reduction benefits and possible adverse effects on obligate seeding species. The large proportion of weed species in the soil seed bank of young rehabilitated areas is a concern, and remains a major consideration for future disturbance of these areas.

Land rehabilitation, mining, prescribed burning, obligate seeder, resilience, resprouter, soil seed banks, fire, Australia, topsoils

111. Sternberg, M., M. Gutman, A. Perevolotsky and J. Kigel. 2203. Effects of grazing on soil seed bank dynamics: An approach with functional groups. *Journal of Vegetation Science* **14**:375-386.

The relationship between intensity and timing of cattle grazing on changes in the size and composition of the soil seed bank were investigated in a 3-yr study in a Mediterranean grassland in northeastern Israel. Treatments included manipulations of stocking rates and of grazing regimes, in a factorial design. The retrieved soil seed bank community was rich in species, with 133 species accounting for 80% of the 166 species recorded at the site. Within the seed bank, 89% of the species were annuals. Seed bank dynamics was analysed in terms of plant functional groups and germination strategies. In terms of total seed bank density and including all functional groups, 42% of the seeds present in the soil did not germinate under watering conditions. The dormancy level differed greatly among functional groups. The seed bank of annual legumes, crucifers, annual thistles and annual forbs had a large fraction of non-germinated seeds and characterized areas grazed early in the growing season under high and very high grazing intensity. These functional groups were considered to have a higher potential for persistent seed banks production. In contrast, short and tall annual grasses and tall perennial grasses, that were dominant in ungrazed or moderately grazed paddocks, generally had seed banks with a very small fraction of non-germinated seeds. Seed bank densities varied widely between grazing treatments and years. Under continuous grazing, heavy grazing pressure reduced seed bank densities of grasses and crucifers in comparison to moderate grazing. The greatest reduction on the seed bank densities resulted from heavy grazing concentrated during the seed-set stages.

Cattle, grazing, seed viability, Israel, Mediterranean region, dormancy, germination, management, persistence, rangeland, regeneration strategy

112. Strickler, G. S., and P. J. Edgerton. 1976. Emergent seedlings from coniferous litter and soil in Eastern Oregon. *Ecology* **57**(4):801-807.

Seedlings emerging from litter and soil samples from three mixed conifer forests were observed for 1 yr in the greenhouse. A total of 536 seedlings emerged from litter, 2- to 2-cm, and 2- to 4-cm soil depth samples subjected to 28°C treated samples under 80% and 92% shade treatments. Identification included 29 species of forbs, four grasses, one sedge, and four shrubs; no conifer seedlings emerged. A significant majority of seedlings emerged from litter, and most were species which produce abundant windborne seed. Only *Epilobium watsonii* Barbey seedlings showed a significant reduction in their emergence under shade. Applicability of the results to post logging management is suggested.

Litter, coniferous forest, Oregon, wind dispersal, logging

113. Thanos, C. A., and P. W. Rundel. 1995. Fire-followers in chaparral: nitrogenous compounds trigger seed germination. *Journal of Ecology* **83**:207-216.

Application of nitrates (optimal concentration c. 10mM) promoted seed germination in the fire annuals *Emmenanthe penduliflora* and *Phacelia grandiflora* and to a lesser extent in the fire-adapted shrub *Salvia mellifera*. Ammonium ions, although virtually inactive in *E. penduliflora*, were as effective as nitrate in both *P. grandiflora*

and *S. mellifera*. Diurnal illuminations and a chilling pretreatment, though of little effect by themselves, significantly enhanced the nitrate-mediated promotion of germination in the two fire annuals. Nitrate was the principal factor inducing germination in *E. penduliflora* (nitrate or ammonium in *P. grandiflora*) whereas in *S. mellifera* light was the principal agent. It was also shown in *E. penduliflora* that nitrates are not required during chilling, i.e. seed sensitisation by chilling and nitrate-mediated induction of germination are entirely different mechanisms. In the three species tested, the effect on seed germination caused by nitrogenous substances was nearly identical to that produced by an extract of charred wood, although chemical analysis of the extract showed that the combined concentrations of nitrates, ammonium ions and free amino acids could not account for the promotive action of charate. However, the nitrate and ammonium concentrations required to induce germination are very close to the increased values encountered after a fire in the otherwise nitrogen-poor chaparral soil. Therefore, in addition to the possible effect of charred wood, the postfire germination flush observed in chaparral may be induced by the increased levels of available nitrogen as well.

Ammonium, nitrate, Emmenanthe penduliflora, Phacelia grandiflora, Salvia mellifera, light, chilling, germination, charate, chaparral, germination signals

114. Thomas, P. B., E. C. Morris, and T.D. Auld. 2003. Interactive effects of heat shock and smoke on germination of nine species forming soil seed banks within the Sydney region. *Austral Ecology* **28**:674-683.

The germination response of seeds from fire-prone vegetation to fire-related cues such as heat shock and smoke has usually been studied by applying the cues singly. The few studies that have applied the cues in combination have shown that interactions between the cues are possible. Here, the response of seeds from a number of species to combined heat shock and smoke is reported. Heat shock (25, 50, 75 and 100°C) and aerosol smoke (0, 5, 10 and 20 min) were applied factorially to nine species that form soil seed banks in the Sydney region of south-eastern Australia. These species were from Epacridaceae (four species), Myrtaceae (four species) and Cyperaceae (one species) and ranged from fire-sensitive obligate seeders to fire-tolerant facultative resprouters. Germination of *Dracophyllum secundum* R. Br and *Sprengelia monticola* (A. Cunn. ex DC.) Druce was low and did not respond to the germination cues. The positive response of *Gahnia sieberiana* Kunth and *Kunzea ambigua* (Sm.) Druce to heat shock and smoke was independent and additive. The positive response of *Kunzea capitata* Rehb. to the interaction between heat shock and smoke was synergistic, and the response of *Baeckea diosmifolia* Rudge and *Baeckea imbricata* (Gaertn.) Druce was unitive, with germination increase only occurring following combined heat and smoke application. *Epacris coriacea* A. Cunn. ex DC. and *Epacris obtusifolia* Sm. had low levels of dormancy and hence it was not possible to find a fire response. *Gahnia sieberiana* and *K. capitata* responded differently to the combination of heat shock and smoke than has previously been reported. Germination of species from habitats that are infrequently burnt was not affected by heat shock or smoke. Low-intensity fire or patches within fire may be important for seedling recruitment as the 50°C heat shock stimulated germination in four of the five species that responded to the heat cue, and germination of *Baeckea imbricata* declined within the 100°C heat shock treatment. Germination of one species, *Baeckea imbricata*, was only stimulated by a specific combination of cues, indicating that

regeneration niches may be narrow for some species and that the application of a range of heat and smoke doses is required to find such responses. Of the species positively responding to heat shock and smoke, a requirement for both cues was prevalent, therefore the response to these cues in isolation cannot be relied upon to give a true indication of the fire response of a species.

Heat shock, smoke, Australia, germination cues, sprouting, fire

115. Trabaud, L. 1980. Influence du feu sur les semences enfouies dans les couches superficielles du sol d'une garrigue de chêne kermés. *Naturalia Monspeliensia*. 39: 1-19.

116. Troumbis, A.Y. 1996. Seed persistence versus soil seed bank persistence: The case of the post-fire seeder *Cistus incanus* L. *Ecoscience* 3(4):461-468.

The paper examines conceptual and methodological questions related to the validation of alternative hypotheses of seed bank size variation in time: the "steady accumulation of seeds in soil" and the "annual fluctuation of seed bank size". Among the examined questions, most effort is allocated to identifying the relative magnitude of temporal variability of seed banks and the establishment of criteria for accepting a hypothesis related to the persistence of single-species soil seed banks. A set of criteria is proposed as a validation scheme of a hypothesis. *Cistus incanus* L., an obligate seeder, has been used during an 8-year study in two different stands, as experimental material for studying seed production and seed storage in soil. Some general conclusions may be proposed: 1) Simple interannual comparisons of seed bank size in order to support a hypothesis on bank persistence must be avoided. 2) The validity of the hypothesis is related to the scale of observation (temporal, spatial and numerical). 3) Although annual fluctuations in soil seed bank size are evident, a minimum number of seeds persist in the soil. In that case, the physiological persistence of the seed is confused with the populational persistence of the soil seed population.

Multiple persistence criteria, steady accumulation of seeds, Cistus incanus, temporal variation, spatial heterogeneity, Mediterranean-type shrubland

117. Tyler, C. M. 1995. Factors contributing to postfire seedling establishment in chaparral: direct and indirect effects of fire. *Journal of Ecology* 83:1009-1020.

In the chaparral, significant seedling establishment occurs only following fire. Mechanisms proposed to explain this abundant recruitment after fire include: direct heating of the soil and seed bank, and a temporary reduction in competition or herbivory. The author tested hypotheses regarding the relative importance of these mechanisms to different plant functional groups using field experiments conducted in burned and nearby unburned chaparral. Competition was manipulated by removing shrubs from mature chaparral, and mammalian herbivory manipulated using small cage exclosures. Burning and reduction in herbivory were primarily responsible for the postburn "flush" of seedlings, although plant functional groups differed in their responses to fire. Shrub seedling density was enhanced only by herbivore exclusion. The abundance of subshrubs and annual herbs was positively affected only by burning. Perennial herbs increased both with burning and herbivore exclusion. The effects of variation in fire intensity or soil heating were also investigated, by comparing unmanipulated plots in the burn to areas in the burn which had been cleared of shrubs prior to the fire. Areas in the burn with reduced soil heating had higher overall seedling densities, cover and biomass; perennial

herbs were the only functional group unaffected by variation in fire intensity. Comparison of the results of this study to those from similar experiments in maritime chaparral suggest that inconsistencies between the response of chaparral communities to fire may be due primarily to differences in species composition.

Burning, competition, fire intensity, herbivory, soil heating, chaparral, exclosures, species composition

118. Valbuena, L. and L. Trabaud. 2001. Contribution of the soil seed bank to post-fire recovery of a heathland. *Plant Ecology* **152**:175-183.

The importance of a soil seed bank was evaluated through its role in the recovery of a burnt shrubland. The study was carried out in a heathland characterized by several ericaceous species. Part of the heathland was burnt in a wildfire on 7 April 1991, while the rest was not affected by the fire and used as a control. Soil samples were collected three days after the wildfire, in the absence of rain; 10 samples (20×25 cm width to a depth of 5 cm) were collected from the burnt area and 10 from the control. Samples were set out in a greenhouse where germinating seedlings were recorded, counted and identified for 17 months. Observations were also carried out twice in the field for 14 months after the wildfire by examining two permanent transects in the study area and recording all regenerating species. The results show a low correspondence between soil seed bank and aboveground vegetation: only 23% of the identified taxa appeared both in the bank and in the field observations. From these species 65% of them have dispersal types like autochory or barochory, that is they generally fall near the mother plant. In the identified species as a whole, therophytes and hemicryptophytes dominate in comparison with chamaephytes, phanerophytes and geophytes; this also applied to the herbaceous species in comparison with the woody ones. Potentially soil possesses an important seed bank, which contributes poorly to the vegetation recovery after fire.

Heathland, post-fire recovery, Spain, shrubland, fire, autochory, barochory

119. Venable, D. L., and L. Lawlor. 1980. Delayed germination and dispersal in desert annuals; escape in space and time. *Oecologia* **46**:272-282.

A model is developed to consider the interplay between dispersibility and delayed germination in desert annuals. The model explores the effect of low levels of dispersal, considered realistic for annual plants, on optimal germination fractions. The model also demonstrates the effect of the amount and accuracy of “predictive” (responsive to the environment) dormancy on the optimal innate germination fraction (not responsive to environmental conditions). Optimal germination fraction is found to be very sensitive to changes in dispersibility especially at the limited dispersibilities that are realistic for annual plants. As dispersibility increases, optimal germination fraction increases. If plants make two kinds of seeds with differing dispersibility, reproduction is maximized if the low dispersal seeds have quick germination. If dormancy mechanisms permit seeds to germinate when environmental conditions allow successful maturation, and remain dormant when environmental conditions do not permit successful maturation, what fraction of seeds should remain dormant under predicted good conditions as a hedge against inaccurate prediction of the environment? If environmental cues that break dormancy are uncorrelated with environmental conditions that permit successful maturation, predictive dormancy has little or no effect on the optimal innate germination

fraction. When predictive dormancy lowers the probability of germinating when environmental conditions preclude successful maturation, the optimal innate germination fraction increases with increasing germination control by predictive dormancy. With a moderate degree of germination control by predictive dormancy, the optimal innate dormancy is still sensitive to changes in dispersal in the low dispersal ranges characteristic of annual plants. Evidence is presented from plant species that have both dispersal and germination dimorphisms to support the predicted correlation of high germination fractions with high dispersal.

Deserts, annual species, seed dispersal, spatial variability, temporal variability, germination, germination cues, dormancy

120. Venable, D.L., C.E. Pake and A.C. Caprio. 1993. Diversity and coexistence of Sonoran Desert winter annuals. *Plant Species Biology* 8:207-216.

Annual plants make up ca. 50% of local floras in the Sonoran Desert. As with most plant communities, there is no shortage of potential coexistence generating mechanisms, and several mechanisms are likely contributors to coexistence at different spatial scales in the Sonoran Desert, e.g. spatial heterogeneity and the behaviors of predators and grazers. The authors explore one mechanism of likely importance for desert annuals: temporal environmental variation. It is widely recognized that coexistence is promoted by temporal variation if species such as desert annuals have “temporal niches” in the sense that each has years in which it out-performs the others. It is usually suggested that some resistant life-history stage, such as a seed bank, is also necessary to buffer each species from the negative population dynamic impact of unfavorable years. Using ten years of demographic data, the authors document the large year-to-year variation in population dynamics of desert annuals and show that ten species respond differently to temporal variation. Competition experiments document reversals in competitive superiority. Also, all species have a between-year seed bank, such that only a proportion of the seed bank germinates in any given year. Thus this system meets the authors’ intuitive requirements for variance-based coexistence. Dynamic models of this system demonstrate that subtle aspects of the species biology determine whether coexistence criteria are actually met. Specifically, variable germination fractions are required and coexistence is most readily favored with “predictive” germination. Germination fractions in this system do vary among years in a species specific fashion. Also, for the three years of available data, germination was predictive, in that each species had greater germination fractions in years of greater demographic success. Thus all of the population dynamic elements necessary for temporal variance mediated coexistence seem to be present in this system.

Sonoran Desert, coexistence, desert annuals, population dynamics, seed bank, temporal variance, spatial variability, germination

121. Vieno, M., M. Komulainen, and S. Neuvonen. 1993. Seed bank composition in a subarctic pine-birch forest in Finnish Lapland: Natural variation and the effect of simulated acid rain. *Canadian Journal of Botany* 71:379-384.

The seed bank composition and seedling densities were determined for a subarctic pine-birch forest. Samples (12 x 12 cm) were taken from plots that had received sulphuric acid and (or) nitric acid irrigation of pH 3 for 5 years and from irrigated control plots.

The average seedling density per plot calculated from seedbank samples was 912/m², varying from 191 to 5240. All the main aboveground taxa were present in the emerging seedlings with *Betula* sp. and *Empetrum nigrum* ssp. *hermaphroditum* being dominant. Other common seed-bank species included *Vaccinium uliginosum*, *Vaccinium vitis-idaea*, and *Festuca ovina*. Acid treatment did not have any significant impact on the composition of the seed bank or on germinative capacity in general. These findings indicate the existence of a viable soil seed bank in northern subarctic forests and the persistence of viability in spite of moderate acid deposition.

Acid rain, subarctic forest, seedling, Finland

122. Vose, J. M., and A. S. White. 1987. Processes of understory seedling recruitment 1 year after prescribed fire in an Arizona ponderosa pine community. *Canadian Journal of Botany* **65**:2280-2290.

The authors monitored seed rain, buried seed germination, and vegetative reproduction to determine the processes of understory species seedling recruitment after prescribed fire in an Arizona ponderosa pine (*Pinus ponderosa*) stand. Stands were burned with both backing and strip head fires. These fires were restricted to surface fuels, with fuel consumption ranging from 25 to 95% and total heat yield ranging from 1,600 to 42,082 kJ/m². They identified seed rain from surviving plants the year after burning, as well as residual seeds surviving the burn, as being the major contributors of propagules for recruitment of herbaceous seedlings. Several seedlings were present in both the early-spring and late-fall inventory. The authors hypothesize that the early recruitment was mainly due to germination of seeds immediately after burning or early the next spring and that seed rain from surviving plants provided propagules for seedlings detected in the late-fall inventory. The pattern of seed rain reflected the phenologies of cool-season and warm-season plants. Buried seed populations were not found to be an important source of new seedlings. *Ceanothus fendleri* was the only species to sprout prolifically after burning.

Arizona, ponderosa pine, Pinus ponderosa, fire, sprouting, Ceanothus fendleri, seed rain

123. Warr, S.J., M. Kent and K. Thompson. 1994. Seed bank composition and variability in five woodlands in south-west England. *Journal of Biogeography* **21**:151-168.

This paper examines the species composition and variability of the seed banks associated with four lowland woodlands and one upland woodland in south-west England. The sites studied are conifer plantations and neglected and coniferized coppice. The sampling covers a range of stand types, stand ages and management systems, on both acidic and basic soils. Within and between site comparisons are made of buried seed densities and of numbers of species present in both seed banks and ground flora. These are then compared with other woodland seed bank studies. The depth distribution of seeds in the soil at the five sites is discussed. The final discussion focuses on the species generally present in and absent from woodland seed banks and the effects of coniferization and neglect.

Lowland woodlands, coniferization, neglected coppices, species diversity, south-west England

124. Whipple, S. A. 1978. The relationship of buried, germinating seeds to vegetation in an old-growth Colorado sub-alpine forest. *Canadian Journal of Botany* **56**:1505-1509.

Species of buried, germinating seeds and species occurring in the vegetation are compared for two Colorado subalpine forest stands, one dry and one mesic, both over 325 years old. The total numbers of seeds found were small and the correspondence with species in the vegetation was poor. This is consistent with reports from other old-growth forests and may be accounted for by a combination of low seed input and rapid loss of viable seeds from the soil reservoir for old-growth forest species.

Colorado, old-growth forest, sub-alpine forest

125. Wienk, C., C. H. Sieg, and G. R. McPherson. 2004. Evaluating the role of prescribed burning, overstory reduction, and soil seed banks in restoring ponderosa pine stands in the Black Hills, South Dakota. *Forest Ecology and Management* **192**:375-393.

Pinus ponderosa Laws. (ponderosa pine) forests have changed considerably during the past century, partly because recurrent fires have been absent for a century or more. A number of studies have explored the influence of timber harvest or burning on understory production in ponderosa pine forests, but study designs incorporating cutting and prescribed burning in an experimental framework are needed to identify mechanisms responsible for the observed changes. In this study, the authors first characterized the disturbance history and the soil seed bank of a ponderosa pine stand in the northern Black Hills. They then experimentally addressed the effects of prescribed burning and overstory reduction on understory vegetation. Before Anglo settlement of the area, the mean fire interval was 14 years and no fires were recorded after 1879. Cessation of fires, prolific regeneration of ponderosa pine, and subsequent logging in 1903 have led to a very dense, even-aged ponderosa pine stand with very little understory vegetation and very few viable seeds in the soil seed bank. Only 57 individual plants, or 186 seeds/m², emerged from 1080 soil samples. Response of understory vegetation during the first growing season after application of treatments was sparse, with no significant treatment effect. There were, however, significant treatment effects during the second growing season. Total understory biomass ranged from 5.8 kg/ha on untreated plots to 1724 kg/ha on clearcut, unburned plots. Herbaceous dicots comprised over 90% of total understory biomass. Both understory species richness and evenness responded to treatments, but understory woody plant density did not respond to either treatment. Paucity of viable seeds in the soil seed bank does not appear to constrain recruitment of understory vegetation in dense ponderosa pine forests of South Dakota.

South Dakota, fire history, Pinus ponderosa, ponderosa pine, fire, stand age

126. Wills, T.J. and J. Read. 2002. Effects of heat and smoke on germination of soil-stored seed in a south-eastern Australia sand heathland. *Australian Journal of Botany* **50**(2): 197-206.

Various fire-related agents, including heat, smoke, ash and charred wood, have been shown to break dormancy and promote germination of soil-stored seed in a broad range of species in mediterranean-type systems. However, relatively little work has been conducted in south-eastern Australian heathlands. This study examined the effects of heat and smoked water on germination of the soil seed bank in a mature sand heathland within the Gippsland Lakes Coastal Park, in south-eastern Australia. Heat was clearly the most

successful treatment for promoting seed germination, followed by smoked water, then controls, with 55% of species present in the germinable soil seed bank requiring a heat or smoke stimulus to promote seed germination. Mean species richness of the germinable soil seed bank was found to be significantly higher in heat-treated soil than in smoke and control treatments. Seedling density of heat-treated soil was almost 10 times that of controls, while smoke-treated soil was almost five times that of controls. Seedling emergence was fastest in heat-treated soil, followed by smoke and control soils. Of the species found in the soil seed bank, 25% were absent from the extant vegetation, suggesting the existence of post-fire colonisers in the soil seed bank. The results have implications for the design of soil seed bank experiments and the use of fire as a tool in vegetation management.

Australia, heathland, heat, smoke, ash, charred wood, dormancy, Mediterranean systems, seedling density, fire

127. Young, J. A., R. A. Evans, and G. J. Cluff. 1987. Seeding on or near the surface of seedbeds in semiarid environments. Pages 57-61 In G. W. Frazier and G. W. Evans, editors. Proceedings of symposium: seed and seedbed ecology of rangeland plants; 1987 April 21-23; Tucson, Arizona. Washington, D.C.: Department of Agriculture, Agricultural Research Service.

Moisture and temperature relations interact to make it difficult for seeds to germinate on the surface of seedbeds. The exposed portion of the seed loses moisture if there is a negative gradient to the atmosphere. At the same time, moisture uptake from the substrate is limited by the points of contact with the seed coat.

Semi-arid environments, rangeland, soil moisture, seeding, germination

128. Zabinski, C., T. Wojtowicz, and D. Cole. 2000. The effects of recreation disturbance on subalpine seed banks in the Rocky Mountains of Montana. Canadian Journal of Botany **78**:577-582.

The authors investigated the soil seed bank in a subalpine ecosystem with patchy disturbance from camping. Soil cores were collected from three site types, heavily impacted, lightly impacted, and undisturbed, that differed in area of bare ground and depth of surface organic matter. They hypothesized that the density and composition of the seed bank would vary with depth of surface organic matter and distance from established vegetation. Seedling emergence was determined in the greenhouse. Seed density was significantly lower on disturbed sites, averaging 441 seeds/m² on heavily impacted sites, 1495 seeds/m² on lightly impacted sites, and 4188 seeds/m² on undisturbed sites. Seed density declined exponentially with distance from established vegetation and increased with depth of surface organic matter. The number of species present did not vary across site types, but 10 species that occurred on lightly impacted and undisturbed sites were not present on heavily impacted sites. The authors concluded that disturbance that causes removal of surface organic matter can affect natural revegetation by lowering the density of propagules and affecting the species represented in the seed bank.

Subalpine, Rocky Mountains, patchy disturbance, recreation impacts.

129. Zammit, C. A., and P. H. Zedler. 1988. The influence of dominant shrubs, fire, and time since fire on soil seed banks in mixed chaparral. *Vegetatio* **75**:175-187.

The composition and density of soil seed banks beneath co-occurring *Adenostoma fasciculatum* and *Ceanothus greggii* shrubs from three chaparral stands last burned 9, 35 and 85 years before 1986 were investigated. The overall density of seeds in the soil, as estimated by germinations under greenhouse conditions, increased with time since fire (ca. 8000 to 25000/m²). However, this increase was due entirely to the accumulation of *A. fasciculatum* seed in the soil (ca.2000/m²). In contrast, the density of *C. greggii* seed was different in each of the three stands, but was not correlated with time since fire: maximum densities were recorded from the 35 year old stand (ca. 2000/m²).

A total of 31 taxa germinated and 17 occurred in sufficient numbers to be analyzed statistically. Germinable seed densities of three herb species were not influenced by soil source (beneath *A. fasciculatum* or *C. greggii*), time since fire, or the direct effects of a controlled fire treatment. Germinable seed densities of a further nine species were significantly influenced by the elapsed time since stands last burned. The densities of four decreased and five increased. Four of the species that increased in seed density over the three stands were annuals, suggesting that the chaparral sub-canopy habitat is not as unfavorable for annuals as is often assumed. The fire treatment decreased germinable seed densities of four annual species by 40 – 70%, but increased the germinable seed densities of the shrubs *A. fasciculatum* will increase in the soil bank for at least 85 years after fire in chaparral where it is dominant. In contrast, seed reserves of *C. greggii* appear to be influenced primarily by site-specific patterns of seed production and by the intensity of post-dispersal seed predation.

Adenostoma fasciculatum, *annual*, *Ceanothus greggii*, *chamise*, *California*, *fire*,

130. Zammit, C. A., and P. H. Zedler. 1994. Organization of the soil seed bank in mixed chaparral. *Vegetatio* **111**:1-16.

Seed densities, estimated from germinations under glasshouse conditions, were determined for fire-treated and control soils sampled from north and south facing stands of mixed *Adenostoma fasciculatum* – *Ceanothus greggii* chaparral that last burned 10, 17, 36, 62, and 86 years before 1987. A total of 53 species was recorded. Total germinable seed density was not influenced by aspect nor by an experimental fire treatment, however, densities varied significantly, but not predictably, over the time since fire sequence. Species diversity was significantly lower in the 86 year old stand, but neither diversity or richness was influenced by the fire treatment. Soils from north facing slopes supported a higher species diversity overall, and seed densities of six species were significantly higher on north than on south slopes.

The authors identify two functional groups in the seed bank on the basis of the direct effects of fire on seed densities: a fire-dependent group, comprising 6 species and about 21% of the total seed bank, in which germinable densities increased after the fire treatment, and a fire-independent group, made up of 11 species and almost two-thirds of the seed bank. The fire-independent group is further separated into two: a shrub-centred sub-group (*Crassula erecta*, *Filago californica*, *Pterostegia drymarioides*, *Streptanthus heterophyllus* and *Senecio vulgaris*) tended to have larger seed banks in younger stands and was associated with canopy gaps. Overall, the soil seed assemblage from this mixed chaparral does not appear to be tightly coupled to fire-generated opportunities for

recruitment. The reason for this is that the fire-dependent group represents only 6 species. In addition, among the fire-independent species, the shrub-centred group of 5 annuals made up almost 40% of total soil seed density. This group shows ecological and taxonomic affinities with desert annuals.

Aspect, California, canopy gaps, fire, functional groups, seed germination, stand age, desert annuals

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