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Methods of soil seed bank estimation: a literature review proposing further work in Africa

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A number of methods are used to assess the soil seed banks of a range of plant species in various habitats around the world, with approaches that differ between countries and continents. An understanding of the differing techniques emphasises the need for further research, especially in Africa. We reviewed 97 articles on soil seed bank estimation, published between 2010 and 2020, and only 13.41% of these were from Africa. Soil sample collection in Africa was based mainly on stratified random sampling, systematic sampling, random sampling or cluster sampling carried out at the end of each region's rainy season. Random and cluster sampling were more widely used in savannas, while stratified random and systematic samplings were more common in forests. The shape of the samples was either circular or quadrilateral (square and rectangular) or they were measured by soil mass or volume. The soil sampler cores most often applied were: circular diameter of 5 cm; square sizes of 10 × 10 cm, 20 × 20 cm and 25 × 25 cm; and rectangular sizes of 20 × 25 cm and 20 × 10 cm. The most-used soil core depths were 5 cm and 10 cm. No specific sample shape was linked with either forest or savanna ecosystems, although the number of samples depended on the land use and land cover. Soil seed bank densities and species composition were mainly assessed with direct greenhouse germination over trial duration depending on the plant species' functional traits. In analysing soil seed bank data, non-parametric statistics were more frequently used than parametric statistics because of the skews in the data. This review will contribute to future soil seed bank studies in Africa.

Keywords: Soil Seed Bank, Sampling Methods, Greenhouse Germination, Literature Review

Introduction

Seeds from a broad range of plant species occur in soil seed banks in various habitats and may be peculiarly important in restoration projects, where preferred species have been lost from the vegetation but survive in the seed bank (Brock et al. 1994). Large amounts of seeds can remain dormant in soil for many years, and can germinate when conditions become favourable (Warr et al. 1993). Soil seed banks are therefore important in understanding vegetation history as the vegetation composition in terms of plant species is influenced by seeds production, dispersal and longevity of seeds as well as soil depth (Sumberová & Ducháček 2017). Significant role can be attributed to seed banks as the determinant of future vegetation, especially after a disturbance (Warr et al. 1993).

In assessing soil seed banks, basic approaches (for example wet sieving and flotation, both of which are followed by identification of seeds under a stereoscopic microscope) are emphasised (Sumberová & Ducháček 2017). Other approaches include the cultivation of soil samples and subsequent identification of the emergent seedlings (Bakker et al. 1996). The advantages and disadvantages of each of these methods have been demonstrated independently by various researchers and have been subject to extensive discussion (Gonzalez & Ghermandi 2012, Mahé et al. 2021). Moreover, the flotation approach was criticised for its inaccuracy (Gross 1990), and therefore the two remaining approaches (cultivation of soil samples approach and wet sieving approach) would have been more widely used in recent soil seed bank analyses.

Although soil seed bank studies have been conducted in many parts of the world, the literature shows a large range of methods from sampling stage to the estimation of species diversity and density and sometime with methodological biases along the study process (Csontos 2007). Thus, no adequacy of soil seed bank assessment methods has been reported yet. For example, in the attempts to minimize sampling method biases, many research dealt with the tedious compensable process of huge amount of soil samples without sufficient guarantee (Brock et al. 1994).

In addition, soil seed bank assessment in different ecosystems was conducted with time and labour investment because of the technicalities of the method procedures (Benoit et al. 1989). It is therefore important to document the soil seed bank assessment method in relation to the ecosystems for further research on the technical and method procedures.

Many African ecosystems are degraded due to multiple factors such as fire, intensive logging, grazing and climatic change (Savadogo et al. 2008). Thus, there is a need for ecosystems restoration and conservation in Africa. The soil seed bank of theses ecosystems may be of interest for

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ecological restoration due to the presence of seeds from the above vegetation in the soil (Savadogo et al. 2017). Moreover, it might be acknowledged that few studies concern this topic in Africa. Despites the few studies on soil seed bank assessment in African ecosystems (Tab. S1 in Supplementary material), there is a lack of reference method for trials experiment, data collection and analysis. The method bias is an issue for seed bank analyses and discussion of the results (Chiquoine & Abella 2018). To make soil seed bank analysis more useful and especially in Africa, it should be important to integrate data from various databases. Combined environmental data (soils, vegetation and climate) would allow modelling of plant species distribution and/or ecological characteristics of stand vegetation (Ewald et al. 2013, Stankevica et al. 2015) to aid landscape restoration. The challenge of this literature review was to find which seed bank assessment methods would be preferentially adopted in soil seed bank assessment in Africa. This paper was then based on soil seed bank literature in relation to vegetation patterns (grassland or savannas and forests) and aims both to highlight the relevant literature on recent methods used in seed bank studies and to emphasise the need for further research within this area in Africa.

Methods of literature search

The Web of Sciences® database was consulted for the papers published in the period of 2010-2020. The keywords used to search the papers included "soil seed bank", "seed bank and methods", "seed bank and soil sample", "soil seed bank and Africa", "seed bank and grassland", "seed bank and savannas", "seed bank and forest", "seed bank and herbaceous", "seed bank and tree species". The papers that did not clearly provide the methods used in soil seed bank assessment were discarded as well as the review papers that did not focus on understanding the seed bank assessment efficiency and/or the accuracy of a method or the comparison of methods. A total of 97 papers were finally considered for this review. Data were analyzed with regard to the objectives of the study, the soil sampling methods, soil sample size, number of samples, seed bank estimation methods, above-ground vegetation analysis methods, soil analysis methods, duration of trial, type of data collected during trial, data analysis methods, plant species studied (herbaceous, trees or both), vegetation type (savanna, grassland, forest), country and continent. Frequency, tables and charts were used to present the findings.

Review of seed bank literature

The main objectives of the studies examining soil seed banks were: (1) to assess the effects and intensity of earlier disturbance on aboveground vegetation (Tessema et al. 2016, Leder et al. 2017, Palmer et al. 2018, Sanou et al. 2018); (2) to evaluate restoration methods (Klooster et al. 2014, Helsen et al. 2015, Luo et al. 2017); and (3) to understand habitat resilience to threat (Davies et al. 2013, Zhang & Chu 2013, Fernández et al. 2018). Others studies have focused on the comparison of ecological habitats in terms of plant species, diversity variation in seed banks (Adereti et al. 2014, Dos Santos et al. 2016, Schwab & Kiehl 2017, Douh et al. 2018) and dynamics of soil seed banks in relation to aboveground vegetation (Franzese et al. 2016).

Studies concerning the methods of soil seed banks assessment were mostly related to the composition and structure of the above-vegetation in relation to the soil seed bank (Ambrosio et al. 2004, Gonzalez & Ghermandi 2012, Shen et al. 2014, Sandra et al. 2016, Plue et al. 2017). Other studies addressed how to reduce bias in greenhouse seed bank data by using post-disturbance gap emergence trials (Plue et al. 2017) and considered whether a large number of small-sized samples are important in forest soil seed bank characterisation (Shen et al. 2014). In addition, these methodologies were widely tested in different ecosystems in North and South America, Asia and Europe. However, few studies addressed the methods of soil seed banks assessment in Africa with diverse ecosystems. Two categories of research questions were addressed in the studies conducted in Africa, such as: (i) how land use or land disturbance affect seed bank richness, density and distribution (Dreber & Esler 2011, Symes 2012, Adereti et al. 2014, Tessema et al. 2016, Galloway et al. 2017, Akande et al. 2018, Sanou et al. 2018); and (ii) the relationship between the soil seed bank and aboveground vegetation and the impact of forest management on seed bank (Daïnou et al. 2011, Gomaa 2012, 2014, Savadogo et al. 2017, Strydom et al. 2017, Douh et al. 2018). This review is therefore an important step to guide future soil seed bank study in Africa.

Seed bank sampling methods

The choice of soil sampling technique in seed bank assessment is as important as the number and dimensions of the sample (Benoit et al. 1989, Mickelson & Stougaard 2003). A total of 75% of the papers considered used stratified random sampling techniques for sample collection, while 14% used systematic sampling, 10% used random sampling and 1% used cluster sampling. The chosen sampling method did not depend on the study location and the objectives of the study, but rather on the homogeneity of the aboveground vegetation of the study area (Hopfensperger 2007, Sumberová & Ducháček 2017), the slopes of the vegetation site surveyed (Shen et al. 2014, Plue et al. 2017) or the intensity of land use and disturbance (Dreber & Esler 2011, Sprengelmeyer & Rebertus 2015, Maia et al. 2016, Deiss et al. 2018, Sharma et al. 2018). Thus, all the sampling methods can be used in Africa ecosystems. Up to now, two sampling methods (systematic and stratified random samplings) were used in the studies carried out in Africa. The systematic sampling concerned three studies in forest ecosystems (Daïnou et al. 2011, Douh et al. 2018), savanna and grassland ecosystems (Sanou et al. 2018). The stratified random concerned 10 studies in woodland and savanna ecosystems (Dreber & Esler 2011, Tessema et al. 2016, Savadogo et al. 2017, Akande et al. 2018), desert ecosystems (Gomaa 2012, 2014), farmland (Adereti et al. 2014) and tree plantations (Symes 2012, Strydom et al. 2017, Galloway et al. 2017).

With the systematic sampling method, a complete description of the units (or individuals) and their arrangement in the population is required. The first unit is drawn at random from the population, and every *n*-th unit is selected until the desired sample size has been obtained. With stratified random sampling, a population is first divided into subpopulations or strata, which may or may not be of equal size. Within each stratum, a sample is selected randomly and independently. With cluster sampling, groups of units are selected randomly from the population. These groups can also be called clusters or primary units and are composed of secondary units. With cluster sampling, all secondary units are sampled. Simple random sampling is a method where each possible sampling unit has an equal (or known) probability of being selected, and the random selection of such units ensures unbiased estimates of population means and sampling variance.

The systematic and stratified random methods were used for trees and herbaceous plants in forest, savanna and grass vegetation patterns. The cluster and random methods were used with herbaceous plants in savannas and grasslands. The stratified random sampling technique was mostly applied in the forest and savanna vegetation (Fig. 1). The choice of method can be due to the heterogeneity in land cover within these ecosystems, to reduce bias (Deiss et al. 2018, Sharma et al. 2018). In Africa, stratified random design method was mostly used due to the spatial heterogeneity within each ecosystem (physical, biological, or environmental characteristics – Mahé et al. 2021). Thus, this method can be the most appropriate within Africa ecosystems when heterogeneity has to be taken into consideration.

Soil sample shape and dimension

The samples taken in soil seed bank studies were circular, square or rectangular. The most common sample shape was the circular method with 47% of studies, followed by quadrilateral at 37%, of which squares made up 58.74% and rectangles 41.26%. There was no specific sample shape linked with either forest or savanna ecosystems. This is due to the land cover heterogeneity within each ecosystem of forest or savanna (Warr et al. 1993). Thus, all the sample shapes can be used in Africa ecosystems. The shapes used in Africa included circular plots in savanna, grassland and tree plantations ecosystems (Dreber & Esler 2011, Akande et al. 2018), square plots in savanna and woodland ecosystems (Sanou et al. 2018, Savadogo et al. 2017) and rectangular plots in desert ecosystems (Gomaa 2012, 2014). More evidences are needed on the relevant shape to consider within each ecosystem in Africa, as the shape used to assess vegetation pattern varied according to the ecosystem (Salako et al. 2013).

The diameter of the circular-shaped plot varied from 1.8 cm to 40 cm, although 5 cm was most commonly applied (55.3%), followed by 1.8 cm (13.03%), 2 cm (10.31%), 2.5 cm (7.19%), 9 cm (6.38%), 12.5 cm (4.51%), 20 cm (2.94%) and 40 cm (0.34%). No specific diameter was attributed to a study area, or to a country or continent. Thus, the different diameters can be used in Africa ecosystems. The diameters used in Africa included 5 and 8.5 cm in savanna and grassland ecosystems, respectively (Dreber & Esler 2011, Akande et al. 2018), 5 cm in pine plantations and 6 cm in *Acacia* plantations (Galloway et al. 2017, Strydom et al. 2017). More research is needed to provide evidence on the specific diameter to consider within each ecosystem in Africa.

With the quadrilateral shape, the square was more widely used than the rectangle. The most common sizes were 10 × 10 cm (48.25%), 20 × 20 cm (25.75%) and 25 × 25 cm (22.59%), with others (15 × 15 cm, 30 × 30 cm, etc.) rarely considered (3.41%). The most-used rectangular shapes were 20 × 25 cm (62.36%) and 20 × 10 cm (23.01%), followed by 15 × 8 cm (8.21%), 25 × 39 cm (3.33%) and others (37 × 27 cm; 30 × 10 cm; 135 × 50 cm, etc.) at 3.09%. Soil volume or soil mass (Adereti et al. 2014, Bourgeois et al. 2017, Forte et al. 2018, Klaus et al. 2018) and sampling area (Van Etten et al. 2014, Vandvik et al. 2016, Londe et al. 2017) were rarely used in soil seed bank assessment studies. The size mostly used in Africa included 15 × 15 cm in savanna and woodland (Savadogo et al. 2017, Sanou et al. 2018) and 20 × 25 cm in desert ecosystem (Gomaa 2014). More research is needed to provide evidence on the specific size to consider within each ecosystem in Africa.

Soil depth also influences soil seed bank estimation (Csontos 2007). The most frequently applied depths of soil cores were 5 cm (53.27%) and 10 cm (40.64%). Other studies assessed the variation in the soil core depths from 0 to 20 cm at intervals of 5 cm (0-5 cm, 5-10 cm, 10-15 cm and 15-20 cm) and its influence on soil seed banks (De Rouw et al. 2014, Sousa et al. 2017, Lipoma et al. 2018). There was no relationship between soil core depth and study area or geographic location. However, soil core depth was linked to the plant species' seed behaviour (seeds mass and shape) or habitat (soil and vegetation type – Warr et al. 1993, O'Donnell et al. 2014, Sanou et al. 2018). While the different soil depth can be considered in Africa ecosystems, further studies are needed to address the relevant soil depth within each ecosystem. The soil depths actually considered in studies conducted in Africa included simple and multi layers. The simple layers included 0-4 cm in savanna and grassland ecosystems (Dreber & Esler 2011), 0-5 cm in desert ecosystems (Gomaa 2012, 2014) and forest ecosystems (Daïnou et al. 2011), 0-10 cm (Galloway et al. 2017) and 0-15 cm (Strydom et al. 2017) in tree plantations. The multi layers included 0-3, 3-6, 6-9 in savanna and woodland ecosystems (Savadogo et al. 2017), 0-5, 5-10, 10-15 cm in savanna and grassland ecosystems (Akande et al. 2018, Sanou et al. 2018), 0-5, 5-10, 10-20 cm in forest ecosystems (Douh et al. 2018).

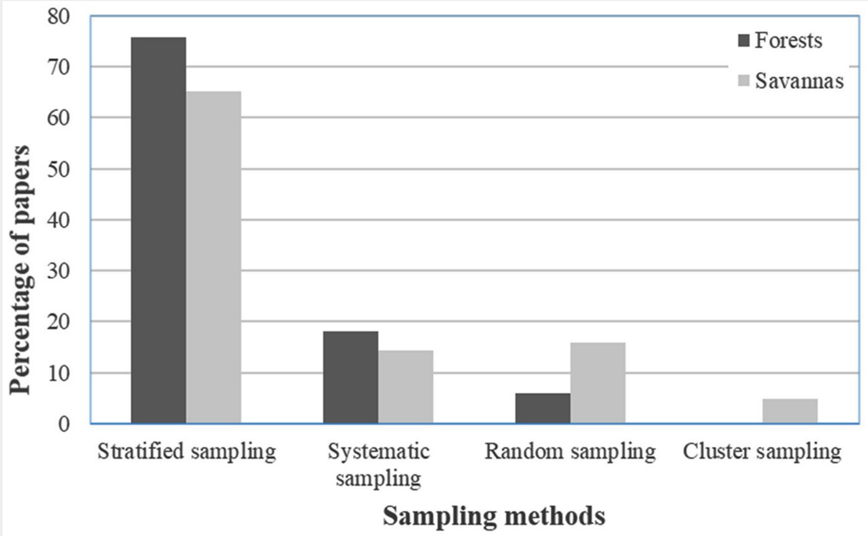

Fig. 1 - Methods of soil sampling applied in forests and savannas.

Sample number

In assessing soil seed banks, the number of soil samples taken is crucial not only to promote the accuracy of the study and the relevance of its results (Mickelson & Stougaard 2003) but is also key to considerations of both time and labour intensity (Benoit et al. 1989, Ambrosio et al. 2004) and hence to cost-benefit (Nadon & Stirling 2006). The challenge of this review is to find which sample number should be preferentially adopted in soil seed bank evaluation, especially in Africa. Regarding this matter, it has been stated that the sampling method can influence the sample number in any given ecosystem (Ambrosio et al. 2004). For example, the sample number can be less from systematic sampling than from random sampling without losing relevance in results while using the same sample dimension. However, regardless of sampling method, accuracy in soil seed bank estimation can be improved by ensuring a sufficient number of samples (Bigwood & Inouye 1988). This is because the precision in gauging seed densities may be under- or overestimated when the number of samples is small (Warr et al. 1993). Therefore, the number of soil samples should be more than 50 to provide a reasonable estimate of the seed density (Bigwood & Inouye 1988). However, this number can be less in areas with high density of seed banks (Mickelson & Stougaard 2003).

Among examples of soil seed bank studies in Africa, Sanou et al. (2018) used 720 soil samples when comparing the aboveground vegetation and soil seed bank composition related to different grazing intensities in Burkina Faso. Tessema et al. (2016) used 544 soil samples to assess changes in grass plant populations and temporal soil seed bank dynamics in a semi-arid African savanna. Gomaa (2014) considered 450 soil samples in a desert ecosystem when reporting on the variation between soil seed banks and stand vegetation in Egypt. In other papers focused on Africa, the number of soil samples depended on the volume of soil available to use (Douh et al. 2018).

Period of soil sampling

The timing of soil sample collection is of great importance in soil seed bank assessment studies (Tiebel et al. 2018). Several papers highlighted the period of field soil sample collection, at least in reference to the seasonal climate of the study area. The end of the rainy season was most cited for soil sampling in tropical regions, particularly those in Africa (Braga et al. 2016, Savadogo et al. 2017, Strydom et al. 2017, Sanou et al. 2018, Souza et al. 2018). During this period, it is easier to investigate the composition, density and vertical distribution of the viable soil seed bank. Seed dispersal in rainy season could attain the peak and the persisting seed from the previous season could still germinate (Savadogo et al. 2017, Strydom et al. 2017, Sanou et al. 2018). The earlier germination of the tran-

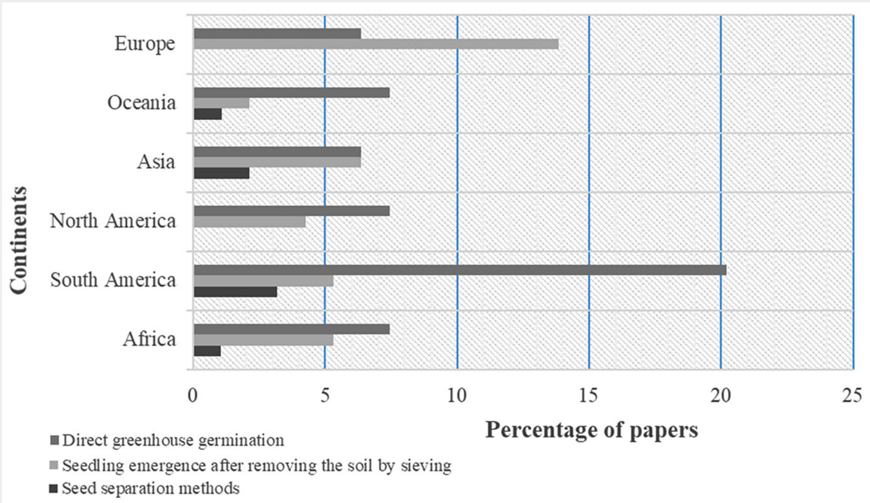

Fig. 2 - Methods of soil seed bank estimation in studies worldwide (2010-2020).

sient seeds can also justify the choice of the end of the rainy season. Moreover, the end of the rainy season can allow collecting information on total soil seed bank, because seed dispersal ended in this period and most transient seeds may already emerge (Mahé et al. 2021).

Other studies generally matched sampling to the period between earlier seed bank germination and when the new seeds had matured and spread (Tessema et al. 2016), which may correspond to the rainy season when there is abundant seed availability in the soil (Sousa et al. 2017, 2018). Moreover, the particular research goal can often lead the timing of soil sampling for vegetation evaluation (Csontos 2007). In these cases, phenological processes of the stand vegetation or of the given species would be important in seed bank composition. Evidently, the life duration of seeds would also be important in setting the time period of sampling (Saatkamp et al. 2017). More literature focusing on the study object would therefore be helpful in further establishing the timing of soil sampling in seed bank characterisation.

Seed bank estimation methods

Many methods have been used in the literature to estimate seed numbers in soil samples. Warr et al. (1993) highlighted the separation of seeds from soil by using water (washing or flotation); this method was not appropriate in several cases because of the non-distinction between viable and unviable seeds and the underestimation of species numbers due to the similarity of different seeds. Also, the risk of washing out of very small seeds makes the method very uncertain. Thus, alternative methods of seed numbering using germination were developed to improve the accuracy in soil seed bank estimation.

Three methods of seed numbering by germination have been used to assess seed banks in soil samples. Direct greenhouse germination was most frequently used to assess soil seed bank densities and species composition (60.22% of the examined studies). This method of quantifying seeds in soil samples was most practised in South America, Oceania, North America, Asia and Africa (Fig. 2). The second method most favoured worldwide was the use of sieving before seed germination (23.86%). Soil seed bank estimation in Europe used this method more than the others. The third approach was the seed separation method (15.92 %), which was less used in all the regions (Fig. 2). Combinations of methods includng the seed concentration method (Ter Heerdt et al. 1996) or sieving (Roberts 1981) before seed germination were used in the estimation of soil seed bank (40% of papers). Therefore, the germination of soil seed (greenhouse trial) can be applied after sieving seeds, for example (seed concentration). The combination of methods can often be used to test when seed already identified is also viable or to confirm the plant species.

Each method has its advantages and disadvantages (Warr et al. 1993). Many authors highlighted that methods in combination could increase precision in seed density estimation (Van Etten et al. 2014). However, the methods can also be used separately, not only to determine seed densities in soil layers, but also to test seed viability *via* germination (Strydom et al. 2017) or to compare the efficacy of different methods (Gonzalez & Ghermandi 2012). Of the entire above, no specificity was found for the methods used and habitat type (Mahé et al. 2021). The same method singly or in combination that is applied in soil seed assessment for forest ecosystem can also be used for savanna ecosystems. Thus, all the methods can be used in Africa ecosystems. Direct greenhouse germination was mostly used in Africa (62%) with samples from savannas ecosystems (Adereti et al. 2014, Tessema et al. 2016, Savadogo et al. 2017), savanna and grassland ecosystems (Akande et al. 2018, Sanou et al. 2018) and tree plantation (Symes 2012, Galloway et al. 2017, Strydom et al. 2017). The combination of the direct greenhouse germination method with either the seed concentration method of Ter Heerdt et al. (1996) or sieving of Roberts (1981) was also used (38%) in seed bank assessment in Africa ecosystems, including forest (Daïnou et al. 2011, Douh et al. 2018), savanna and grassland ecosystems (Dreber & Esler 2011) and desert ecosystems (Gomaa 2012, 2014). More research is needed to provide evidence on the appropriate methods for each ecosystem in Africa.

Data collection and seed bank analysis methods

In the greenhouse, the frequency of data collection on seed germination, seedling growth and radicle elongation was daily, weekly or monthly, depending on plant species biology. More than 83% of the examined papers showed that data on the emerged seedlings were collected during the growth trial in the greenhouse. Many authors noted that the trays needed to be checked at regular intervals for new emergent seedlings (O'Donnell et al. 2014, Dos Santos et al. 2016, Savadogo et al. 2017, Sanou et al. 2018). Each germinated seed was counted, recorded and removed. When seedling identification was not easy, it was transplanted elsewhere and grown until species identification was possible. Therefore, the trial duration depended on the plant species under study and could vary from two weeks to two years. The study area or habitat had no link with the duration of the trial for species identification. This variation can also be applied in Africa ecosystems where the actual duration of trial germination varied from 3 weeks (Adereti et al. 2014, Akande et al. 2018) to 9 months (Tessema et al. 2016, Galloway et al. 2017) for samples collected from savanna ecosystems (Adereti et al. 2014, Tessema et al. 2016, Savadogo et al. 2017) or grassland ecosystems (Akande et al. 2018, Sanou et al. 2018).

Seed density or diversity indices (stand vegetation and seedling) were mostly calculated in the published papers regarding soil seed bank assessment. Thereby, in order to compare diversity between areas of seed banks, the coefficients of similarity were often used (Warr et al. 1993). Therefore, the Sørensen's similarity index between seed bank and aboveground vegetation was calculated using presence-absence data (Shang et al. 2016, Fragoso et al. 2018, Sharma et al. 2018). Other statistical methods were also used to compare the seed bank density with aboveground vegetation. In this case, non-parametric statistics were found to be more relevant than parametric statistics because of the skews in seed bank data (even after data transformation) in order to meet the statistical requirements (Warr et al. 1993). Several studies used the Kruskal-Wallis test or the Mann-Whitney U test to compare density of emerged seedlings, floristic composition, richness and diversity of species (Cubiña & Mitchell Aide 2001, De Andrade & Miranda 2014, Franzese et al. 2016, Lacerda et al. 2016, Maia et al. 2016, Jaroszewicz et al. 2017, Schwab & Kiehl 2017, Sousa et al. 2017). However, parametric statistics were still used either with or without data transformation to compare seed banks with standing vegetation. Analysis of variance (ANOVA) followed by *post-hoc* Tukey's test were applied to structural differences by Kunz & Martins (2016), Shang et al. (2016), Galloway et al. (2017), Luo et al. (2017), Forte et al. (2018) and Sharma et al. (2018). Data can also be analysed by performing a generalised linear mixed model to highlight the relationship between seed density and species composition (Havrdová et al. 2015, Strydom et al. 2017, Fernández et al. 2018, Palmer et al. 2018, Vanstockem et al. 2018).

Conclusion

This study reviewed the existing literature on soil seed bank assessment and the methodologies used from sampling to data analysis. Of the 97 scientific papers reviewed, only 13.40% were from Africa. The stratified random sampling method was the most applied for soil sampling due to heterogeneity in the land cover within the ecosystems. The circular sample with 5 cm diameter and 5 cm depth was most widely used to sample the soil. For soil seed bank estimation, the greenhouse germination method was the most adopted. Data on seed germinated, seedling growth and radicle elongation were collected at daily, weekly or monthly intervals based on species behaviour. For data analysis, floristic data were generally analysed with the Sørensen's similarity index, while ANOVA or the Kruskal-Wallis test were used for density data. Generalized linear models were used to show the relationship between seed density and species composition. The methods used in soil seed bank assessment are not specific to a region and can be transferred in all ecosystems in Africa for ecological restoration. This review is an important step in furthering soil seed bank estimation in Africa for ecosystems restoration.

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Supplementary Material

Tab. S1 - Published articles on soil seed banks worldwide in 2010-2020.

Appendix 1 - References of papers cited in Tab. S1.

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