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# An Introduction to Wetland Seed Banks etland Seed Banks

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## Introduction

One of the most important structural components of wetland ecosystems is the seed bank. Seed banks are present in nearly all ecosystems, and can be defined as "[an] aggregation of ungerminated seed potentially capable of replacing adult plants that may be annuals, dying a natural or unnatural death, or perennials, susceptible to death by disease, disturbance, or consumption by animals including man" (Baker 1989). They are a critical component in the establishment and development of vegetation communities in wetlands (van der Valk 1981).

Practical principles concerning the "behavior" of seeds in the soil in different wetland types may be derived from past research. The purpose of this and technical report number 00-4 is to present to the reader a general overview of seed bank ecology and the role seed banks play in wetland succession processes. In this report we introduce the concepts of seed physiology and ecology as applied to seed storage in the soil. We conclude with a short introduction to our current understanding of wetland seed banks. Report number 00-4 discusses recent literature on wetland seed banks in natural and created or restored systems, and defines the role seed banks play in created and restored wetland management.

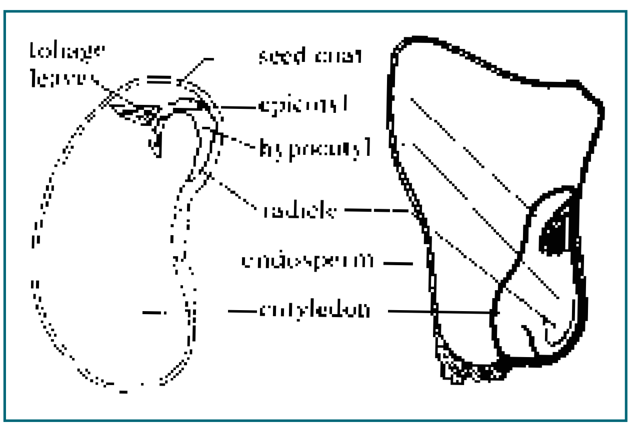


*Figure 1. Diagram of a dicot and monocot seeds. The embryos in these seeds consist of epicotyl, hypocotyl, radicle, and cotyledon. Left: A dicot seed (bean) in which one cotyledon has been removed to reveal remaining parts of embryo. Right: A monocot seed (corn) has only one cotyledon, but a large endosperm. Modified from Keeton and Gould (1993). Endosperm of mature dicot is indistinguishable from cotyledon.*

## Seeds and Seed Ecology

Regeneration of wetland plant communities occurs by sexual reproduction through either the development of seeds, or by asexual reproduction through clonal propagation by rhizomes or other vegetative organs. A plant may employ the former (e.g. annuals), the latter (e.g. submerged aquatics), or both (e.g. herbaceous perennials) as a principal reproductive strategy (Fenner 1985). Much of the literature on seed bank research deals with sexually produced propagules in angiosperms (flowering plants) (Leck 1989).

### Seeds

Seeds of angiosperms develop from a fertilized ovule and consist of the following: 1) the embryo (includes the epicotyl, hypocotyl, radicle, and cotyledon) which eventually grows into the young plant; 2) the endosperm (internal food source for developing seed); and 3) the seed coat (Raven *et al.* 1992, figure 1). Although all mature seeds contain an embryo, even if only poorly developed, and most are surrounded by a seed coat, the extent to which the endosperm and perisperm persist varies among species. In some cases, the seed coat is in rudimentary form and the seed is contained within the pericarp (fruit coat) derived from the ovary wall. In this condition, the primary dispersal unit is not a seed, but a fruit (Fenner 1985, Bewley and Black 1994). In mature dicots (e.g. beans) the endosperm is stored in the cotyledon and is indistinguishable.

## Dispersal mechanism

Growth of the seed embryo is usually delayed while the seed matures and is dispersed (Baskin and Baskin 1989). Several dispersal mechanisms are available to seed plants, including wind (anemonochory), water (hydrochory), and animals (zoochory - birds in particular) (Fenner 1985). Wind dispersed seeds of various species have morphological adaptations designed to exploit a particular dispersal vector, such as high surface to volume ratio in small seeds (e.g. many grasses and sedges), or the presence of appendages such as plumes, hairs, or wings to increase air resistance for wind dispersal (e.g. sea side goldenrod). Adaptations that facilitate dispersal by animals include burrs, hooks, or adhesive substances, which increase the opportunities for a seed to cling to an animal (ectozoochory, e.g. marsh beggar ticks). Certain seeds develop special seed coats that increase buoyancy for water transport (e.g. arrow arum). Special oil bodies (elaiosomes) are also present on some seeds as an attractant for insects, such as ants, which are exploited in dispersal (myrmecochory). Many plant species have developed large, nutritious fruits (e.g. persimmons) which attract frugivores (fruit-eating animals). The seeds within the fruit are not susceptible to the digestive acids of an animal's stomach and are, therefore, viable when eliminated from the animal that ingests the fruit (endozoochory). In some species, the foliage of the plant may serve as an attractant, alleviating the necessity for fruit development (e.g. flowering and silky dogwoods) (Willson 1992, Raven *et al.* 1992, Fenner 1985).

## Germination requirements

Seed germination depends on both internal and external factors (Bewley and Black 1994). The three most important external (environmental) factors include the proper amounts of water and oxygen and appropriate temperature range. Too little or too much water, too little oxygen, and temperatures that stay too low may lead to delay or lack of germination. Some seeds from the temperate climate zone may require freezing temperatures for several consecutive days to sclarify (see discussion on stratification below). In addition, some seeds have a light requirement for germination (Leck 1989).

Most mature seeds have low moisture content, containing only about 5-20% water by weight (Fenner 1985), and must imbibe (absorb) water in order to activate enzymes and initiate metabolism. During the early stages of germination, respiration may be entirely anaerobic (i.e. carried out in the lack of oxygen), but as soon as the seed coat is ruptured, the seed switches to aerobic respiration (Bewley and Black 1994). Too much water may also be a problem since if the seed becomes waterlogged, the amount of oxygen available will be limited and can be inadequate for seedling establishment (Karssen and

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Hilhorst 1992). In wetlands, seeds must therefore maintain adaptations to overcome the low oxygen levels associated with saturated soil conditions.

## Dormancy as an adaptation for seedling survival

Even in favorable conditions some viable seeds will fail to germinate and are said to be dormant. Common causes of dormancy include physiological immaturity of the embryo and impermeability of the seed coat to water and oxygen (Baskin and Baskin 1989). Seeds with a physiological dormancy will sometimes require a complex series of enzymatic and biochemical changes, referred to as "after-ripening," in order to germinate. In temperate climates, after-ripening is triggered by the low temperatures of winter (stratification). The after-ripening requirement, therefore, is seen as an adaptation that delays germination through the stressful winter climate until warmer temperatures when conditions are more conducive to seedling survival (Raven *et al.* 1992). Seed dormancy may also be induced by burial in the soil, underdevelopment of the embryo, and chemical inhibition, among other factors (Fenner 1985). These dormancy mechanisms represent adaptations that adjust germination timing for the seed to coincide with favorable environmental conditions.

## Seed Bank

The seed bank includes all viable seeds present on, or in, the soil or associated litter. Contributions are derived from the seed rain, which includes dispersal from the local vegetation, but may also include major contributions from spatially and temporally distant sources (Simpson *et al.* 1989). Seed losses from the soil are generally due to germination, fire, predation, decomposition, physiological death induced by deep burial, and physical removal due to erosion or other disturbances (Leck 1989, Fenner 1985).

In general, seeds of species forming seed banks must be viable for long periods of time. This requires extended periods of dormancy thus ensuring viability and persistence in the seed bank until conditions are favorable for germination (Murdoch and Ellis 1992). Species that tend to form seed banks are those typically found in habitats appearing unpredictably in nature (e.g. bare soil). Such species are typically annuals, often referred to as early colonizers or volunteer species (Pickett and McDonnell 1989). Therefore, certain annual species may be perennially represented in the seed bank, and will become established when disturbance or some other factor removes the competitive influence of existing vegetation (Fenner 1985).

## Seed Bank Dynamics

The mobility of seeds in the soil is poorly understood, but appears to follow some disturbance mechanism which may be facilitated by the activity of burrowing animals or shrink-swell fissuring of the soil during alternating wet and dry periods. Some seed migration may occur by ground water percolation, with smaller seeds moving more rapidly than larger ones (Leck 1989). By far, human disturbance through tilling and other practices provides the most immediate mechanism for vertical transport of seeds within the soil (Simpson *et al* 1989). For many soil seed banks, a physical disturbance mechanism must be present in order to bring buried seeds to the surface where germination may occur (Fenner 1985).

## Methods for Studying Seed Banks

The most common method of seed bank analysis is the seedling emergence technique, where soil samples are extracted and brought back to a greenhouse or lab to be observed under conditions favorable for germination. Under this method, germinating species are removed from the soil as they are identified, and the treatment continues until all seedlings have emerged from the soil. In a review of several methods for estimating seed numbers in the soil, Gross (1990) found that the seedling emergence technique underestimates the seed bank because, under any experimental condition, germination requirements for some species will not be met. However, Gross also noted that this method does provide the most complete listing of species present in the seed bank. Other methods employed by researchers include direct counts using sieves to separate seeds (Bonis *et al.* 1995), and elutriation, a system that recognizes fine root production from seeds in the soil (Gross 1990). As Gross points out, either of these alternative methods gives better results of actual seed numbers in the soil; however, the methods are severely limited by the necessity of identifying species by seed alone.

## Wetland Seed Banks

Much of our knowledge of wetland seed bank ecology has been developed through research carried out in tidal salt and freshwater marshes and/or seasonal and temporary non-tidal wetlands (Leck 1989). Nearly all of these studies indicate that seed banks play an important role in the composition and succession of vegetation communities (Thompson 1992). Several generalizations may be drawn from the literature (Leck 1989):

- Wetland seed bank composition and size are highly variable, with individual samples ranging from 0 to 59 species and 0 to 377,041 seeds $m^2$. Fewer seeds are found at continually inundated sites.

- Increasing water depth and salinity decreases size and diversity of wetland seed banks.

- Dominant species represented in wetland seed banks are most often graminoids (grasses or grass-like plants); and seed banks are most often dominated by one species (15-90%).

- Woody species are often poorly represented or lacking in wetland seed banks (including forested wetlands).

- Vertical distribution of seeds is variable among wetland habitats with 80% of all viable seeds occurring in the top 4-5cm of soil for lacustrine, temporary, and freshwater tidal wetlands. Only 20-50% of viable seeds occur in the top 5cm of the soil in swamps, prairie marshes, and bogs (wetland systems for which deep burial is more characteristic).

- Low oxygen levels in consistently saturated or flooded wetland soils may reduce deterioration and increase longevity in seeds.

- Inundation is the most important factor influencing the recruitment of vegetation from the seed bank in wetlands. Germination response to the drawdown frequency (periodicity of alternating flooded and dry conditions) favors submersed aquatic species during flooded conditions, and mudflat annuals or emergent perennials during drawdown conditions.

- Species composition in the seed bank is most often correlated with the standing vegetation in wetland systems dominated by herbaceous vegetation. Forested wetlands tend to support seed banks that do not reflect the standing vegetation.

- Wind and water are two of the most important dispersal vectors operating in wetland systems. In some wetlands, waterfowl dispersal is also an important vector, allowing for a much broader potential geographic distribution for wetland plant species that utilize this mechanism.

The importance of drawdown conditions as a recruitment alternative for species present in the seed bank is the most recurrent subject of review in the literature. van der Valk (1981) describes this phenomenon as an "environmental sieve" where the influence of water level fluctuation determines which species can become established in the wetland at any given time. Certain annuals may only become established in the wetland when sediments are exposed and will die back upon inundation. However, if these species can set seed and establish a presence in the seed bank, a flood event will not extirpate the species from the wetland. A species with an annual life history may, therefore, have a perennial component in the soil seed bank (van der Valk 1981, van der Valk and Davis 1978).

The unpredictability of drawdown frequency in certain wetlands, induced by stochastic events such as drought, presents a problem to scientists who wish to make predictions on successional sequences in wetlands. This effect is most notable in seasonal wetlands, for which precipitation is the principal hydrologic component (Poiani and Johnson 1989).

Another factor that may affect diversity in wetland ecosystems is the potential for development of aggressive weed species from the seed bank (Leck 1989). Invasive or exotic species present in the seed bank may proliferate during favorable drawdown conditions. Once established, these species may reproduce by seed and rhizome, and may competitively exclude annuals that persist only in the seed bank (van der Valk and Penderson 1989). The presence of invasive species in the seed bank is thus a threat to the maintenance of diversity in wetland systems.

## Conclusion

The seed bank represents an important component of the overall wetland ecosystem. Stresses at the seed bank level imposed by flooding, low oxygen levels, and other site-specific environmental conditions in wetlands (e.g. salinity, burial, etc.), select for species with physical and/or physiological adaptations to overcome environmental stresses for successful seed germination and seedling establishment. The seed bank provides a storage medium for plants that might otherwise not survive through stressful conditions. In general, the function of the wetland seed bank is to maintain genetic continuity and diversity at the species level, and to maintain species diversity at the community level. Therefore, a comprehensive understanding of plant dynamics in wetlands should not stop at the soil surface.

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