

Urban domestic gardens (VII): a preliminary survey of soil seed banks

Ken Thompson*, Stephen Colsell, Jennifer Carpenter, Richard M. Smith, Philip H. Warren and Kevin J. Gaston

Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

Abstract

As part of a larger survey of biodiversity in private gardens in Sheffield, UK, we examined the composition and diversity of the soil seed banks in each of 56 gardens. Six soil cores from each garden revealed 2759 seedlings of 119 taxa, although the real species richness is likely to be much higher than this. By far the most abundant species were weedy natives, while the most common alien was *Buddleja davidii*. Seeds of perennial herbs were more abundant than hundreds of all other life forms combined. More frequent species were also more abundant, but the relationship was weak. Numbers of species in the seed bank and in the garden flora were positively but very weakly related. Seeds were quite evenly distributed between 0–5 cm and 5–10 cm soil layers, and most seeds were of species known to have persistent seed banks. Seeds of some species were largely confined to gardens in which the plant was growing, but others were not.

Keywords: alien plants, biodiversity, urban ecology, urban flora

Introduction

Urban areas continue to grow, as a consequence of human population increase, development and social trends. Green space within such environments is fundamental to the maintenance, or restoration, of biodiversity in areas impacted by development, to the provision of ecosystem services in urban regions, to the quality of life (including physical and mental health) for the large proportion of the human

population who live in them (Niemelä, 1999) and for educating and engaging people in habitat management and conservation.

Against this background, the Biodiversity in Urban Gardens in Sheffield (BUGS) project used the city of Sheffield, UK, as a model system to discover: (1) the size and composition of the resource that domestic gardens provide for biodiversity and ecosystem functioning (Gaston *et al.*, 2005b); (2) factors that influence the levels of biodiversity associated with different gardens (Thompson *et al.*, 2003, 2004); and (3) the effect of simple manipulations of garden features designed to enhance the native biodiversity associated with them (Gaston *et al.*, 2005a). The BUGS project also provided the first opportunity to look at the seed banks of garden soils. Despite the large literature on soil seed banks (Thompson *et al.*, 1997), seed banks of urban soils seem to have been almost completely ignored (Sukopp and Starfinger, 1999). Certainly, despite the huge amount of time and money invested in private gardens, we are unaware of any previous investigation of their soil seed banks. Seed banks form an active part of the flora, especially in disturbed habitats such as gardens, which provide frequent opportunities for regeneration from buried seeds. Viable seeds in the soil are also an indication of the ability of introduced plants to reproduce in gardens and, perhaps, of their ability to escape into the wider environment.

We know that gardens are extremely rich in plant species, especially aliens (Thompson *et al.*, 2003), but we do not know if any of this diversity is represented in the seed bank. Specifically, we address the following questions: are garden seed banks dominated by the same weedy species that are most frequent in the above-ground flora? Which cultivated garden plants contribute to the soil seed bank, and are the seeds of these species confined to gardens where the plant is present in the flora? Small-seeded species are normally more abundant, and more deeply buried, than large-seeded species. Does this also apply to garden seed banks?

*Correspondence

Fax: +44 0114 2220015

Email: ken.thompson@sheffield.ac.uk

Methods

Study sites

Survey gardens were in the city of Sheffield, South Yorkshire, UK (53°23'N, 1°28'W; OS grid reference SK 38). Sheffield lies in the centre of England and is largely surrounded by agricultural land, except where the urban area merges with that of Rotherham to the north-east. The administrative boundaries of the city enclose an area of more than 360 km², including farmland and a portion of the Peak District National Park. The study was carried out in the rear gardens (hereafter called 'gardens') of 56 private, owner-occupied houses in the predominantly urbanized region of the city (about 143 km², defined as those 1 km × 1 km cells having more than 25% coverage by residential or industrial zones, as judged by eye from Ordnance Survey 1:25 000 scale maps). The study focused on rear gardens because they form the major garden component of most properties.

Gardens were selected from a pool of 161 householders who had either volunteered, or been approached, to participate in the study. Because the sample was chosen to maximize variation in house age, garden size and location within the urban area, it does not reflect the proportions of housing types in the city. Properties were distributed throughout the urban area and were aged between 5 and 165 years. Rear gardens ranged from 32 to 940 m² in area.

Survey methods

Seed banks are notoriously patchy at all scales and, with such a large number of gardens under investigation, it was not possible to study both within- and between-garden variation. For this exploratory study, our approach was to ignore within-garden variation. Six soil cores (3.5 cm diameter, 10 cm deep) were taken from cultivated parts of each garden. Cores were taken in every case from flower beds and, where available, from vegetable patches, in rough proportion to their contribution to garden area. Each core was divided into two by depth: 0–5 cm and 5–10 cm. For each depth, the six cores from each garden were combined and mixed before being placed on top of a 1 cm deep layer of sterile sand in a seed tray (21 × 35 cm), to give a soil layer of approximately 0.5 cm. This shallow layer of soil ensured that all germinable seeds germinated reasonably rapidly. Samples were collected in June and July 2001 and processed immediately. Sampling preceded dispersal of seeds of most species, although seeds of vernalis and winter annuals would already have been dispersed. Trays were randomly arranged in an unheated greenhouse and watered regularly. Seedlings were

identified and removed as soon as possible, while those that could not be identified were transplanted into pots of potting compost and grown, until flowering if necessary. Seedling emergence had ceased after 3 months, but some perennials were not identified until 2003. Trays of sterile sand were placed among the soil trays to detect contaminants, but the only species that appeared in these trays and in the sample trays was the greenhouse weed, *Oxalis corniculata*. The 5–10 cm fraction from one garden was accidentally discarded; results from this garden are therefore excluded from any analysis involving the depth distribution of seeds. Note that although we actually counted seedlings, we refer throughout to numbers of seeds.

All seedlings were identified to species as far as possible. *Epilobium* seedlings could not be identified and were too numerous to grow to a stage at which they could be identified to species, so they were recorded only as *Epilobium* spp. They almost certainly included the common and weedy *E. ciliatum*, *E. obscurum*, *E. montanum* and probably other species, and are, therefore, a mixture of an alien and several natives. Seedlings recorded as *Sonchus oleraceus* may have included *S. asper* and *S. arvensis*, while the very numerous seedlings of *Sagina procumbens* almost certainly included some *S. apetala*. All *Betula* seedlings were recorded as *B. pendula*, but other species (native and alien) also occur in gardens. The single seedling identified as *Fallopia japonica* was presumably a hybrid (Stace, 1997).

A complete list was also made of all vascular plant taxa present in each garden in 2000.

Data analysis

To determine whether species that were more frequent in the seed bank were also more abundant in the seed bank, we regressed number of gardens occupied against mean density (where present) of individual species. We also estimated the likely true species richness of the seed bank by a jackknife procedure (Burnham and Overton, 1979). To attempt to account for differences between gardens, we regressed numbers of seeds and numbers of species in the seed bank against both garden area and total number of taxa recorded in the above-ground flora. To test whether small-seeded species were more abundant in the seed bank than large-seeded species, we regressed total numbers of seedlings against seed weight. Small-seeded species are normally more persistent in the soil than large-seeded species (Thompson *et al.*, 1993), and one consistent feature of persistent seeds is a high proportion of seeds in lower soil layers (Thompson *et al.*, 1997; Bekker *et al.*, 1998). To see if this applies to garden seed banks, we regressed the upper/lower

ratio against seed weight for the more abundant taxa in the seed bank (those for which ≥ 10 seeds were recorded). Seed weights were obtained from an unpublished database or from the Kew Seed Information Database (<http://www.rbgekew.org.uk/data/sid/>). We also examined the distribution of seed longevity indices (Thompson *et al.*, 1998) among both species and seeds. Variables were log transformed before analysis where necessary.

For several reasons, a simple comparison of garden seed banks and above-ground floras (e.g. by calculating a similarity index) is unlikely to prove very illuminating. First, most seeds in the soil are of common weed species with very persistent seeds, which were found growing in almost all the gardens studied, e.g. *Ranunculus repens* and *Poa annua*. Secondly, even among planted species, many of the more abundant species in the seed bank are rather transient members of the garden flora. Whether *Lobelia erinus* or *Viola × wittrockiana* were recorded in the flora of a particular garden in a single year may depend on whether they were actively grown in that year, but their presence in the seed bank may reflect their presence in the garden over many previous years. Therefore we confined our attention to: (1) five relatively 'permanent' planted species (long-lived woody plants or perennials) that were found in the seed banks of at least three gardens; and (2) two commonly planted perennial herbs that abundantly self-seed and, therefore, whether planted or not, are probably more-or-less permanent members of garden floras.

Results

A total of 2759 seedlings was identified, comprising 119 taxa, of which 53 occurred in only a single garden (Table 1). Our jackknife estimate of the likely true species richness of the seed bank is 225.9 ± 22.8 (SE). Numbers of seedlings per individual garden varied from 8 to 185, and numbers of taxa varied from 4 to 20 (Table 2). Natives outnumbered aliens in terms of both seedlings (1890:325) and taxa (74:44; *Epilobium* excluded in both cases). No taxon was present in every garden, but *Epilobium* was absent from only two gardens (Table 1). Perennial herbs, with 1896 seedlings, were more abundant than all other life forms combined, followed by annuals (498), biennials (218), shrubs (124) and trees (23). Natives outnumbered aliens in all categories except shrubs, where the three most abundant species were aliens (*Buddleja*, *Fuchsia magellanica* and *Leycesteria formosa*). The most abundant species were short-lived, weedy natives, with *Sagina procumbens*, *Cardamine hirsuta*, *Digitalis purpurea*, *Poa annua*, *Rumex obtusifolius* and *Ranunculus repens* being the most important. By far the

most abundant positively identified alien was *Buddleja davidii*, with 102 seedlings in 21 gardens, although North American *Epilobium ciliatum* may well have been more abundant. More frequent species were also generally more abundant, but the relationship was relatively weak ($R^2 = 0.30$, $n = 56$), and several species were present (and numerous) in only a single garden.

Numbers of seeds and species recovered from individual gardens were unrelated to garden area ($R^2 \approx 0$ in both cases). Numbers of seeds were also unrelated to total garden floristic richness, but the relationship between number of species in the seed bank and in the flora was only marginally non-significant ($R^2 = 0.062$, $P = 0.064$, $n = 56$).

The ratio of total numbers of seedlings in the upper 5 cm to the lower 5 cm varied from 0.2 to 3.8, with a single outlier of 17.5. Including this outlier the mean ratio was 1.6, but only 1.3 if the outlier was excluded. In other words, although there were, on average, more seeds in the upper layer than the lower layer, the difference was not large, and in 19 gardens there were more seeds in the lower layer. The ratio of seeds in the upper layer to numbers in the lower layer was not related to seed weight ($R^2 = 0.01$, NS, $n = 30$). Smaller seeds were more abundant than large ones, but the proportion of variance in abundance explained by seed weight was very small ($R^2 = 0.04$, $P < 0.05$, $n = 102$). Most species recorded had moderate to high seed longevity indices, and the overwhelming majority of seeds came from species with very persistent seeds (Fig. 1). Therefore, most seeds in our samples seemed to represent a persistent seed bank, rather than seed production of the current year.

As a predictor of presence in the seed bank, presence in the flora was very variable. Seeds of the shrubs *Buddleja* and *Leycesteria*, and the herbs *Aquilegia vulgaris* and *Alchemilla mollis*, were almost all confined to gardens in which the species were recorded in the flora, but seeds of *Hypericum androsaemum*, *Betula pendula* and *Carex pendula* were commonly found in gardens in which the species was absent (Table 3). Fifteen species were not recorded from the flora of any garden (Table 1).

Discussion

Because soil was collected in summer and not kept over winter, we may have underestimated the numbers of species that require a period of chilling to break the dormancy of seeds. However, seeds in the persistent seed bank would have been cold-stratified during the previous winter; thus we were able to detect seeds of species with persistent seed banks and a known requirement for chilling, e.g. *Plantago major* and *Carex pendula* (Grime *et al.*, 1981; Schütz, 2000).

Table 1. Species recorded in the soil seed banks of 56 gardens in Sheffield, UK, including native/alien status, growth form, total number of gardens where present, and numbers of seeds in upper and lower soil layers. *Species not recorded from the flora of any garden

Name	Native/alien	Growth form	Number of gardens	Number of seeds		
				Total	0–5 cm	5–10 cm
<i>Sagina procumbens</i>	Native	Perennial herb	39	589	322	267
<i>Digitalis purpurea</i>	Native	Biennial	34	196	87	109
<i>Poa annua</i>	Native	Annual	30	143	92	51
<i>Cardamine hirsuta</i>	Native	Annual	25	245	207	38
<i>Juncus effusus</i>	Native	Perennial herb	22	65	35	30
<i>Rumex obtusifolius</i>	Native	Perennial herb	17	99	75	24
<i>Agrostis capillaris</i>	Native	Perennial herb	16	34	10	24
<i>Plantago major</i>	Native	Perennial herb	16	28	8	20
<i>Ranunculus repens</i>	Native	Perennial herb	15	80	48	32
<i>Agrostis stolonifera</i>	Native	Perennial herb	13	15	6	9
<i>Poa trivialis</i>	Native	Perennial herb	13	25	17	8
<i>Sonchus oleraceus</i>	Native	Annual	11	16	6	10
<i>Aquilegia vulgaris</i>	Native	Perennial herb	9	20	14	6
<i>Betula pendula</i>	Native	Tree	9	21	15	6
<i>Myosotis sylvatica</i>	Native	Perennial herb	9	17	13	4
<i>Rorippa palustris</i> *	Native	Perennial herb	9	13	8	5
<i>Hypericum androsaemum</i>	Native	Perennial herb	7	61	46	15
<i>Urtica dioica</i>	Native	Perennial herb	7	16	7	9
<i>Euphorbia peplus</i>	Native	Annual	6	6	4	2
<i>Taraxacum officinale</i>	Native	Perennial herb	6	13	8	5
<i>Calluna vulgaris</i>	Native	Shrub	5	5	4	1
<i>Carex pendula</i>	Native	Perennial herb	5	20	6	14
<i>Geranium robertianum</i>	Native	Annual	5	10	6	4
<i>Holcus lanatus</i>	Native	Perennial herb	5	10	4	6
<i>Juncus bulbosus</i> *	Native	Perennial herb	5	5	2	3
<i>Lapsana communis</i>	Native	Annual	5	7	3	4
<i>Stachys sylvatica</i>	Native	Perennial herb	5	9	7	2
<i>Stellaria media</i>	Native	Annual	5	5	2	3
<i>Arabidopsis thaliana</i>	Native	Annual	4	4	2	2
<i>Capsella bursa-pastoris</i>	Native	Annual	4	7	2	5
<i>Prunella vulgaris</i>	Native	Perennial herb	4	4	4	0
<i>Rubus fruticosus</i>	Native	Perennial herb	4	5	1	4
<i>Chenopodium album</i> *	Native	Annual	3	3	0	3
<i>Fragaria vesca</i>	Native	Perennial herb	3	7	1	6
<i>Geum urbanum</i>	Native	Perennial herb	3	4	4	0
<i>Polygonum aviculare</i>	Native	Annual	3	4	2	2
<i>Rubus idaeus</i>	Native	Perennial herb	3	5	2	3
<i>Rumex acetosella</i>	Native	Perennial herb	3	3	2	1
<i>Tripleurospermum inodorum</i>	Native	Annual	3	4	1	3
<i>Centaurea nigra</i>	Native	Perennial herb	2	2	1	1
<i>Dipsacus fullonum</i>	Native	Biennial	2	2	1	1
<i>Gnaphalium uliginosum</i> *	Native	Annual	2	6	1	5
<i>Juncus articulatus</i> *	Native	Perennial herb	2	2	1	1
<i>Leucanthemum vulgare</i>	Native	Perennial herb	2	2	0	2
<i>Rumex crispus</i>	Native	Perennial herb	2	2	1	1
<i>Senecio jacobaea</i>	Native	Biennial	2	2	1	1
<i>Stachys arvensis</i>	Native	Annual	2	2	1	1
<i>Veronica serpyllifolia</i>	Native	Perennial herb	2	2	2	0
<i>Ajuga reptans</i>	Native	Perennial herb	1	1	0	1
<i>Alnus glutinosa</i>	Native	Tree	1	1	0	1
<i>Anagallis arvensis</i>	Native	Annual	1	1	0	1
<i>Arrhenatherum elatius</i>	Native	Perennial herb	1	1	0	1
<i>Atriplex patula</i>	Native	Annual	1	2	1	1
<i>Bellis perennis</i>	Native	Perennial herb	1	1	0	1
<i>Chamerion angustifolium</i>	Native	Perennial herb	1	1	1	0

Table 1. Continued

Name	Native/alien	Growth form	Number of gardens	Number of seeds		
				Total	0–5 cm	5–10 cm
<i>Chenopodium polyspermum</i> *	Native	Annual	1	2	0	2
<i>Chenopodium rubrum</i> *	Native	Annual	1	3	2	1
<i>Cirsium arvense</i>	Native	Perennial herb	1	1	0	1
<i>Cytisus scoparius</i>	Native	Shrub	1	1	1	0
<i>Hypericum perforatum</i>	Native	Perennial herb	1	1	0	1
<i>Hypericum tetrapterum</i> *	Native	Perennial herb	1	2	1	1
<i>Juncus inflexus</i> *	Native	Perennial herb	1	1	0	1
<i>Medicago lupulina</i>	Native	Annual	1	2	1	1
<i>Milium effusum</i> 'Aureum'	Native	Perennial herb	1	1	1	0
<i>Persicaria maculosa</i>	Native	Annual	1	1	0	1
<i>Poa pratensis</i>	Native	Perennial herb	1	1	1	0
<i>Scrophularia auriculata</i>	Native	Perennial herb	1	14	9	5
<i>Silene dioica</i>	Native	Perennial herb	1	1	0	1
<i>Thlaspi arvense</i> *	Native	Annual	1	1	0	1
<i>Trifolium repens</i>	Native	Perennial herb	1	1	0	1
<i>Typha latifolia</i> *	Native	Perennial herb	1	1	1	0
<i>Verbascum thapsus</i>	Native	Biennial	1	1	0	1
<i>Veronica agrestis</i>	Native	Annual	1	1	1	0
<i>Veronica beccabunga</i>	Native	Perennial herb	1	1	1	0
<i>Buddleja davidii</i>	Alien	Shrub	21	102	66	36
<i>Lobelia erinus</i>	Alien	Annual	10	13	5	8
<i>Tanacetum parthenium</i>	Alien	Perennial herb	10	17	6	11
<i>Alchemilla mollis</i>	Alien	Perennial herb	8	19	10	9
<i>Viola</i> × <i>wittrockiana</i>	Alien	Perennial herb	7	55	34	21
<i>Antirrhinum majus</i>	Alien	Perennial herb	4	4	2	2
<i>Fuchsia magellanica</i>	Alien	Shrub	4	8	6	2
<i>Leycesteria formosa</i>	Alien	Shrub	3	7	6	1
<i>Oenothera glazioviana</i>	Alien	Biennial	3	17	13	4
<i>Viola labradorica</i>	Alien	Perennial herb	3	6	1	5
<i>Fragaria</i> × <i>ananassa</i>	Alien	Perennial herb	2	4	2	2
<i>Heuchera sanguinea</i>	Alien	Perennial herb	2	3	1	2
<i>Melissa officinalis</i>	Alien	Perennial herb	2	11	6	5
<i>Mimulus guttatus</i>	Alien	Perennial herb	2	2	0	2
<i>Petunia</i> × <i>hybrida</i>	Alien	Annual	2	2	2	0
<i>Sedum spurium</i>	Alien	Perennial herb	2	2	1	1
<i>Veronica persica</i>	Alien	Annual	2	2	0	2
<i>Ageratum houstonianum</i>	Alien	Annual	1	1	0	1
<i>Begonia cucullata</i>	Alien	Perennial herb	1	1	0	1
<i>Brassica rapa</i> *	Alien	Annual	1	2	0	2
<i>Campanula persicifolia</i>	Alien	Perennial herb	1	1	0	1
<i>Conyza canadensis</i>	Alien	Annual	1	1	1	0
<i>Coronopus didymus</i>	Alien	Annual	1	1	1	0
<i>Crocosmia masoniorum</i>	Alien	Perennial herb	1	5	0	5
<i>Cymbalaria muralis</i>	Alien	Perennial herb	1	1	0	1
<i>Escallonia macrantha</i>	Alien	Shrub	1	1	1	0
<i>Fallopia japonica</i>	Alien	Perennial herb	1	1	0	1
<i>Laburnum anagyroides</i>	Alien	Tree	1	1	1	0
<i>Linaria purpurea</i>	Alien	Perennial herb	1	1	0	1
<i>Lychnis coronaria</i>	Alien	Perennial herb	1	1	1	0
<i>Mentha requienii</i>	Alien	Perennial herb	1	1	0	1
<i>Mentha</i> × <i>spicata</i>	Alien	Perennial herb	1	1	1	0
<i>Oxalis exilis</i>	Alien	Perennial herb	1	1	0	1
<i>Panicum miliaceum</i> *	Alien	Annual	1	1	1	0
<i>Papaver atlanticum</i> *	Alien	Perennial herb	1	20	10	10
<i>Petroselinum crispum</i>	Alien	Perennial herb	1	1	1	0
<i>Potentilla recta</i>	Alien	Perennial herb	1	1	0	1
<i>Primula denticulata</i>	Alien	Perennial herb	1	1	0	1

Table 1. *Continued*

Name	Native/alien	Growth form	Number of gardens	Number of seeds		
				Total	0–5 cm	5–10 cm
<i>Sedum rupestre</i>	Alien	Perennial herb	1	1	0	1
<i>Sisyrinchium californicum</i>	Alien	Perennial herb	1	1	1	0
<i>Sisyrinchium montanum</i>	Alien	Perennial herb	1	1	1	0
<i>Tellima grandiflora</i>	Alien	Perennial herb	1	1	0	1
<i>Verbena bonariensis</i>	Alien	Perennial herb	1	1	1	0
<i>Veronica longifolia</i>	Alien	Perennial herb	1	1	1	0
<i>Epilobium</i> spp.	–	Perennial herb	54	544	323	221

Surprisingly, we were even able to detect *Polygonum aviculare*, which should have re-entered secondary dormancy by July (Courtney, 1968), although we may have underestimated the numbers of seeds of this species. Nevertheless, there remains a possibility that some species with a chilling requirement were missed, but it is impossible to estimate the size of this problem. *Meconopsis cambrica*, generally common in our gardens and known to self-seed (Thompson *et al.*, 2003), but requiring chilling to break dormancy (Baskin and Baskin, 1998) and not detected in this study, is one obvious candidate. Quite apart from this problem, it is also clear from our jackknife estimate that our sampling missed many of the less common constituents of the seed bank.

The seed banks of private gardens, as revealed by this study, were dominated by the seeds of short-lived, mainly native species (Table 1). Most of these are typical weeds of cultivated soil, although some (e.g. *Ranunculus repens*) are also frequent in lawns (Thompson *et al.*, 2004). Although most abundant species are common weeds, some native species frequently self-seed in gardens and are tolerated or even encouraged as ornamental species (e.g. *Digitalis purpurea*, *Aquilegia vulgaris*). It is also clear that most species recorded, and the huge majority of seeds, were very persistent (Fig. 1). This impression is reinforced by the finding that the distribution of seeds between soil layers was remarkably even; abundant seeds in lower soil layers are a characteristic of persistent seeds. The paucity of species with short-lived seeds probably contributed to the absence of any relationship between seed weight and depth distribution. Another factor is probably the highly disturbed nature of most gardens; regular cultivation probably ensures that seeds rapidly become distributed throughout the top 10 cm of soil.

The results reveal the importance of the production of viable seeds for the naturalization process. All alien species found in the seed bank (with one exception: *Begonia cucullata* Willdenow) can be found in Stace (1997), which lists all British natives, naturalized aliens and recurrent casuals. Although some aliens

have been conspicuously successful without producing seed (e.g. *Veronica filiformis*, *Petasites fragrans*), it is clear that for most aliens, seed production is a prerequisite for escaping from gardens into the wild. It is probably no accident that the most abundant alien species, *Buddleja davidii*, is also one of the most common and widely distributed naturalized aliens in the British flora. All the abundant aliens we found in the seed bank are well known as either frequently escaping from gardens, or at least freely self-seeding within them. In some cases, our results suggest that perceptions of a plant species may need revising. Stace (1997) reports that *Heuchera sanguinea* 'rarely sets seed'. Given that we found three seeds from two gardens, in only a tiny sample of soil, seed production in this species must be moderately frequent.

Since only a very small volume of soil was sampled, we should not infer too much from the many species that were abundant in the flora, but absent from the seed bank. Of more interest are species that were present in the seed bank of gardens where the plant was absent from the flora. In this respect, the seven species we investigated were remarkably variable (Table 3). In two alien shrubs and two perennial herbs, one alien and one native, seeds were largely confined to gardens where the species was present. In three commonly planted native species, most occurrences in the seed bank were in gardens where the species was absent from the above-ground flora. All three can perhaps be explained by effective seed dispersal (*Hypericum*, *Betula*) or a long-persistent seed bank (*Carex*), but this cannot be the whole story, since *Leycesteria* is also effectively bird-dispersed (Stace, 1997). The 15 species that were found in the seed bank, but not recorded in the flora of any garden, were mostly native weeds known to possess very persistent seed banks (Table 1). Therefore, it is possible that most of these species had previously occurred in these gardens, but they were not present when the floristic recording was conducted. A further effect that may be of importance in gardens is the combination of their generally small sizes and the abrupt changes in flora that can occur between neighbouring gardens:

Table 2. Numbers of seeds and species recorded in the soil seed banks of 56 gardens in Sheffield, UK, and the ratio of the number of seeds in the upper and lower soil layers

Garden code	Number of seeds			Upper/lower ratio	Number of species
	0–5 cm	5–10 cm	Total		
100	91	94	185	1.0	9
96	184	–	184	–	11
87	99	53	152	1.9	15
16	98	50	148	2.0	11
147	83	36	119	2.3	10
25	69	33	102	2.1	19
51	52	33	85	1.6	20
121	42	36	78	1.2	13
89	39	35	74	1.1	17
88	25	43	68	0.6	16
24	41	27	68	1.5	12
141	44	24	68	1.8	9
61	48	20	68	2.4	14
97	35	27	62	1.3	12
17	17	42	59	0.4	8
64	23	33	56	0.7	17
109	38	17	55	2.2	15
70	27	24	51	1.1	10
3	30	20	50	1.5	9
30	29	20	49	1.5	11
1	23	24	47	1.0	10
4	24	23	47	1.0	13
112	17	27	44	0.6	13
99	26	18	44	1.4	14
46	25	18	43	1.4	16
32	28	15	43	1.9	11
6	23	19	42	1.2	9
81	22	17	39	1.3	7
21	19	18	37	1.1	9
8	35	2	37	17.5	7
68	20	16	36	1.3	13
128	12	22	34	0.5	8
43	15	19	34	0.8	12
9	18	15	33	1.2	12
10	8	23	31	0.3	10
106	16	15	31	1.1	13
94	11	13	24	0.8	7
152	5	17	22	0.3	9
44	11	11	22	1.0	11
56	16	6	22	2.7	8
11	8	13	21	0.6	11
38	14	7	21	2.0	9
47	7	13	20	0.5	5
78	15	5	20	3.0	14
72	4	15	19	0.3	12
91	7	12	19	0.6	10
57	11	8	19	1.4	9
123	15	4	19	3.8	10
5	3	15	18	0.2	9
76	11	7	18	1.6	9
50	7	10	17	0.7	7
49	9	6	15	1.5	6
101	4	9	13	0.4	6
7	4	6	10	0.7	4
48	6	3	9	2.0	6
52	6	2	8	3.0	5

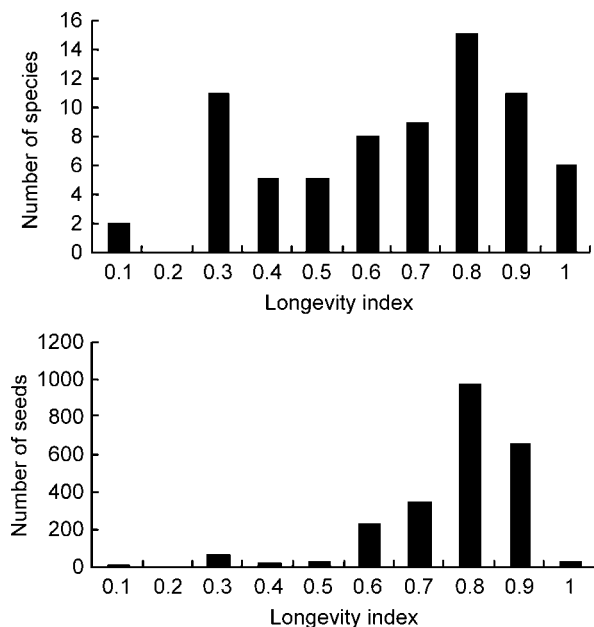


Figure 1. The distributions of longevity indices (Thompson *et al.*, 1998) among species found in the soil of 56 gardens, and the same data expressed in terms of numbers of seeds.

the floras of adjacent gardens are rarely similar (Thompson *et al.*, 2003, unpublished data). It is quite possible that seeds occurring in one garden may have originated in an adjacent garden, an effect likely to be exacerbated by the fact that flowerbeds are often along garden edges.

One surprising finding was seeds of *Rumex obtusifolius* in 17 gardens (and *R. crispus* in two of the 17). *R. obtusifolius* can hardly be described as attractive, and it would probably be actively encouraged by only the most fanatical wildlife gardener. The fact that this species has been allowed to set seed in at least 17 gardens probably tells us that management of many private gardens is, at least periodically, surprisingly lax. Another oddity is the presence of *Juncus effusus* in the soil of 22 gardens – it was found

Table 3. Number of gardens in which seven planted species were present in the above-ground flora, in the soil and in both

	Present in flora	Present in seed bank	Present in flora and seed bank
<i>Alchemilla mollis</i>	25	8	7
<i>Aquilegia vulgaris</i>	36	9	6
<i>Betula pendula</i>	11	9	3
<i>Buddleja davidii</i>	36	21	18
<i>Carex pendula</i>	5	5	1
<i>Hypericum androsaemum</i>	1	7	0
<i>Leycesteria formosa</i>	3	3	2

growing in only eight. One can only assume that its wide distribution (in this study and elsewhere) reflects both its prodigious seed production and the extreme persistence of its seeds.

Finally, what are garden seed banks worth? We checked a popular online nursery to see what it would cost to buy the garden perennials that emerged from our soil samples. At 2004 prices, our seed bank was worth £1488.75. Perhaps gardeners should take more care of their seed banks.

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References

- Baskin, C.C. and Baskin, J.M. (1998) *Seeds; Ecology, biogeography and evolution of dormancy and germination*. San Diego, Academic Press.
- Bekker, R.M., Bakker, J.P., Grandin, U., Kalamees, R., Milberg, P., Poschlod, P., Thompson, K. and Willems, J.H. (1998) Seed size, shape and vertical distribution in the soil: indicators of seed longevity. *Functional Ecology* **12**, 834–842.
- Burnham, K.P. and Overton, W.S. (1979) Robust estimation of population size when capture probabilities vary among animals. *Ecology* **60**, 927–936.
- Courtney, A.D. (1968) Seed dormancy and field emergence in *Polygonum aviculare*. *Journal of Applied Ecology* **5**, 675–684.
- Gaston, K.J., Smith, R.M., Thompson, K. and Warren, P.H. (2005a) Urban domestic gardens (II): experimental tests of methods for increasing biodiversity. *Biodiversity and Conservation* **14**, 395–413.
- Gaston, K.J., Warren, P.H., Thompson, K. and Smith, R.M. (2005b) Urban domestic gardens (IV): the extent of the resource and its associated features. *Biodiversity and Conservation* (in press).
- Grime, J., Mason, G., Curtis, A.V., Rodman, J., Band, S.R., Mowforth, M.A.G., Neal, A.M. and Shaw, S. (1981) A comparative study of germination characteristics in a local flora. *Journal of Ecology* **69**, 1017–1059.
- Niemelä, J. (1999) Ecology and urban planning. *Biodiversity and Conservation* **8**, 119–131.
- Schütz, W. (2000) Ecology of seed dormancy and germination in sedges (*Carex*). *Perspectives in Plant Ecology, Evolution and Systematics* **3**, 67–89.
- Stace, C.A. (1997) *New flora of the British Isles* (2nd edition). Cambridge, Cambridge University Press.
- Sukopp, H. and Starfinger, U. (1999) Disturbance in urban ecosystems. pp. 397–412 in Walker, L.R. (Ed.) *Ecosystems of disturbed ground*. Vol. 16. Amsterdam, Elsevier.

- Thompson, K., Band, S.R. and Hodgson, J.G.** (1993) Seed size and shape predict persistence in soil. *Functional Ecology* **7**, 236–241.
- Thompson, K., Bakker, J.P. and Bekker, R.M.** (1997) *The soil seed banks of north west Europe: Methodology, density and longevity*. Cambridge, Cambridge University Press.
- Thompson, K., Bakker, J.P., Bekker, R.M. and Hodgson, J.G.** (1998) Ecological correlates of seed persistence in soil in the NW European flora. *Journal of Ecology* **86**, 163–169.
- Thompson, K., Austin, K.C., Smith, R.M., Warren, P.H., Angold, P.G. and Gaston, K.J.** (2003) Urban domestic gardens (I): Putting small-scale plant diversity in context. *Journal of Vegetation Science* **14**, 71–78.
- Thompson, K., Hodgson, J.G., Smith, R.M., Warren, P.H. and Gaston, K.J.** (2004) Urban domestic gardens (III): Composition and diversity of lawn floras. *Journal of Vegetation Science* **15**, 373–378.

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