

Successional Changes in Seed Banks in Abandoned Rice Fields in Gwangneung, Central Korea

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ABSTRACT: In order to understand the role of seed banks for restoration, seed banks in abandoned rice fields in the Gwangneung National Arboretum, central Korea were investigated using the seedling emergence method. The study sites represented three stages: an initial stage dominated by forbs such as *Persicaria thunbergii* and *Juncus effuses* var. *decipiens*, a middle stage dominated by *Salix*, and a late stage dominated by *Quercus aliena* and *Prunus padus* (in nearby riparian forest chosen as a reference stand). DCA ordination arranged the stands according to the number of years since abandonment. CCA ordination identified the dominant environmental variables correlated most closely with Axes 1 and 2 as Mg^{2+} (intraset correlation was 0.827) and K^+ (intraset correlation was -0.677), respectively. Species richness and diversity decreased from the initial stage ($H'=2.61$) to the middle ($H'=1.79$) and late ($H'=0.75$) stages. A total of 49 species ($/m^2$) and 18,620 seedlings ($/m^2$) emerged out of the seed bank samples. The DCA ordination and similarity analysis detected a large discrepancy between the composition of the actual vegetation and the seed bank. We conclude that the contribution of seed bank to restoration is low. However, seed bank may help the recovery of forbs after disturbance. Some of our results are consistent with the tolerance model of succession whereas others follow the trajectory of the facilitation model. More research on succession will be required to understand the underlying mechanisms.

Key words: Abandoned rice fields, Gwangneung, Restoration, Seed bank, Succession

INTRODUCTION

In Asian countries where people depend on rice as a food source, most floodplains of rivers and streams have been transformed to rice fields (Lee et al. 2006). Until the late 20th century, rice fields were rarely abandoned because rice production was not adequate to meet demand. In recent years, however, people are moving in large numbers from rural areas to urban areas (Lee et al. 2002). As a result, inaccessible and terraced rice fields are being increasingly abandoned. Only highly productive and easily accessible rice paddy remains in cultivation (Tasser et al. 2006). Therefore, frequent opportunities for habitat restoration occur as a result of land abandonment (Young 2000).

Seed banks are defined as the ungerminated but viable seeds that can remain dormant for periods ranging from several years to several decades in the soil until environmental conditions are appropriate for germination (Grime 1989, Simpson et al. 1989). Plants usually delay germination by permitting their seeds to enter a dormant state, forming a seed bank (Baskin and Baskin 1998). The species composition of seed banks is affected by the established

vegetation, seed longevity, regeneration strategies of individual species, and surrounding environmental conditions (Harper 1977). Seed banks can significantly affect vegetation diversity, revegetation of disturbed areas, and initial vegetation composition. Thus, they have been examined in studies of succession, vegetation history, and seed germination properties (van der Valk and Davis 1979, Haag 1981, Galatowitsh and van der Valk 1996, Brock and Rogers 1998, Harwell and Havens 2003). Seed banks are an important factor affecting the reestablishment of vegetation in disturbed areas (e.g. van der Valk and Pederson 1989, Chambers and MacMahon 1994, Zabinski et al. 2000). Nowadays, the study of seed banks is an important feature of the basic surveys for wetland restoration (Kim and Ju 2005). Understanding the role of seed banks is also important in the design of restoration projects (Richter and Stromberg 2005).

In Korea, there have been very few studies of the abandoned rice fields. Lee et al. (1998) clarified the vegetation sere and the underlying mechanisms by analyzing soil environmental factors and vegetation in abandoned rice fields at different time intervals after abandonment, and Lee et al. (2002) clarified the regenerative aspects of succession as a tool for habitat restoration.

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Studies of seed banks have also been very rare in Korea. Kim and Ju (2005) studied soil seed banks in an ecological preserve area in Seoul and Kim and Lee (2005) clarified the role of seed banks in the establishment of vegetation in landfills.

The purposes of this paper are to 1) analyze the species diversity and composition of seed banks in abandoned rice fields, 2) examine the relationship between the soil seed bank and the actual vegetation, 3) verify successional changes, and 4) evaluate the possibility of using the existing seed bank for restoration.

STUDY AREA AND METHODS

The study area was located in the Gwangneung National Arboretum, central Korea (Fig. 1, 37° 42' 36" ~ 47' 41" N and 127° 8' 20" ~ 11' 58" E). This area is in a cool-temperate broadleaved forest region (Lim et al. 2003). Mean annual precipitation and temperature were 1,365 mm and 11.3°C, respectively (Forest Practice Research Center, internal data file). The study area includes fields that have been abandoned for various numbers of years. We examined fields in three developmental stages: an initial stage dominated by forbs such as *Persicaria thunbergii* and *Juncus effuses* var. *decipiens*, a middle stage dominated by *Salix*, and a late stage, exemplified by a nearby riparian forest chosen as a reference stand, dominated by *Quercus aliena* and *Prunus padus*. All study sites in the three stages of succession are located within 200 m of each other, at an elevation of 100 m above sea level. Therefore, those sites do not vary substantially in environmental factors except developmental stage.

Vegetation surveys were performed from April to September 2006 in 29 plots, including 10 study plots in the initial stage, 9 in the middle stage, and 10 in the late stage. Quadrats of 10 × 10 m and 1 × 1 m were used for stands dominated by trees and forbs, respectively. Field surveys were carried out using quadrat and point methods in stands dominated by trees and forbs, respectively (Barbour et al. 1999).

Seed bank data were collected using the seedling emergence method. We sampled the soil in March 2006 before germination occurred. A total of 75 samples were obtained including 25 samples from each stage. After removal of the litter layer, topsoil was collected using a soil auger with a volume of 157 cm³ (19.625 cm² surface area × 8 cm depth) from ten random points within the quadrats (1 × 1 m) and those ten soil cores were pooled to produce one sample (ter Heerd et al. 1996). The aboveground vegetation at the sampling sites was also recorded. The samples were not sieved, because the coarse materials include seeds (Kim and Lee 2005). The soil samples were thinly spread on a mixture of vermiculate, peat moss, and perlite in plastic trays (length 49 cm, width 33 cm, depth 8 cm). The trays were randomly placed in a plant nursery in Seoul

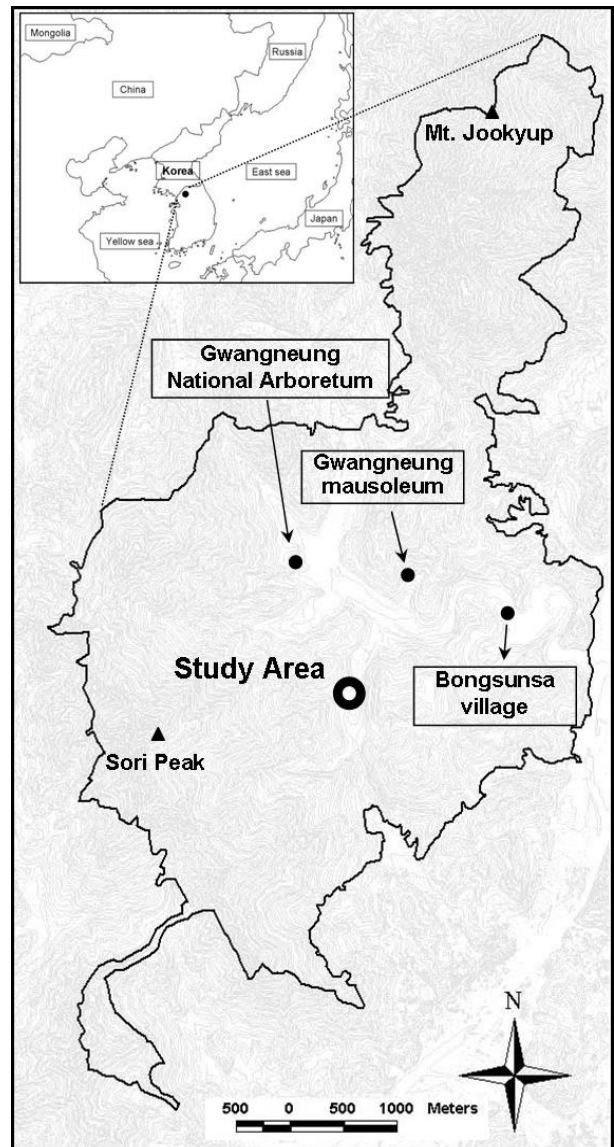


Fig. 1. Map showing the study areas. The marginal line indicates the boundary of Gwangneung national arboretum.

Women's University to prevent invasion of other seeds from outside. Seedlings that emerged were identified to the species or genus level, and were removed after counting to promote the emergence of additional seedlings. If immediate identification was impossible, seedlings were transplanted to other pots to allow further growth.

Differences in species composition among study sites were analyzed with Detrended Correspondence Analysis (DCA, Hill 1979) and the relationship between species composition and soil properties was analyzed with Canonical Correspondence Analysis (CCA, ter Braak 1986) by using PC-ORD 4 (McCune and Mefford 1999). For the matrix of importance values, we conducted relativization by species column, and the results were subjected to Detrended Corre-

spondence Analysis (DCA) for ordination (Hill 1979). Nomenclature followed Lee (1985), Park (1995), Ryang et al (2004), and the Korean Plant Names Index (2003).

Similarity between the actual vegetation and the seed bank was calculated using Sorensen's similarity index (IS_s ; Greig-Smith 1983):

$$IS_s = (2C/A + B) \times 100$$

where A is the number of species in the vegetation, B is the number of species in the seed bank and C is the number of species common to both.

Soil samples were collected and vegetation surveys were conducted in 29 plots. In each sample plot, five soil cores were taken from the top 10 cm. Soil samples were dried under shaded conditions in the laboratory for 10 days and sieved through 2 mm mesh. Before drying, a part of the soil samples was used to measure soil moisture content. Soil moisture content was calculated from the percentage of pure water weight of fresh soil, using the following equation:

$$SM (\%) = \frac{S_f - S_d}{S_f} \times 100$$

(S_f : soil weight before drying, S_d : soil weight after drying)

The soil pH was measured with a bench top probe after mixing the soil with distilled water (1:5 ratio, w/v) and filtering the extract (Whatman No. 44 paper). The soil organic matter content was obtained by measuring the loss after ignition for four hours in a muffle furnace at 400 °C. Total nitrogen was measured using the micro-Kjeldahl method (Jackson 1967). Exchangeable K^+ , Ca^{2+} and Mg^{2+} contents were measured from an extract in 1N ammonium acetate solution at pH 7.0 by ICP (inductively coupled plasma atomic emission spectrometry; Shimadzu ICPQ-1000; National Institute of Agricultural Science and Technology 2000).

RESULTS

Change of Species Composition

The eigenvalues of Axes 1 and 2 from the DCA ordination based on the seed bank data were 0.493 and 0.188, respectively (Fig. 2). Older abandoned rice fields tended to fall on the left of Axis 1, and younger ones were on the right of Axis 1. The dominance of *Pilea mongolica* and *Bidens frondosa* increased from left to right on Axis 1, whereas that of *Carex neurocarpa* and *Pimpinella brachycarpa* decreased. The dominance of *Lipocarpha microcephala* increased from bottom to top on Axis 2, whereas that of *Eragrostis multicaulis* and *Stellaria alsine* var. *undulata* decreased.

The eigenvalues of Axes 1 and 2 from the CCA ordination based on the seed bank and soil data were 0.458 and 0.081, respectively (Fig. 3). The arrangement of stands was closely correlated with the

order of Mg^{2+} , total-N, pH, organic matter, K^+ , and Ca^{2+} . Mg^{2+} showed the highest correlation with Axis 1, and K^+ showed the highest correlation with the Axis 2 (Table 1). Soil moisture content tended to decrease from the initial stage to the late stage (Fig. 4).

Changes in Species Diversity

Species rank-abundance curves and Shannon indices of the seed

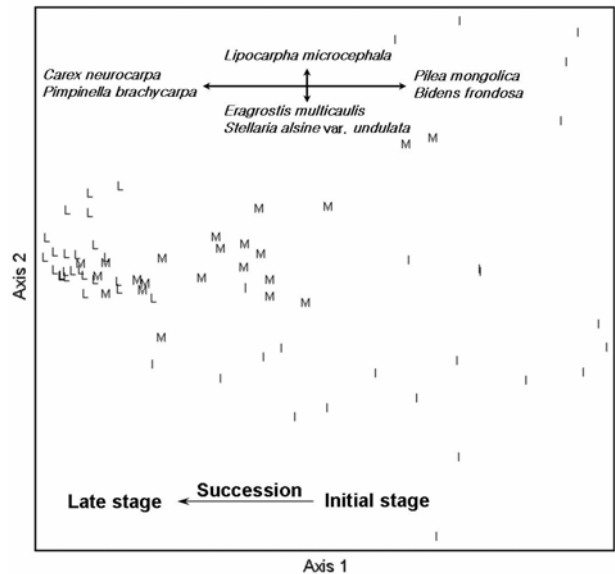


Fig. 2. DCA ordination of stands based on the seed bank data collected in rice fields of three successional stages, including the initial (I), middle (M), and late stages (L).

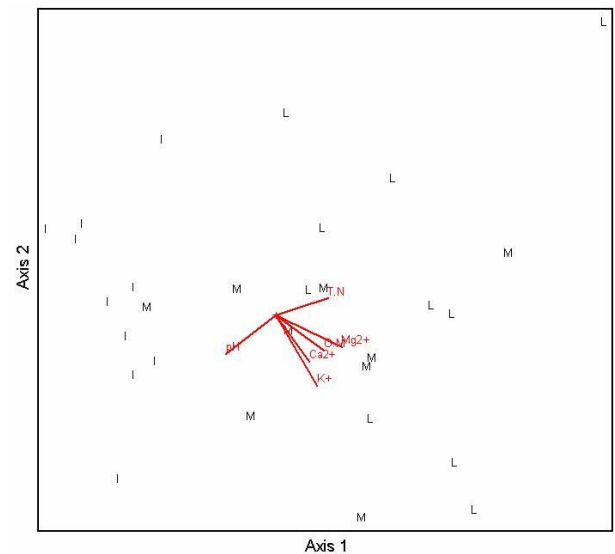


Fig. 3. CCA ordination based on seed bank and soil data collected in the rice fields of three successional stages, including the initial (I), middle (M), and late stages (L).

Table 1. Intraset correlations for six soil variables

Variable	Axis 1	Axis 2
pH	-0.623	-0.374
Organic matter	0.601	-0.337
Total-N	0.655	0.163
K ⁺	0.519	-0.677
Ca ²⁺	0.422	-0.449
Mg ²⁺	0.827	-0.304

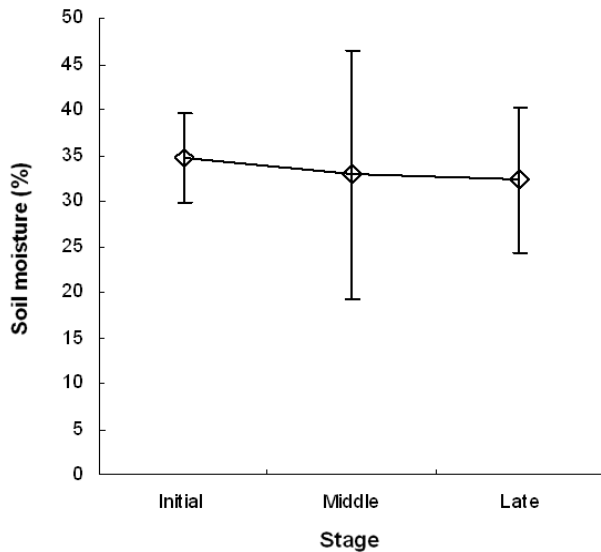


Fig. 4. Soil moisture contents based on soil data collected in abandoned rice fields in the initial, middle, and late stages of succession.

banks are shown in Fig. 5. The initial stage showed the highest species richness and diversity ($H'=2.61$), and species richness and diversity decreased in the middle ($H'=1.79$), and late ($H'=0.75$) stages.

The total number of species in the seed bank and the number of seedlings appearing in the seed bank at each stage are shown in Fig. 6. A total of 49 species /m² and 18,620 /m² seedlings emerged. The highest number of species and seedlings germinated in the initial stage, and germination rates decreased with advances in the successional stage.

A Comparison of Species Composition Based on the Seed Bank and Actual Vegetation Data

Fig. 7 shows the result of DCA ordination based on data from the seed bank and the woody vegetation. Eigenvalues of Axes 1 and 2 were 0.987 and 0.750, respectively. On Axis 1, there is a clear separation between on the seed bank and woody vegetation data.

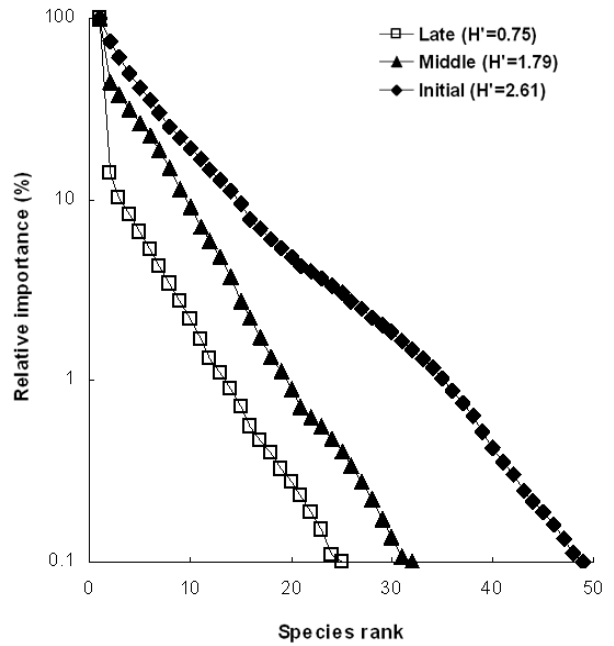


Fig. 5. Rank-abundance curves and Shannon indices (H') based on seed bank data collected in abandoned rice fields in the initial (I), middle (M), and late (L) stages of succession.

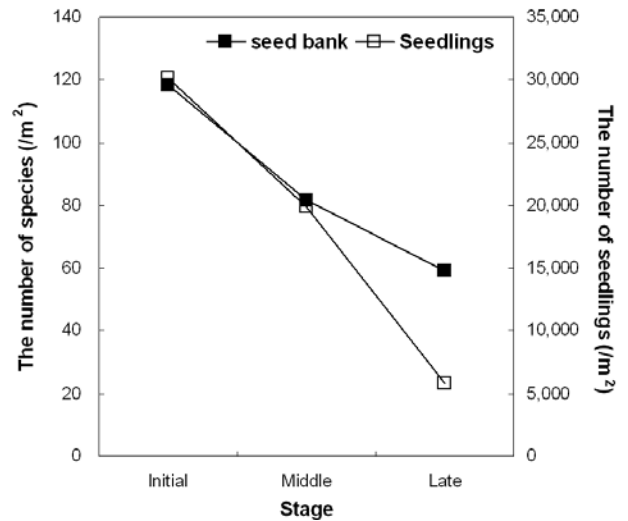


Fig. 6. Changes in the number of species represented in the seed bank and seedlings with advancing successional stage from the initial (I) to the middle (M) and late (L) stages.

Stands based on seed bank data were concentrated on the left on Axis 1 and those using woody vegetation data tended to be arranged on the right of Axis 1. The dominance of *Quercus aliena* and *Styrax obassia* increased from the left to the right on Axis 1, whereas that of *Persicaria conspicua* decreased. The dominance of *Q. aliena* and *S. obassia* increased from the bottom to the top on Axis

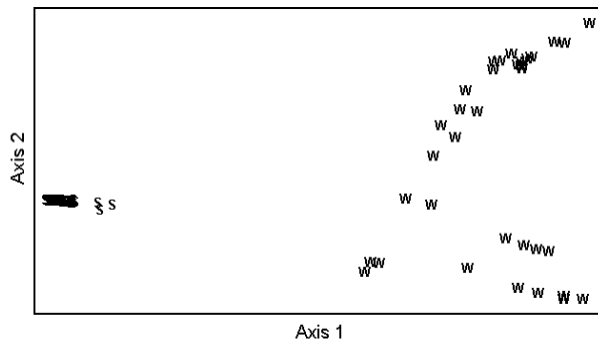


Fig. 7. DCA ordination of stands based on woody vegetation and seed bank data. W: woody vegetation, S: seed bank.

2, whereas that of *S. gracilistyla* and *S. integra* decreased.

Similarly, the DCA ordination based on seed bank and herbaceous vegetation data resulted in a clear separation between stands according to the source of the data (Fig. 8). However, the distance between stands based on the seed bank and herbaceous vegetation was shorter than that for the seed bank and woody vegetation. The Eigen values of Axes 1 and 2 were 0.953 and 0.483, respectively. Stands based on seed bank data were distributed on the left of Axis 1 and those from herbaceous vegetation data tended to be located on the right side of Axis 1. The dominance of *Persicaria filiformis* and *Corydalis ochotensis* increased from the left to the right on Axis 1, whereas that of *Galinsoga ciliate* and *Sagittaria pygmaea* decreased. The dominance of *Echinochloa crusgalli* var. *frumentacea* and *Adenocaulon himalaicum* increased from the bottom to the top on Axis 2, whereas that of *Athyrium yokoscense* and *Desmodium podocarpum* var. *oxyphyllum* decreased.

Based on the Sorensen's similarity indices, the similarity of the species composition in the seed bank and actual vegetation for the three stages ranged from 2.1% to 29.3%, and similarity decreased from the initial to the later stages (Table 2).

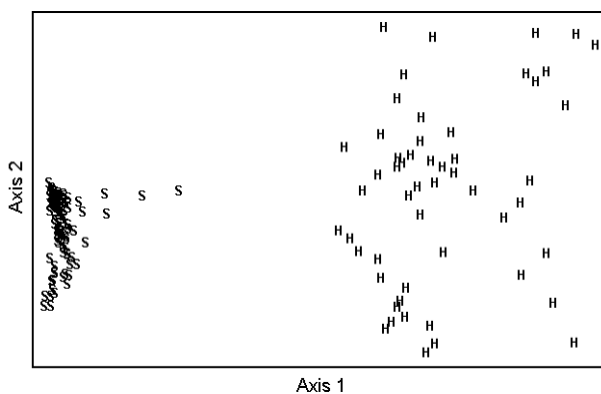


Fig. 8. DCA ordination of stands based on herbaceous vegetation and seed bank data. H: herbaceous vegetation, S: seed bank.

Table 2. A comparison of similarities between actual vegetation and seed bank data in abandoned rice fields of three successional stages

Stage	I	M	L
Similarity (%)	29.3	10.8	2.1

I: initial stage, M: middle stage, and L: late stage.

DISCUSSION

Analysis and Evaluation of Seed Banks

Seed banks were rich during the early stages of stand development or just after abandonment as shown in Figs. 5 and 6 (Oosting and Humpreys 1940, Livingston and Allesio 1968, Roberts et al. 1984). However, there was low similarity between the actual vegetation and the seed bank (Table 2, Figs. 7 and 8), which is similar to the results from other studies (Douglas 1965, Johnston et al. 1969, Thompson and Grime 1979, Rabinowitz 1981, Pratt et al. 1984, Hassan and West 1986, Bertiller 1992, Warr et al. 1994, Jutila 1998, Falinska 1999, Olano et al. 2002, Bossuyt et al. 2002, Kim and Lee 2005, Solomon et al. 2006, Roovers et al. 2006, Godfroid et al. 2006). These results imply that there is little similarity between the vegetation that may be recruited from the seed bank and the actual vegetation (Roovers et al. 2006).

The forest species that constitute the late successional stage are usually rare in the seed bank (Olano et al. 2002). Even in stable plant communities with a long history, many species appearing in the vegetation are absent from the seed bank (Thompson 2000). This could be due to the fact that their reproductive capacity is limited, while their large seeds are vulnerable to predation and decay, and have restricted longevity (Bekker et al. 1998). Another reason for the rich flora of early successional species is that early successional species produce overwhelming numbers of long-living seeds, whereas most forest species form a transient seed bank (Roovers et al. 2006). In addition, the abundance of earlier successional species in the seed bank could be due to the suppression of seedling emergence by litter in old forests (Amiaud and Touzard 2004).

Consideration on Succession Model Perspectives

Connell and Slatyer (1977) proposed three models or mechanisms by which succession may be driven. The facilitation model proposes that early successional species may improve their environments in such a way that new species of the next seral stage are at a competitive advantage and thus supplant species from the previous stage. The driving force behind succession in this model, therefore, is the reaction of the site to the plants growing on it. The tolerance model is a revision of Egler's IFC (Initial Floristic Com-

position) model, which suggests that all pioneer, seral, and climax species are present initially following disturbance. Some germinate and become established quickly, others germinate quickly but grow more slowly for a longer period, and others may become established still later. Larger, longer-lived, slower-growing species eventually outcompete small pioneer species and thus community dominance shifts and succession proceeds. The inhibition model de-emphasized biotic interactions such as competition, and suggested that all species resist invasion by competitors by preempting space and continue to inhibit invasion until they die or are damaged (Barbour et al. 1999).

Our results show that although all species did not emerge in the initial stage, species of the next stage were already invading in the current stage (Figs. 2 and 3). This result implies that the process of succession is continuous and thereby supports the tolerance model. But changes in the species composition were closely related to changes in the soil environment, which follows the trajectory of the facilitation model (Fig. 3). In fact, Walker and Chapin (1987) characterized the Connell-Slatyer models as simplistic, and suggested that succession is an inherently complex phenomenon driven by interactions among numerous mechanisms. Accordingly, no single model is sufficient to interpret our results for succession in abandoned rice fields. More studies of succession will be required to develop adequate models to explain the mechanisms driving plant succession.

Implication of Seed Banks for Restoration

Ecological restoration is the return of a degraded ecosystem to a close approximation of its original state before disturbance (National Research Council (NRC) 1992). The goal of ecological restoration is to reestablish a functionally complete ecosystem (Stanturf et al. 2001), and methods for restoration are different depending on the degree of disturbance. There are three methods for ecosystem restoration: allowing natural recovery as a passive form of restoration, minimal intervention to accelerate succession, and constructive intervention such as planting trees and sowing seeds (Bradshaw 1984).

Knowledge about the seed bank in these abandoned paddy fields will be crucial in guiding ecological restoration efforts. Seed banks can speed up secondary succession on abandoned bare soils such as old fields and some ruderal urban sites (Prach and Pyšek, 2001). Some studies have reported that the lack of desirable seeds is the key limiting factor when cultivated land is restored to its original grassland with diverse plant communities (Pywell et al. 2002, Walker et al. 2004). Our data on seed banks in abandoned rice fields indicate that herbaceous species are abundant but woody plants are very restricted. Identifying critical constraints is often the first step in ecological restoration of degraded ecosystems (Zhan et al. 2007).

Table 3. Total number of seeds and the number of *Salix* species seeds emerging in three stages of succession

	I	M	L
The number of <i>Salix</i> seedlings (/m ²)	43	155	0
Total number of seedlings (/m ²)	30,111	19,924	5,825

I: initial stage, M: middle stage, and L: late stage.

The DCA ordination indicated that the abandoned rice fields experienced successional change over time after abandonment (Figs. 2 and 3), but both the number of species and seeds decreased with advancing succession. Moreover, the numbers of the representative woody plant, *Salix* species, in the abandoned rice fields were highest in the middle stage and then very low in the late stage, when no *Salix* seedlings emerged. In addition, there was a large discrepancy between the species composition of the seed bank and that of the actual vegetation (Table 3). We conclude that the seed bank can be a useful source for the recovery of annual species following disturbance (Baskin and Baskin 1980); however, it is insufficient for the restoration of woody species. We suggest that restoration of abandoned rice fields can be accelerated by introducing *Salix* species, which are usually easy to establish with cuttings.

ACKNOWLEDGMENTS

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LITERATURE CITED

- Amiaud B, Touzard B. 2004. The relationships between soil seed bank, aboveground vegetation and disturbances in old embanked marshlands of Western France. *Flora* 199: 25-35.
- Barbour MG, Burk JH, Pitts WD, Gilliam FS, Schwartz MW. 1999. *Terrestrial Plant Ecology*. 3rd Ed. Addison Wesley Longman, New York.
- Baskin CC, Baskin JM. 1998. *Seed-ecology, Biogeography and Evolution of Dormancy and Germination*. Academic Press, London.
- Baskin JM, Baskin CC. 1980. Role of seed reserves in the persistence of a local population of *Sedum pulchellum*: a direct field observation. *Bull Torrey Bot Club* 107: 429-430.
- Bekker RM, Bakker JP, Grandin U, Kalamess R, Milberg P, Poschold P, Thompson K, Willems JH. 1998. Seed size and vertical distribution in the soil: indicators of seed longevity. *Funct Ecol* 12: 834-842.
- Bertiller MB. 1992. Seasonal variation in the seed bank of a Patagonian grassland in relation to grazing and topography. *J Veg Sci* 3: 47-54.
- Bossuyt B, Heyn M, Hermy M. 2002. Seed bank and vegetation com-

- position of forest stands of varying age in central Belgium: consequences for regeneration of ancient forest vegetation. *Plant Ecol* 162: 33-48.
- Bradshaw AD. 1984. Ecological principles and land reclamation practice. *Landscape Plan* 11: 35-48.
- Brock MA, Rogers KH. 1998. The regeneration potential of the seed bank of an ephemeral floodplain in South Africa. *Aquat Bot* 61: 123-135.
- Chambers JC, MacMahon JA. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. *Ann Rev Ecol Syst* 25: 263-292.
- Connell JH, Slatyer RO. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am Nat* 111: 1119-1124.
- Douglas G. 1965. The weed flora of chemically-renewed lowland swards. *J Brit Grassland Soc* 4: 189-194.
- Falinska K. 1999. Seed bank dynamics in abandoned meadows during a 20-years period in the Bialowieza National Park. *Ecology* 87: 461-475.
- Galatowitsh SM, van der Valk AG. 1996. The vegetation of restored and natural prairie wetlands. *Ecol Appl* 6: 102-112.
- Godefroid S, Phartyal SS, Koedam N. 2006. Depth distribution and composition of seed banks under different tree layers in a managed temperate forest ecosystem. *Acta Oecol* 29: 283-292.
- Greig-Smith P. 1983. *Quantitative Plant Ecology*. Blackwell Scientific Publications, Oxford, pp 171-226.
- Grime JP. 1989. Seed banks in ecological perspective. In: *Ecology of Soil Seed Banks* (Leck MA, Parker VT, Simpson RL, eds). Academic Press, London, pp 15-22.
- Haag RW. 1981. Emergence of seedlings of aquatic macrophytes from lake sediments. *Can J Bot* 61: 148-156.
- Harper JL. 1977. *The Population Biology of Plants*. Academic Press, New York.
- Harwell MC, Havens KE. 2003. Experimental studies on the recovery potential of submerged aquatic vegetation after flooding and desiccation in a large subtropical lake. *Aquat Bot* 77: 131-151.
- Hassan MA, West NE. 1986. Dynamics of soil seed pools in burned and unburned sagebrush semi desert. *Ecology* 67: 269-272.
- Hill MO. 1979. DECORANA - A FORTRAN Program for Detrended Correspondence Analysis and Reciprocal Averaging. Cornell University Ithaca, New York.
- Jackson MC. 1967. *Soil Chemical Analysis*. Prentice-Hall, New York.
- Johnston A, Smoliak S, Stringer PW. 1969. Viable seed population in Alberta prairie top soils. *Can J Plant Sci* 49: 75-82.
- Jutila HM. 1998. Seed banks of grazed and ungrazed Baltic seashore meadows. *J Veg Sci* 9: 395-408.
- Kim JG, Ju EJ. 2005. Soil seed banks at three ecological preservation areas in Seoul. *Korean J Ecol* 28(5): 271-279 (In Korean with English abstract).
- Kim KD, Lee EJ. 2005. Soil seed bank of the waste landfills in South Korea. *Plant Soil* 271: 109-121.
- Korean Plant Names Index. 2003. <http://www.koreaplants.go.kr:9090/>
- Lee CS, Cho YC, Shin HC, Moon JS, Lee BC, Bae YS, Byun HG, Yi HB. 2006. Ecological response of streams in Korea under different management regimes. *Korean Water Resources Association* 6(3): 131-147.
- Lee CS, Park HS, You YH, Kim SK. 1998. A study on vegetation succession in abandoned paddy fields. *J Natural Sci Ins, Seoul Women's University*, Vol. 10. pp 29-43 (In Korean).
- Lee CS, You YH, Robinson GR. 2002. Secondary succession and natural habitat restoration in abandoned rice fields of central Korea. *Rest Ecol* 10(2): 306-314.
- Lee TB. 1985. *Illustrated Flora of Korea*. Hyangmoonsa (In Korean).
- Lim JW, Shin JH, Jin GZ, Chun JH, Oh JS. 2003. Forest stand structure, site characteristics and carbon budget of the Kwangneung natural forest in Korea. *Korean J Agri For Meteo* 5: 101-109.
- Livingston RB, Allesio ML. 1968. Buried viable seed in successional fields and forest stands Harvard Forest, M.A. *Bull Torrey Bot Club* 95: 58-69.
- McCune B, Mefford MJ. 1999. PC-ORD, multivariate analysis of ecological data. Version 4. MjM Software Design, Glenden Beach, Oregon.
- National Institute of Agricultural Science and Technology. 2000. *Methods of analysis for soils and plants*. Rural Development Administration.
- National Research Council. 1992. *Restoration of Aquatic Ecosystems*. National Academy Press, Washington, DC.
- Olano JM, Caballero I, Laskurain NA, Loidi J, Escudero A. 2002. Seed bank spatial pattern in a temperate secondary forest. *J Veg Sci* 13: 775-784.
- Oosting HF, Humpreys ME. 1940. Buried viable seeds in successional series of old fields and forests. *Bull Torrey Bot Club* 67: 253-273.
- Park SH. 1995. *Colored Illustrations of Naturalized Plants of Korea*. Ilchokak.
- Prach K, Pyšek P. 2001. Using spontaneous succession for restoration of human-disturbed habitats: experience from Central Europe. *Ecol Eng* 17: 55-62.
- Pratt DW, Black RA, Zamora BA. 1984. Buried viable seed in a ponderosa pine community. *Can J Bot* 62: 44-52.
- Pywell RF, Bullock JM, Hopkins A, Walker KJ, Sparks TH, Burke MJW, Peel S. 2002. Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. *J Appl Ecol* 39: 294-309.
- Rabinowitz D. 1981. Buried viable seeds in a North American tall-grass prairie: the resemblance of their abundance and composition to dispersing seeds. *Oikos* 36: 191-195.
- Richter R, Stromberg JC. 2005. Soil seed banks of two montane riparian areas: implications for restoration. *Biol Cons* 14: 993-1016.
- Roberts TL, Carson WP, Vankat JL. 1984. The seed bank and the initial revegetation of disturbance sites in Hueston Woods State Nature Preserve. In: *Houston Woods State Park and Nature Preserve* (Wilkeke GE, ed). Miami University, Oxford, OH, pp 150-155.
- Roovers P, Bossuyt B, Igodt B. 2006. May seed banks contribute to vegetation restoration on paths in temperate deciduous forest? *Plant Ecol* 187: 25-38.
- Ryang HS, Kim DS, Park SH. 2004. *Weed of Korea*. Rijeon Agricultural Resources Publications (In Korean).
- Simpson RL, Leck MA, Parker TV. 1989. Seed banks: General concepts and methodological issues. In: *Ecology of Soil Seed Banks*

- (Leck MA, Parker VT, Simpson RL, eds). Academic Press, London, pp 1-8.
- Solomon TB, Snyman HA, Smit GN. 2006. Soil seed bank characteristics in relation to land use systems and distance from water in a semi-arid rangeland of southern Ethiopia. *South Afr J Bot* 72: 263-271.
- Stanturf JA, Schoenholtz SH, Schweitzer CJ, Shepard JP. 2001. Achieving restoration success: myths in bottomland hardwood forests. *Rest Ecol* 9(2): 189-200.
- Tasser E, Walde J, Tappeiner U, Teutsch A, Noggler W. 2006. Land-use changes and natural reforestation in the Eastern Central Alps. *Agri Ecosys Environ* 118: 115-129.
- Ter Braak CJF. 1986. Canonical correspondence analysis: a new Eigen-vector technique for multivariate direct gradient analysis. *Ecology* 67(5): 1167-1179.
- Ter Heerdt GNJ, Verweij GL, Bekker RM, Bekker JP. 1996. An improved method for seed-bank analysis: seedling emergence after removing the soil by sieving. *Funct Ecol* 10: 144-151.
- Thompson K, Grime JP. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *J Ecol* 67: 893-921.
- Thompson K. 2000. The functional ecology of soil seed banks. In: *Seeds: The Ecology of Regeneration in Plant Communities*, Second ed (Fenner M, ed). ABI Publishing, New York, pp 215-235.
- Van der Valk AG, Davis CB. 1979. A reconstruction of the recent vegetational history of a prairie marsh, eagle lake, Iowa from its seed bank. *Aquat Bot* 6: 29-51.
- Van der Valk EG, Pederson RL. 1989. Seed banks and the management and restoration of natural vegetation. In: *Ecology of Soil Seed Banks* (Leck MA, Parker VT, Simpson RL, eds). Academic Press, Inc., London, pp 329-344.
- Walker KJ, Stevens PA, Stevens DP, Mountford JO, Manchester SJ, Pywell RF. 2004. The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. *Biol Cons* 119: 1-18.
- Walker, LR, Chapin, FS. 1987. Interactions among processes controlling successional change. *Oikos* 50: 131-135.
- Warr JS, Kent M, Thompson K. 1994. Seed bank composition and variability in five woodlands in south-west England. *J Biogeo* 21: 151-168.
- Young TP. 2000. Restoration ecology and conservation biology. *Biol Conserv* 92: 73-83.
- Zabinski CA, Wojtowicz T, Cole DN. 2000. The effect of recreation disturbance on subalpine seed banks in the Rocky Mountains of Montana. *Can J Bot* 78: 577-582.
- Zhan X, Li L, Cheng W. 2007. Restoration of *Stipa krylovi* steppes in inner Mongolia of China: Assessment of seed banks and vegetation composition. *J Arid Environ* 68: 298-307.

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