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Soil seed bank and regeneration of a *Calluna vulgaris* community after forest clearing

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SUMMARY

After tree cutting of a margin of a deciduous forest (Querceto petraeae-Betuletum) on acid gravel deposits in South-Limburg, The Netherlands, a *Calluna vulgaris* community re-established as a result of germination from the soil seed bank.

The greater part of the extensive seed bank of *Calluna* probably originated from heathland vegetation, which was present on the site until half a century ago.

The number of viable seeds of *Calluna* present in the soil samples varied tremendously in time and space. The maximal density found was *c.* 300 seeds per dm^2 to a depth of 20 cm.

From a viewpoint of nature preservation, it is important to estimate the feasibility of re-creating former plant communities based upon the seed bank in the soil.

Key-words: Calluna vulgaris, heathland regeneration, Querceto petraeae-Betuletum, seed bank.

INTRODUCTION

The species composition of the bank of viable seeds buried in the soil is often not similar to the acutal above-ground vegetation (Ryser & Gigon 1985), but reflects an earlier stage in vegetation succession (Chippindale & Milton 1934, Roberts 1981). This phenomenon can be applied in nature preservation to re-create former or endangered plant communities.

The present paper gives a description of the re-appearance of an open heathland community after enlarging a glade in a forest by felling a number of trees, in order to save a species-rich grassland.

Special attention was given to the role *Calluna vulgaris* (subsequently referred to as *Calluna*) plays in the re-establishment of the heathland community, since it is well known that this dwarf shrub once was the predominant plant species in heathland communities (Genisto pilosae-Callunetum) on dry, acid soils in the area (Hillegers 1980). Analyses of the soil seed bank have been carried out over several years, after tree felling, and a description of both the former forest community and the present vegetation will be given.

Some remarks will be made on the longevity of *Calluna* seeds in the soil and on the possible function of the seed bank in nature conservation.

SITE DESCRIPTION

The research site named Zure Dries, is situated in the forest Savelsbosch, a few kilometres east of Maastricht, in the province of Limburg (5°45′E, 51°47′N), in the southernmost part of The Netherlands (van de Broek & Diemont 1966). The Zure Dries is a centuries-old glade. The chalk grassland occurring in this glade can be reckoned to the association Mesobrometum erecti (Diemont & van de Ven 1953; Willems 1987).

The chalk grassland is situated in the middle part of a south facing slope (20°) which borders a deep erosion gully leading towards the valley of the River Meuse. The subsoil on the middle part of the slope consists of Upper-Senonian chalk deposits. Although the chalk grassland was mown during the past decades, the grasslands area had decreased to only 500 m^2 in 1980 by spontaneous encroachment of shrubs and trees. Adjacent trees had been grown very high, due to the absence of the former coppicing regime. Because of the exceptional floristical importance of the chalk grassland (10 rare and endangered indigenous species occur in this site), the State Forestry Commission enlarged the gap to *c.* 4000 m^2 by cutting trees, in order to improve light conditions for this grassland.

Enlarging of the open area took place uphill, too, where the soil consists of fluvial acid sand and gravel deposits from Pleistocene origin. The forest vegetation type occurring here (*Querceto petraeae-Betuletum;* synonym: *Querco roboris-Betuletum*), is widespread on the acid soil of the edges of the plateaus, bordering the valleys of the River Meuse and tributaries. Apart from the species mentioned in Table 1 (column B), the community is characterized by the trees *Quercus petraea, Q. robur, Betula pendula* and *Populus tremula.* Until World War II this type of forest was partly coppiced every 7–10 years (van den Broek & Diemont 1966; fieldwork carried out in 1955). Tree felling took place in April 1982. From that time onwards the site was surrounded by a fence and irregularly grazed by a few sheep during the greater part of the year in order to prevent the re-establishment of woodland.

This paper will be restricted to the development of the vegetation on the acid soil.

METHODS

Soil samples analysed on their viable seed content were taken with a root auger, diameter 8 cm to a depth of 15 or 20 cm. The samples were taken over several years in spring and autumn to record the eventual effects on seed bank size by seed germination of *Calluna* in autumn (Bruggink 1987). At every sampling date a soil sample was taken within three fixed plots (1 × 1 m). The distance between these plots was *c.* 15 m.

The soil column was divided into subsamples of 5 cm height each. After drying (24 h, 20°C) the roots and stones were removed and the volume of the remaining soil was measured. This made it possible to calculate the number of seeds per pure soil, and to compare the number of seeds of the several (sub-)samples. Numbers of seeds per area were calculated by multiplying the number of emerging seedlings in a subsample by the ratio between the volume sampled in the field and the volume left after drying and cleaning the subsample. The soil was spread in trays in thin layers (< 3 mm) on sterilized, moist sand and put in a greenhouse. Seedlings were recorded three times a week during the first 2 months. After this period recording took place only once a week. After 2 and 4 months, respectively, the samples were kept dry during 1 week and were then watered again. Generally, the soil samples were kept in the greenhouse for 6 months, with supplementary lighting during the winter months up to a light intensity of 40–50 W m^{-2} during 12 h. Temperature varied between *c.* 20°C (25°C in summertime) during the day and 18°C during the night.

Vegetation records were made after the methods of the French-Swiss School for Phytosociology (Braun-Blanquet 1964). Plant nomenclature follows Heukels & van der Meijden (1983) for phanerogams.

Table 1. Synoptic table of vegetation relevees

Species	Constancy and cover degree (%)			
	A clearing (1987) (Hindriks & de Wit 1987) ($n=48$)		B forest (1955) van den broek & Diemont 1966) ($n=20$)	
Pteridium aquilinum	V	(1–25)	V	(1–75)
Deschampsia flexuosa	IV	(1–25)	IV	(1–75)
Rubus caesius	V	(1–50)	IV	(1–25)
*Agrostis stolonifera/capillaris**	V	(1–5)	IV	(1–25)
*Carex pilulifera**	V	(1–25)	V	(1–5)
Teucrium scorodonia	IV	(1–5)	V	(1–25)
*Betula pendula**	IV	(1–5)	V	(1–50)
*Anthoxanthum odoratum**	IV	(5–25)	III	(1)
Lonicera periclimenum	II	(1)	V	(1–25)
Sorbus aucuparia	+	(1)	V	(1–25)
Quercus petraea	+	(1)	V	(1–100)
Holcus lanatus	+	(1–10)	V	(1–25)
Convallaria majalis	II	(1–25)	IV	(1–50)
*Calluna vulgaris**	II	(1–15)	III	(1)
Festuca ovina	I	(5)	II	(1)
Rumex acetosella	+	(1–25)	I	(1)
Verbascum thapsus	I	(1)	II	(1)
Cytisus scoparius	+	(1)	II	(1)
Hypericum perforatum	+	(1)	I	(1)
*Veronica officinalis**	V	(1–15)	I	(1)
Origanum vulgare	IV	(1–5)		
*Cerastium arvense**	IV	(1–5)		
*Myosotis ramosissima**	III	(1–2)		
Poa trivialis	III	(1–5)		
Luzula campestris	III	(1–5)		
Carduus crispus	III	(1)		
Trisetum flavescens	II	(1–5)		
Geum urbanum	II	(1)		
Fragaria vesca	II	(1)		
Crataegus monogyna	II	(1)		
Lamium galeobdolon	II	(1–5)		
Arenaria serpyllifolia	II	(1)		
Fraxinus excelsior	II	(1)		
Festuca rubra	+	(5)		
Lithospermum officinale	+	(1)		
Taraxacum sect. vulgare	+	(1)		
Urtica dioica	+	(1)		
Poa pratensis	+	(10)		
Stellaria media	+	(1)		
Centaurium erythraea	+	(1)		
*Hedera helix**	+	(1)		
Capsella bursa-pastoris	+	(1)		
Viola riviniana	+	(1)		
*Galium aparine**	+	(1)		
*Poa annua**	+	(1)		

*Present in seed bank.

RESULTS

Vegetation

Five years after tree felling a vegetation occurred in which a number of species already present in the former forest was abundant, e.g. *Pteridium aquilinum, Rubus caesius, Teucrium scorodonia, Deschampsia flexuosa, Agrostis stolonifera/capillaris, Carex pilulifera,* and *Anthoxanthum odoratum* (Table 1). *Betula pendula* was present only by a large number of juvenile plants of a few centimetres height.

A number of plant species turned up in the clearing. Some of these species originated from the chalk grassland downhill (*Lithospermum officinale, Origanum vulgare, Arenaria serpyllifolia*), whereas some consisted of weeds and ruderals with effective dispersal capacity (*Taraxacum* sp., *Cerastium arvense, Capsella bursa-pastoris, Urtica dioica, Carduus crispus*) (Table 1). Also some species, characteristic for the forest community (Querceto-Carpinetum) occurring on the basic soil downhill, appeared in the clearing (*Geum urbanum, Fraxinus excelsior, Hedera helix, Fragaria vesca, Lamium galeobdolon*).

One year after tree felling, some juvenile plants of *Calluna* were encountered between the tree stumps of *Quercus petraea, Q. robur,* and *Betula pendula.* A year later a substantial increase in *Calluna* was recorded with numbers amounting to 130 plants per m^2. The present day situation shows *Calluna* plants scattered all over the clearing and locally, on small spots (< 1 m^2), it is even the dominant species (cover $> 50\%$).

Seed bank

Viable seeds of 13 species were found in the soil samples during the period May 1984 to September 1987; this number is low compared to the number of above-ground species. The greater part of this number consisted of short-lived weeds (*Poa annua, Cerastium arvense, Verbascum thapsus, Myosotis ramosissima, Galium aparine, Solanum nigrum*). Seeds of only a few species already present in the forest before clearing, were encountered in the soil seed bank (*Anthoxanthum odoratum, Agrostis* spp., *Veronica officinalis, Carex pilulifera*). All of these species were present in low quantities ($< 6\%$), compared with the total number of seedlings present in the soil samples. *Betula pubescens* seeds were found more frequently in the soil (13·8%). This is due to the continuous input of seeds by the surrounding mature trees. The dominant species in the seed bank was *Calluna* (63·0%) (Table 2).

The number of *Calluna* seeds encountered in the soil samples varied enormously. The depth distribution of the seed in the soil was also very variable (Table 3). In general, most of the seeds were present in the upper 10 cm, though a fairly large number were present in the lower soil layers (10–20 cm). Due to the increasing amount of coarse gravel and pebbles it was not possible to sample adequately lower than 15 or 20 cm.

The highest number of viable *Calluna* seeds was always found within the same sampling plot (1). This was also the spot with the highest density of juvenile *Calluna* plants. The number of juvenile *Calluna* plants was a low percentage of the total amount of seedlings in a given area (Bruggink 1987).

Calluna seedlings were not counted during the present investigation. Due to the high turnover rate of the tiny *Calluna* seedlings, which are very sensitive to drought (Bruggink 1987). Accurate insight into the number of these seedlings is only possible with a high frequency of recording.

Evident decrease in *Calluna* seeds in the soil could not be observed during the period May 1984 to September 1987, despite the loss of seeds by germination. This is not caused

Table 2. Number of species and their relative frequency in the seed bank samples in 1984–87

Species	%
Calluna vulgaris	63·0
Betula pendula	13·8
Poa annua	5·4
Anthoxanthum odoratum	3·8
Veronica officinalis	3·4
Agrostis stolonifera	2·9
Cerastium arvense	2·0
Verbascum thapsus	1·9
Carex pilulifera	1·7
Myosotis ramosissima	1·2
Galium aparine	0·4
Hedera helix	0·3
Solanum nigrum	0·2

Table 3. Depth distribution of *Calluna* seeds per dm^{-2} in the soil of a forest clearing

Plot no.	Depth (cm)	1984 May	1984 November	1986 March	1986 October	1987 September
1	0–5	55	25	0	182	20
	5–10	100	10	40	45	85
	10–15	77	5	15	74	50
	15–20	75	*	*	3	35
2	0–5	0	5	0	0	5
	5–10	3	5	0	0	10
	10–15	11	15	0	0	0
	15–20	0	*	*	0	10
3	0–5	3	0	5	3	30
	5–10	12	15	40	3	75
	10–15	21	0	15	0	0
	15–20	3	*	*	0	10

*Not sampled.

by input of recent seeds of the established young plants, because the grazing sheep eat these plants before flowering.

DISCUSSION

The species composition of the herb layer on the 5-year-old clearing is partly due to either expansion of species already present in the forest (e.g. *Rubus caesius*), or by establishment from the soil seed bank (e.g. *Cerastium arvense, Myosotis ramosissima*), or by a combination of both (e.g. *Anthoxanthum odoratum, Veronica officinalis*) (Table 1).

The seeds of some newly established species (e.g. *Origanum vulgare, Poa trivialis, Trisetum flavescens, Lithospermum officinale, Arenaria serpyllifolia*) undoubtedly originated from the chalk grassland situated some tens of metres downhill, since they did not occur in the seed bank in the acid soil. Migration uphill probably took place by grazing sheep, since it is known that sheep can transport large amounts of seeds, especially in their fleece (Hillegers 1983; Shmida & Ellner 1984). These seeds must have germinated soon after arriving in the cleared area because they were not present in the soil samples. Moreover, the number of soil samples was probably not sufficient to encounter species sparsely present in the soil seed bank (Ryser & Gigon 1985). In the soil under the chalk grassland these species were present in large numbers in a persistent seed bank (J.H. Willems personal observation). *Calluna* seedlings originated from one seed bank, since it is known that *c*. 20 years ago the last few plants of this species, growing in a nearby roadside verge, disappeared. Until the 1950s, *Calluna* plants could be found in the Querceto petraceae-Betuletum community, though the individuals were limited in their distribution and never gained a 1% cover per vegetation relevee (Van den Broek & Diemont 1966). In this part of Europe *Calluna* plants can maintain themselves for a number of years in the shade of a tree canopy, but with reduced flowering capacity (Gimingham 1972). Whether these scarcely flowering individuals build up the extensive seed bank is doubtful.

It is more likely that the bulk of the *Calluna* seed bank originated from a treeless, *Calluna* dominated heathland which was present on this site until *c*. 1930 (Hillegers 1980). Old photographs show *Calluna* dominated heathland of several hectares on the edges of the plateaus in this area. Floristical data indicate the presence of these heathlands already in the middle of the 19th century (a.o. Dumolin 1868). All of these heathlands gradually disappeared after sheep grazing ceased in the late 1920s (Hillegers 1980).

Large quantities of seeds were produced in the period after the grazing regime ended and before the spontaneous reafforestation caused too much shade to allow optimal growing and flowering conditions to *Calluna* (Gimingham 1972). Measurements of seed production in a Dutch, *Calluna* dominated heathland amounted to some hundred-thousands of seeds per m^2 (Bruggink 1987). Probably, this was the period in which the larger part of the *Calluna* seed bank was accumulated; from which the seedlings originated after tree felling in 1982. During the period of wholsesale seed production there was probably hardly any decrease in seeds by germination. Germination of *Calluna* seeds was prevented by the low red/far-red ratio of the light initially due to the ungrazed heathland vegetation and, later on, to the canopy of the upgrowing trees (Hill & Stevens 1981; Pons & Elings 1985). Moreover, the very small *Calluna* seeds dropped into the increasing litter layer of *Calluna* after sheep grazing ceased, a process which negatively influenced the germination of this species, due to the absence of appropriate light conditions (Pons & Elings 1985; Heil 1985; Bruggink 1987). These conditions can be considered responsible for an increasing number of *Calluna* seeds in the soil implying that a large number of seeds probably survived in the soil for at least half a century. This confirms the statement that *Calluna* has a long-lived persistent seed bank (Hill & Stevens 1981; Stieperaere & Timmerman 1983; Heil 1984).

Stieperaere & Timmerman (1983) found *Calluna* seeds in improved grassland soil of 20 years old, but not in soil under a 40-year-old production grassland. Probably, the conservation conditions for *Calluna* seeds are less suitable under similar grassland than they are in forest soil.

The presence of a fairly large number of seeds in the deeper soil layers (> 15 cm), also indicates that the seeds are already present in the soil for a long time (Roberts

1981, Harper 1977). The combination of a coarse soil texture of sand and gravel and the very small *Calluna* seeds (Helsper & Klerken 1984; Pons & Elings 1985) can explain the fairly large numbers of seeds in the deeper soil layers of the Zure Dries.

The species composition of the former *Calluna* community of the site is not known with certainty. A number of species, which probably occurred in this community, such as *Genista pilosa, G. anglica* and *Danthonia decumbens* (Hillegers 1980), were not found in the seed bank. Seeds of species which perhaps formed a part of this community, like *Carex pilulifera, Veronica officinalis* and *Agrostis* spp., may have originated from recent input in the soil, since these species survived after spontaneous afforestation. *Calluna* proved to be the only plant species from this former community with a long-lived soil seed bank.

The average number of *Calluna* seeds in the seed bank of this site can be considered as very large. Harper (1977, Table 4/1) summarizes the number of viable seeds found in the soil beneath different vegetation types. This number can amount to up to some ten-thousands of seeds per m^2 in arable fields soil. The largest number of viable seeds of *Calluna* found on the Zure Dries on one spot was *c.* 300 seeds per dm^2, which corresponds to 30 000 per m^2. This number is in accordance with the number of viable seeds found elsewhere in The Netherlands under heathland communities (de Smidt 1985; Bruggink 1987).

The fluctuation of the seed bank size of *Calluna* at different times during the years of observation is striking. Due to the preference of sheep to eat *Calluna* shoots rather frequently, the fluctuation in seed numbers in the soil is not a result of input of recently produced *Calluna* seeds, but reflects their very heterogeneous distribution in the soil (Ryser & Gigon 1985). In combination with the spatially varying germination conditions, this causes the present patchy distribution pattern of the young *Calluna* plants. In the South-Limburg area almost all remnants of the former plateau-edge heathlands disappeared after World War II and even *Calluna* as a species was near to extinction at the end of the 1970s (Hillegers 1980). As an unexpected result of tree cutting on a suitable site, a *Calluna* community is gradually regenerating now from the soil seed bank.

In The Netherlands much attention has been paid during the recent past to restore species-rich, semi-natural vegetation which once, approximately until World War II, was an integrated part of the former agricultural system (a.o. Bakker 1987). The present study shows the possibility to utilize the soil seed bank, originating from earlier vegetation types in restoration attempts. An assessment of the seed bank before starting restoration measures can indicate which species assortment can be expected. This is more important because spontaneous dispersal capacity of species is often very limited (Verkaar *et al.* 1983); it may last many years before the seed of a species can reach a suitable habitat, even if the distance to a potential source is only some hundreds of metres (Stieperaere & Timmerman 1983).

If the type of semi-natural vegetation to be restored is fixed, knowledge of the seed bank composition may help to indicate how long it will take before acceptable results can be achieved. If, however, the aim of restoration is still open, a seed bank study will be an important instrument in choosing the vegetation type to be restored, and thus, the appropriate management regime to be applied.

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