



**Annotated Bibliography on the
Ecology and Management of Invasive Species:**

Early Hairgrass (*Aira praecox*)

Prepared by Kersti Vaino

For the Garry Oak Ecosystems Recovery Team

February 2009

**Funding supplied by the Habitat Stewardship Program for Species at Risk of
Environment Canada**



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Peer-Reviewed Journal Articles

Best, R. J. 2008. Exotic grasses and feces deposition by an exotic herbivore combine to reduce the relative abundance of native forbs. *Oecologia* 158 (2): 319-327.

Abstract: Increased resource availability can facilitate establishment of exotic plant species, especially when coincident with propagule supply. Following establishment, increased resource availability may also facilitate the spread of exotic plant species if it enhances their competitive abilities relative to native species. Exotic Canada geese (*Branta canadensis*) introduce both exotic grass seed and nutrients to an endangered plant community on the Gulf Islands of southwestern British Columbia, Canada. I used greenhouse experiments to assess the competitive advantage of the exotic grasses relative to native and exotic forbs in this community and to test the impacts of nutrient addition from goose feces on competitive outcomes. I grew experimental communities varying in their proportion of forbs versus exotic grasses, and added goose feces as a nutrient source. I found that both native and exotic forbs produced significantly more biomass in competition with conspecifics than in competition with the grasses, and that the proportional abundance of two out of three native forbs was lowest in the combined presence of exotic grasses and nutrient addition. In a second experiment, I found that in monoculture all species of forbs and grasses showed equal growth responses to nutrients. The exotic species did not convert additional nutrients into additional biomass at a higher rate, but did germinate earlier and grow larger than the native species regardless of nutrient availability. This suggests that the exotic species may have achieved their competitive advantage partly by pre-empting resources in community mixtures. Small and late-germinating native forbs may be particularly vulnerable to competitive suppression from exotic grasses and forbs and may be at an even greater disadvantage if their competitors are benefiting from early access to additional nutrients. In combination, the input of exotic propagules and additional nutrients by nesting geese may compromise efforts to maintain native community composition in this system.

Bossuyt, B., E. Cosyns, and M. Hoffman. 2007. The role of soil seed banks in the restoration of dry acidic dune grassland after burning of *Ulex europaeus* scrub (abstract). *Applied Vegetation Science* 10 (1): 131-138.

Abstract: Question: Can the seed bank play a significant role in the restoration of plant communities of dry acidic dune grassland where fire has destroyed *Ulex europaeus* scrub? Location: Northern French Atlantic coast. Methods: One year after the fire, the seed bank and vegetation were sampled in 1 m × 1 m plots along three transects from the oldest scrub vegetation towards the grassland. Differences in species richness, seed density and contribution of ecological groups in the seed bank and vegetation along the transects were analysed. Results: Seed density and species richness in the seed bank decreased significantly from the grassland towards the centre of the scrub vegetation; 50% of the seed bank consisted of core species of the target plant community, such as *Carex arenaria*, *Aira praecox*, *Rumex acetosella* and *Agrostis capillaris*. Seeds of these species were also found in the deeper soil layers beneath the oldest scrub vegetation, indicating that they can be considered to be long-term persistent. Beneath the youngest scrub vegetation, seeds of rare satellite target species also occurred. However, no target species were established on the burned site after one year, resulting in a large discrepancy between seed bank and vegetation. Conclusions: Although the seeds present in the soil indicate that restoration of the acidic grassland based on the seed bank is possible, additional management actions such as mowing and soil disturbance may be necessary to restrict resprouting of *Ulex* and to stimulate the germination of seeds of target species in the deeper soil layers.

Didham, R. K., J. M. Tylianakis, M. A. Hutchison, R. M. Ewers, and N. J. Gemmell. 2005. Are invasive species the drivers of ecological change? *Trends in Ecology and Evolution* 20 (9): 470-474.

Abstract: Invasive species are widely accepted as one of the leading direct causes of biodiversity loss. However, much of the evidence for this contention is based on simple correlations between exotic dominance and native species decline in degraded systems. Although appealing, direct causality is not the only possible interpretation. A plausible alternative hypothesis is that exotic dominance could be the indirect consequence of habitat modification driving native species loss. In a new paper, MacDougall and Turkington now provide the first direct test of whether invasive species are the drivers of community change, or merely 'passengers' along for the environmental ride.

Keeley, J. E., M. Baer-Keeley, and C. J. Fotheringham. 2005. Alien plant dynamics following fire in Mediterranean-climate California shrublands. *Ecological Applications* 15 (6): 2109-2125.

Abstract: Over 75 species of alien plants were recorded during the first five years after fire in southern California shrublands, most of which were European annuals. Both cover and richness of aliens varied between years and plant association. Alien cover was lowest in the first postfire year in all plant associations and remained low during succession in chaparral but increased in sage scrub. Alien cover and richness were significantly correlated with year (time since disturbance) and with precipitation in both coastal and interior sage scrub associations. Hypothesized factors determining alien dominance were tested with structural equation modeling. Models that included nitrogen deposition and distance from the coast were not significant, but with those variables removed we obtained a significant model that gave an $R^2=0.60$ for the response variable of fifth year alien dominance. Factors directly affecting alien dominance were (1) woody canopy closure and (2) alien seed banks. Significant indirect effects were (3) fire intensity, (4) fire history, (5) prefire stand structure, (6) aridity, and (7) community type. According to this model the most critical factor influencing aliens is the rapid return of the shrub and subshrub canopy. Thus, in these communities a single functional type (woody plants) appears to be the most critical element controlling alien invasion and persistence. Fire history is an important indirect factor because it affects both prefire stand structure and postfire alien seed banks. Despite being fire-prone ecosystems, these shrublands are not adapted to fire per se, but rather to a particular fire regime. Alterations in the fire regime produce a very different selective environment, and high fire frequency changes the selective regime to favor aliens. This study does not support the widely held belief that prescription burning is a viable management practice for controlling alien species on semiarid landscapes.

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MacDougall, A. S. and R. Turkington. 2005. Does the type of disturbance matter when restoring disturbance-dependent grasslands? *Restoration Ecology* 15 (2): 263-272.

Abstract: The reintroduction of burning is usually viewed as critical for grassland restoration; but its ecological necessity is often untested. On the one hand, fire may be irreplaceable because it suppresses dominant competitors, eliminates litter, and modifies resource availability. On the other hand, its impacts could be mimicked by other disturbances such as mowing or weeding that suppress dominants but without the risks sometimes associated with burning. Using a 5-year field experiment in a degraded oak savanna, we tested the impacts of fire, cutting and raking, and weeding on two factors critical for restoration: controlling dominant invasive grasses and increasing subordinate native flora. We manipulated the season of treatment application and used sites with different soil depths because both factors influence fire behavior. We found no significant difference among the treatments—all were similarly effective at suppressing exotics and increasing native plant growth. This occurred because light is the primary limiting resource for many native species and each treatment increased its availability. The effectiveness of disturbance for restoration depended more on the timing of application and site factors than on the type of treatment used. Summer disturbances occurred near their reproductive peak of the exotics, so their mortality approached 100%. Positive responses by native species were significantly greater on shallow soils because these areas had higher native diversity prior to treatment. Although likely not applicable to all disturbance-dependent ecosystems, these results emphasize the importance of testing the effectiveness of alternative restoration treatments prior to their application.

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Owen, N. W., M. Kent, and M. P. Dale. 2001. Spatial and temporal variability in seed dynamics of machair sand dune plant communities, the Outer Hebrides, Scotland. *Journal of Biogeography* 28 (5): 565-588.

Abstract: Aim: The subjects of seed banks and seed rain represent comparatively neglected areas of biogeography, yet at the community scale, exhibit interesting patterns in both space and time. This paper describes the seed bank and seed rain characteristics of the machair sand dune communities of the Outer Hebrides. As well as looking at individual species distributions and variability, the seed banks and seed rain are examined in terms of their detailed subcommunity composition and its local spatial and temporal variation. The machair plant (sub)communities show extensive degrees of anthropogenic modification because of past and present agricultural management, including cultivation for cereals over wide areas and for potatoes in large numbers of 'lazy beds' or small patches. Thus over the historical period, large areas of machair have undergone regular ploughing and cultivation, which have provided the opportunity for a patchwork of secondary succession to occur. This pattern continues to the present day. Furthermore, most other non-cultivated plant (sub)communities are intensively grazed, primarily by cattle and also by sheep and rabbits. Location: South Uist, the Outer Hebrides, north-west Scotland. Methods: At two carefully selected locations, a range of these various successional subcommunities have been sampled for their seed banks, by taking cores and for their seed rain, by using specially designed traps located where each seed bank sample was removed. This paired sampling strategy allowed direct comparison of the seed bank and the seed rain. Both individual species distributions and the community assemblages of seed bank/seed rain species are examined in space and time using techniques of numerical classification [two-way indicator species analysis (TWINSPAN)] and ordination [detrended correspondence analysis (DCA)]. Results and conclusions: There is considerable heterogeneity within and between machair subcommunities in terms of seed bank and seed rain characteristics. The soil seed banks and seed rain of the agriculturally disturbed machair subcommunities are consistently more dense and more species rich than non-cultivated areas of the machair. Overall, machair seed banks are small and stable with no discernible seasonal trends in either size or species composition. In contrast, seed rain on the machair is characterized by a distinct temporal trend. Both seed banks and seed rain are potentially very poor sources of propagules for recolonization following disturbance, indicating that the majority of revegetation following anthropogenic and/or environmental interference is through vegetative reproduction.

Pakeman, R. J., J. P. Attwood, and J. Engelen. 1998. Sources of plants colonizing experimentally disturbed patches in an acidic grassland, in eastern England. *Journal of Ecology* 86 (6): 1032-1041.

Abstract: 1. The sources of propagules for regeneration in an acidic grassland were identified from analysis of differences in colonization between plots subject to surface (0-5 cm) soil disturbance and plots where surface soil had been replaced by 'seedfree' soil from deeper soil horizons (30-35 cm), and between plots with and without the removal of rabbit pellets. 2. After 1 year, 10 species had a significantly higher cover on plots where the seed bank had been left intact. These included *Agrostis capillaris* (the dominant species prior to disturbance), *Myosotis arvensis* and *Veronica arvensis*. 3. Five species, including *Sagina apetala*, *Senecio jacobaea* and *Veronica arvensis*, showed significantly higher cover on plots where rabbit pellets were left in situ. 4. From calculations it appeared that rabbit-dispersed seeds accounted for 15% of the developing higher plant cover, other means of dispersal from outside the plot accounted for 40%, and regeneration from the seed bank accounted for 45%. 5. Similar calculations suggested that three higher plant species, *Geranium molle*, *Myosotis arvensis* and *Senecio jacobaea*, appeared to depend most on non-rabbit dispersed seed for colonization of bare ground. 6. High concentrations of *Urtica dioica* in pellets contrasted with its poor establishment in the experiment. However, the other common species in the pellets, *Sagina apetala*, *Senecio jacobaea* and *Veronica arvensis*, all established in greater numbers on the plots where the pellets were not removed. 7. Seed bank content correlated well with the pattern of regeneration for *Agrostis*

capillaris, *Holcus lanatus*, *Myosotis arvensis* and *Veronica arvensis*. However, removal of the seed bank did not have a significant effect on the regeneration of either of the most common species in the seed bank, *Rumex acetosella* and *Sagina apetala*. 8. No species appeared to be reliant on only one mechanism for regeneration from seed in disturbed areas in this community.

Perchemlides, K. A., P. S. Muir, and P. E. Hosten. 2008. Responses of chaparral and oak woodland plant communities to fuel-reduction thinning in Southwestern Oregon. *Rangeland Ecology and Management* 61 (1): 98-109.

Abstract: Fire suppression has led to large fuel accumulations in many regions of the United States. In response to concerns about associated wildfire hazards, land managers in the western United States are carrying out extensive fuel-reduction thinning programs. Although reductions in cover by woody vegetation seem likely to cause changes in herbaceous communities, few published studies have reported on consequences of such treatments for native or exotic plant species. We compared vegetation and abiotic characteristics between paired thinned and unthinned chaparral and oak woodland communities of southwestern Oregon 4-7 yr posttreatment and contrasted impacts of manual vs. mechanical treatments. Herbaceous cover increased on thinned sites, but species richness did not change. Herbaceous communities at thinned sites had an early postdisturbance type of composition dominated by native annual forbs and exotic annual grasses; cover by annuals was nearly twice as high on treated as on untreated sites. Absolute and proportional cover of native annual forbs increased more than any other trait group, whereas exotic annual forbs and native perennial forbs declined. Exotic annual grass cover (absolute and proportional) increased, whereas cover by native perennial grasses did not. Shrub reestablishment was sparse after thinning, probably because of a lack of fire-stimulated germination. Manual and mechanical treatment impacts on abiotic site conditions differed, but differences in vegetation impacts were not statistically significant. Fuel-reduction thinning may have some unintended negative impacts, including expansion of exotic grasses, reductions in native perennial species cover, persistent domination by annuals, and increased surface fuels. Coupled with sparse tree or shrub regeneration, these alterations suggest that ecological-state changes may occur in treated communities. Such changes might be mitigated by retaining more woody cover than is currently retained, seeding with native perennials after treatment, or other practices; further research is needed to inform management in these ecosystems.

Pickart, A. J., L. M. Miller, and T. E. Duebendorfer. 1998. Yellow bush lupine invasion in Northern California coastal dunes I. Ecological impacts and manual restoration techniques. *Restoration Ecology* 6 (1): 59-68.

Abstract: We studied the ecological effects of the invasion of coastal dunes by *Lupinus arboreus* (yellow bush lupine), an introduced species, and used the results to develop manual restoration techniques on the North Spit of Humboldt Bay. Vegetation and soil data were collected in five vegetation types representing points along a continuum of bush lupine's invasive influence. We collected data on the number and size of shrubs, vegetation cover, and soil nutrients. One set of plots was subjected to two restoration treatments: removal of lupine shrubs only, or removal of all nonnative vegetation and removal of litter and duff. Treatments were repeated annually for four years, and emerging lupine seedlings were monitored for three years. Prior to treatment, ammonium and nitrate were found to increase along the lupine continuum, but organic matter decreased at the extreme lupine end. Yellow bush lupine was not the most significant variable affecting variation in soil nutrients. After four years, nonnative grasses, including *Vulpia bromoides*, *Holcus lanatus* (velvet grass), *Bromus* spp. (brome), and *Aira* spp. (European hairgrass), were significantly reduced in those restoration plots from which litter and duff was removed. Native species increased significantly in vegetation types that were less influenced by lupine. By the third year, soil variables differed among vegetation types but not by treatment. Bush lupine seedling emergence was higher, however, in plots receiving the litter and duff removal treatment. Based on these results, we conclude that bush lupine invasion results in

both direct soil enrichment and indirect enrichment as a result of the associated encroachment of other nonnative species, particularly grasses. Although treatment did not affect soil nutrients during the period of this study, it did reduce establishment of nonnative grasses and recruitment of new bush lupine seedlings. Restoration should therefore include litter and duff removal. In areas that are heavily influenced by lupine and contain few native propagules, revegetation is also required.

Roberts, H. A. 1986. Persistence of seeds of some grass species in cultivated soil. *Grass and Forage Science* 41: 273-276.

Abstract: Freshly collected ripe caryopses of twenty-five indigenous grasses were mixed with the top 7-5 cm of sterilized soil confined in cylinders sunk in the ground and cultivated three times yearly. There was a flush of seedlings of most species shortly after sowing, but species differed in the persistence of viable seeds. About one third, including *Bromus sterilis*, *B. hordeaceus*, *Lolium perenne* ssp. *perenne*, *Arrhenatherum elatius* and *Alopecurus pratensis*, produced few seedlings after the initial flush. Others such as *Deschampsia cespitosa*, *Holcus lanatus* and *Poa trivialis*, recognized as forming persistent seed banks in grassland soils, produced appreciable numbers of seedlings in the second year after sowing. Most persistent were species that occur as arable weeds (*Avena fatua*, *Poa annua*) or in wetlands (*Glyceria plicata*, *G. maxima*, *Alopecurus geniculatus*). Emergence from the seed bank generally followed soil disturbance but some species (*Aira praecox*, *Avena fatua*, *A. sterilis* ssp. *ludoviciana*, *Danthonia decumbens*) exhibited consistent seasonal patterns which may be associated with cyclic changes in germination requirements of the buried seeds.

Rozijn, N. A. M. G. and D. C. van der Werf. 1986. Effect of drought during different stages in the life-cycle on the growth and biomass allocation of two *Aira* species (abstract). *Journal of Ecology* 74 (2): 507-523.

Abstract: The effects of drought treatments applied in different stages of the life-cycle on the growth and allocation of biomass in the vegetative and reproductive phases of *Aira caryophylla* and *A. praecox* have been studied. Drought treatment in the vegetative phase had no effect on growth in the reproductive phase in either species. In the reproductive phase *A. praecox* grew exponentially, while *A. caryophylla* did not grow. The biomass allocation showed greater differences between the species than between the treatments, especially in the reproductive phase. The proportion of biomass allocated to reproductive organs was affected by the drought treatments. The production of caryopses was reduced by drought if it occurred in vegetative as well as in the reproductive phase. In contrast to *A. caryophylla*, *A. praecox* showed both somatic and reproductive growth after inflorescence emergence.

Online Resources

Clayton, W. D., K. T. Harman, and H. Williamson. 2008. GrassBase - The Online World Grass Flora. <http://www.kew.org/data/grasses-db.html>. The Board of Trustees, Royal Botanic Gardens, Kew.

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