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The potential of soil seed banks for revegetation of bogs in SW Finland after long-term aerial pollution

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We studied a soil seed bank composition using the germination method in three clearly polluted bogs, and in one bog farther away from the pollution source, in SW Finland. Total number of seedlings that emerged from the surface (0–5 cm deep) soil samples was significantly smaller in the farthest site (5.9 km, 939 seedlings m^{-2}) as compared with sites situated 2.1 or 3.2 km (2 882 and 3 687 seedlings m^{-2}, respectively) from the pollution source. The most common taxa in the seed banks were *Calluna vulgaris* and *Betula* spp. Only 18%–31% of the spermatophyte species were common to both seed bank and vegetation. The monodominance of *Calluna* was smallest, and the number of emergent seedlings of other mire species was highest in the farthest site. The high numbers of emergent seedlings show that seeds of some species can persist viable in the soil in polluted bogs.

Key words: bogs, pollution, recovery, seed bank

INTRODUCTION

The role of soil seed banks in the recovery of vegetation in degraded sites depends on the type and severity of the disturbance. Seed banks can be important in revegetation after fire (Vavrek *et al.* 1999) and clear-cutting (Granström 1988), whereas in cut-away peatlands they play only a minor role (Salonen 1987, Huopalainen *et al.* 1998). Seed banks have been found to have the potential to enhance vegetation recovery in pollution-damaged forests both in mineral soils (Komulainen *et al.* 1994) and in drained pine mires (Huopalainen *et al.* 2000).

Many studies have shown that pollution has serious effects on vegetation composition close to smelters (e.g., Laaksovirta & Silvola 1975, Freedman & Hutchinson 1980, Folkeson & Andersson-Bringmark 1988), and thereby on the composition of the potential seed source. Pollen germination is believed to be one of the most sensitive indicators of pollution in plants (e.g., Cox 1988a, 1988b), whereas several studies have shown that seed germination is not affected (e.g., Patterson & Olson 1982, Scherbatskoy *et al.* 1987), or is influenced only slightly (Komulainen *et al.* 1994) by pollutants.

Recovery of polluted areas in many industrial countries is of general concern. The successful reduction of industrial emissions, as in the heavily polluted industrial area Harjavalta, SW Finland, makes it possible to restore areas in the vicinity of pollution sources. If seed banks play a significant role in vegetation development in bogs they might be expected to have importance in the recovery of mire vegetation. Knowledge of natural recovery mechanisms, including seed banks, also would be beneficial for artificial revegetation (Bradshaw 1983). There is, however, only little information concerning the potential of soil seed banks to contribute to the recovery from pollution-induced damage (Vieno *et al.* 1993, Komulainen *et al.* 1994, Winterhalder 1996, Huopalainen *et al.* 2000). Moreover, studies on the role of soil seed banks in the population dynamics of bog plants are rare (Moore & Wein 1977, McGraw 1987, Poschlod 1995, Jauhiainen 1998).

We investigated the composition of soil seed banks in three boreal bogs located near a copper and nickel smelter, and in one boreal bog outside the main zone of impact of the smelter in the Harjavalta industrialized area in SW Finland. Our objectives were (1) to describe the composition of soil seed banks in clearly polluted bogs and in a bog that resembled undisturbed bogs of the same site type, (2) to compare the species composition of the soil seed banks with that of the existing spermatophyte vegetation, and (3) to assess the potential of the soil seed banks to contribute to the regeneration of mire vegetation in bogs under pollution stress.

MATERIAL AND METHODS

Study area

The study area, Harjavalta township, is located in SW Finland (61°20´N, 22°10´E) in the concentric raised bog region (Ruuhijärvi 1983) of the southern boreal coniferous forest zone (Ahti *et al.* 1968). Prevailing winds in the area blow from the southern direction. The copper smeltering of Outokumpu Harjavalta Metals started in 1945, and the nickel smeltering in 1960. Because the stack of the smelter was low, the emissions were deposited mainly within five kilometres of the smelter (Veijalainen 1998). A decrease in the concentrations of sulphur and heavy metals in the uppermost surface layer of peat humus from 0.9 to 10.0 km from the smelter has been observed (Veijalainen 1998). Because of changes in the process technology, installation of new filters and increase in stack height the sulphur and metallic dust emissions have decreased considerably. In 1985, the dust emissions containing Cu, Ni, Zn, Pb, Cd, As, and Hg were 1 100 tonnes, but in 1995 only approximately 70 tonnes. The SO_2 emissions decreased from 30 000 to 3 300 tonnes between 1945 and 1995 (Helmisaari 1998).

Study sites

The four study sites were within six kilometres of the smelter and generally north of it. They were undrained nutrient-poor ridge-hollow pine bogs (KeR) (site type *sensu* Laine & Vasander 1996) with sparse tree cover. The closest, 2.1 km to the smelter, is Lammaistensuo, where a large part of the site consisted of unvegetated peat surfaces. The field layer was dominated by *Eriophorum vaginatum*, and only two species, *Pohlia nutans* and *Cladopodiella fluitans*, occurred in the ground layer. Kotosuo was divided into two separate study sites in the opposite ends of the bog: 2.6 km and 3.2 km from the smelter. In both, *E. vaginatum* and *Rubus chamaemorus* were the most common species in the field layer. *Pohlia nutans* and lichens characterized ground layer vegetation, and

Sphagnum mosses were rare. The farthest site Pyhäsuo (5.9 km) is located outside the main zone of impact of the smelter. Its vegetation resembled that of an undisturbed bog (Vasander 1982): the vegetation was dominated by *Sphagnum* spp. (e.g., *S. balticum*, *S. fuscum*, *S. cuspidatum* and *S. angustifolium*), *E. vaginatum*, *Calluna vulgaris*, *Andromeda polifolia* and *R. chamaemorus*. In general, oligotrophic mixed pine-birch forests surrounded the study sites.

Data collection

The vegetation was sampled during the summers of 1993 and 1994 (A. Reinikainen, H. Nousiainen & I. Vanha-Majamaa, unpubl.). In the present study, we used the presence/absence data of spermatophyte species collected from 31 sample plots from each study site. The 0.25 m^2 sample plots were laid out on a transect through the middle part of each study site. Distance between the sample plots was regular along the transects, but the length of the transects varied between sites from 150 to 400 metres. The nomenclature follows that of D. M. Moore (1982) for vascular plants, Ahti (1993) for lichens, and Koponen *et al*. (1977) for bryophytes.

Soil sampling was carried out between 27 and 29 September 1995, so that both the current year's seed rain and the long-term seed bank were included in the germination assay. Surface samples (0–5 cm deep) were taken from the top of moss layer at each site from 31 sample points situated at lawn level about two metres left from the vegetation sample plots. The samples were collected with a corer measuring 5 × 10 cm. At each site six samples were also taken from the 5–10 cm peat layer. Samples were placed in airtight plastic bags and stored in a dark room at 5 °C for five weeks (chilling).

After chilling, the soil samples were taken to a greenhouse, cleaned of living plants and plant parts capable of vegetative reproduction, and evenly spread out on a layer of a mixture of horticultural peat and quartz sand in trays measuring 18.5 × 20.5 cm. The samples formed approximately a 1-cm deep layer on top of the peat-sand mixture in the trays. Each sample was treated separately. Thirty-six control trays containing only a mixture of horticultural peat and quartz sand were placed among the seed bank sample trays. All trays (control and seed bank samples) were protected against contamination with airborne seeds by spreading a white, thin gauze layer over the trays. Air temperature in the greenhouse was kept at 20 °C for 16 h (day) and at 15 °C for 8 h (night). The relative humidity of the air was maintained at approximately 60%, and the samples were watered regularly.

The soil samples were monitored for seedlings at weekly intervals. Seedlings that emerged from germinated seeds were counted and identified. Seedlings, which died soon after the development of the cotyledons could not be identified with certainty, and thus are referred to as "dicotyledons". After 14 weeks, all seedlings were removed, and the soil samples were stored in the dark at 5 °C for additional four weeks. Seedlings of unidentified species were transferred to pots and grown until they could be positively identified. After the second chilling treatment the surface of the samples was carefully broken by scratching since it was colonized by mosses and liverworts which could hinder germination. The samples were then cultivated for 11 additional weeks.

Data analysis

In order to study the variation of species composition in the seed bank and in the vegetation at various distances from the smelter, seed bank data of the surface (0–5 cm) peat layer were analysed together with vegetation data (frequency) by global non-metric multidimensional scaling (GNMDS) with the DECODA software package (Minchin 1991). GNMDS is an ordination method in which site points are positioned in rank order within a few dimensions or axes according to their compositional dissimilarities. Points that are close together correspond to sites that are similar in species composition (ter Braak 1987).

In this study, we used the Bray-Curtis coefficient (Bray & Curtis 1957) as the dissimilarity parameter. We performed one- to four-dimensional global multidimensional scalings using 20 random starts. In each dimensionality, minimum stress configurations were compared with Procrustean analysis. Distance from the smelter, dominance, i.e. proportion of the two most frequent species, and Simpson's diversity index (Simpson 1949) were fitted as vectors of maximum correlation in the sample ordination spaces according to linear regression (Minchin 1987). The significance of the correlations was tested using the Monte-Carlo test (Minchin 1991).

ANOVA was applied to compare means among the four sites in the numbers of germinated seeds from the 0–5 cm layer of the seed bank. Tests were carried out for the most common taxa (*Calluna vulgaris* and *Betula* spp.), dicotyledons and the total number of germinated seeds. To improve normality, the data were log-transformed ($y' = \log(y + 1)$). ANOVA tests were also carried out for the relative proportions of *Calluna* and dicotyledons of all germinated seeds in the surface (0–5 cm) samples. Following ANOVA, the similarity of means was tested with Tukey's HSD pairwise comparison. All the calculations were done with the SYSTAT software package (SYSTAT 1998).

RESULTS

Seed bank composition

Altogether 1 543 seedlings emerged from 124 surface (0–5 cm) soil samples and 96 seedlings from 24 soil samples from the deeper (5–10 cm) peat layer. This is equivalent to 9 953 and 3 199 seedlings per square metre, respectively. The total number per site of seedlings that emerged from the surface soil samples varied between 939 m^{-2} at the farthest site and 3 687 m^{-2} at the site 3.2 km from the smelter (Table 1). Total number of emerged seedlings in the surface (0–5 cm) soil samples in the farthest site was significantly smaller than in the closest site (2.1 km) ($p = 0.02$) and in the site 3.2 km from the smelter ($p < 0.01$).

Seedlings of five to nine taxa emerged from the soil samples of the study sites (Table 1). The species with the highest number of emerged seedlings was *Calluna vulgaris*, which occurred in 86% of the soil samples. Dominance of *Calluna* was particularly obvious at the closest site (2.1 km from the smelter). Other taxa common to all sites were *Betula* spp. (16% of all samples) and *Epilobium angustifolium* (7%). Some species were clearly restricted to certain sites, e.g., *Vaccinium* spp. which were found from only the two most distant sites (3.2 and 5.9 km from the smelter) (Table 1). *Calluna* was the only species frequently found in the samples collected from the 5–10 cm deep peat layer (Table 1).

The farthest site had significantly smaller number of emerged *Calluna* seedlings (632 seedlings m^{-2}) in the surface (0–5 cm) peat than the other sites (2 116–3 206 seedlings m^{-2}) ($p < 0.02$). Also the relative proportion of *Calluna* of all emerged seedlings in the surface (0–5 cm) peat was significantly lower ($p < 0.01$) in the farthest site (67%) than in the clearly polluted sites (85%–87%).

There was an increasing trend in the number of emerged *Betula* seedlings with distance from the smelter (Table 1). According to Tukey's comparison the closest site (2.1 km from the smelter) and the farthest site (5.9 km from the smelter) differed significantly from each other ($p = 0.02$).

The majority of seedlings, which died soon after the development of cotyledons, resembled seedlings of *Calluna*. However, they could not be identified with certainty. Only 6 short-lived dicotyledons m^{-2} emerged from the farthest site, whereas from the clearly polluted sites altogether 252–406 short-lived seedlings m^{-2} emerged (Table 1). The differences between the farthest site and clearly polluted sites were significant ($p < 0.02$). The relative proportion of short-lived dicotyledons of all emerged seedlings in the surface (0–5 cm) peat was significantly higher ($p < 0.05$) at clearly polluted sites (10–14%) than at the farthest site (< 1%).

Variation in seedling numbers per square metre between individual samples within sites was high. Quartile deviations for the sites 2.1 km, 2.6 km, 3.2 km and 5.9 km from the smelter were 58 (median (Md) = 71), 29 (Md = 38), 71 (Md = 84) and 18 (Md = 19), respectively. A few *Calluna* seedlings emerged from the trays with horticultural peat and quartz sand only (mean 1.4 in the first cultivation and 0.3 in the second).

Seed bank versus existing vegetation

The most frequent species in the vegetation were either very rare or absent in the seed bank (Table 2). Five of the species present in the seed bank were not observed in the vegetation. Only 18%–31% of the total spermatophyte flora (seed bank and vegetation) of the sites was common to seed bank and vegetation. The proportion increased with distance from the smelter.

A two-dimensional solution of GNMDS was sufficient to describe the variation of species composition in seed bank and vegetation. The main variation in the data was connected to clear difference between the seed bank and vegetation. The analysis distinctly separated their scores at the opposite ends of the first axis in the ordination space (Fig. 1). The variation along the second axis was connected to differences within the seed bank and vegetation sites. The seed bank composition of clearly polluted sites was very similar, but the farthest site was separated from them (Fig. 1). For vegetation, the site in close vicinity of the smelter (2.1 km) differed from the other sites (Fig. 1). The

Table 1. Numbers of seedlings per square metre that emerged from the seed bank samples from two depths at four distances from the smelter. The number of samples from the 0–5 cm depth is 31 and that from the 5–10 cm depth is 6. The category “dicotyledons” are seedlings that died before they could be identified.

Taxa	Depth (cm)	Distance (km) 2.1	2.6	3.2	5.9
Betula spp.*	0–5	6	39	58	77
	5–10	0	0	0	0
Calluna vulgaris	0–5	2 439	2 116	3 206	632
	5–10	600	467	1 400	467
Carex canescens	0–5	0	0	6	0
	5–10	0	0	0	0
Drosera rotundifolia	0–5	6	0	6	0
	5–10	0	0	0	0
Epilobium adenocaulon	0–5	0	0	6	19
	5–10	0	0	0	0
Epilobium angustifolium	0–5	13	13	6	26
	5–10	0	33	0	33
Epilobium ciliatum	0–5	6	0	0	6
	5–10	0	0	0	0
Eriophorum vaginatum	0–5	0	19	19	6
	5–10	0	0	0	0
Lapsana communis	0–5	0	6	0	0
	5–10	0	0	0	0
Ledum palustre	0–5	6	0	0	0
	5–10	0	0	0	0
Vaccinium microcarpum	0–5	0	0	0	13
	5–10	0	0	0	0
Vaccinium oxycoccos	0–5	0	0	6	148
	5–10	0	0	0	33
Vaccinium uliginosum	0–5	0	0	0	6
	5–10	0	0	0	0
Dicotyledons	0–5	406	252	374	6
	5–10	0	33	133	0
Total	0–5	2 882	2 445	3 687	939
	5–10	600	533	1 533	533
Number of taxa		6	5	8	9

* Includes *B. pendula* and *B. pubescens*

fitted vectors for distance, dominance and diversity (Simpson) were parallel to the second axis (Fig. 1). Diversity increased and dominance decreased with distance.

DISCUSSION

The total number of seedlings that emerged from the surface soil samples in our study was smaller than reported for bogs by McGraw (1987) and Poschlod (1995), but larger than by Moore and Wein (1977) and Jauhiainen (1998). The largest seed bank was not found in the close vicinity of the smelter or in the farthest site, but between them. Owing presumably to high amounts of pollution close to the smelter there are fewer seed sources, which may have led to restricted seed bank formation. On the other hand, because pristine bogs are relatively stable ecosystems, seed bank formation, which is an adaptation to unstable environmental conditions (P. Moore 1982), might not be very common in them. Jauhiainen (1998) concluded that vegetative growth seems to be a more important regenerative strategy among mire species.

The dominance of only a few taxa in the seed banks, found in our study for bogs, is in accordance with several earlier studies in various habitats (e.g. McGraw 1987, Kiirikki 1993, Komulainen *et al*. 1994, Rydgren & Hestmark 1997, Mitchell *et al*. 1998). The most dominant species in our

Table 2. Taxa in soil seed banks of the surface (0–5 cm) peat layer and in the vegetation in bogs at four distances from the smelter. *B* = percentage occurrence in 31 seed bank samples, *V* = percentage occurrence in 31 vegetation sample plots. The category "dicotyledons" are seedlings that died before they could be identified.

	Distance (km)							
	2.1		2.6		3.2		5.9	
	B	*V*	*B*	*V*	*B*	*V*	*B*	*V*
Present only in seed bank								
Carex canescens	–		–		3		–	
Epilobium adenocaulon	–		–		3		10	
Epilobium angustifolium	6		6		3		13	
Epilobium ciliatum	3		–		–		3	
Lapsana communis	–		3		–		–	
Dicotyledons	55		45		61		3	
Present in both seed bank and vegetation								
Betula spp.*	3	3	16	–	23	–	32	–
Calluna vulgaris	97	–	94	29	97	23	71	48
Drosera rotundifolia	3	–	–	–	3	–	–	3
Eriophorum vaginatum	–	100	3	97	10	100	3	100
Ledum palustre	3	6	–	–	–	–	–	10
Vaccinium microcarpum	–	–	–	–	3	6	55	
Vaccinium oxycoccos	–	3	–	26	3	35	39	74
Vaccinium uliginosum	–	–	–	6	–	6	3	35
Present only in vegetation								
Andromeda polifolia		–		29		26		90
Empetrum nigrum ssp. *hermaphroditum*		–		10		13		13
Empetrum nigrum ssp. *nigrum*		–		–		10		48
Eriophorum angustifolium		3		–		–		–
Pinus sylvestris		23		10		3		13
Rubus chamaemorus		13		58		58		61

* Includes *B. pendula* and *B. pubescens*

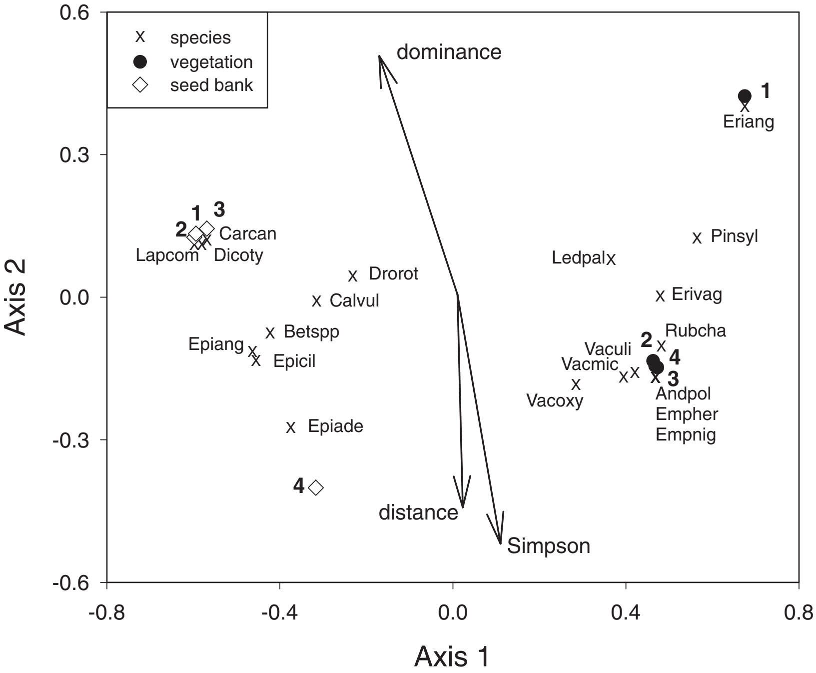

Fig 1. GNMDS ordination diagram of species, seed bank, vegetation and environmental variables in bogs at four distances from the smelter in Harjavalta, SW Finland. Species: Andpol = *Andromeda polifolia*, Betspp = *Betula* spp. (*B. pendula* and *B. pubescens*), Carcan = *Carex canescens*, Calvul = *Calluna vulgaris*, Drorot = *Drosera rotundifolia*, Empher = *Empetrum nigrum* ssp. *hermaphroditum*, Empnig = *Empetrum nigrum* ssp. *nigrum*, Epiade = *Epilobium adenocaulon*, Epiang = *Epilobium angustifolium*, Epicil = *Epilobium ciliatum*, Eriang = *Eriophorum angustifolium*, Erivag = *Eriophorum vaginatum*, Lapcom = *Lapsana communis*, Ledpal = *Ledum palustre*, Pinsyl = *Pinus sylvestris*, Rubcha = *Rubus chamaemorus*, Vacmic = *Vaccinium microcarpum*, Vacoxy = *Vaccinium oxycoccos*, Vaculi = *Vaccinium uliginosum*, Dicoty = dicotyledons not identified. Sites: 1 = site at 2.1 km, 2 = site at 2.6 km, 3 = site at 3.2 km and 4 = site at 5.9 km from the smelter. Environmental variables ($p < 0.1$) (arrows): distance = distance from the smelter, dominance = proportion of the two most frequent species, Simpson = Simpson's diversity index. The direction of the arrow shows the direction of an increasing trend and the length indicates the strength of the correlation.

study, *Calluna vulgaris*, has small, long-lived seeds that are easily buried in deep soil layers and can remain viable in the soil for decades (Mitchell *et al*. 1998). *Calluna* has a resistance to high Cu concentrations (Monni *et al*. 2000) and it is also a characteristic species to the maritime ridge-hollow pine bogs (KeR) in the south-west of Finland (Eurola 1962).

Betula, frequent in the soil samples and the surrounding areas, often produces very large numbers of seeds, but the seeds tend to be short-lived (Granström & Fries 1985). The increase in the number of germinated *Betula* seeds with distance from the smelter (*see* also Komulainen *et al*. 1994), as well as the large number of short-lived dicotyledons in the polluted sites, may be pollution-related, but the causal mechanisms can not be distinguished on the basis of this study.

Only few *Eriophorum vaginatum* seedlings emerged from the seed bank samples, although it was the most frequent species in the vegetation of the study sites. *Eriophorum* does not seem to have seed dormancy (Wein & MacLean 1973, Poschlod 1990) and the light and temperature requirements for germination (Wein & MacLean 1973, Gartner *et al*. 1986) were fulfilled in the germination assay. This may indicate that the majority of viable *Eriophorum* seeds already have germinated in the field during the summer prior to the soil sampling (*see* also Huopalainen *et al*. 1998).

However, germination assay provides only a conservative estimate of seed density in the soil because germination conditions may not have been met for all species. It was also noticed that many individuals of *Andromeda*, *Empetrum*, *Ledum*, *Rubus* and *Vaccinium* species growing in the vicinity of the smelter were sterile (A. Reinikainen, H. Nousiainen & I. Vanha-Majamaa, unpubl.).

Viable seeds of *Empetrum* (Granström 1982), *Ledum* (Granström 1982, 1988), *Vaccinium oxycoccos* (Granström 1988), *V. uliginosum* (Granström 1982, Jauhiainen 1998), *Andromeda* and *Rubus* (Jauhiainen 1998) have previously been found in boreal seed banks. *Rubus chamaemorus*, however, very rarely reproduces sexually in the field (Rantala 1977). To our knowledge, this is the first report of viable *Vaccinium microcarpum* seeds in seed banks. Absence of *Pinus sylvestris* seedlings may be due to lack of seed dormancy in the soil (Granström 1987).

Our result that fewer seeds were found in the deep (5–10 cm) peat layer than in the upper one was in agreement with earlier findings that most viable seeds are usually concentrated in the topmost centimetres of the soil (Harper 1977). Although the seed number decreases with depth, viable seeds have been found over 40 cm deep in mires (McGraw 1987, Jauhiainen 1998), which are organic matter accumulating ecosystems. In this study the small number of samples collected from the deeper (5–10 cm) layer may result in imprecise seed density estimates.

CONCLUSIONS

Our results show that seeds of some species can persist viable in the soil despite a heavy pollution load. This also supports earlier findings of Komulainen *et al*. (1994). The presence of *Epilobium* species, typical of disturbed habitats, absence of some characteristic bog species and the monodominance of *Calluna* indicate that the species composition can be different from that of undisturbed bogs. However, most of the species found in the seed banks were characteristic to bog vegetation. Overall high numbers of viable seeds in the seed banks found in undrained bogs in this study, as also in drained pine mires (Huopalainen *et al*. 2000), indicate their potential to stimulate vegetation recovery in polluted peatlands.

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