

DEMOGRAPHIC STUDIES OF A DIOECIOUS TREE. I. COLONIZATION, SEX AND AGE STRUCTURE OF A POPULATION OF *SALIX CINEREA*

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SUMMARY

(1) The distribution of individuals of *Salix cinerea* was mapped in a site in Anglesey, N. Wales. The age structure of individual genets was estimated from morphological characteristics and used to describe the age structure of the whole population. The sex ratio and the spatial distribution of the two sexes and of juvenile (non-flowering) individuals were determined.

(2) The colonization of the study site apparently commenced when two female trees became established before 1967. The population increased rapidly until 1980, after which few new individuals became established and these were restricted to a few small areas on the site.

(3) The overall sex ratio was female biased, with a ratio of 2:1. The sex ratio of each age cohort was also female biased, except at age 6. At other sampled sites the sex ratio was also female biased, with one exception.

(4) There was no evidence of spatial segregation of the sexes, but juvenile plants tended to be spatially segregated from adults.

(5) Analysis of the distribution of individuals by Thiessen polygons showed few differences between the area occupied by male and female plants. The younger male plants were further from neighbours, and male plants overall had higher polygon displacement values than females. The polygon areas of juvenile plants were smaller than those of reproductive plants of the same age.

(6) Nearest-neighbour distance was the density measure best correlated with plant performance. Measures of plant growth were more strongly correlated with measures of density in female and juvenile plants than in males.

(7) No differences in size were detected between male and female plants. Reproductive individuals were usually larger than juveniles.

INTRODUCTION

In dioecious plants, males and females might be expected to make different demands on environmental resources because of the difference in magnitude and timing of their reproductive effort. Such differences might lead to a division of labour between the sexes (Darwin 1877) and ecological differentiation (Onyekwelu & Harper 1979). Freeman, Klikoff & Harper (1976) have demonstrated that differential resource allocation does indeed occur between the sexes of some dioecious herbs, and Cox (1981) gives examples of herbs in which the sexes appear to occupy different patches in space or make their major growth at slightly different seasons or exploit different layers in a mixed canopy.

If there are ecological differences between the sexes of higher plants, this might be expected to result in changing sex ratios along environmental gradients and to increase

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the frequency with which nearest neighbours are of the same sex. Meagher (1980) analysed detailed maps of the distribution of male and female plants of *Chamaelirion luteum* and found significant spatial segregation of the sexes. Melampy (1981) also found some spatial segregation and significantly biased sex ratios in *Thalictrum dioicum*. Others have looked for spatial segregation and failed to find it (e.g. Bawa & Opler 1977; Melampy & Howe 1977). In a review of literature on the spatial distribution of the sexes in dioecious plants, Bierzychudek & Eckhart (1988) noted that spatial segregation had been detected in twenty-one out of thirty-two species studied but conclude that this may overestimate its true frequency.

A number of studies have made of the sex ratios in populations of *Salix* spp. (Falinski 1980, 1986; Ietswaart, Offerijns & van der Waal 1984). In most dioecious species in which the sex ratio departs significantly from unity, it is males that predominate (Opler & Bawa 1978), but among *Salix* spp. female-biased ratios are common. Physiological differences between the sexes have been found in *Salix polaris* (Crawford & Balfour 1983), and also in *Salix arctica* (Dawson & Bliss 1989) in which the sex ratio is especially female biased in cooler, wetter habitats.

In this paper we report the results of a study of a population of *Salix cinerea* in which we traced the developing spatial distribution of individuals of both sexes from the establishment of the first colonists.

MATERIALS AND METHODS

The study site

The study was made at Newborough Warren National Nature Reserve, Isle of Anglesey, Gwynedd, Wales (National Grid reference SH 415625). The vegetation in the area has been greatly affected by the diminished population of rabbits since the introduction of the myxoma virus in 1954. Rabbits had grazed the seedlings of many shrubs and trees and prevented their establishment (Ranwell 1960). In various parts of the dune system, woody shrubs and trees have become successful colonists, especially *Pinus* spp., *Betula* spp., *Crataegus monogyna* and *Salix atrocinerea* (*Salix cinerea* ssp. *atrocinerea*) (Hodgkin 1984). (Nomenclature follows Clapham, Tutin & Moore (1987).) In the wetter dune slacks, where the study site was located, *S. cinerea* was the only woody invader except for a very few plants of *Salix aurita*.

The site is a 4-ha field at the site of a small lake, Llyn Rhos Ddu, that drains into the site. The water table is high throughout the year. The area has a wet marsh vegetation in which the shrub stratum is dominated by *Salix cinerea*. The herb layer is dominated in the wetter areas by *Equisetum fluviatile*, *E. arvense*, *Juncus effusus* and *Mentha aquatica*, and in the drier areas by *Holcus lanatus* and *Arrhenatherum elatius*.

Mapping of the study site

A map of the population of *Salix cinerea* was constructed with the help of an aerial photograph of the area taken in 1984 and kindly made available by the N.E.R.C. Institute of Terrestrial Ecology at Bangor. All plants of *S. cinerea* that could be recognized in the aerial photograph were marked on the map and plants that were not visible in the photograph were located and included in the map with the help of reference plants. Differences in sex, phenology, morphology and leaf colour allowed individual genets to be distinguished. Each tree at the site was labelled. The sex ratio of *Salix cinerea* was also

determined at seven other sites in the Isle of Anglesey on 1 May 1984, when flowering was at its peak.

The spatial arrangement of individuals was analysed by drawing Voronoi (Thiessen) polygons (i.e. drawing the perpendicular bisectors of the lines linking each plant with its immediate neighbours). The procedure and the analysis of derived measurements are described by Mithen, Harper & Weiner (1984) and Bülow-Olsen, Sackville Hamilton & Hutchings (1984). All parameters of the polygons, and also the distances between nearest neighbours and the mean distance between neighbours, were calculated from the map of the population using a modified version of a FORTRAN program developed by Green & Sibson (1978) and adapted for the Bangor computer by N. R. Sackville Hamilton. The edge polygons were excluded from the analyses.

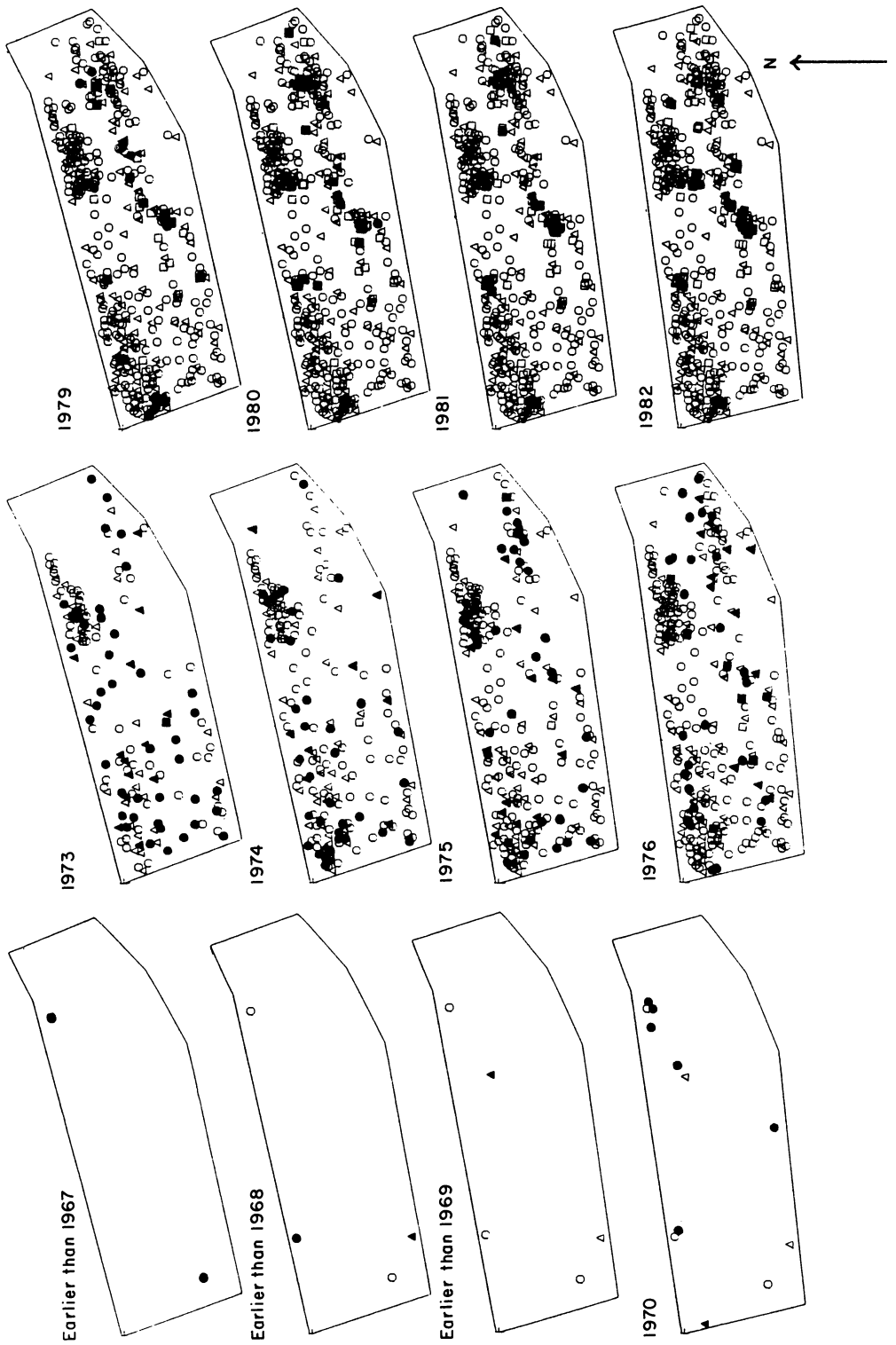
Measurements made on individual plants

Each individual was described in terms of its sex, age, height, canopy volume and mean annual increment, and its position was defined by the coordinates of its axis at ground level. The gender of individuals was noted throughout the study period 1983–85. No hermaphrodite or intersexual plants were detected. Plants that flowered early in the study also flowered in subsequent years; the intensity of flowering of individual trees was strongly correlated over the three-year period of study ($P < 0.001$). Plants that were never observed to flower during the study period were classified as juveniles.

Salix cinerea has sympodial growth. The apical meristem usually dies during winter and vegetative growth resumes from the nearest lateral meristems. The young plants have orthotropic branches that arise very close to the base and two or more persistent laterals are usually formed close together on each sympodium (including the first which forms a short, quite distinct, abbreviated trunk). Many of the thinner twigs are shed. On young shoots the twigs form narrow angles to the sympodia but as they age the branching becomes markedly divaricate, with some branch angles even becoming obtuse. The progressive widening of branch angles with age has the effect that the first formed branches often come to lie close to ground level. Branches that were marked when they were breast height had become waist height after three years. Although many young shoots are shed within a year, most of those that persist are long-lived, even though some remain short and thin. The effect of this pattern of growth is that on isolated plants (or on their isolated sides) the young shoots scarcely shade each other. In the older specimens the highly divaricate form sometimes makes it difficult for the observer to gain access to the trunk. The characteristic branching system is illustrated in Phillips (1978).

Thiébaud, Cuguen & Dupré (1985) named the growth mode of such a sympodial system a 'sympodial fork' and, from the scars left from dormant overwintering buds, were able to reconstruct the development of the axis of beech (*Fagus sylvatica*) trees for twenty to thirty years back. In *Salix cinerea* it was similarly possible to identify the elongation that each branch arising from the basal trunk had made in successive years, from the scars of overwintering buds, characteristic bends at each sympodial junction and the positions of the long persistent lateral branches or occasionally their scars. Even at the centre and base of the plants the annually formed sympodia could be clearly distinguished.

We have never observed a secondary flush of (sylleptic) growth in the shoots of any of the plants studied, and the number of successive sympodia is therefore taken to be a measure of the age of a branch. The basal branches normally develop in the first year, on the first sympodium formed as the plant grows from seed. The accuracy of this method for ageing the plants (i.e. genets) was checked by counting annual rings at the base of five



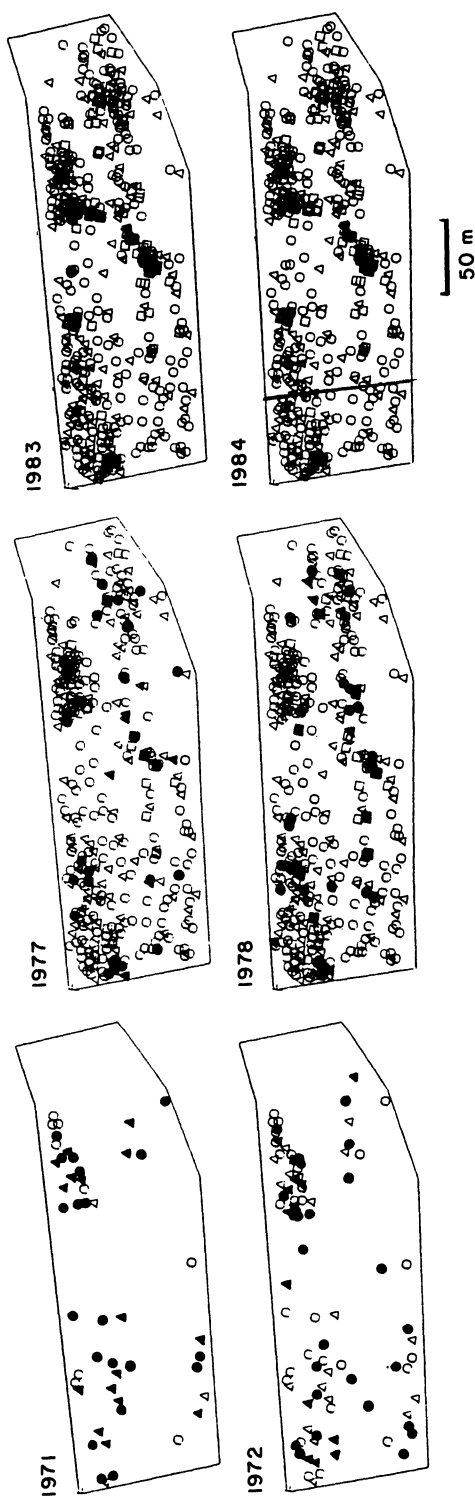


FIG. 1. Reconstruction of the colonization of the study site at Newborough Warren, Anglesey, Wales by *Salix cinerea*. These figures were constructed by adding each year the new cohort of plants. The new cohort is represented by the darkened symbols; female (O), male (Δ) and plants that did not flower during the period of observation, 1983–85 (juveniles) (\square). The area to the west of the line drawn on the map for 1984 was used in the study of herbivory described in Allienne (1989).

branches that had previously been estimated to be eight years old. In all samples the predicted age and ring counts gave the same values. Individual genets could be clearly identified because the basal branches typically arise from the abbreviated trunk above ground level. The age of each tree was estimated from the age of basal branches arising from the trunk plus one year (for the trunk). The age estimates were made by two independent observers when no leaves were present. Disagreement between observers was rare and when it occurred the plant was re-examined and the disagreement was resolved. As with the other woody colonists in this community (except *Crataegus monogyna*), it is not possible to estimate the age of plants by coring and counting annual rings at the base of the stem (Hodgkin 1984).

In very large plants (more than sixteen years old) the centre was sometimes difficult to access and the age estimates may then be less reliable. However, the main source of error in estimating the age of a plant from the morphology of its basal branches is that in the earliest stages of colonization of the site some established seedlings may have been repeatedly grazed to ground level and then regenerated. As indicated previously, the colonization of the site was possible because of the sudden decline in the rabbit population, and the oldest plants may have suffered from grazing. If such damage and regeneration had occurred, the ages of the oldest individuals would have been underestimated. This will of course be true for all estimates of the age structure of populations of species of tree that regenerate—even when [as in the elegant study of Falinski (1986)] most of a large population is cut at ground level to make ring counts.

In the present study it was possible to confirm the presence and distribution of the pioneer plants from aerial photographs taken of the site in 1966 (Meridian Airmaps), 1970 (Ordnance Survey), 1972 (Cambridge University Collection k17-AA163), 1983 (Cambridge University Collection RC8-E5-1H3) and a photograph taken in 1984 and made available by courtesy of the Nature Conservancy Council and the Natural Environment Research Council, Institute of Terrestrial Ecology.

The height of each plant was measured in July 1983 and again in 1984 (the tallest plants were then trees more than 4 m high and their canopy extended to form a crown up to about 4 m radius). The canopy volume was estimated by an approximation to a half spheroid using the formula of Ludwig, Reynolds & Whitson (1975). The mean annual increment was calculated as the canopy volume divided by the estimated age.

Statistical analysis

Tests of the extent of spatial segregation of male, female and juvenile trees were made in three ways: (i) the map was divided into three plot sizes (25 m × 25 m, 50 m × 50 m and 100 m × 100 m), and the numbers of male and female trees were counted in each plot. Differences in sex ratio at the different plot sizes were tested with chi-square and heterogeneity chi-square. (ii) The nearest-neighbour test developed by Pielou (1961, 1977) for examining segregation between pairs of species was used to test for segregation between the sexes within the single species. (iii) Analyses of variance were made of the area and displacement of polygons (Bulow-Olsen, Sackville Hamilton & Hutchings 1984) and neighbour distances, with base plant (male, female or juvenile) and nearest neighbours (male, female or juvenile) as factors. Variables were analysed statistically using two-way analysis of variance with log transformations when required (Zar 1984). Chi-square, heterogeneity chi-square and Pearson correlation coefficients were calculated according to Zar (1984). All analyses were performed using SPSS-X statistical package.

RESULTS

Maps of the distribution of *Salix cinerea* at various times after the start of colonization were constructed using the ages of each tree as estimated in 1983–85 and adding successive annual cohorts to the population of the two trees that must have established before 1967 (Fig. 1). It is certain that the two oldest individuals were both female. The precise year in which the first males became established is difficult to determine with precision, but it was before 1969. The maps of successive colonists suggest that the oldest female trees acted as foci from which the population started to spread. They may not, however, have been the parents. It is possible that the rapid growth of the population occurred because seed

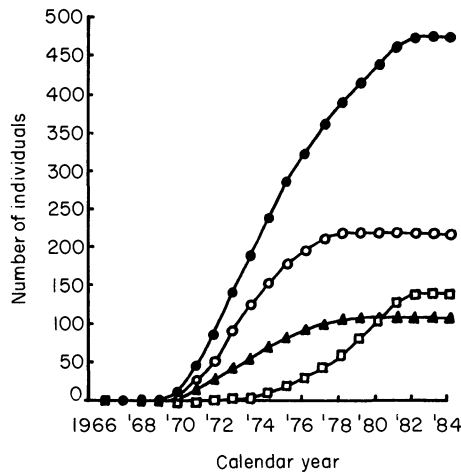


FIG. 2. The growth of the population of *Salix cinerea* at Newborough Warren, Anglesey, Wales. Females (○), males (▲), plants that did not flower during the study (□) and total plants (●).

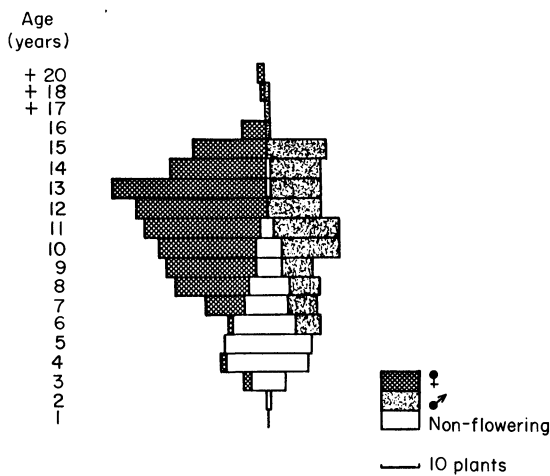


FIG. 3. Pyramid of age and sex of the population of *Salix cinerea* at the Newborough Warren, Anglesey, Wales in 1984. Female plants, male plants and non-flowering (juvenile) plants.

TABLE 1. Sex ratio in several *Salix cinerea* populations in North Wales.

Name of site	Grid reference	Female	Male	Not flowering	F:M	Chi-square
Llyn Rhos-ddu	SH 426648	92	41	13	2.24	19.56†
Llyn Bodgylched	SH 584773	68	30	116	2.27	14.73†
Red Wharf Bay	SH 547802	37	57	2	0.65	4.26‡
Cors Goch	SH 503815	25	12	1	2.08	4.57‡
Siglan	SH 533727	82	45	10	1.82	10.78†
Cyttir Mawr	SH 577752	82	33	19	2.48	20.88†
Perfeddgoed	SH 566698	54	30	10	1.80	6.86§

Pooled chi-square = 81.44; heterogeneity chi-square = 27.86.

‡ $P < 0.05$, § $P < 0.01$, † $P < 0.001$.

TABLE 2. Quadrat size and sex ratio of adult plants of *Salix cinerea* at the study site on Newborough Warren, Anglesey.

Quadrat size	n	Range of adult plants per quadrat	Quadrats with more female plants	Chi-square	
				Pooled	Heterogeneity
100 m × 100 m	3	87–163	3	44.92	0.07 N.S.
50 m × 50 m	12	16–71	11	55.34	10.49 N.S.
25 m × 25 m	43	1–26	35	68.48	23.63 N.S.

N.S., not significant.

sources outside the study area were increasing in size and rate of seed production. The population increased in a classic population growth curve (Fig. 2), and the carrying capacity of the site appears to have been reached by 1983–85. At this time young plants were present in only a few local areas on the site.

Sex ratios in populations of S. cinerea

The ratio of female to male plants at the site was 2:1, strongly biased towards females. The age structure of the population in 1985 is subdivided to show the sex ratios in successive annual cohorts. Females predominated in every cohort except that which was estimated to have become established in 1980 (i.e. plants that were estimated to be six years old) (Fig. 3).

The populations contained juvenile (i.e. non-flowering) individuals of which the sex was unknown. Most plants flowered first when they were six to ten years old, though there were a few precocious females.

The sex ratio of populations of *S. cinerea* determined at seven other sites on the island of Anglesey was significantly female biased at six of the sites but male biased at one, Red Wharf Bay. There was significant heterogeneity in sex ratio *between* the sites (Table 1).

Spatial segregation of the sexes within the main study site

Any tendency for males, females and juveniles to show a segregated distribution was determined by detailed examination of the maps of the study site. A comparison of the sex ratios in quadrats of different sizes is shown in Table 2. The sex ratio was female biased at all quadrat sizes and there was no significant heterogeneity among them. This test gave no evidence of spatial segregation of the sexes.

Plants in the population were grouped into pairs composed of each plant (the base plant) and its nearest neighbour, according to Pielou's test for spatial segregation. The contingency analysis for pairs composed of known males and females (i.e. excluding

TABLE 3. Pielou's test for spatial segregation applied to the segregation of (a) sexes and (b) sexual state of *Salix cinerea* at the study sites on Newborough Warren, Anglesey.

(a) Chi-square = 1.211, $P > 0.05$, $S = 0.07$

		Sex of nearest neighbour	
		Female	Male
Sex of base plant	Female	138	75
	Male	73	29

(b) Chi-square = 83.91, $P < 0.001$; $S = 0.58$

		Nearest neighbour	
		Adult	Juvenile
Base plant	Adult	315	56
	Juvenile	50	67

S , segregation coefficient (Pielou 1961).

TABLE 4. Analysis of variance for polygon area and neighbour distances between base plant and nearest-neighbour plant of *Salix cinerea*. Mean values for different 'sex pairs' are presented in Fig. 4.

Factors	Nearest-neighbour distance			Area of polygon*		
	d.f.	s.s.	P	d.f.	s.s.	P
Within cells	471	2280.177		399	71.322	
Total	479	2666.960		407	80.620	
Base plant sex	2	133.478	<0.001	2	3.725	<0.001
Neighbour sex	2	85.610	<0.001	2	1.545	0.014
Base sex \times neighbour sex	4	18.842	0.422	4	0.691	0.426

* Log + 1 transformation.

juveniles) shows no evidence of segregation of the sexes (Table 3a). However, the contingency analysis for pairs composed of individuals of known sex (i.e. males plus females) and juveniles shows evidence of spatial segregation (Table 3b). Meagher & Burdick (1980) have shown that Pielou's contingency table, analysed with the chi-square test, may be over-sensitive. However, visual inspection of the maps of the populations shows clear clustering of the juveniles (i.e. non-flowering plants) which tend to occur in very localized areas.

Polygon areas and the distances between each nearest neighbour pair, classified according to their sexual state, were computed. The results of analysis of variance (Table 4) show an influence of both base plant and nearest neighbour. This is because all pairs involving juveniles (M-J, F-J, J-M, J-F and J-J) had closer inter-plant distances than pairs composed of mature plants (F-F, M-M, F-M and M-F). The closest pairs were of two juveniles (J-J) and these also involved the smallest polygon areas, whereas pairs of mature plants showed no significant differences (Fig. 4a, b).

The effects of age and sexual state on polygon characteristics, nearest-neighbour distances and size

There was a significant effect of age on polygon area, whether juvenile plants were included (Table 5a) or excluded (Table 5b) from the analysis. Male plants appeared to have larger polygon areas and greater distances between neighbours, especially among

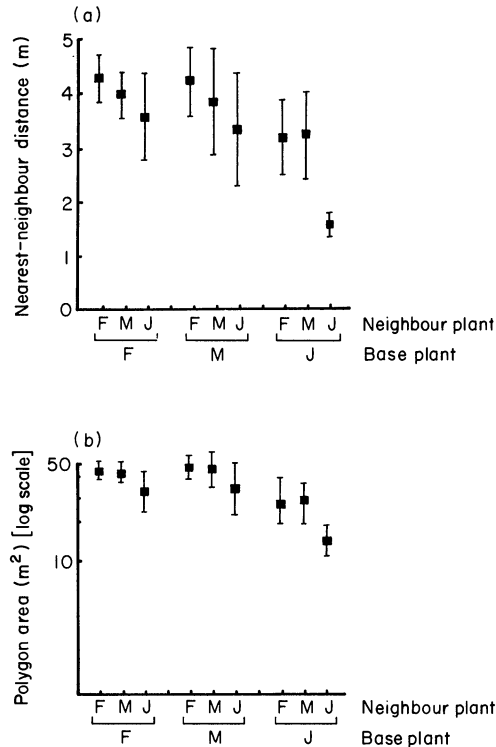


FIG. 4 (a) Nearest-neighbour distance and (b) polygon area of each 'sex pair' of *Salix cinerea* at Newborough Warren, Anglesey, Wales. The bars represent the interval of confidence at 5% for each mean. F, female; M, male; J, non-flowering (juvenile) plants.

the younger age groups. Male plants were also more displaced from the centres of their polygons than females or juveniles (Fig. 5, Table 5).

Height, canopy volume and mean annual increment were the measures of plant size available to analyse the relationships between size and neighbour distances, polygon area and displacement (Fig. 6). No difference could be detected between the sexes. Young plants were, as expected, smaller than older plants. A significant difference was detected between juvenile and flowering plants of the same age; the former were smaller and made significantly smaller mean annual increments (Table 5). Pearson correlation coefficients are given in Table 6 for the various measures of plant size considered in relation to nearest (and mean)-neighbour distance, polygon area and displacement calculated separately for all plants, males, females and juveniles. The correlations are strongest for canopy volume and mean annual increment and are weak for both the absolute and relative growth in height of flowering plants. The height of juveniles is quite strongly correlated with their distance from nearest neighbours, however, perhaps implying a degree of etiolation. Canopy volume and mean annual increment are more strongly correlated with the distance from the nearest neighbour than with mean neighbour distance, and correlations of the same measures with the areas of polygons are stronger than with the displacement of individuals within them.

TABLE 5. Analysis of variance for neighbour distances, polygon characteristics and size measures for *Salix cinerea* at the study site on Newborough Warren, Anglesey. (a) From ages 7 to 15 factor sex includes male and female plants; (b) from ages 7 to 11 factor sex includes male, female and juvenile plants.

Factors	Nearest neighbour distance*			Mean neighbour distance*			Area of polygon*			Displacement of polygon			Height			Canopy			Mean annual increment*		
	d.f.	S.S.	P	d.f.	S.S.	P	d.f.	S.S.	P	d.f.	S.S.	P	d.f.	S.S.	P	d.f.	S.S.	P	d.f.	S.S.	P
(a)																					
Within cells	321	9.252		321	10.862		259	38.806		259	571.086		321	276.431		321	42.879		321	25.665	
Total	338	11.080		338	12.364		276	46.200		276	632.982		338	554.735		338	107.817		203	49.028	
Sex	1	0.001	0.914	1	0.147	0.038	1	0.168	0.290	1	7.769	0.062	1	0.756	0.350	1	0.104	0.379	1	0.075	0.783
Age	8	1.466	<0.001	8	1.004	<0.001	8	4.733	<0.001	8	22.776	0.248	8	265.817	<0.001	8	63.850	<0.001	8	22.793	<0.001
Sex × age	8	0.362	0.133	8	0.385	0.187	8	2.496	0.038	8	31.840	0.076	8	11.415	0.108	8	0.942	0.532	8	0.527	0.881
(b)																					
Within cells	189	5.773		189	7.213		167	29.294		167	474.645		189	151.906		189	1.606		189	14.597	
Total	203	7.023		203	8.456		181	35.309		181	527.500		203	236.607		203	56.562		203	22.462	
Sex	2	0.061	0.368	2	0.285	0.026	2	1.149	0.040	2	14.755	0.026	2	4.378	0.068	2	1.670	0.008	2	0.758	0.008
Age	4	0.643	<0.001	4	0.590	0.005	4	2.668	0.002	4	1.978	0.530	4	50.270	<0.001	4	3.622	<0.001	4	3.846	<0.001
Sex × age	8	0.272	0.355	8	0.404	0.234	8	1.799	0.256	8	35.790	0.136	8	7.362	0.335	8	0.845	0.751	8	0.356	0.773

* Log + 1 transformation.

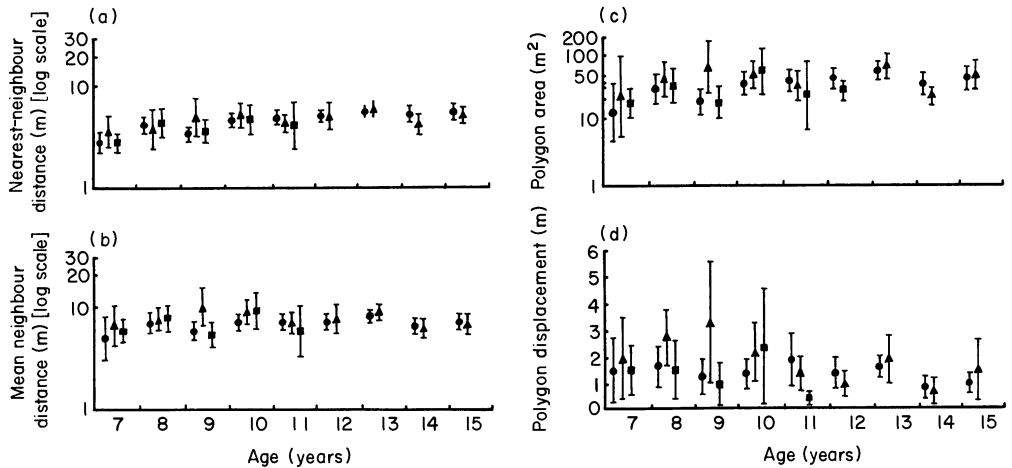


FIG. 5 (a) Nearest neighbour distance, (b) mean neighbour distance, (c) polygon area and (d) polygon displacement of each 'sex' and age, group of *Salix cinerea* at Newborough Warren, Anglesey, Wales. The bars represent the interval of confidence at 5% for each mean. Female (●), male (▲) and non-flowering (juvenile) plants (■).

DISCUSSION

The increase in the number of established trees of *Salix cinerea* followed a typical population growth curve, apparently now approaching its maximum. Invasion by *Crataegus monogyna* on drier sites followed a similar pattern but its population growth started much earlier and reached its maximum in 1970 (Hodgkin 1984). The first colonists of *Salix cinerea* were both female. The distribution of later arrivals appeared to spread outwards from these earliest colonists. This may be because the early colonists were the seed parents of those that colonized later, but it may be that the sites colonized by the early plants were especially favourable for seed arriving later. It is not possible to judge how far seed production locally was accelerated when the first males on the site started to flower: plants did not flower until they were six to ten years old. The later aerial photographs and maps of the site (Fig. 1) show some areas in which colonization has failed to occur. Some of these areas were water logged (in areas draining directly from Llyn Rhos Ddu) and others were dry throughout the year. This suggests that soil moisture conditions may have determined which sites were available to be colonized by the species.

At present the population appears to be reaching carrying capacity and occasional new recruitment is occurring in very local sites. Colonization of a Dutch island, Schiermonnikoog, by *Salix pentandra* occurred in a similar way (Ietswaart, Offerijns & van der Waal 1984). A very similar process of colonization has been revealed by age-structure analysis of populations of *Juniperus communis* in Poland (Falinski 1986). The oldest individuals in Falinski's study were estimated to be fifty-five years old and the population of junipers, like the *Salix* population in our study, had become increasingly female biased over time.

The sex ratio

The sex ratio of the population of *S. cinerea* on the study site was female biased, with an overall sex ratio of 2:1. The proportion of female plants was higher than that of males in all age cohorts, except in the cohort that was five years old in 1984: rather surprisingly, the

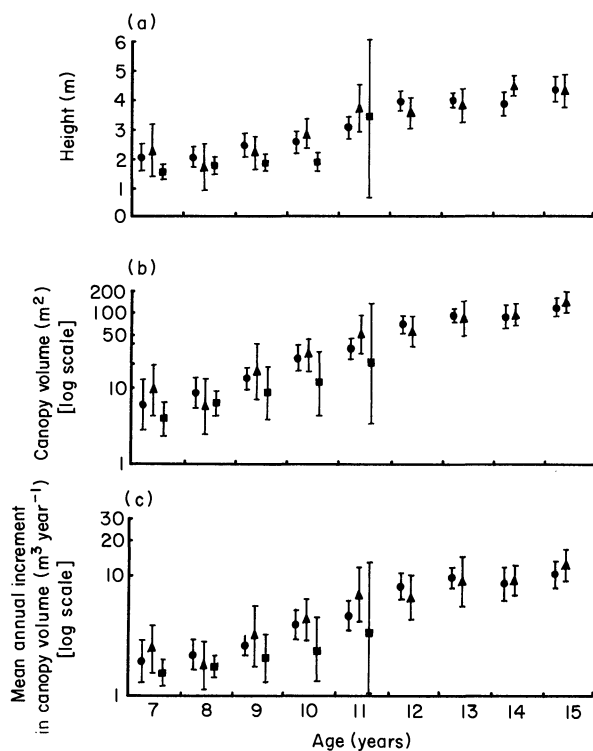


FIG. 6 (a) Height, (b) canopy volume and (c) mean annual increment of each 'sex' and age group of *Salix cinerea* at Newborough Warren, Anglesey, Wales. Bar represents the interval of confidence at 5% for each mean. Female (●), male (▲) and non-flowering (juvenile) (■) plants.

youngest flowering plants were females of which a few flowered when only two or three years old. There is almost always a problem in determining true sex ratios in perennial plants that have a prolonged juvenile period, because the populations contain non-flowering juveniles of unknown sex. If there is precocious flowering by one of the sexes this can easily give the false impression of a biased sex ratio. This problem does not arise in the present study because the age cohorts were separated. In cohorts more than twelve years old all individuals had flowered by the end of the study and the bias in the sex ratio was not confused by the presence of juveniles.

The sex structures of populations of various *Salix* and *Populus* spp. have been studied by Falinski (1986) in the temperate lowland primeval forests of Białowieża, Poland. *Populus tremula* spreads clonally and the males form compact clones that are only rarely penetrated by females. Groups of females appeared against the background of larger areas dominated by agglomerations of male trees. The males flowered first when the main stems were thirteen or more years old. Females did not flower until they were older, taller and had thicker trunks. Falinski points out that it is difficult to obtain meaningful sex ratios from species which form clonal patches. In eleven of the thirty areas (each of 1000 m²) that he examined, the populations of *P. tremula* were exclusively or predominantly male and on nine areas exclusively or predominantly female, presumably the result of cloning.

TABLE 6. Pearson correlation coefficients between polygon characteristics and neighbour distances and plant performance of *Salix cinerea* on Newborough Warren, Anglesey.

	All plants ($n=407$)				
	Height	Canopy volume	Mean annual increment	Growth in height	Relative growth in height
Nearest-neighbour distance	0.416	0.602	0.584	0.160	-0.148
Mean neighbour distance	0.226	0.393	0.369	0.114	NS
Area of polygon	0.215	0.388	0.369	0.115	N.S.
Displacement of polygon	-0.176	-0.114	-0.136	N.S.	0.099
	Female plants ($n=195$)				
Nearest-neighbour distance	0.230	0.478	0.503	N.S.	N.S.
Mean neighbour distance	N.S.	0.296	0.304	N.S.	N.S.
Area of polygon	N.S.	0.302	0.315	N.S.	N.S.
Displacement of polygon	-0.144	-0.120	-0.140	N.S.	0.132
	Male plants ($n=96$)				
Nearest-neighbour distance	N.S.	0.413	0.382	N.S.	N.S.
Mean neighbour distance	N.S.	N.S.	N.S.	N.S.	N.S.
Area of polygon	N.S.	N.S.	N.S.	N.S.	N.S.
Displacement of polygon	-0.409	-0.316	-0.333	N.S.	0.253
	Juvenile plants ($n=116$)				
Nearest-neighbour distance	0.405	0.587	0.553	N.S.	N.S.
Mean neighbour distance	0.174	0.377	0.360	N.S.	N.S.
Area of polygon	0.159	0.360	0.353	N.S.	N.S.
Displacement of polygon	N.S.	N.S.	N.S.	N.S.	N.S.

N.S., not significant.

Other reports of sex ratios in the Salicaceae are summarized in Table 7. Female-biased sex ratios occur throughout the genera *Populus* and *Salix*, especially in the subgenera of *Salix*, *Vetris* and *Chamaetia*.

Mulcahy (1967) and Kaplan (1972) have argued that a female-biased sex ratio might be favoured by natural selection because it would optimize seed production of the population. Crawford & Balfour (1983) make a similar argument to explain the female-biased sex ratios in *S. polaris* and *S. herbacea*. This is essentially a group-selectionist argument, and selection at the level of the individual would be expected to favour a sex ratio near to equality, because in a population with a biased sex ratio the minority sex will have an advantage over the majority (Lewis 1942; Charnov 1982).

Lloyd (1974) and Opler & Bawa (1978) have noted that biased sex ratios are associated with certain taxa: *Rumex*, *Silene*, *Cannabis* and *Humulus*. They suggest that genetic differentiation of sex chromosomes with a consequence of differential fertilization offers a likely proximate explanation of biased sex ratios. Heslop-Harrison (1924) had argued earlier that this was the explanation of female-biased sex ratios in *Salix*. If we are to understand the biased sex ratios in *Salix* we need to know the nature of the sex-determining mechanism and, in particular, whether apomixis occurs in the populations, as has already been detected in the dioecious *Pandanus tectorius* (Cox 1985).

Spatial segregation

There have been many reports of spatial segregation between the sexes of dioecious plants. Sex ratios biased in different directions at different sites have been found by Davey & Gibson (1917), Harris (1968), Freeman, Klikoff & Harper (1976), Opler & Bawa (1978),

TABLE 7. Sex ratio in the family *Salicaceae*

	Sex ratio (F:M)	Reference
Genus <i>Populus</i> *		
<i>P. tremuloides</i>	1:1	Santamour (1956) in Lester (1966)†
<i>P. tremuloides</i>	1:3	Pauley & Mennel (1957) in Lester (1966)†
<i>P. tremuloides</i>	1:1	Einspahr (1960)
<i>P. tremuloides</i>	1:1	Lester (1966)
<i>P. tremuloides</i>	1:1	Farmer (1964)
<i>P. tremuloides</i>	1:1	Grant & Mitton (1979)
<i>P. tremula</i>	1:1	Langhammer (1963) in Muhle-Larsen (1970)
<i>P. tremula</i>	1:1	Muhle-Larsen (1970)
<i>P. tremula</i>	1:100	Falinski (1980)
<i>P. tremula</i>	50:1	Falinski (1980)
<i>P. deltoides</i>	1:1	Muhle-Larsen (1970)
<i>P. deltoides</i>	1:1	Kaul & Kaul (1984)
Genus <i>Salix</i>		
Subgenus <i>Salix</i>		
<i>S. pentandra</i>	1:1	Falinski (1980)
<i>S. pentandra</i>	2:1	Ietswaart, Offerijns & van der Waal (1984)
<i>S. amygdaloides</i>	1:1	Kaul & Kaul (1984)
Subgenus <i>Vetrix</i>		
<i>S. caprea</i>	2:1	Falinski (1980)
<i>S. cinerea</i>	2:1	Falinski (1980)
<i>S. cinerea</i>	3:1	Kay & Stevens (1986)
<i>S. aurita</i>	4:1	Falinski (1980)
<i>S. rosmarinifolia</i>	3:1	Falinski (1980)
<i>S. repens</i>	3:2	Alliende (1986)
Subgenus <i>Chamaetia</i>		
<i>S. herbacea</i>	3:1	Crawford & Balfour (1983)
<i>S. polaris</i>	3:1	Crawford & Balfour (1983)

*Taxonomic subdivisions according to Meikle (1984).

†A small number of bisexual trees are reported.

Note that in *P. tremula* and *P. tremuloides* genets spread clonally and the true sex ratios may become distorted.

Grant & Mitton (1979), Cox (1981), Fox & Harrison (1981) and Crawford & Balfour (1983). However, tests for spatial segregation of sexes within sites, using Pielou's nearest-neighbour technique, have often proved negative (Bawa & Opler 1977; Melampy & Howe 1977; Melampy 1981). Few of these studies have taken into account the fact that males and females may flower with different frequency (Meagher 1981) and that shoots of the same genet may, in the case of clonal species, sometimes be counted as different individuals. Differences in the phenology of males and females might be more common under extreme conditions. Freeman, Klikoff & Harper (1976) found spatial segregation of the sexes in *Acer negundo* with a predominance of male plants in drier areas, but this effect might have been due to sexual dimorphism in the flowering phenology.

The only studies comparable with the present one are those of Meagher (1980) and Cavigelli *et al.* (1986), who used mapping techniques to study sexual segregation. Meagher (1980) obtained strong evidence for spatial segregation of the sexes in the lily *Chamaelirion luteum* and Cavigelli *et al.* (1986) found weak segregation of the sexes in the dioecious tree *Ilex montana*. The study of *S. cinerea* reported here found seven sites at which the sex ratio was female biased (agreeing with the values reported by others for *S. cinerea* and several other species of *Salix* (Table 7), but one site in which the population was significantly male biased. We could detect no spatial segregation within the

Newborough Warren site using Pielou's nearest-neighbour technique, different plot sizes or the analysis of polygons. The techniques were, however, sufficiently sensitive to detect the spatial segregation of juveniles and flowering plants. Juveniles were closer to each other than to flowering plants.

There were only slight differences in the polygon areas defined around male and female plants. Both male and female plants were significantly displaced from the centre of gravity of their polygons and the males were more displaced than the females. Such displacement means that each plant tended to have one or a few especially close neighbours.

The positive correlations between plant performance (height, canopy volume and mean annual increment) and distance from nearest neighbour, mean neighbour distance and polygon size indicate that the larger plants pre-empt larger areas of the field. That the correlations were stronger in female and juvenile plants suggests that they suffer more than males from the presence of neighbours.

Size and growth of Salix cinerea

Male and female plants of *S. cinerea* of the same age did not differ significantly in height, canopy volume or mean annual increment. Other authors have reported different growth rates between males and females in *Salix* and *Populus*. It has been claimed that male plants of *Populus* spp. are taller and grow more vigorously than females (Muhle-Larsen 1954, 1970; Farmer 1964). However, Muhle-Larsen later reinterpreted his results and attributed most of the effects to differences between families rather than between the sexes. He also presented new evidence in which he found no differences in growth rate between the sexes. Einspahr (1960) found no difference in the size and growth rates of the sexes in *Populus tremuloides*. However, Grant & Mitton (1979) found that female trees of *Populus tremuloides* made greater annual radial growth than males, and Sakai & Burris (1985) showed that, relative to male clones, female clones had a larger number of ramets, greater basal area and a greater area of spread over a twenty-five-year period. Ietswaart, Offerijns & van der Waal (1984) claimed (but without giving statistics) that in *S. pentandra* it was the males that were taller and grew faster than the females.

Comparisons of the growth of male and female trees have sometimes been made by comparing diameters at breast height (dbh) (Falinski 1980 with *Juniperus communis*; Bullock & Bawa 1981 with *Jacaratia dolichaula*, Kaul & Kaul 1984 with *Populus deltoides*). This method detected a higher proportion of males in the lower dbh classes and no difference between the sexes in the higher classes. These observations suggest that males of these species start flowering (and so their sex can be determined) earlier than females rather than that males have the slower growth rate. No size differences between the sexes were detected in *Guarea rhopalocarpa* (Bullock, Beach & Bawa 1983), *Compsoneura sprucei* (Bullock 1982) and *Ilex montana* (Cavigelli *et al.* 1986). Earlier literature is reviewed by Lloyd & Webb (1977).

In the present study, when male, female and juvenile plants of *S. cinerea* were compared at the same age, juvenile plants were smaller. This suggests that plants that remain juvenile when they are more than seven years old are the more suppressed individuals. These 'old juveniles' occurred under crowded conditions and their polygon areas, displacement values and distances to nearest neighbours were smaller than those of trees that flowered earlier. In the field site, 'vigorous' plants started to flower only after six to ten years, although, given ideal conditions in cultivation, *S. cinerea* is capable of flowering when only one year old (Alliende 1986). Even the most vigorous plants in the field must have developed under conditions that were far from optimal.

The cause of the strikingly biased sex ratios in many *Salix* spp. remains unknown—it may be that males suffer a greater risk of mortality before they start to flower. Differential predation of seedlings cannot be detected without a technology that allows their sex to be determined. However, Elmquist *et al.* (1988) transplanted young shoots, 0.3 m long, of known sex of *Salix myrsinifolia-phylicifolia* into an area in which two species of vole (*Clethrionomys glareolus* Schreber and *Microtus agrestis* L.) were abundant. The voles foraged in a density-responsive fashion and male shoots were consumed or removed on average three times more frequently than females. The sex bias may be influenced even earlier if some seed is produced by apomixis and therefore yields only female plants.

Most of the analysis of the distribution and growth of the sexes of *S. cinerea* described in this paper has depended on the detailed mapping of individuals at the site and the knowledge of their ages as well as sexual states. Without this information correlations between size, sex and distribution patterns could have been seriously misleading.

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