THE FLORA OF DURHAM WALLS

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INTRODUCTION

Walls provide a variety of habitats for plants; they are constructed of different materials; they are built for many purposes; their dampness and aspects are of great importance to the plants upon them. They provide ample opportunity for the study of colonization, and they pose problems in dispersal. It is surprising, therefore, that comparatively few accounts of their vegetation have appeared; possibly their very ubiquity causes the plants upon them to be taken for granted. Of the accounts that have appeared, only those of Richard (1888), Salisbury (in Fitter, 1945) and Rishbeth (1948) have dealt with the flora in much detail, and that of Salisbury is not strictly confined to walls, though the bombed site substratum is essentially similar.

The observations discussed in this paper were made over a period of three years, 1953-56. The work was mainly confined to Durham City, though a few lists were made in the Pennine Dales. It was felt that the problem was better served by concentrating our attention on a small area, than by compiling a rather formidable list of species from all over the county. Brief mention is, however, made of some of the plants we saw elsewhere.

Among the advantages of confining the investigation to the city of Durham was the fact that each wall could be easily revisited, and so a series of visits over the whole year enabled us to record plants, especially annuals, that lived only for short periods. As far as was possible, each wall was visited at least once in each of the three years, to give us some idea of the persistence of the flora.

Walls, in this study, have been taken as including not only simple walls, but bridges, old buildings and stone buttresses. The composition and aspect of each wall and its function (dividing or retaining) was recorded. Some preliminary experiments on seed dispersal were carried out.

THE WALL FLORA

a. *Species present*

Table 1 contains a list of the species found on the walls of Durham City and its environs. The inclusion of a species on this list does not necessarily mean that it was present throughout the

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period of the study, but very few were not; these were a few annuals, and one or two that for some reason or other died. The prolonged drought of the summer of 1955 caused the death of some plants, as is only to be expected in a habitat so prone to drying out.

The number of species recorded was much larger than a preliminary survey had led us to believe, and the length of the list is surprising, considering the small size of the city. Atmospheric pollution, though sufficient to restrict lichens and bryophytes severely, is apparently not enough to affect the higher plants adversely. Factors contributing to the high number of species present are the great age of many of the buildings and walls in the city, and the present state of neglect of many of them.

A list of species found on half-a-dozen walls elsewhere in the county, all but one in Weardale and Teesdale, contained 94 species. The length of this list indicates that a detailed survey of walls in the area would reveal a very rich flora.

The 14 species that have 15 or more records on the walls are listed in Table 2. 66 walls were listed, and so this is a list of the species that occurred on approximately 25% of the walls or more. Of the remaining 158 species recorded, 8 were recorded between 10 and 14 times, 21 between 5 and 9 times, and 129 less than 5 times, 74 of these only once. The rarity of so many of the species recorded puts the total in a somewhat different light. Only 45 species occurred on more than 5 walls.

Included in Table 2 are the normal habitats of the species. These will be discussed later.

Of the 14 species listed here, 6 (42·9%) are normally wind-distributed, 6 (42·9%) are not equipped with any special means of dispersal, and two (14·3%) are animal-distributed. These figures do not differ greatly from the percentages of different dispersal mechanisms in the complete list of species (see Table 8).

TABLE 1
LIST OF DURHAM WALL PLANTS

ANGIOSPERMAE

Acer pseudoplatanus L.
Achillea millefolium L.
Aethusa cynapium L.
Agropyron repens (L.) Beauv.
Agrostis stolonifera L.
A. tenuis Sibth.
Alliaria petiolata (Bieb.) Cavara & Grande
Alnus glutinosa (L.) Gaertn.
Alopecurus pratensis L.
Anthoxanthum odoratum L.
Anthriscus sylvestris (L.) Hoffm.
Antirrhinum majus L.
Aquilegia vulgaris L.
Arctium sp.
Arrhenatherum elatius (L.) Beauv. ex J. & C. Presl
Artemisia vulgaris L.
Aster lanceolatus Willd.
A. novi-belgii L.
Atriplex patula L.
Ballota nigra L.
Bellis perennis L.
Betula pubescens Ehrh.
B. pendula Roth
Bromus mollis L.
B. ramosus Huds.
B. sterilis L.

Buddleja davidii Franch.
Calendula officinalis L.
Calystegia silvatica (Kit.) Griseb.
Campanula rotundifolia L.
Capsella bursa-pastoris (L.) Medic.
Centaurea nigra L.
Cerastium tomentosum L.
C. holosteoides Fr.
Chamaenerion angustifolium (L.) Scop.
Cheiranthus cheiri L.
Chrysanthemum parthenium (L.) Bernh.
Cirsium arvense (L.) Scop.
C. vulgare (Savi) Ten.
Convolvulus arvensis L.
Corylus avellana L.
Cotoneaster frigidus Wall. ex Lindl.
Crataegus monogyna Jacq.
Cymbalaria muralis Gaertn., Mey. & Scherb.
Cynosurus cristatus L.
Dactylis glomerata L.
Deschampsia cespitosa (L.) Beauv.
D. flexuosa (L.) Trin.
Dianthus caryophyllus L.
Digitalis purpurea L.
Epilobium hirsutum L.
E. montanum L.
E. parviflorum Schreb.
Festuca ovina L.
F. pratensis Huds.
F. rubra L.
Ficus carica L.
Fragaria ananassa Duchesne
F. vesca L.
Fraxinus excelsior L.
Galium aparine L.
G. saxatile L.
Genista radiata (L.) Scop.
Geranium lucidum L.
G. robertianum L.
Geum urbanum L.
Glechoma hederacea L.
Hedera helix L.
Heracleum mantegazzianum Somm. & Levier
H. sphondylium L.
Hieracium perpropinquum (Zahn) Druce
H. pilosella L.
Holcus mollis L.
Hordeum murinum L.
Hypericum perforatum L.
Hypochoeris radicata L.
Impatiens glandulifera Royle
Iris germanica L.
Laburnum anagyroides Medic.
Lamium album L.
L. purpureum L.
Lapsana communis L.
Lathyrus odoratus L.
Leontodon autumnalis L.
L. hispidus L.
Ligustrum vulgare L.
Lolium multiflorum Lam.
L. perenne L.
Lupinus nootkatensis Donn ex Sims
Lycium halimifolium Mill.
Matricaria matricarioides (Less.) Porter
Mentha spicata L.
Mercurialis perennis L.
Milium effusum L.
Myrrhis odorata (L.) Scop.
Papaver rhoeas L.
Petasites hybridus (L.) Gaertn., Mey. & Scherb.
Phalaris arundinacea L.
Pisum sativum L.
Plantago lanceolata L.
P. major L.
P. media L.
Poa annua L.
P. compressa L.
P. pratensis L. agg.
Polygonum baldschuanicum Regel
P. cuspidatum Sieb. & Zucc.
P. convolvulus L.
Potentilla anserina L.
Prunus padus L.
Quercus petraea (Mattuschka) Liebl.
Ranunculus acris L.
R. repens L.
Reseda luteola L.
Ribes rubrum L. agg.

R. uva-crispa L.
Rosa canina L.
R. dumetorum Thuill.
Rubus fruticosus L. agg.
R. idaeus L.
Rumex acetosa L.
R. acetosella L.
R. longifolius DC.
R. obtusifolius L.
Sagina apetala Ard.
Salix cinerea subsp. *atrocinerea* (Brot.) Silva & Sobrinho
S. caprea L.
Sambucus nigra L.
Sarothamnus scoparius (L.) Wimm. ex Koch
Saxifraga umbrosa L.
Sedum acre L.
Sempervivum tectorum L.
Senecio jacobaea L.
S. viscosus L.
S. vulgaris L.
Silene vulgaris (Moench) Garcke
Sinapis arvensis L.
Sisymbrium officinale (L.) Scop.
Solidago altissima L.
Sonchus asper (L.) Hill
S. oleraceus L.
Sorbus intermedia (Ehrh.) Pers. *sensu lato*
S. aucuparia L.
Stachys sylvatica L.
Stellaria holostea L.
S. media (L.) Vill.
S. nemorum L.
Symphytum officinale L.
Taraxacum officinale Weber
Trifolium pratense L.
T. repens L.
Tripleurospermum maritimum (L.) Koch
Tussilago farfara L.
Ulmus glabra Huds.
Urtica dioica L.
U. urens L.
Verbascum thapsus L.
Veronica chamaedrys L.
V. arvensis L.
Vicia sepium L.
Vinca minor L.

GYMNOSPERMAE

Taxus baccata L.

PTERIDOPHYTA

Asplenium ruta-muraria L.
A. trichomanes L.
Dryopteris filix-mas (L.) Schott agg.
Equisetum arvense L.
Phyllitis scolopendrium (L.) Newm.
Pteridium aquilinum (L.) Kuhn

BRYOPHYTA

Amblystegium serpens (Hedw.) Bruch, Schimp. & Guemb.
Barbula unguiculata Hedw.
B. sp.
Brachythecium rutabulum (Hedw.) Bruch, Schimp. & Guemb.
Bryum argenteum Hedw.
B. caespiticium Hedw.
Ceratodon purpureus (Hedw.) Brid.
Conocephalum conicum (L.) Dumort.
Funaria hygrometrica Hedw.
Grimmia pulvinata (Hedw.) Sm.
Hypnum cupressiforme Hedw.
Lunularia cruciata (L.) Dum.
Tortula muralis Hedw.

FUNGI

Psalliota arvensis (Fr.) Quélet

ALGAE

Pleurococcus sp.
Cladophora sp.
Oedogonium sp.

TABLE 2

THE COMMONER WALL PLANTS OF DURHAM CITY AND THEIR NORMAL HABITATS

	No. of records	Normal habitat
Taraxacum officinale	42	Waste ground, lawns, pasture
Chamaenerion angustifolium	35	Open ground, walls, rocks
Sambucus nigra	27	Open wastes, scrub
Dactylis glomerata	26	Waste ground, meadows
Poa annua	26	General distribution
Epilobium montanum	25	Woods, walls, rocks
Acer pseudoplatanus	23	Woods, hedges
Senecio vulgaris	18	Waste and cultivated ground
Lolium perenne	15	Waste ground, meadows
Plantago lanceolata	15	Waste ground, grassland
Poa pratensis	15	Grassy places, meadows
Rubus fruticosus agg.	15	Woods, scrub, hedgerows
Rumex obtusifolius	15	Waste ground, hedgerows
Senecio jacobaea	15	Waste and cultivated ground

b. *Comparison with other wall floras*

Table 3 gives a comparison of the Durham list with 12 others. 8 of these are wall flora lists, a ninth is a bombed site list, another is of dustcarts, and the remainder are records from pollard willows or epiphytes on trees. Tree epiphytes are not strictly comparable but to a certain extent the problems of dispersal are similar, though not entirely, as will be pointed out later.

There are two interesting observations to be made on this table. Rishbeth (1948) made a comparison with the same lists and we have repeated it. In every case more than 50% of the species recorded in other lists also occurred on the walls of Cambridge. In fact in the least similar list he had 55% common to the Cambridge walls. On the other hand, although some of the lists contained many species that occur in Durham, some others showed a much smaller number common to both.

Thus, with the exception of the Durham Dales, which would be expected to have a closer affinity to Durham City, the Cambridge walls have more species in common with every other wall list than do the Durham walls. The reason for this is not obvious. Durham's northern position may have some bearing on these differences, but it is doubtful, especially in the light of the data for Cambridge dustcarts (Table 3). Of 99 species distributed by dustcarts in Cambridge, 39 are found on Cambridge walls. However, 39 are also found on Durham walls.

Rishbeth suggested that several species are found fairly regularly on walls throughout Britain. He listed as examples *Cheiranthus cheiri, Cymbalaria muralis, Parietaria diffusa, Poa compressa* and *Asplenium ruta-muraria.* We have analysed the lists in Table 3 (with the exception of the mosses and the dustcart list) and our

own, a total of 10, to see which are the most commonly recorded species. There are 2 species recorded on 8 of these lists, namely *Dactylis glomerata* and *Poa annua*. 9 species are present on 7 lists: *Acer pseudoplatanus, Taraxacum officinale, Achillea millefolium, Poa pratensis, Ribes uva-crispa, Rubus fruticosus* agg., *Sambucus nigra, Stellaria media* and *Urtica dioica*. 2 ferns were present on 6 of the lists: *Asplenium trichomanes* and *Polypodium vulgare*. Angiosperms with 6 records were *Bromus mollis, Hypochoeris radicata, Lolium perenne, Senecio jacobaea Sonchus oleraceus, Fraxinus excelsior,* and *Senecio vulgaris*. Species on 5 lists (50% of lists) were *Asplenium ruta-muraria, Anthriscus sylvestris, Capsella bursa-pastoris, Cymbalaria muralis, Epilobium parviflorum, Galium aparine, Plantago lanceolata, Rumex acetosa*.

On the basis of published lists these 28 species are the most likely to be found on walls. It is interesting to note that 11 of the 14 most frequent species on Durham walls and 7 of the 12 commonest on Cambridge walls, are on this list of 28 common wall species.

TABLE 3

COMPARISON OF THE SPECIES LIST ON CAMBRIDGE AND DURHAM WALLS WITH OTHER RECORDS

Place, habitat and author	*Species listed*	*Common to Durham*		*Cambridge*	
		No.	*%*	*No.*	*%*
Poitiers; churches (Richard, 1888)	76	23	30·2	43	
Cambridge; pollard willows (Willis & Burkill, 1893)	80	40	50·0	50	
Oxford District; walls (Church, 1922)	33	12	36·3	20	
Pays Basque; walls (Jovet, 1941)	23	5	21·5	8	
London; bombed sites (Salisbury, in Fitter, 1945)	126	62	49·2	70	
Cambridge; walls (Rishbeth, 1948)	185	87	47·0		
Flatford; pollard willows (Cannon & Cannon, 1957)	35	25	71·4	24	
Durham Dales; walls (Present authors)	94	59	62·7	48	
Middlesex; walls (bryophytes) (Richards, 1928)	19	8	42·1	10	
Cambridge; walls (bryophytes) (Rishbeth, 1948)	32	8	25·0		
Cambridge; dustcarts (Burkill, 1893)	99	39	40·0	39	
Kristiansand; trees (Grødem, 1940)	100	42	42·0	36	36·0

c. *Life-form*

Table 4 lists the life-forms of 168 species found on Durham walls, both by number of species and number of site records.

TABLE 4

LIFE-FORMS OF DURHAM WALL PLANTS

	Species		*Site records*	
	No.	%	*No.*	%
Phanerophytes	29	17·3	127	16·7
Chamaephytes	13	7·7	53	6·9
Hemicryptophytes	92	54·7	48	58·7
Geophytes	6	3·5	16	2·1
Therophytes	27	16·2	115	15·2
Helophytes	1	0·6	3	0·4
Totals	168	100·0		100·0

Hemicryptophytes account for over half the species on Durham walls, and the number of phanerophytes and chamaephytes is large. Therophytes, on the other hand, are under-represented. These figures are best discussed in the light of other life-form spectra, and a selection of these is given in Table 5.

TABLE 5

COMPARISON OF THE LIFE-FORM SPECTRUM OF THE FLORA OF DURHAM WALLS WITH OTHER WALL FLORAS AND GENERAL SPECTRA

(*General spectra from Raunkiaer, 1934*)	*Phan.*	*Ch.*	*H.*	*G.*	*Th.*	*Hel.*
Clova (Scotland)	9·0	7·0	59·0	7·0	13·0	5·0
Denmark	7·0	3·0	50·0	11·0	18·0	11·0
Stuttgart region	9·0	3·0	54·0	10·0	17·0	7·0
Durham walls	17·3	7·7	54·7	3·5	16·2	0·6
Cambridge walls	15·0	4·0	49·0	5·0	27·0	—
Poitiers churches	5·0	4·0	49·0	3·0	39·0	—
London bombed sites	5·0	2·0	44·0	5·0	44·0	—
Kristiansand epiphytes	27·0	2·0	59·0	5·0	7·0	—
22 commonest spp. on Durham walls	18·2	4·5	63·6	—	13·7	—
12 commonest on Cambridge walls	16·6	8·3	45·9	—	29·2	—
28 commonest on published lists	14·8	11·1	59·3	—	14·8	—

The high percentage of phanerophytes on Durham walls, like that in Cambridge, can be explained by the fact that many of the walls are old and surrounded by large numbers of trees and shrubs. Less easily explained is the high number of these forms in the list of commonest recorded wall plants, unless it be that walls in general tend to be in places where trees and shrubs are common. Some of the trees on Durham walls are quite large, notably some specimens of *Ulmus glabra, Ficus carica* and

Sambucus nigra. Though many seedlings of phanerophytes occur, the only species of phanerophytes to be found only as seedlings were *Quercus petraea* and *Taxus baccata.* The successful establishment of so many trees and shrubs indicate the age of the walls and their condition of neglect. Many of them are being slowly destroyed by the root action of plants.

The slightly higher percentage of hemicryptophytes on Durham walls, in comparison with Cambridge and London bombed sites, is probably a reflection of the very low percentage of therophytes. Yet the commonest species in published lists of wall floras include only 15% of therophytes, though many of the lists contain a much higher therophyte percentage. The high percentage in London is no doubt due to the very recent colonization and the open habitat. It would appear that as the walls become older and more fully overgrown with vegetation, the opportunity for annuals to gain a foothold is much reduced. This trend is evident in Cambridge. In Durham it is much more marked, and it is relevant to point out here that many of the therophytes that were found in Durham were either on rubble from recently demolished buildings, or on relatively new (less than 50 years old) brick walls, which had not yet had time to become fully colonized. In fact, the percentages of annuals on Durham walls, and among the commonest wall species, are comparable with those in the life-form spectra for Scotland, Denmark and Stuttgart. It would seem that the mature wall flora closely approaches that of the surrounding vegetation in its life form composition. The extremely low percentage of therophytes found on Kristiansand trees cannot be explained without further evidence.

d. *Normal habitats of wall plants*

One might expect that walls would provide a suitable habitat for plants of open ground to colonize. The species that normally first appear on waste or cultivated ground are adapted to take rapid advantage of such situations. They also generally have high reproductive capacities, which enable them rapidly to exploit such areas.

Table 6 summarises the usual habitats in which the species found on Durham walls occur. Since many of the species can be classified under more than one of the types of habitat, the total is higher than the total number of species. The percentages, however, are calculated as percentages of total number of species. The result is that the percentages total more than 100%, but to present them in this way gives, we think, a truer picture of the numbers of species which occur in any one habitat.

It will be seen that our surmise is to some extent borne out by the result in Table 6. The habitat typical of the highest number of species from the walls is waste ground. The importance of garden escapes is emphasised by the fact that 16·6% of the species found on walls are garden plants, including all the aliens found on the walls of Durham. The high percentage of grassland species

is partly due to the fact that many of the plants of waste ground are also, according to Clapham, Tutin and Warburg (1952) (from whose flora these data have been extracted), said to occur in grassland. The large number of woodland species results partly from the fact that many of the walls along the river gorge are among woodland and are colonised by woodland plants.

The commonest plants recorded on walls have also been treated in the same way as in Table 6, and the results show the same trend.

TABLE 6
USUAL HABITATS OF DURHAM WALL PLANTS

Habitat	*No. of species occurring in this habitat*	*% (of total number of species on walls)*
Walls	19	11·3
Rocks, cliffs, scree	19	11·3
Roadsides, paths	9	5·4
Waste ground	55	32·7
Cultivated ground	18	10·7
Gardens	28	16·6
General distribution	4	2·4
Hedgerows	34	20·2
Heathland	11	6·5
Grassland	41	24·4
Scrub	15	9·0
Woodland	46	27·4
Streams, damp places	15	9·0

HABITAT FACTORS

Wall vegetation is likely to be affected by the aspect, construction, shading and moisture content of the substratum. Rishbeth (1948) made some observations on this, particularly on aspect. Although in this study we were mainly concerned with problems of distribution, we made a few comparisons between different walls and their flora.

a. *Construction*

Most Durham walls are constructed of either brick or sandstone, with the exception of a few concrete river walls. The sandstone walls are usually very old. They are constantly crumbling, and so it is difficult for plants to become established on the stone itself, except on the wall tops. The mortar acts as a better substratum, and provides crevices in which plants are found. There are a few old brick walls, and these are well covered, but the majority of brick walls are more recent in origin, and they do not carry many plants. In spite of this, the average number of plants on these walls is the same as on stone and old brick walls had more plants than the average. Brick, it would seem, is the better substratum for plants. The few concrete walls

carried a very large number of plants. This is due to the fact that they are all riverside walls, and drainage from the steep bank above them keeps them moist and carries down seeds from above.

Retaining walls, it was thought, being kept constantly damp, would probably have more plants than dividing walls. The majority of the retaining walls are of stone, and a count of plant numbers on them revealed that they are no more heavily covered with vegetation than the rest. The difference is in distribution more than numbers. Dividing walls have a dense plant cover on top whereas retaining walls have a much more scattered plant cover. It is difficult at times to determine whether a plant on the side of such a wall has extended its roots through to the soil behind.

b. *Moisture*

What has been said above about retaining walls is, of course, related to their moisture-holding capacity. Rishbeth noted that where a wall had an intermittent flow of water from a pipe or overflow, there was often a quite well established plant cover. We noted this also in Durham; algae, in particular (mainly *Pleurococcus* sp.), liverworts and mosses were especially rich in these positions.

The fact that the riverside walls, constantly damp, have a rich plant cover is indicative of the importance of moisture. The probable reason for the failure of the plants to establish themselves on moist retaining stone walls may be that in a rainstorm the scouring action of rain and debris carried over from the soil behind prevents seedlings from getting a good hold. The concrete river walls are less affected by this, as they are properly drained.

While agreeing with the general premise that moist walls will be a more suitable habitat for plants, we are inclined to discount the importance of moisture for well established plants. Mosses and algae are very sensitive to drying out, and a drought will often result in the drying out and blowing away of moss. Seedlings and small annuals will suffer likewise. Well established plants, on the other hand, do not seem to be much affected, even in a prolonged dry summer such as that of 1955. Among the annuals we noted only one striking example of dwarfing, presumably through water deficit. This was in *Impatiens glandulifera,* which was present on one or two river walls. The wall specimens were stunted and weakly, whereas their probable parents, rooted in the muddy bank a few feet away, reached heights of up to 9 feet. The rarity of such dwarfing is not really surprising, since we have established that a large number of species found on the walls are normally found in open dry habitats, where they will be subjected to lack of water from time to time.

c. *Shade*

An investigation of the richness of the flora of different aspects of walls did not produce any convincing evidence that the higher

plants were much affected by shading from the sun. Mosses and seedlings were affected, and moisture is directly related to shade in many cases. In general, the westerly or northerly aspects of walls are apparently more favourable to plant growth than the easterly or southerly.

Some walls in Durham are very heavily shaded by trees. This increases their general moistness, of course. They rarely had any plants on them, and those that were present were usually normal woodland species.

One moss, *Amblystegium serpens,* deserves mention. It occurs only on a few walls in the city, all deeply shaded. It cannot apparently tolerate dry or bright conditions. It forms dense mats on the top of one wall, and is the only plant, other than algae, that is present.

d. *Flora of walls in different situations*

It is obvious that the flora of any particular wall will be influenced not only by its composition, aspect, and exposure, but also by the character of the surrounding vegetation, i.e. the available source of colonisation. Table 7 gives lists of a few walls in rather different situations.

TABLE 7

THE FLORAL COVER OF DIFFERENTLY SITUATED WALLS

1. Brick wall by foot passage in town.	2. River banks, on edge of wood.
Chamaenerion angustifolium	*Geranium robertianum*
Epilobium montanum	*Milium effusum*
Festuca rubra	*Rumex acetosa*
Poa annua	*Hedera helix*
Rumex obtusifolius	*Geum urbanum*
Senecio vulgaris	*Mercurialis perennis*
Sorbus aucuparia	*Lamium album*
Taraxacum officinale	*Stellaria nemorum*
3. Brick kiln, in large meadow near river.	4. Stone wall, rear of College.
Agrostis stolonifera	*Acer pseudoplatanus*
Alopecurus pratensis	*Achillea millefolium*
Anthoxanthum odoratum	*Antirrhinum majus*
Bellis perennis	*Buddleja davidii*
Bromus mollis	*Chamaenerion angustifolium*
B. sterilis	*Convolvulus arvensis*
Crataegus monogyna	*Cotoneaster frigidus*
Dactylis glomerata	*Crataegus monogyna*
Festuca ovina	*Cymbalaria muralis*
F. rubra	*Dactylis glomerata*
Hieracium pilosella	*Dryopteris filix-mas*
Leontodon hispidus	*Epilobium hirsutum*
Plantago lanceolata	*E. montanum*

TABLE 7—*Continued*

Poa compressa	*Geum urbanum*
P. pratensis	*Hedera helix*
Pteridium aquilinum	*Heracleum mantegazzianum*
Rubus fruticosus agg.	*Laburnum anagyroides*
Rumex acetosa	*Pisum sativum*
R. acetosella	*Polygonum cuspidatum*
Sambucus nigra	*Rubus idaeus*
Sorbus aucuparia	*Rumex obtusifolius*
Taraxacum officinale	*Sambucus nigra*
Rosa canina	*Sorbus aucuparia*
R. dumetorum	*S. intermedia*
Salix caprea	*Taraxacum officinale*
S. cinerea subsp. *atrocinerea*	

These lists do show that although the quantity of plants on different types of walls may not differ, the species composition may vary very much indeed. To a large extent the variation is a reflection of the available disseminules. The 8 species on a wall in the town include 4 that are adapted to wind-distribution, and two more that are probably wind dispersed. One of the remainder is carried by birds. All have had to travel some distance to the wall. The river-bank wall, partly shaded by the trees, has several woodland plants among its flora. The brick kiln, in a field on the riverside at the town outskirts, has a high proportion of meadow and scrub plants, and the old college wall, as might be expected, includes 8 or 9 species of garden origin in its flora. This confirms Rishbeth's observation that short-distance dispersal is important in wall floras, and in addition suggests that walls that are somewhat isolated from the nearest sources of re-invasion are liable to include a high proportion of wind-carried plants in their flora.

e. *Air pollution*

Though Durham is not obviously suffering from polluted air, careful observation shows that the amount of smoke and soot is rather high. Being partly in a hollow, smoke tends to hang about over the lower parts of the town. The absence of lichens in all but a few places, and the low number of bryophyte species are indicative of the extent of the pollution. Not only is the number of moss species low, but also the percentage cover. A comparison with walls in more rural areas confirms this. It is doubtful if the higher plants are affected very much by this factor, however.

ESTABLISHMENT

Though detailed observations were not carried out on the establishment and succession of plants on the walls, a few notes were made which indicate that the generally accepted pattern of

succession is not necessarily always followed. The pioneers are indeed lichens (where the atmosphere allows) or simple algae. Mosses appear next, or are themselves pioneers. However, the mosses, at least in Durham, do not usually produce enough humus for the establishment of higher plants. We observed seedlings in three successive years, and in almost every case the first dry spell killed the seedlings in moss carpets on the top of walls. On the other hand, in many instances, vascular plants become established without the help of mosses.

We would suggest that where a moss carpet overlies cracks in a wall, into which the roots of seedlings can penetrate, they stand a very good chance of survival. On walls with little or no moss, deep cracks, or spaces left by the crumbling of mortar, tend to become filled with debris, and if a seed becomes wedged in such a crevice and germinates, it is protected somewhat against the effects of a drought, and often survives. It is noticeable in Durham, where mosses are relatively scarce on the walls, that many walls support an abundance of vascular plants and very few mosses, and these plants often must have become established without the aid of mosses. Chance is probably the most important factor in the arrival and establishment of many wall plants.

Dispersal

No study of wall floras is complete unless a good deal of attention is paid to the problems of dispersal. The species list has been classified into plants with particular types of dispersal mechanism. However, as can be seen from Table 8, over 60% of the species present apparently do not possess any special dispersal mechanism. The immediate conclusion is that their seeds are carried on to walls by wind, but though this may be the correct conclusion, it is very difficult to obtain any real evidence for such dispersal. Ridley (1932) records many species of this type as occurring high on cliffs and rock faces, and suggests that they can only have been carried there by wind. Rishbeth merely states that Cambridge walls have a high proportion of wind-distributed plants that have no special wind-dispersal mechanism.

Some interesting points are brought out by Table 8. Both Cambridge and Durham walls have a large percentage (16% and 14·9% respectively) of animal-dispersed species, compared with London and Poitiers. London's bombed sites would presumably be colonised at first by wind-carried plants, and this probably accounts for the difference here. The reason for the low number of animal-dispersed species on Poitiers walls is obscure.

The increased efficiency of dispersal of plants specially modified for wind dispersal over those not so modified is shown by the fact that, whereas in Durham only 20% of the species have such modifications, they are represented in 30% of the site records. Also, since a site record merely means that the species concerned is present on a certain wall, it gives no idea of the abundance

Table 8

Dispersal of Wall Plants

	Durham walls				*Cambridge walls*				*London bombed sites*				*Poitiers*		*Flatford willows*		*Kristiansand epiphytes*	
	Species		Site Records		Species		Site Records		Species		Site Records		Species		Species		Species	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Animal																		
Fleshy	21	12·5	100	13·1	20	13	89	7	5	4	27	3	3	4	12	34·25	17	17.0
Adhesive	4	2·4	17	2·2	5	3	44	4	3	2	14	1	—	—	1	2·9	3	3·0
Total	(25)	(14·9)	(117)	(15·3)	(25)	(16)	(133)	(11)	(8)	(6)	(41)	(4)	(3)	(4)	(13)	(37·15)	(20)	(20·0)
Wind	34	20·2	229	30·1	79	50	564	45	45	36	723	75	32	42	9	25·7	23	23·0
No Special Mechanism	106	63·1	402	52·8	58	34	560	44	73	58	202	21	41	54	13	37·15	57	57·0
Others (Explosive, etc.)	3	1·8	14	1·8	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Total	168	100·0	762	100·0	162	100·0	1257	100·0	126	100·0	966	100·0	76	100·0	35	100·0	100	100·0

For Durham walls, only fruits with pappus or well-developed wings are regarded as being especially modified for wind dispersal, e.g. grasses are not included. Other figures from Rishbeth (1948).

of some of these species, and some rough estimates showed that plants with special wind-dispersal mechanisms were more abundant than those without.

The flora of dustcarts, investigated by Burkill (1893), contains many plants also commonly found on walls. It is possible that passing dustcarts could scatter a certain amount of seed on to roadside walls. Even more likely is the possibility that swirling air currents in the wake of passing vehicles will carry seeds up on to such walls. Both these suggestions are invoking air currents for seed dispersal, and so can really be classified under wind. There remains the possibility that animals (including man) carry seeds on to walls.

Birds are the most likely candidates here, but before considering them, a few other possibilities should be mentioned. Some of these walls are used as climbing grounds by children. Clifford (1956) has shown that a large number of plants are carried as seed on human footwear, and he has suggested (personal communication) that some seeds may reach walls in this way. Two other common frequenters of walls are cats and snails. Domestic animals may carry a few seeds in their fur. It has been reported to us that snails do occasionally have seeds adhering to them. Both these means of seed dispersal are very unlikely to be of great importance, but they deserve mention.

A good deal has been written about the action of birds in carrying seeds from place to place. They have been shown to carry them in mud on their feet; among the materials used in nest building; as food, which either gets dropped before being eaten, or passes through their gut unharmed.

Table 9 contains a list of species, not normally considered as being animal-dispersed, which occur on Durham walls, and have been recorded as being carried in some way or other by birds. This list has been compiled from various sources, especially Ridley (1932), Cannon & Cannon (1957), Willis & Burkill (1893) and personal observations. The importance of birds as carriers of seeds is especially seen in the flora of the pollard willows at Flatford. Here over 37% of the species found are either fleshy or adhesive. Cannon & Cannon actually list 30 of the 35 species as being birds' food, and eight as occurring in birds' nests.

Thus, of the species on Durham walls with no special adaptation for dispersal by animals, 44, or 30%, have been recorded as being carried in one way or another by birds. (*Galium aparine* is included, though it is not normally considered as being carried as food.) It is almost certain that others are carried in this way, but have never been recorded. This rather remarkable fact means that the possibility of at least a few of the plants on the walls having been deposited there by birds, though not specially adapted for such dispersal, is quite high. Birds often use walls as perches, as the number of bird droppings on walls testifies, and droppings have been shown to contain viable seed (Ridley, 1932). It is hoped to investigate this aspect of seed dispersal further.

TABLE 9

SPECIES FOR WHICH BIRD DISTRIBUTION IS RECORDED

Species	Droppings or food	Nests
Acer pseudoplatanus	X	—
**Achillea millefolium*	Sparrow	—
**Agropyron repens*	X	Thrush
Alliaria petiolata	X	—
**Alopecurus pratensis*	—	Sparrow
Anthriscus sylvestris	—	Sparrow, Thrush, Blackbird
Bellis perennis	Sparrow	—
Bromus mollis	—	X
B. sterilis	X	Thrush
Capsella bursa-pastoris	Magpie	—
Cerastium holosteoides	—	Woodpigeon
Cirsium arvense	X	—
C. vulgare	X	X
Convolvulus arvensis	Woodpigeon	—
Cynosurus cristatus	—	Sparrow
Dactylis glomerata	X	Thrush, Sparrow
Deschampsia cespitosa	—	Sparrow
Festuca ovina	—	Sparrow
Galium aparine	Greenfinch	Thrush, Wren, Garden Warbler
**Geranium robertianum*	X	—
**Glechoma hederacea*	X	—
Hieracium pilosella	Bullfinch	—
Lamium purpureum	—	Thrush
Lolium perenne	X	Sparrow
Papaver rhoeas	Woodpigeon	—
Plantago lanceolata	Woodpigeon Sparrow	—
P. major	Greenfinch, Bullfinch	—
Poa annua	X	Thrush, Sparrow
P. pratensis	—	Thrush, Sparrow
**Ranunculus acris*	Woodpigeon	—
R. repens	Sparrow	—
Rumex acetosa	Sparrow	—
**R. acetosella*	Sparrow, Magpie	—
Senecio jacobaea	Bullfinch	—
S. vulgaris	Sparrow, Bullfinch, Goldfinch	—
Sinapis arvensis	Greenfinch, Bullfinch	—
Sonchus oleraceus	Bullfinch	—
Stachys sylvatica	Marsh Tit	—
**Stellaria media*	Sparrow	—
Taraxacum officinale	Greenfinch, Goldfinch	—
Trifolium repens	Starling	—
Tussilago farfara	Woodpigeon	—
**Urtica dioica*	Magpie	Blackbird
U. urens	Woodpigeon	—

Species indicated where known. Where plants are known to be either food, droppings or in nests, but bird species not known, they are indicated by X; * by Magpie, Blackbird, Fieldfare (Grødem, 1940).

Some preliminary experiments have been carried out to test the validity of the hypothesis that the majority of seeds on walls are carried there by wind, and again it is hoped to pursue this subject more actively. Two experiments were carried out, using nets and sticky traps of the type often used to catch small

insects. These were placed at varying heights above ground, in a reasonably open space where the wind had the chance of attaining moderate velocities, and also near buildings which would be expected to cause eddying currents in which seeds could be carried. The sticky traps were tested by throwing seeds at them to see if they would stick.

The nets were examined every morning and afternoon during a period which included some high winds. They were found to contain seeds of *Betula* species and *Chamaenerion angustifolium*. These are normally wind-carried so their presence was not surprising. The sticky traps were left up for periods of several weeks, and examined at intervals. Apart from numerous insects, they collected seeds of *Chamaenerion, Taraxacum officinale* and another unknown Composite. No other seeds were found, but evidence of the carriage of large particles by the wind was the large number of soil particles on "the traps". These experiments then were inconclusive, and further more prolonged tests may prove more rewarding.

We gratefully acknowledge the assistance of Professor D. H. Valentine, both during the progress of the work and in criticising the manuscript. Mr. P. J. Wanstall has also offered valuable criticism. We wish to thank Mr. William Sykes of the Royal Horticultural Society's Gardens at Wisley for his assistance in identifying garden plants. Those others who have offered suggestions are too numerous to mention and must be thanked collectively. The work was carried out under the auspices of the Durham Colleges Natural History Society.

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