

*Review*

# **“Ecology of soil seed banks: Implications for conservation and restoration of natural vegetation”: A review**

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**Seed bank (henceforth referred to as SB) refers to viable seed which is present on or in soil and associated with litter/humus. Under different land use/land cover systems and climatic regions, density of seeds in the soil is variable both in space and time. SB density decreases with increasing depth and age of seeds in the soil. Smaller seeds are more easily incorporated, moved to deeper soil layers and persist longer in the soil, whereas large sized seeds without hard seed coats lack persistence in the soil. Moreover, small and elongated seeds are more persistent than large and round seeds. In most vegetation types, grass and herbs have denser seeds in the soil than woody species. Due to shade intolerant properties, density of grasses and forbs are also higher in forest gaps and farmlands than under shade of trees. In most of vegetation types and under medium disturbances e.g. under grazing, density and diversity of species are higher than that of lower and higher disturbance intensities. Tillage practices also have negative impacts on density, composition and abundance of SB. Hence, seeds decline under conventional tillage than under conservational tillage practices. In several studies, seeds in the SB are not similar to above ground vegetation. Similarly, density and diversity of seeds in a SB exceeds that of standing vegetation. Persistence seeds in soil are essential in maintaining individual species and the plant community, conservation of genetic biodiversity and restoration of plant communities of degraded lands after disturbances under harsh environmental conditions, especially in arid regions. As a result, SB characteristics are used to elucidate seed dynamics in various vegetation types. Overall, scientific knowledge of SB is used for land use planning, to make recommendations for future cost effective measures and to establish policies for conservation or restoration programmes.**

**Keywords:** Seed bank (SB), dispersal, persistence, restoration, vegetation type.

## **INTRODUCTION**

Seed bank (SB) is the feasible seeds that exist on the surface or dormant in the soil (Li et al., 2017). All viable seeds present on, or in, the soil and associated with

litter/humus (Mekonnen, 2016). It is the reservoir of viable seeds or vegetative propagules that are present in the soil and that are able to recompose a natural

regeneration. The reservoir corresponds to the seeds not germinated but potentially capable of replacing the annual adult plants, which had disappeared by natural death or not, and perennial plants that are susceptible to plant diseases, disturbances and animal consumption including man (Taiwo et al., 2018).

In comparison to above ground vegetation, researches on SBs were underestimated by many scholars throughout the world. The reason might be the difficulties in isolation of viable seeds from the soil samples (Abella et al., 2013). However, SB is an important component of ecosystem resilience and represents a stock of regeneration potential in many plant assemblages. Understanding the diversity and density level of SB is important for designing conservation and restoration programs in degraded ecosystems, especially in arid ecosystems. SBs are therefore considered as essential constituents of plant communities since the reclaimed communities after disturbances is believed to lie mainly in the buried seed populations (Song et al., 2017). Information of the SB is further essential for the ecological restoration and a better understanding of the species composition, storage capacity size, seasonal dynamics and the distributing patterns, which will be helpful to conserve and restore deforested and degraded vegetation types. However, the biodiversity of below-ground (that is, the SB) and its relationship to biodiversity of above-ground plants are less understood so far. In order to investigate complete diversity of plant communities in space and time, it is therefore vital to document informations of SBs with above ground vegetation. Therefore, this paper aims to provide answers for the following questions: (1) what are the trends of soil seeds under different land use/land cover dynamics? (2) What are characteristics of SBs under different climatic conditions and vegetation types? (3) How are different traits limiting, the seed persistence in the soil? (4) What are the fates of seeds in the soil? (5) What are the relationships between SBs and above ground vegetation? and (6) What are the contributions of SBs in conservation of genetic diversity and restoration of natural vegetation types?

## MATERIALS AND METHODS

In order to highlight the ecology of SBs, different materials such as journals, manuals, books and other secondary data were used. Tables, figures and results of different written materials were used to illustrate the review suitable for the readers about the topics raised in this paper.

## RESULTS AND DISCUSSION

### Ecology of seed banks

#### *Seed dispersal*

A series of events occur in the process of regeneration, namely flowering, seed production and dispersal, incorporation of seeds into the soil, seed predation which is used to enhance germination, seedling establishment and growth and formation of SBs (Savadogo et al., 2016). Some terminologies in the process of seed dispersal are defined for the convenience of the reader. Seed rain is flow of seeds dispersed and deposited into a given site. On the other hand, seed shadow refers to the pattern of spatial deposition of seeds relative to parent plants. Seed dispersal consists of the removal and deposition of seeds away from parent plants (Hamalainen et al., 2017). Seed dispersal plays a vital role in conserving community diversity (Bufalo et al., 2016).

After fertilization, seeds will be formed in different plant species under different vegetation types. It is important for the seeds to be dispersed away from each other and from the parent plant. This helps to avoid overcrowding and the competition for light, water and mineral nutrients. Dispersal also enables species to take advantage of new opportunities and to survive if conditions for the parent plant become unsuitable (Traveset et al., 2014). All plants need water, sun and space in order to grow. A seed cannot get the things it needs to grow if it falls immediately below its parent plant because its parent is already using the resources in that location. Seed dispersal has long been a topic of interest to naturalists, but it has not been until the last three decades that the ecology of dispersal has received much rigorous scientific attention (Fingesi et al., 2017). Seed dispersal has a major influence on plant fitness because it determines the locations in which seeds and subsequently seedlings live or die. Seed dispersal can be advantageous in escaping density-dependent mortality near parent plants. Seed dispersal causes seedling mortality and colonization of suitable sites unpredictable in space and time. However, directed-dispersal (that is, non-random dispersal such as by predators or other biota that carry the seeds to favorable sites) is particular for sites with a relatively high probability of seedling survival. Most previous researches on the consequences of seed dispersal has focused on escape and colonization because adaptations ensuring directed dispersal are not expected under the paradigm of disperse mutualism that characterizes the modern view of seed dispersal evolution (Robledo-Arnuncio et al., 2014).

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### **Soil seed characteristics in various climatic regions and climatic types**

Natural regeneration is the cheapest approach for rehabilitation of vegetation types, provided that the previous disturbance has left some residuals (e.g., SBs, mother trees or root shoots) that can serve as succession pioneers. The very low relationship of similarity between the SBs and aboveground flora implying that the role of SBs in the regeneration is low and dispersal of seeds from the adjacent natural forest plays an important role in the process (Ssali et al., 2018). This problem may exist in any vegetation ecosystems provided that environmental drivers, topographic features, land uses and management and anthropogenic activities vary in specific areas.

According to Madawala et al. (2016), SBs are dominated by seeds of herbaceous species, although they can be highly variable in features such as species number and composition, seed longevity and viability, germination strategies and depth distribution of seeds in the soil. SBs have the capacity to survive for a longer period of time in the soil, and overcome the poor establishment and low survival rates of seedlings during drier years, which are typical of the afro-montane vegetation types (Santos et al., 2018) and contribute to the re-establishment of plant species lost from the original plant community. Thus, the SB acts as a reserve out of which new recruitment may occur if environmental conditions are favorable (Kolodziejek and Patykowski, 2015).

Seed populations in the soil are heterogeneous and abnormally distributed. The problem in describing the seed distribution in soil is associated with its inherent heterogeneity. Seeds often are shed close to the parent plant. This leads to strong departures from randomness in the seed distribution of populations on the surface and in the soil. Although the most abundant species often have a normal distribution, the less abundant ones usually have a Poisson or an aggregated distribution (Zhang et al., 2012). Natural forests in the tropics have been and continue to be subjected to natural and human induced disturbances, which have resulted in their degradation or complete destruction.

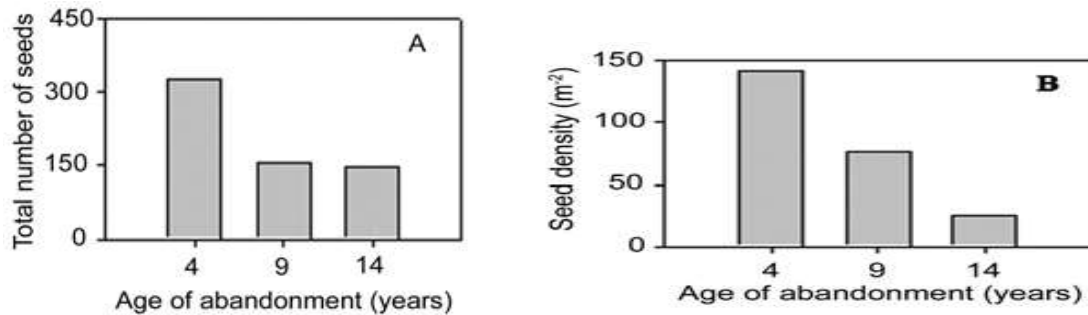
In places where the sites are left without further interference, the processes of succession that will ultimately lead to re-vegetation of the sites may be initiated. Here, the SBs serve as one of the major sources of plant re-growth. In most tropical areas, however, the degraded or completely destroyed forest sites are changed either to other land uses, establishment of monoculture plantations of fast growing trees, or permanent arable lands, which is a common practice in the tropics, e.g. in Ethiopia. They are continuously eliminated through weeding practices and ultimately completely exhausted. In these cases, the SBs have the potential to initiate re-vegetation of the sites. Another scenario could be the conversion of the destroyed forest

sites to permanent arable lands followed by their abandonment. In this case, some of the persistent seeds in the soil and the seed rain may lead to restoration of the vegetation (Senbeta and Teketay, 2002).

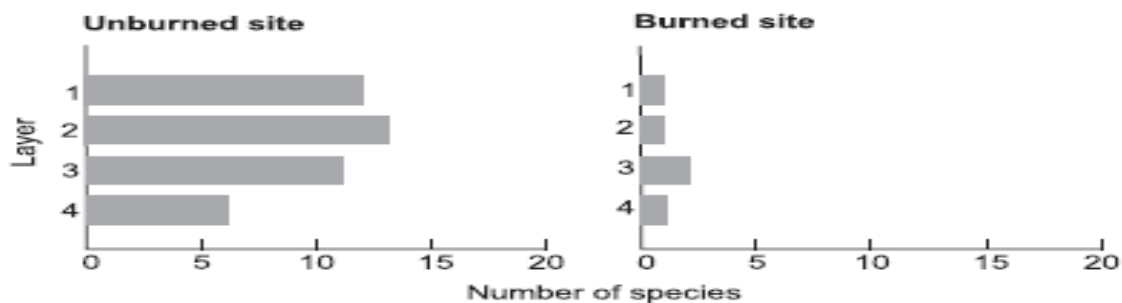
In agro-ecosystems, the SB is closely related to weed studies. This allows building models of population establishment through time, making possible control of weed programs. The knowledge of emergence rate of the different species from a SB can be used for the adequacy of soil and crop management programs, which can result in a rational use of herbicides (Christoffoleti and Caetano, 1998). In the dry afro-montane region of Ethiopia, adjacent plantation and dry afro-montane forests in central and southern parts of the country could be characterized as possessing large numbers of buried seeds of forbs, grasses and sedges. Only a few woody plants were represented by a few seeds in the SB, suggesting that most woody plants typically use the seed rain, or coppicing from stumps, as alternative regeneration routes (Senbeta and Teketay, 2002).

In the vast majority of SB studies, SB density declines monotonically with soil depth. This pattern is assumed to reflect regular seed input at the surface and a more or less gradual decline in viability as seeds aged and move vertically down soil profiles. This is because older seeds have more time to become deeply buried and depth distribution is often a reasonably good indicator of seed longevity (Thompson et al., 1997; Bekker et al., 1998). For instance, in abandoned croplands on the hilly-gullied Loess Plateau in China, the potential for vegetation restoration from SB survey for germination and correspondence analysis showed that the seed density of SBs ranged from 900 to 6,467 seeds per m<sup>2</sup> at 0 to 5 cm depth and 117 to 2,467 seeds per m<sup>2</sup> at 5 to 10 cm depth; with species richness of 7 to 14 (Jiao et al., 2007).

According to Teketay (1997a), in afro-montane forest belt of east Ethiopia while comparing SB of forests, gaps between forest and arable lands and in arable lands, the highest number of species was recorded from the forests, while the highest seed density was found in the arable land for herbaceous species. Herbs were represented by the largest numbers of species in SBs in all sampling habitats. Contribution of woody species to the SB was 15% in the forest, while it was less than 1% in gaps and arable lands. In this study, seed density and number of species were also decreased with increasing depth, although species differed in the depth distribution of their seeds and age of seeds in the soil. According to Gonzalez-Rivas et al. (2009), SB investigation of agricultural fields abandoned for 4, 9 and 14 years of Nicaragua, in Central America showed that a total of 3, 5 and 9 species were found on sites abandoned for 4, 9 and 14 years, respectively. Among different life forms, trees were highly represented in the SB of 9-year (60%) and 14-year (33%) old sites compared to a 4-year old site entirely dominated by non-woody flora. The total number of seeds was 327, 156 and 146 for 4, 9 and 14 years,



**Figure 1.** Total number of seeds (A) and density of viable seeds (B) in soil samples collected from three secondary forests developed on sites abandoned 4, 9 and 14 years ago in Nicaragua, Central America. Source: Gonzalez-Rivas et al. (2009).



**Figure 2.** Number of species found in each soil layer sample at the unburned and burned sites. Soil layers: 1 = litter, 2 = 0-3 cm, 3 = 3-6 cm, and 4 = 6-9 cm. Source: Tesfaye et al. (2000).

respectively (Figure 1A). The corresponding density of viable seed decreased from 141 seeds per m<sup>2</sup> in 4 years to 76 seeds per m<sup>2</sup> for sites of 9 years and 26 seeds per m<sup>2</sup> for site of 14 years (Figure 1B).

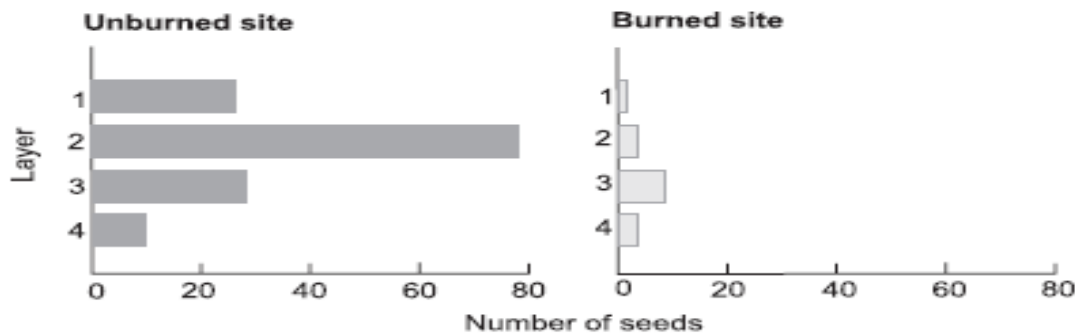
For most of the species, the viability of seeds recovered from the soil samples was low. They also concluded that species composition of SBs assembled gradually during secondary succession, but the overall seed density was still low for natural regeneration of trees to rely on. To expedite the recovery of secondary forests on such abandoned fields, the SB needs to be supplemented by direct seeding, enrichment planting of desired species and installing artificial perches for facilitating seed dispersal (Senbeta and Teketay, 2002).

According to Tesfaye et al. (2000), in Southeast Ethiopia in the Harena forest, 155 seedlings were germinated from the soil samples of which 140 and 15 seedlings were from the unburned and burned sites, respectively (Figure 2). The proportion of woody species found on the unburned site was 47%, while on the burned site only one woody species was recorded. Overall mean densities were 621 ± 15 and 66 ± 2 seeds per m<sup>2</sup> on the unburned and burned sites, respectively. The greatest diversity was found in the upper soil layer, followed by the

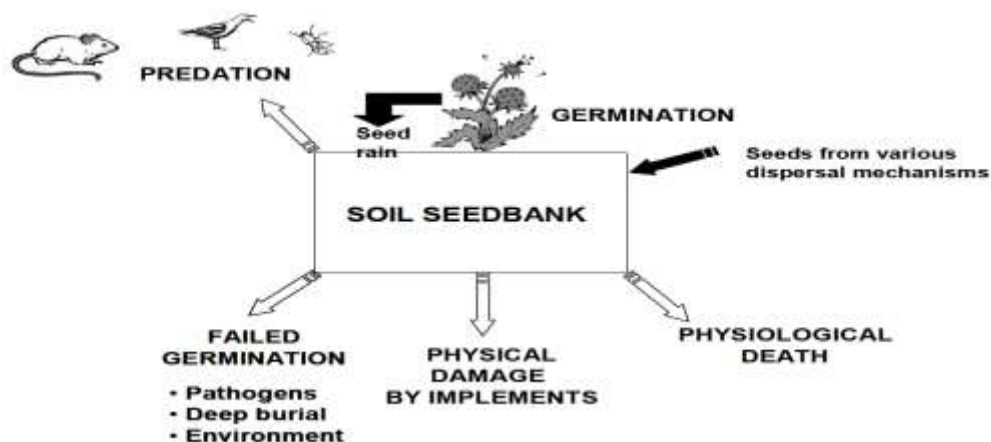
middle, litter, and lower soil layers collected from the unburned site.

The greatest diversity was found in the upper soil layer, followed by the middle, litter, and lower soil layers collected from the unburned site. Eighteen months after the fire, the burned site was covered with 32 species of dense vegetation, which attained a height of 3.5 m (Figure 3). Their results revealed that although the fire exhausted the SB, the vegetation could regenerate quickly with pioneer species, which differed in composition from the neighboring unburned stand (Tesfaye et al., 2000).

There are two types of dispersal stages (Stoner and Henry, 2002): (1) Primary dispersal: this consists of the removal of a fruit from a tree and the deposition of seeds from this fruit in a particular area, typically by a predator. In addition to factors that affect animals choice for feed that determines if a fruit is consumed or not, once the fruit is swallowed a series of factors affect primary seed dispersal and the ultimate fate of the consumed seeds. These factors include body size, digestive strategies, ranging behavior and defecation of the animals. Larger animals can swallow bigger seeds than smaller ones. The time required for seeds to pass through the digestive



**Figure 3.** Number of seeds found in each soil layer sample at the unburned and burned sites. Soil layers: 1 = litter, 2 = 0-3 cm, 3 = 3-6 cm, and 4 = 6-9 cm. Source: Bekele et al. (2000).



**Figure 4.** SB flow chart which shows dynamics of the seed population. Source: Christoffoleti and Caetano (1998).

tract affects the fate of swallowed seeds in that seeds that spend more time in the digestive tract are generally deposited at greater distances from the mother plant and frequently consist of one species. (2) Secondary dispersal: this consists of the removal of seeds once they have been deposited by their primary disperser. Spit seeds and dropped, and wasted fruit may be exploited by other seed dispersers such as rodents, and deer, who may then serve either as secondary dispersal agents or seed predators. Spit seeds and dropped, wasted fruit may be exploited by other seed dispersers such as: rodents, deer and peccaries or any of several piglike hoofed mammals of the family Tayassuidae found in North and South America that may then serve either as secondary dispersal agents or seed predators. Some invertebrates like ants and dung beetles may also contribute to secondary dispersal of small seeds, but their effect on final seed germination and establishment is poorly known compared to that of mammals (Stoner and Henry, 2002).

### **The fate of seeds in the soil**

Several things can happen to seeds in SBs (Figure 4). They may be preyed upon by insects or other vertebrates, die or become dormant due to physiological reasons, attacked by pathogens, get buried too deep in the soil preventing emergence, physically damaged by agricultural implements, or germinate, emerge, grow and produce more seeds (Dalling et al., 2011).

In dry afro-montane forest of South Wollo in Ethiopia, a SB evaluation made by Bekele (2000) depicted that herbs comprised the majority of the SB species (75%), followed by grasses, climbers, shrubs and trees (Table 1). Herbs were dominant in all the vegetation classes.

In New Zealand, persistence of viable seeds after 1, 2, 3, 5, 11, 16 and 28 years was evaluated by using a seed burial method using five seeds. The species were Scotch thistle (*Cirsium vulgare*, in Asteraceae family), Californian thistle (*Cirsium arvense*), nodding thistle (*Carduus nutans*, in Asteraceae family), ragwort (*Jacobaea*

**Table 1.** Number of species of the different life-forms occurring in the SB and in the standing vegetation (Bekele, 2000).

Life form	NSB <sup>a</sup>	NSEB <sup>b</sup>	NSC <sup>c</sup>	NSEV <sup>d</sup>	NSV <sup>e</sup>
Trees	2	0	2	30	32
Climbers	6	1	5	4	9
Shrubs	3	1	2	50	52
Grasses	7	3	4	34	38
Herbs	53	24	29	98	127
Total	71	29	42	216	258

NSB<sup>a</sup>: Number of species in seed bank; NSEB<sup>b</sup>: Number of species exclusive the seed bank; NSC<sup>c</sup>: Number of species common to the seed bank and the standing vegetation; NSEV<sup>d</sup>: Number of species exclusive to the standing vegetation; NSV<sup>e</sup>: Number of species in the standing vegetation.

**Table 2.** Means  $\pm$  SD of diversity indices and density of SB as well as the similarity between SB and the above-ground vegetation in the different habitats (Gomaa, 2012a).

Diversity index	Habitat		
	Desert salinized land	Desert Wadi	Reclaimed land
Species richness	2.2 <sup>a</sup> $\pm$ 0.4	4.7 <sup>b</sup> $\pm$ 1.4	9.3 <sup>c</sup> $\pm$ 2.3
Shannon index	0.74 <sup>a</sup> $\pm$ 0.16	1.12 <sup>a</sup> $\pm$ 0.36	1.57 <sup>a</sup> $\pm$ 0.49
Evenness	0.95 <sup>a</sup> $\pm$ 0.06	0.73 <sup>b</sup> $\pm$ 0.18	0.71 $\pm$ 0.20
Density of seed bank (seed/m <sup>2</sup> )	28.0 <sup>a</sup> $\pm$ 9.2	174.7 <sup>b</sup> $\pm$ 83.6	471.3 <sup>b</sup> $\pm$ 177.0
Motyka's similarity index	36.5 <sup>a</sup> $\pm$ 3.7	38.4 <sup>a</sup> $\pm$ 10.3	75.1 <sup>b</sup> $\pm$ 5.0

*vulgaris*) and giant buttercup (*Ranunculus acris*). The results showed that some herbaceous broadleaf weed species are major weeds of pastures and are difficult to manage, largely because of ongoing re-infestation from the persistent soil weed SB. Very few of the seeds were viable after being buried for 28 years in a clay soil, while in a sandy soil seeds of the three thistle species remained viable when buried at 200 mm depth. It is estimated that these seeds may remain viable for up to 66 years (James et al., 2010). This result indicated that soil texture is detrimental for soil seed longevity.

In the Eastern Desert of Egypt, the floristic composition and species diversity of the germinable SB were studied in three different habitats, namely desert salinized land, Desert Wadi, and reclaimed land (Gomaa, 2012a). Consequently, Gomaa recorded 43 annuals and 18 perennials species, which he had recovered from soil samples. The reclaimed land had the highest values of the following indices: species richness, Shannon-Weiner index of diversity and the density of the germinable SB, following with lower values in the habitats of Desert Wadi and desert salinized land. Motyka's similarity index between the SB and the above-ground vegetation is significantly higher in reclaimed land (75.1%) compared to Desert Wadi (38.4%) and desert salinized land (36.5%) (Table 2).

Under different grazing systems on the natural rangelands of the Kargapazari Mountain (Erzurum,

Turkey), a total of 73 taxa were recorded, 22 of them were annual species on the experimental area. The species number in the SB changed between 26 and 36 among the sites. The winter grazing system sites had the highest species richness, while spring grazing system sites had the lower species richness. The highest perennial grasses seedlings were recorded for a spring to autumn grazing system and for the season-long grazing system sites compared to all of the others. Similar differences were also recorded for the other functional groups and common species among the range sites. The differences in spatial distribution of plant species in the SBs were mainly addressed to geo-morphological heterogeneity, rather than grazing system effect. The differences in SB composition among range sites were mainly addressed in the difference of grazing season and pressure that originated from grazing system practices (Koc et al., 2013).

In a moist tropical forest, part of the Harena forest in Southeastern parts of Ethiopia, Jara (2006) recorded that the recovery of most of woody species from SBs was very low and seed densities were also higher in the top 3-cm of the soil layer and decreasing vertically down the soil depths. In wetlands of Mount St. Helens in USA, research reports made by Tu et al. (1998) showed that seedling emergence density in the top 5 cm was highly variable, and ranged from 15,700 $\pm$ 15,200 to 38,000  $\pm$ 31,500 seeds per m<sup>-2</sup>. Seedling emergence from soil at

5 to 10 cm depth varied from  $800 \pm 600$  to  $18,000 \pm 24,800$  seeds per  $m^{-2}$ , and averaged one third as many seeds as the surface. The high proportion of buried seeds might be due to continuing deposition of upland sediments.

### **Seed dormancy**

Despite the importance of the subject, there is no clear and unique definition for seed dormancy. This lack of agreement may be due to dissimilar perspectives from different disciplines about this phenomenon. For example, what a seed physiologist considers to be a dormant seed may be different from what an ecologist or seed technologist considers a dormant seed (Baskin and Baskin, 2004). Sometimes sown seeds do not have a capacity to germinate, even in the presence of favorable environmental conditions (Nasreen et al., 2002).

According to their manner of seed origin, different categories of seed dormancy can be categorized into two kinds: (1) Primary dormancy and (2) Secondary Dormancy. Each are explained in the following.

Primary dormancy is a dormancy inherent in the seed at the end of its development on the mother plant. Within primary dormancy there are three recognized groups. These include: (A) exogenous; (B) endogenous; and (C) combinational dormancy (Geneve, 1998). (A) Exogenous: Hard seeds are characteristic of members of the Cannaceae, Convolvulaceae, Fabaceae, Geraniaceae, and Malvaceae. (B) Endogenous: is related to dormancy factors within the embryo. There are two types of endogenous dormancy, morphological and physiological (Geneve, 1998). Morphological dormancy is where the embryo has not completed development at the time the seed is shed from the plant. The second type of endogenous dormancy is physiological dormancy. This involves physiological changes within the embryo that results in a change in its growth potential that allows the radicle to escape the restraint of the seed coverings. Physiological dormancy includes non-deep, intermediate and deep categories. (C) Combinational: includes a combination of exogenous and/or endogenous dormancies. This category of dormancy is also called double dormancy. These dormancy factors must be removed sequentially to allow germination. This combinational dormancy condition combines two or more types of primary dormancy. Examples include exoendodormancy (seed coat dormancy and intermediate physiological dormancy), or morpho-physiological dormancy (an undeveloped embryo combined with physiological dormancy).

Secondary dormancy occurs when seeds, whose germination has been inhibited, fail to recover when the inhibitory factor is removed. These seeds are said to enter in a state of dormancy called secondary or induced dormancy. It is induced in certain non-dormant seeds when the germination environment is unfavorable for

germination (Hartmann et al., 1997 cited in Geneve, 1998).

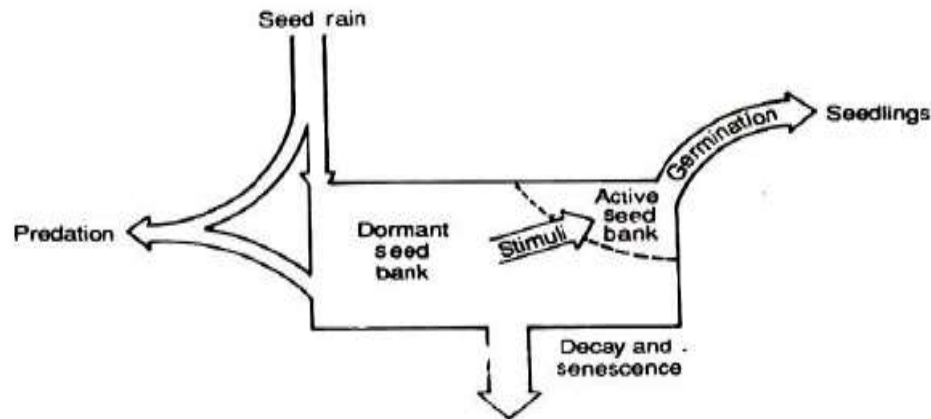
The biological significance of dormancy involves several factors. Seed dormancy is a device for optimizing the distribution of germination in time or space and its importance is therefore best seen in an ecological context. Distribution in time can be achieved by spreading germination over an extended period. This is because seeds of many species show variability in depth of dormancy. Basic patterns with respect to the temporal distribution of germination were recognized by Nasreen et al. (2002), which are: (1) Quasi-simultaneous, when germination of all the seeds occurs over a relative brief period; (2) Intermittent, irregular germination over long time periods, showing essentially multi-modal distribution; (3) Continuous, in which members of the population germinate over an extended time period, with no clear peaks and (4) Periodic, which is multi-modal but shows more regular periodicity.

### **Types of seed banks**

Viable seeds stored in the soil at a given time make up the SB (Bueno and Baruch, 2011). SB studies are of great importance for the understanding of the secondary succession, and it is considered as a necessary first step for the design of ecological restoration plans in which SBs contribute to the diversity and dynamics of most plant communities (Lang, 2006). On the basis of seed longevity in the soil, SBs are classified into two general types. These are persistent and transient seeds (Thompson and Grime, 1979; Teketay, 2005a). Thompson et al. (1997) suggested that a classification of SB types based on seed longevity subdivided into two categories: (1) transient: < 1 year; short-term persistent: 1-5 year(s) and (2) long-term persistent: > 5 years. Only the latter category may play a significant role in the restoration of species richness (Esmaeilzadeh et al., 2010). Thus, SB persistence is a key factor in the regeneration of plant communities and for the assessment of the local extinction risk (Saatkamp et al., 2011).

### **Dynamics of seed banks**

The dynamics of SBs involve a series of events of seeds from the bank in relation to time (Christoffoleti and Caetano, 1998). The SB is the natural storage of seeds, often dormant, within the soil of most ecosystems (Dekker, 1997). SB dynamics occurred with different functional, adaptable traits of seeds and associated ecosystems processes carried out on mother plant and in the soil. These resulted in dynamics of the seed population (Christoffoleti and Caetano, 1998): (1) Dormant SB ("deposit SB account"): majorities are dormant seed waiting stimuli or conditions before germination; (2) Active



**Figure 5.** SB flow chart which shows dynamics of the seed population.  
Source: Christoffoleti and Caetano (1998).

SB ("current SB account"): another part of SB in temporary stage, requiring only favorable temperature and moisture to germinate such as: dispersed seed with simple germination requirements, dispersed seed whose stimulus requirements have already been met and seed recruited from the dormant SB. (3) Two-way flow between two accounts; seed continually added from seed rain and represents an historical record of the past vegetation that grew on or near the area (Figure 5).

### **Functional and adaptive traits of seed banks**

Functional traits refer to well-defined and measurable properties of organisms that strongly influence or are strongly coordinated with ecological performances (Wright et al., 2010). Functional traits are morphological, biochemical, physiological, structural, phenological, or behavioral characteristics that are expressed in phenotypes of individual organisms and are considered relevant to the response of such organisms to the environment and/or their effects on ecosystem properties. This crucial position of functional traits at the junctions between responses to the environment and ecosystem properties explains the increasing attention given to them by both evolutionary biologists and functional ecologists (Diaz et al., 2013). For instance, functional traits include seed mass, leaf mass per area, wood density, maximum height, etc.

There is a growing consensus that wood density, seed mass, leaf mass per area and maximum adult height are key functional traits among forest trees providing insight into biogeochemical cycles (Wright et al., 2010), including: (1) life history variation (wood density, seed mass, and leaf area index), (2) the ability to disperse to new sites (seed mass), (3) acquire resources (leaf mass per area), (4) grow quickly (wood density, leaf mass per area), and (5) compete with neighbors (leaf mass per

area) maximum adult height and tolerate pests and other hazards. On the other hand, plant species have their own adaptive traits. Adaptive traits are the strategies of plants react towards abiotic and biotic (environmental) conditions.

Plant resistance to drought relies on adaptive strategies based on the timing of phenophases and on the presence of structural traits mainly related to: (1) increase of water uptake and storage, (2) reduction of water loss during dry periods and (3) mechanical reinforcement of tissues to prevent wilting that may lead to irreversible collapse and damage of cells. Various combinations of anatomical features can contribute in different degrees to the adaptive capacity of plants to drought (Micco and Aronne, 2012). Woody species predominated in the SB of plots with richer soils, deeper litter, and more closed canopies. Herbaceous species predominated in the SB of plots with more open canopies, more mesic water regimes, and greater species richness in the aboveground vegetation. Contrary to earlier results suggesting forest SBs primarily include shade-intolerant species associated with canopy disturbance or secondary succession, the SB in this old-growth; primary forest contains many shade-tolerant forest species (Leckie et al., 2000). These are adaptive trait strategies of plants to environmental conditions.

### **Seed longevity**

Longevity of seeds is viable seeds and persistence after maturity on the mother plant or germination media (litter/humus or in the soil). Seed persistence has a vital role in restoration ecology and population changing aspects (Abdi, 2013). Longevity of seeds is very variable and depends on many factors; few species exceed 100 years (Thompson et al., 1997). In typical soils, longevity of seeds can range from nearly zero to several hundred years. Some of the oldest still-viable seeds were those of



Lotus (*Nelumbo nucifera* in Nymphaeaceae family) found buried in the soil of a pond; these seeds were estimated by carbon dating to be around 1,200 years old (Bewley et al., 2006).

### **Environmental processes**

SBs play an important role in the natural environment of many ecosystems. For example, the rapid re-vegetation of sites disturbed by wildfire, catastrophic weather, agricultural operations and timber harvesting is largely due to SBs. Forest ecosystems and wetlands contain a number of specialized plant species forming persistent SBs (Christoffoleti and Caetano, 1998).

### **Population densities and diversity**

The mortality of seeds in the soil is one of the key factors for the persistence and density fluctuations of plant populations especially for annual plants. Studies on the genetic structure of *Erythrophysa septentrionalis* populations (Sapindaceae family) in the SB compared to those of established plants showed that diversity within populations is higher below ground than above ground (Ross and Lembi, 2008).

### **Associated ecosystem processes**

The term soil diaspore bank can also be used to include non-flowering plants such as ferns and bryophytes. In addition to seeds, perennial plants have vegetative propagules to facilitate forming new plants, migration into new ground, or reestablishment after being top-killed. These propagules are collectively called the 'soil bud bank' which includes dormant and adventitious buds on stolons, rhizomes and bulbs (Dekker, 1997). Numbers of SB studies have shown that SBs vary from one ecosystem to other ecosystems. For instance, SBs in moist temperate deciduous forests are fewer than in other ecosystems. For these kinds of forests, past studies have demonstrated that importance of buried seed for regeneration following infrequent but severe disturbances. SBs are rich during early stages of stand development or just after agricultural abandonment (Ashton et al., 1998). Furthermore, the amount of seeds in soil progressively declines with the development of close-canopied forests but increases can occur when stands enter the old growth stage.

### **Disturbance, succession and seed banks**

Whatever the reasons, the co-existence of species with contrasting SBs (transient vs. persistent) varies, because

disturbances will not equally affect the recovery of plant populations in transient as compared to persistent SSBs. Plant communities also differ in the abundance of viable seeds in soil banks, and therefore the success of restoration from them varies significantly. Moreover, even plants with notoriously persistent seed banks depend crucially on the time since land-use change to recover (Saatkamp et al., 2014). In a given time, vegetation ecosystems particularly mature forests undergo a series of changes, which are prompted by different types of disturbances. In response to disturbances, succession starts in which different plants use varying strategies to regenerate themselves (Teketay, 2005b). As the result, forest canopies are dynamic, changing continually as trees grow up, die and others replace them. Various disturbances initiate a forest growth cycle with three phases: gap, building and mature phases. Fire is a major natural disturbance factor in the boreal forest ecosystem and has great influence over stand development. Fire, though initially destructive, is considered to encourage colonization of deciduous trees. Increased diversity in the tree layer after fire disturbance should make fire an important tool for forest conservation. Browsing is another disturbance factor which can have great impact on stand development. Browsing alters the structural complexity of forest ecosystems and affects successional development by arresting or retarding height development (Eriksson, 2010). These disturbances improved SB's potential of the respective vegetation ecosystems. Therefore, secondary succession, conservation and restoration potential of degraded areas.

### **Seed banks, invasive species and climate change**

Much of the current understanding of the impact of invasive species on plant communities is based on patterns occurring in the above-ground vegetation, while only few studies have examined changes in SBs associated with plant invasions, despite their important role as determinants of vegetation dynamics (Gioria et al., 2014). The extent of transformation and degradation of ecosystems due to alien invasions is a global ecological and economic problem (Fourie, 2012). Invasions by invasive alien plant species significantly affect biodiversity and ecosystem functioning.

Investigations of the SBs of invasive plant species and changes in the composition and structure of resident seed banks following plant invasions can provide valuable insight into the long-term implications of plant invasions. SBs play a major role as reservoirs of species, genetic diversity and allow for the persistence of a species at a locality, buffering environmental changes that may occur over time (Gioria et al., 2012). On the other hand, climate change plays a powerful and diverse role in ecosystems all over the world. Wet areas are becoming dry, dry areas are experiencing more rainfall

and CO<sub>2</sub> is increasing at an alarming rate. These changes are not only visible in vegetation growth and distribution; they are also affecting the seed banks. The seeds are dormant and can stay in the bank with the potential to germinate for several years. Biotic and abiotic factors affect seed movement after a seed leaves its parent.

Climate change also aggravates invasive alien species to colonize easily and in turn invasive alien species can induce climate change. For example, climate change can facilitate invasive alien species to become more competitive and proliferate. Invasive species will be entering regions due to climate change and species hierarchies in ecosystems will change leading to new dominants that may have invasive tendencies. Climate induced stresses in an ecosystem will facilitate invasive pathways. Alternatively, invasive alien species can also facilitate climatic stress by increasing ecosystem susceptibility to climatic perturbation, through reducing the number of species and their functional types within the ecosystem (Masters and Norgrove, 2009).

### Methods of separation of seeds from soil samples

The fate of seeds in soil is one of the important features of plant ecology, because most of all potential plants die during the seed stage or as new seedlings. Nevertheless, seed demography (separation and identification) has been largely ignored because of the lack of suitable methods for the recovery of seeds from soil (Tsuyuzaki, 1993). Moreover, buried seeds are distributed heterogeneously even in a small area. Such information is lacking especially for many weed species and cropping systems because weeds cause yield loss in valuable crops in agriculture and horticulture. There are two general methods for enumerations of seeds from soil samples; e.g., for weed seeds. The first separation method is when seeds are collected from the soil sample and counted-extraction (physical methods) which involves sieving, floatation, bag methods etc. and subsequent viability determination.

The second method is vegetation method, when the seeds are left in sampled soil to germinate. Then, individual species are identified based on morphological characteristics of species (Smutny and Kren, 2002). Extraction methods are labor intensive; but are better suited to quantifying changes in seed banks, which require repeated sampling over time. Other advantages with extraction are that samples can be temporarily stored for dry processing when final results are obtained (Jones and Medd, 1984). Methods based on physical separation consist of isolating and identifying seeds from soil samples, whereas in seedling emergence methods soil samples are placed under suitable conditions for seed germination, and emergent seedlings are identified and counted as viable seeds. In general, estimates derived by physical separation are higher than those

derived by seedling emergence, since the former include non-viable, apparently healthy seeds, and the latter do not detect viable seeds whose appropriate germination stimuli are not provided (Ferrandis et al., 1999).

Thompson et al. (1997) concluded that methods based on physical separation are costly, time consuming and rather inaccurate. Therefore, They suggested designing use of a standardized seedling emergence method originally. The germination method may estimate the seed bank size more accurately. However, the germination method also has its specific limitations, one being the long-time seedlings may need to germinate and emerge. For example, Mesgaran et al. (2007) suggested continuing the process for 2 years. According to their results, in floatation method, a high capacity centrifugation is necessary and limited number and volume of centrifugal vials, as well as the needs for chemical solutions, are among other constraints. Accordingly, the bag method could be recommended as it was as time consuming as the floatation method, but requiring the same minimum equipment and costs as the sieving method.

A more desirable floatation method would shorten seed exposure to the floatation solution to save time and reduce loss of seed viability and provide reliable recovery of all species of interest. Counting seed after extraction from soil represents another constraint on conducting efficient seed bank assessments. Fatigue from counting large numbers of seed for long periods of time may result in errors. Seeds of many weed species are also very small, increasing the difficulty of making accurate counts. Seed counting may be automated with a seed counter or image capture device. Image capture and analysis technology has many applications, including seed morphology analysis by the seed industry. Seed count accuracy decreased with increased number of seed and smaller seed sizes. In general, the image capture technique compared favorably with manual seed counting and has the potential to further improve seed bank assessment methods (Mesgaran et al., 2007).

Using the most effective, efficient, precise and less costly seed separation methods, enumeration and assessment of SB potential is very important under different conditions for complete assessment of density and diversity seeds in the soil. These preconditions are also used to design correct land use planning for land management, restoration of degraded lands and deliver correct recommendations for land managers and policy maker for different land use/land cover dynamics in different vegetation types.

### The relationship between seed bank and standing vegetation

The relationship between the composition of the SB and standing vegetation is particularly important for the vegetation that appears under different management

regimes (Lopez-Marino et al., 2000). Studies from many plant communities have shown that importance of the SB to ecosystem development following disturbances. Whether a SB is either transient or persistent (Thompson and Grime 1979) has been proposed to be related to successional age and disturbance regimes (Paul and Gibson, 1995). However, the nature of this relationship is ambiguous, mainly because few studies compare the SB of a diversity of habitats. In several studies, the SB did not resemble the above-ground vegetation closely (Thompson and Grime, 1979). The composition and abundance of seed species in the soil, as well as the distribution of life forms, are influenced by factors such as floristic composition, phenology of local vegetation and disturbances occurring at forest edge (Esmailzadeh et al., 2011).

### **Seed banks, management and restoration of natural vegetation**

SB is the reservoir of seed capable of germinating in favorable conditions in the soil or on the surface (Jaganathan and Dalrymple, 2016). SBs are also considered to be an important potential seed source for the restoration of plant communities (Bossuyt and Honnay, 2008). SBs usually in desert ecosystems are composed of very small seed that typically lack dispersal structures (Thompson and Grime, 1979) and are characterized by temporal and spatial fluctuations in seed density.

SBs are a crucial component in desert ecosystems and other stressful habitats where favorable conditions for seed germination and seedling establishment are quite unpredictable both in space and time (Gomaa, 2012b). In such vegetation types, SBs play a critical role in vegetation maintenance, succession ecosystem restoration, differential species management and conservation of genetic variability (Gomaa, 2012a). Native forests are characteristically scarce in urban areas and constantly under threat from surrounding development, invasion by exotic pest plants, animals and disturbance from human activities. Restoration of native forest vegetation in urban environments may be limited due to isolation from native seed sources and to the prevalence of exotic plant species (Overdyck, 2014).

Further research into a few persistent SB traits and seedling establishment is needed to refine effective management strategies for successful restoration of urban native forests. Enrichment planting will also be required for those native species with limited dispersal or short-lived seeds, thus improving native seed availability in urban forests as more planted species mature reproductively (Overdyck et al., 2012). In general, understanding the diversity and density level of SB is important for designing conservation and restoration programs in degraded ecosystems especially in arid

ecosystems. SBs, therefore, are considered as essential constituents of plant communities. This is because they contribute significantly to ecological processes, and then recoverability of vegetation after disturbances is believed to lie mainly in the buried seed populations (Zaghloul, 2008). The replacement of individuals from the SB may have profound effects on the composition and patterns of the vegetation within the community (Royo and Ristau, 2013). Therefore, conservation and restoration of plant species diversity rely on understanding the available levels of density and seed diversity, spatial distribution and processes that influence these levels and which have implications for the pathways by which plant species will colonize sites.

### **CONCLUSION AND RECOMMENDATIONS**

Seeds disperse from the mother plant by different mechanisms and incorporated into the soil and become part of a store or bank of seeds based on different dispersal syndromes. The dispersal mechanisms of seeds vary in different plants though the purpose is the same. The dispersal of seeds is commonly influenced by abiotic and biotic factors. The effectiveness of seed dispersal agents depends mainly on the number and quality of seeds dispersed. Once seeds are incorporated into SBs they face different environmental conditions, which entirely determine their fates. The fates of a seed population in the soil depend upon the fluctuation of seeds into an area by dispersal and the loss of seeds through the activity of predators and pathogens, senescence, and germination. Seeds in SBs are distributed at different depths starting from the upper soil surface both in dry and vegetation types.

Forest SBs, mostly studied in managed forests, proved to be small, species poor and not reflecting above ground species composition. Studies conducted in undisturbed communities indicated different SB characteristics. For an ecologist, the longevity of seeds in the soil is very important. The persistence of SBs in the soil is a major component of the phenomenon of plant succession and plays an important role in the evolution of plant communities.

Depending on internal and external environmental factors and types of species; the period of seed viability in the soil varies. Viability is also affected by ageing; with increase in age, the viability of seeds decreases until it stops completely. Seed survival in the soil contributes to population persistence and community diversity, which are creating a need for reliable measures of SB persistence. SBs are known for maintaining a gene pool, which ensures continual occupation of a site after disturbance; that in turn is a complementary mechanism of regeneration involved in the maintenance of floristic diversity. The SBs are also found in different environments or vegetation types represent a record of past as

well as present vegetation growing on the area and nearby.

In general, SBs play a critical role in vegetation maintenance, succession, ecosystem restoration, differential species management and conservation of genetic variability. Therefore, evidence based information on SBs can be used as input for agriculturalists and natural resource managers so as to manage crops from weed invasions, and to protect natural vegetations from invasive plant species. Data in relation to SB reserves are also crucial for natural regeneration management and restoration of degraded ecosystems. To carry out such activities, further studies are needed in all semi-natural and natural ecosystems to quantify and know quality of seeds in SBs. Hence, each ecosystem evaluation will be used as input to prepare land use management planning guidelines which incorporate conservation and restoration programmes particularly for degraded and arid areas. If an existing vegetation stand is destroyed by various causes, the SB will immediately serve as a source from which new vegetation arises.

Research-driven improvements in SB use efficiency for restoration should be available by natural resource managers are available at landscape levels. Communities need knowledge on using SBs and restoring landscapes. Biodiversity conservation institutes for instance expand their mandate from ex-situ germplasm conservation to in-situ conservation (air-dry storage) for restoration of degraded lands. To achieve these, new, enclosed botanic gardens should be encouraged in all regions in the country. Regeneration by seeding and enrichment planting will be recommended if SB is poor in the soil for plants. Local communities should be trained, especially through developing and delivering in-country restoration capacity. It is also highly recommended that these local practices are augmented with worldwide partnership experiences through trained experts of natural resource managers.

## CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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