



Seed banks: ecological definitions and sampling considerations

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Abstract: Definitions of seed banks are discussed in the introductory part of the paper. In the second part, a literature review regarding sampling problems in soil seed bank ecology is presented. Regarding sampling depth, a rapid decline in soil seed content is demonstrated from example studies. The use of soil cores with 5 cm or 10 cm depth is suggested to ensure comparability of results. For determination of optimal sample volumes for various communities, the species saturation model is suggested such that “minimal volume” can be defined for soil seed banks in the same way that “minimal area” can be defined in phytosociological studies. Although sampling time may depend on research goals for vegetation types with a winter standstill period, late autumn sampling is suggested for detecting the entire soil seed bank, whilst late spring sampling is recommended for the examination of its persistent part. Studies looking at medium (plant community level) and fine scales (patch level) have demonstrated that soil seed bank distributions show horizontal aggregation for most of the cases and for most of the species. Seed dispersal processes which are among major factors responsible for such aggregated patterns are also discussed.

Seed bank definitions

The expression ‘seed bank’ can be defined as all the viable (dormant as well as ready to germinate) seeds contained in the soil in a given area (Harper 1977). Roberts (1981) uses practically the same definition but expands it to include all seeds lying on the soil surface. (Although, from a botanical point of view, we often consider fruits rather than seeds, the literature does not make a distinction here and applies the expression ‘seed bank’ to include all dispersal units no matter whether seeds or fruits.) These definitions seem useful in a practical sense but they are not completely accurate as a scientific definition. This is because: (a) there are many species in which significant part of the seed bank is not preserved in the soil; and (b) just the opposite, certain seeds found in the soil, though viable, are not part of the seed bank.

Well-known examples of situation (a) are *Pinus banksiana* Lamb. and *P. attenuata* Lemm. of North America. In these species, the mature seeds are retained in cones on the mother tree for several years. They are usually dispersed only after the heat of a forest fire triggers cone

opening, thus ensuring the appearance of a new seedling generation (Keeley et al. 1999). Many species of the *Proteaceae* family and the genus *Allocasuarina* and *Eucalyptus* are also characterized by ‘canopy-stored seed banks’ (Zammit and Westoby 1987, 1988, Pannell and Myerscough 1993), most of them also fire adapted (Lamont et al. 1991, Pausas et al. 2004). Certain herbaceous plants can also bear their mature fruits for a prolonged period (this is a so-called ‘aerial seed bank’). According to Narita and Wada (1998), this is most important in cases where there is a great risk of seed predation on the soil surface and where the wet period suitable for germination is short and unpredictable.

In the case of epiphytes (e.g., tree-dwelling bromeliads) and especially of true parasites (e.g., mistletoe species), the seed bank exists in the cracks of the host plant’s bark and in the forks of its branches.

A special case of the above-surface seed bank is when birds use seeds equipped with soft hairs to build their nests (Dean et al. 1990). This poorly studied phenomenon provides an opportunity for the plants to spread their

Table 1. Subordinate seed bank categories and terms proposed for distinction.

'seed bank'				
l i m i t i n g c o r r i t e r i a	medium (spatial allocation)	seeds stored in the soil or on the soil surface 'soil seed bank'	seeds floating in or drifted by water 'aquatic seed bank'	seeds held by above- ground parts of plants, (also includes passive storage, e.g. in bird nests) 'aerial seed bank' ('canopy-stored seed bank' for serotinous woody plants)
	seed longevity	survival time is up to 1 year 'transient seed bank'	survival time from 1 year to 5 years 'short-term persistent seed bank'	survival time longer than 5 years 'long-term persistent seed bank'
	biological organiza- tion level	a single species studied 'specific seed bank'	phytosociologically undefined units (e.g. ploughed lands, flower beds, etc.) with respect of total seed pool 'seed bank assemblage' *	natural, semi-natural vegetation units (asso- ciations) studied with respect of total seed pool 'seed bank community'

* 'Seed bank assemblage' is suggested also to name subsets (e.g. grasses *vs.* herbs or annuals *vs.* perennials, etc.) of a total species pool of either natural or man-made habitats.

seeds but is only possible when coupled with appropriate seed longevity.

Aquatic plants or plants living near water often have seeds and fruits that float. Bill et al. (1999) have performed detailed studies in this field, using seed traps on Alpine rivers and also some laboratory flotation experiments. Further studies related to lowland streams were also published (Boedeltje et al. 2003). The role of water as a seed carrying medium can be even greater in the case of seashore plants. Their seeds can drift with the currents for months until they reach the shore and begin to germinate (*Hibiscus tiliaceus* L., *Ipomoea pes-caprae* Sweet., *Cocos nucifera* L., *Entada phaseoloides* (L.) Merr., *Ricinus communis* L., etc., Nakanishi 1983, 1987, 1988). A significant proportion of the seed bank of such species exists in the water.

In situation (b), where viable seeds found in the soil are not part of the seed bank, we must consider that the seeds of certain species get into the soil unripe, that is before they become a functioning part of the seed bank, e.g., *Arachis hypogaea* L. and *Trifolium subterraneum* L. Amphicarpic plants, which produce both subterranean and aerial seeds (e.g. *Amphicarpum purshii* Kunth, *Cardamine chenopodifolia* Pers. *Catananthe lutea* L.) can also be considered here (for complete list of amphicarpic species, see Cheplick 1987).

Taking into consideration the above-mentioned facts, we can give the following general seed bank definition: *The seed bank includes all naturally occurring seeds that have a metabolism independent of the mother plant and that are viable (able to germinate or will potentially become able to germinate in the future).*

In many cases, we find more restricted uses of the term seed bank. Authors very often limit the medium of occurrence of seeds and speak about the 'soil seed bank'. Another regularly used restriction is autecological limitation, when we find data on the seed bank of only a single species. Sometimes it may also be useful to differentiate between the currently germinable proportion of the seed bank (the active seed bank) and the part that will become germinable in the future (the dormant seed bank, Harper 1977). However, "active" and "dormant" seed bank are confusing and should be abandoned, because: 1) not all seeds that remain ungerminated do this because of dormancy, and dormancy is neither a necessary nor a sufficient condition for persistence in the soil (Thompson et al. 2003); 2) "active" means something happening while in this context "active" means the potential to become activated. Perhaps, the most frequent reduction is of functional kind and is related to seed bank classification. When seed bank types are defined, a distinction between transient and persistent types has high priority (Csontos and Tamás 2003). Researchers tending to simplify the term "seed bank" used to consider it as would be the per-

sistent fraction only, and this simplification often happens when restoration ecology is being discussed, since long-lived seeds have crucial importance in vegetation recovery (Bakker et al. 1996a). However, to preserve the clarity of terminology I would recommend to apply the term 'seed bank' in its widest meaning and using terms "transient ~", "short-term persistent ~" and "long-term persistent seed bank" (*sensu* Thompson 1993) when survival time of seeds is in the focus of interest. A proposed system of terms is given in Table 1.

Sampling in the study of soil seed banks

As soon as we set out to study a seed bank, we encounter a number of questions, several of which are discussed below. The optimal answer to each of these depends on the research question, but for the development of theories and hypotheses, we often need to compare wide range of conditions. Hence, it would be of value if more studies adopted comparable methodology. In research projects where the number or size of samples taken is practically unlimited (in the case of seed banks, samples are taken from the habitat's soil) perhaps the first question to answer is: how large a sample do we need?

Sampling depth

As the depth of soil layer increases, the number of seeds present, as would be expected, decreases, in general drastically.

Leck and Simpson (1987) found that in the soil of flood-plain meadows, the layer between 4 and 6 cm contained only about 7-18% of the seeds found in the top 2 cm. The seed content of the layer between 8 and 10 cm was only 1.8-5.4%. Using the same method of calculation, the seed content of the 15-17 cm layer was an insignificant 0.2-0.5%.

A review of the results obtained at one *Calluna* heath and seven meadow sites confirms the special importance of the top layer of soil (Harper 1977). In the case of the heath, 78% of the seed bank was present in the top 2.5 cm. The seed content of the layers below 10 cm was very low at the seven meadow sites. A sampling depth of 10 cm also proved to be deep enough in some English woods (Warr et al. 1994), and Symonides (1986) found that irrespective of the successional stage of a sere at least 70% of seeds are accumulated in the top layer (0.5-2.5 cm) of the soil.

Graham and Hutchings (1988) point out that the decrease in quantity of seed bank with soil depth may differ with species group. The decrease is faster in the grass seed bank assemblage and slower in the case of perennial

forbs. The reason for this could be that the elongated shape of the grass caryopses makes them less susceptible to being buried (Thompson et al. 1993, Csontos 1998).

If the seed bank is extremely well-developed (as in the case of riparian vegetation), then there may be a relatively high number of seeds in even the deeper layers (Welling and Becker 1990). In case of *Striga asiatica* (L.) Kuntze, a species with extremely small seeds, studies found a seed density of 2 seeds/100 grams of soil at a depth of 140-150 cm (Robinson and Kust 1962).

When considering sampling depth, we must mention the phenomenon of seed bank "profile inversion". This describes situations where the largest proportion of seeds occurs in the deeper layers. Profile inversion occurs most frequently in the case of the much studied plough-land seed banks, when the inversion is due to the regular ploughing of the soil (Fekete 1975, Hunyadi and Pathy 1976). The inversion can be limited to the specific seed bank of certain species only or may involve the whole seed bank assemblage. This latter was studied by Máthé and Précsényi (1971) in the plough-lands of the IBP model area at Újszentmargita (East-Hungary), and by Hunyadi and Pathy (1976) in meadow soils that were turned into plough-lands near Lake Balaton.

The phenomenon of seed bank profile inversion in natural vegetation has been observed only in a few cases: Jerling (1983), McGraw (1987) and Kjellsson (1992) reported it for some species of a sea-shore meadow, of an Appalachian *Sphagnum*-bog and of Danish deciduous forests, respectively, whereas a seasonal inversion of the seed bank community was detected by Symonides (1978) in *Spergulo-Corynephorum* in Poland.

Sample volume

When studying soil seed banks, we must know the minimum soil volume (the 'minimal volume') that will determine the species occurring in the seed bank of a given area with satisfactory accuracy. This concept is similar to the phytosociological concept of 'minimal area'.

The first attempts to determine this minimal volume were made by Numata and Hayashi between 1964 and 1971 (Hayashi and Numata 1964, 1971). (Their series of articles written in English and Japanese were reviewed by Roberts in 1981.) According to their research, the minimal volume – with a sampling depth of 10 cm – is 400 cm³ in weed communities in the early stages of succession, 500-600 cm³ in grasslands and 4000-6000 cm³ in climax forests.

However, Forcella (1984) has found that the minimal volume in a grassland (a former plough-land that had been fallow for five years) was $10\,000\text{ cm}^3$. In another disturbed grassland in Michigan, USA, the minimal volume was found to be about 7300 cm^3 . However, in this case the samples were taken from a depth of up to 15 centimetres (Gross 1990). Nakagoshi performed similar studies in woodland communities. He found that it is necessary to use a soil volume between $20\,000$ and $50\,000\text{ cm}^3$ in secondary forests and a volume of $40\,000\text{ cm}^3$ in climax forests with sampling depth of 10 cm (Nakagoshi 1984a, b, 1996).

Although not directly indicating minimal volume, we must mention an early work by Champness. He stated that to estimate the specific seed bank of the most frequently occurring species in a community, with 10% accuracy, two hundred soil cores are necessary (Champness 1949, cit. Warr et al. 1993). As these soil cores were taken from an area of 25 cm^2 and supposing a sampling depth of 5 cm, it is easy to calculate that the sample volume was $25\,000\text{ cm}^3$. This value was for the most frequent species only!

These results clearly show that the problem of minimal volume cannot be considered solved. The only certain thing is that the study of pioneer communities requires a smaller quantity of soil sampled than the study of those older successional and climax communities.

The remaining uncertainty is partly caused by the relatively low number of minimal volume studies that have been performed to date. We do not have data for many vegetation types and for some significant geographical areas. Therefore, additional minimal volume studies to fill these gaps would be welcome.

The other factor making research on minimal volume difficult is a matter of methodology. As previously discussed, a significant proportion of the seed bank is concentrated in the top layer of the soil. Therefore, a sampling unit taken from a large area but from a small depth (e.g., 0-5 cm) is more effective than a sampling unit with the same volume but collected from a smaller area and greater depth. However, certain research projects may require the study of deeper soil layers (e.g. 5-10 cm).

Accordingly we feel that the best solution is i) to take samples to a soil depth of 5 or 10 centimetres, which are the most frequently mentioned depths in existing publications (thus ensuring comparability of results); and ii) to document the sampling method as accurately as possible, always mentioning surface area (or sampling depth) and total volume of the sample. It is also advised to calculate seed density per square metre (Thompson et al. 1997).

Because deciding soil volume to sample is one of the most important steps of the sampling process, a list of comparative data with emphasis on non-forest communities is given from published studies reporting soil seed bank records of various European vegetation types (see Appendix). Similar tables limited to forest studies were published by Warr et al. (1994) and Jankowska-Błaszczuk (1998).

Timing of sampling

In areas where vegetation changes are governed by an annual cycle, the amount and composition of the seed bank changes seasonally (Thompson and Grime 1979). This must be taken into consideration when selecting sampling dates.

If we wish to get as full a picture as possible on the soil seed bank of a given area with a single sampling, sampling should be performed in October in Central Europe and areas with a similar climate (van der Valk and Verhoeven 1988, Virágh and Gerencsér 1988, Csontos et al. 1996). By October, practically all plant species will have dispersed their annual seed crop but species germinating in the autumn will not yet have begun to develop. In a warmer climate this date is much later, for example in the southern part of the island of Honshu the best period for sampling is the end of November (Nakagoshi 1984a) if the aim is to maximise species and seeds recorded. In a cooler climate, like Scandinavia, September is recommended for the same research goal.

If we are only interested in those species that retain their seed bank for more than 12 months, we should sample in May in Central Europe. By this time, species germinating in the spring have begun to develop but no fresh seeds have been dispersed. Using the same consideration, the ideal period for sampling in Scandinavia is the end of June (Milberg 1992, Milberg and Persson 1994).

As the seed bank size for a given species can also be influenced by chance events, results will be more valuable if sampling is repeated on the same date in consecutive years (Roberts 1981). Studies performed on short-grass prairie with erratic rainfall have shown that the time of soil seed bank maximum for a given species can differ by one or two months in two consecutive years (Coffin and Lauenroth 1989). Therefore, it is particularly advisable to observe Robert's recommendation when studying areas with an unpredictable climate.

The scientific value of data can be increased further if sampling is carried out twice annually: once at the time of maximum seed bank saturation and once at the time when the seed bank is at a minimum level (Nakagoshi 1984a,b,

Krinke et al. 2005). The first occasion provides data on the whole seed bank while the second helps to assess the persistent seed bank fraction. Here we must note that the other way to assess the transient and persistent fraction of the seed bank is to treat the samples taken from the upper (0-5 cm) and the deeper (5-10 cm) soil layers separately (Thompson 1993, Thompson et al. 1997). This is because it takes years for seeds to reach the deeper soil layers and so all transient seeds will lose their viability by the time, and if, they reach these deeper layers. However, the cut off depth at 5 cm was arbitrarily decided in the absence of precise information on seeds' sinking speed in soil. Thus, this question would be worth studying regarding both for species with different seed morphology and for soil types with different texture. Of course, it does not apply to cultivated soils, and in agricultural fields sampling time depends principally on the crop rotation cycle of the given area (Tuesca et al. 2004).

If we wish to determine the seed bank dynamics for a given area, we must take and study a series of samples. One of the most detailed studies of this kind was published by Graham and Hutchings (1988) from England, who sampled an area every month, for two vegetation periods. Russi et al. (1992) had the same objective when they worked with samples taken bimonthly for three vegetation periods from a Mediterranean grassland in Syria. In their much cited study, Thompson and Grime (1979) recommend sampling eight times annually in order to determine soil seed bank dynamics. This entails sampling approximately every six weeks.

Further considerations for planning sampling

It would be easy to suppose that the horizontal distribution of seeds in soil, following seed rain and burial, is likely to be nearly random. However, ecological experience places strong doubts on this supposition. The reasoning for these doubts can be related to the hypotheses for the dispersal of plant propagules.

The so-called 'escape' hypothesis supposes that there is a special advantage for offspring in moving far away from the mother plant. If offspring stay in the proximity of parent plants, they have to compete with numerous other seedlings for resources. This is in addition to competition from an adult individual, the mother plant (cf. Howe and Smallwood 1982, Howe 1986).

Although scattering widely has advantages, it also involves the risk that offspring leave the suitable habitat. Therefore, the seed scattering ability of species characterized by the escape hypothesis is not unlimited and most of their seeds fall in a relatively small area. This results in

an aggregated seed distribution. In addition, the distribution of the "escaped" seeds is also often aggregated. This is especially likely if their distributing agent is, for example, a frugivorous mammal or bird. Studying the faeces of medium-sized frugivorous mammals revealed 4-9 seeds in each dropping of the white-faced capuchin (*Cebus capuchinus* L.), an average of 9 seeds in each dropping of the howler monkey (*Alouatta palliata* Gray), and 6-45 (average 19) seeds in each dropping of the white-nosed coati (*Nasua narica* L.) (Howe 1989).

Large mammals - for European landscapes especially cow and red deer (*Cervus elaphus* L.) - can cause even greater local seed concentrations (Malo and Suarez 1995, Ortiz et al. 1995, Malo et al. 2000). The record-holder may be the Indian rhinoceros (*Rhinoceros unicornis* L.) which uses its so-called latrines for long periods of time. At one of these sites, more than 4000 viable *Trewia nudiflora* L. (Euphorbiaceae) seeds were found (Howe 1989). Fragoso (1997) reported that tapirs have a similar role in Amazonia.

Another possible method of propagule scattering is described by the 'directed dispersal' hypothesis, which also results in an aggregated seed bank. One of the most frequently studied phenomena here is myrmecochory, which has been found to exist in all climates for numerous plant species (Lisci and Pacini 1997, Dostál 2005, Mayer et al. 2005), though probably it is most pronounced in the Australian flora (Berg 1975, Ness et al. 2004). The seed storing activities of various mouse and vole species also contribute to aggregation of propagules (Jensen 1985, Jensen and Nielsen 1986). Although these small animals are primarily seed-predators, some of their seed hoard often remains untouched because of the death of the animals or because the rodents simply forget some of their caches (Vander Wall 2002).

The random seed distribution patterns can be most expected from dispersion according to the 'colonization' hypothesis. This characterizes those species that have a habitat which is quite extreme and unpredictable in space and time. Therefore, plants try to disperse their seeds over the greatest possible area, to ensure that at least some will be able to develop into adult plants. The best method for achieving this is anemochory. Light seeds, often equipped with mechanisms to improve their flying abilities, can be carried great distances by the wind and distributed randomly in some other area. However, local geographical characteristics (like depressions or other types of surface heterogeneity) can cause secondary seed accumulation, and also in the case of open vegetation grass tufts or other vegetation patches can collect drifting seeds (Symonides 1978, Bertiller 1998). When the propagule is a fruit or in-

fructescence with several seeds in it, rather than a single seed, the chance of aggregation is even more likely (Czarnecka 2004), not only because of the “morphologically clumped” seeds, but also because of shorter expected dispersal distance of the fruit and inflorescence.

The above-mentioned circumstances indicate that aggregated soil seed banks should occur fairly frequently. This supposition can now be compared with results obtained from corresponding studies.

Mattlack and Good (1990) studied the seed banks of 34 forests, each older than 100 years, in New Jersey. They took 25 soil cores of $10 \times 10 \times 10$ centimetres from each forest. During the glasshouse germination of these samples they found a total of 46 species. Only 10 of these species were present in numbers large enough for statistical analysis; of these the researchers found that the seeds showed aggregated distribution in nine cases.

A study performed in Danish deciduous forests detected an aggregated distribution in 60% of the 25 species involved. Of the 40% with a random distribution, two third were wind dispersed species which behaved according to the colonization hypothesis (Kjellsson 1992). We must note, however, that Kjellsson’s samples were obtained by aggregating four sub-samples collected a few meters from each other, a method that is likely to bias results towards random distribution by averaging seed number heterogeneity at the sub-sample scale.

In the above examples, the large number of soil samples collected for such extensive studies allowed investigation into the degree of seed bank aggregation at a large (community) scale. In addition to such studies, some direct research has also been conducted to learn more about the distribution of the soil seed bank at a finer scale.

Thompson (1986) collected a 8×16 grid of 7×7 cm neighbouring soil prisms from an English pasture, thereby completely removing a relatively large rectangular piece of soil. After determination of the seed content of the soil samples, it became obvious that the seed bank of the pasture’s most important species was quite aggregated. Similarly, a clustered spatial structure of the soil seed bank community was demonstrated by Symonides (1986) from about 30 m^2 areas of old fields in Poland. Further studies involving both the seed bank community and the specific seed bank of dominants led to analogous results regarding Alpine soils (Hatt 1991) and xerothermic grasslands (Czarnecka 2004).

It was perhaps Bigwood and Inouye (1988) who demonstrated most convincingly the spatial heterogeneity of the distribution of seeds in the soil. In their study, several

2 cm deep sampling units with a 50×50 cm area were taken from the soil of a tobacco field that was lying fallow for 20 years. Care was taken not to disturb the structure of the sampling units. During germination in a glasshouse, the location of each seedling was recorded to one millimetre accuracy. This method enabled preparation of a digitized map of seedlings, from which small quadrats of 31 sizes ($1\text{--}625 \text{ cm}^2$) were taken by computer and evaluated statistically. It was found that the great majority of species had an aggregated seed bank distribution and that the measure of non-randomness of the seeds’ distribution was different for each species. The final conclusion from this study was that the most accurate estimation can be achieved by using numerous small samples – to the extent allowed by practical constraints. This is supported by other studies. In addition, Bigwood and Inouye note that it is practically impossible to collect enough samples to allow a statistically reliable result for the rarest species in the seed bank.

Finally, I would like to highlight some practical ideas when soil seed bank of plant communities are aimed to be sampled. The sub-samples collected to reach the minimal volume should be collected from a distance of at least 5-6 metres from each other. It is advisable to select the sampling points in advance in a randomized way. In some cases the sampling could be performed by tracing a ‘W’, or – if the purpose is to demonstrate a gradient – to take samples along a transect (Jankowska-Błaszczuk and Grubb 1997, Davies and Waite 1998, Grandin 2001). Finally, the accuracy of the estimate can be increased by collecting two or more times the necessary soil volume, mixing it thoroughly and taking the minimal volume from this to study the seed bank (Livingston and Allesio 1968, Jensen 1998).

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Appendix. Soil seed bank studies in various European vegetation types. Seed banks were determined by the seedling emergence method (greenhouse germination).

Vegetation type	Soil volume cm ³	Sampling depth, cm	Seed bank		Reference
			species number	density seeds/m ²	
Grasslands and other non-forest vegetation types					
Limestone grassland, <i>Medicago falcatae-Mesobrometum</i> ; Switzerland	26600	10	37	3000	Ryser, Gigon 1985
Limestone grassland on stony rendzina, <i>Dauco-Salvio-Mesobrometum</i> ; Switzerland	13300	5	46	5000	Ryser, Gigon 1985
Acidic grassland, dominants: <i>Agrostis capillaris, Luzula campestris</i> ; England	31500 ⁽¹⁾	5	11	1325	Thompson 1986
Open grassland in abandoned chalk quarries; England	31800	10	42-51	2400	Jefferson, Usher 1987
<i>Urtica dioica</i> community; Germany	3000	8	17-25	60970-96290	Jensen 1988
<i>Carex acutiformis</i> community; Germany	3000	8	25-26	27580-71450	Jensen 1988
<i>Angelico-Cirsietum oleracei</i> ; Germany	3000	8	20-30	90180-133780	Jensen 1988
<i>Phalaris arundinaceae</i> community; Germany	3000	8	24	34400	Jensen 1988
Semi-natural grassland on clay, treatments: grazed, mowed, fertilized with controls; Sweden	3420	10	15-24	8650-20700	Milberg 1992

Semi-natural grassland on sand, treatments: grazed, mown fertilized with controls; Sweden	3420	10	10-30	13200-73800	Milberg 1992
Limestone grassland, <i>Veronica spicata</i> - <i>Avenula pratensis</i> ass.; Sweden	1280	10	70	10060	Milberg, Hansson 1994
Road verge grassland, mown once a year, hay not removed; Sweden	18500	6	56	5800	Milberg, Persson 1994
Alvar grassland grazed by cattle, <i>Veronica spicata</i> - <i>Avenula pratensis</i> ass.; Sweden	1257	10	51	13400	Bakker et al. 1996b
Alvar grassland overgrown by 80 yrs old <i>Juniperus</i> shrubs; Sweden	1257	10	44	2740	Bakker et al. 1996b
Meadow community, <i>Cirsietum rivularis</i> ; Poland	12000	3	40	1890 ⁽²⁾	Falińska 1998
<i>Cirsietum rivularis</i> meadow after 10 yrs of abandonment; Poland	12000	3	30	4150 ⁽²⁾	Falińska 1998
<i>Cirsietum rivularis</i> after 20 yrs of abandonment (willow brush-wood formation stage); Poland	12000	3	27	1245 ⁽²⁾	Falińska 1998
Grazed and ungrazed seashore meadows; Finland	5430-15380	10	23-44	7100-26600	Jutila 1998
Xerothermic vegetation in abandoned vineyards; Hungary	1750	7	76 ⁽³⁾	4017	Sendtko 1999
Riverine wetland, <i>Polygono hydropiperis</i> - <i>Bidentetum tripartitae</i> ; Italy	9600	8	20	1560 ⁽⁴⁾	Assini 2001
Calcareous grassland, <i>Sesleria caerulea</i> - <i>Filipendula vulgaris</i> ass., mown traditionally; Estonia	125700	10	51	2362	Kalamees, Zobel 2002
Sparse shrub community on gypsum, <i>Gypsophylo struthii</i> - <i>Centaureetum hyssopifoliae</i> ; Spain	5484	3	51	14175	Caballero et al. 2003
Perennial tussock on gypsum, <i>Limonio</i> - <i>Lygeetum spartii</i> ; Spain	1330	3	39	21534	Caballero et al. 2003
Fen meadow, <i>Cirsio dissecti</i> - <i>Molinietum</i> ; The Netherlands	12566	10	23-42	25000-140000	Matus et al. 2003
Submontane <i>Calluna</i> - <i>Vaccinium</i> heath; Scotland	4070	5	7	51000-69000	Miller, Cummins 2003
Montane <i>Calluna</i> - <i>Vaccinium</i> and <i>Calluna</i> - <i>Cladonia</i> heath; Scotland	4070	5	4	11000-41000	Miller, Cummins 2003
Montane <i>Vaccinium</i> - <i>Cladonia</i> heath; Scotland	4070	5	5	600	Miller, Cummins 2003
Submontane <i>Festuca</i> - <i>Agrostis</i> - <i>Galium</i> grassland; Scotland	4070	5	10	21000	Miller, Cummins 2003
Montane <i>Nardus</i> - <i>Carex</i> grass-heath; Scotland	4070	5	2-6	200-700	Miller, Cummins 2003
Hedge banks in agricultural landscape; France	--	10	38-42	16300-91500	Pellissier et al. 2004
Dry sandy grassland, <i>Cynodonti</i> - <i>Festucetum pseudovinae</i> ; Hungary	3770	10	32-51	13900-24600	Matus et al. 2005

Domestic gardens, flower beds and vegetable patches; England	577	10	4-20 ⁽⁵⁾	1386-32046	Thompson et al. 2005
Forest vegetation ⁽⁶⁾					
Mixed <i>Quercus robur</i> - <i>Fagus sylvatica</i> stand of archaic character; Denmark	24250	17.5	10	4700	Kjellsson 1992
<i>Tilia cordata</i> - <i>Betula pubescens</i> - <i>Alnus glutinosa</i> stand on water-logged soil; Denmark	12120	10	22	15630	Kjellsson 1992
Mixed deciduous forest, dominants: <i>Quercus robur</i> , <i>Betula pendula</i> and <i>Fraxinus excelsior</i> , Sweden	7540	5	20	1074	Eriksson 1995
Mixed deciduous forest, dominants: <i>Quercus robur</i> , <i>Fagus sylvatica</i> , <i>Castanea sativa</i> , Basque Country	15000	10	21	317	Onaindia, Amezaga 2000
<i>Pinus radiata</i> plantation, stand age 35 yrs; Basque Country	15000	10	26	401	Onaindia, Amezaga 2000
Typical <i>Potentillo albae-Quercetum</i> ; Poland	200000	10	55	1892	Panufnik-Mędrzycka, Kwiatkowska-Falińska 2001
<i>Potentillo albae-Quercetum</i> ; invaded by hornbeam; Poland	200000	10	20	738	Panufnik-Mędrzycka, Kwiatkowska-Falińska 2001
Mixed <i>Fagus sylvatica</i> , <i>Quercus robur</i> forest, <i>Milio-Fagetum</i> ; Belgium	3846	20	39	8667-9400 ⁽⁷⁾	Bossuyt et al. 2002
<i>Betula</i> , <i>Fagus</i> and <i>Quercus</i> dominated secondary forest; Basque Country	55400	10	28	7057	Olano et al. 2002
Evergreen <i>Quercus suber</i> forest; Spain	2010	4	24	11240	Díaz-Villa et al. 2003
Semi-deciduous <i>Quercus canariensis</i> forest; Spain	2010	4	29	14125	Díaz-Villa et al. 2003
Submontane <i>Pinus sylvestris</i> woodland with <i>Calluna</i> in the ground layer; Scotland	4070	5	7	83000	Miller, Cummins 2003
Submontane <i>Pinus sylvestris</i> woodland with <i>Vaccinium spp.</i> in the ground layer; Scotland	4070	5	5	11000	Miller, Cummins 2003
Submontane <i>Quercus-Betula</i> woodland; Scotland	4070	5	10	13000	Miller, Cummins 2003

(1) Represents a single surface area of 0.63 m².

(2) Higher densities were detected by seed separation method.

(3) Number of xerothermic species indigenous to the studied communities.

(4) Germination did not ceased until the end of the experiment.

(5) A total of 119 species was found in the 56 gardens studied.

(6) Works reported by Warr et al. (1994) and Jankowska-Błaszczuk (1998) are not included.

(7) In average 84% of total density was formed by *Juncus effusus*.