Ecological Research (1999) 14, 9–21

Recruitment of fleshy-fruited species under different shrub species: Control by under-canopy environment

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Seedling densities and the mortality of fleshy-fruited species under 10 European tall-shrub species and the tree *Sorbus aria* were analyzed in 10-year-old experimental scrub for one growing season. The mean total densities of seedlings of 18 fleshy-fruited species differed under the different 'hosts', being highest under *Crataegus monogyna*, *Viburnum opulus* and *Rosa canina* (24–20 m^{-2}); intermediate under *Sorbus aria, Rhamnus catharticus, Cornus sanguinea*, *Ligustrum vulgare* and *Juniperus communis* (17–12 m^{-2}); and lowest under *Euonymus europaeus*, *Viburnum lantana* and *Prunus spinosa* (10–9 m^{-2}). This ranking was similar for the 11 planted species and for nine bird-dispersed, non-planted species which invaded the site, notably *Hedera helix* and *Solanum dulcamara*. Within the experimental scrub as a whole mortality of seedlings differed significantly among species, being highest in those with the smallest number of recruits. Mortality ranged from 94% and 89% for *Solanum dulcamara* and *Viburnum opulus* to 26% for *Hedera helix* and *Ligustrum vulgare*. The mean mortality across all species of seedlings did not differ significantly between host species, although it was slightly higher under *Juniperus* and *Cornus* (56%, 53%) and lower under *Viburnum lantana* and *Rhamnus* (42%, 41%). In four species, the mortality of seedlings was significantly higher under conspecific adults. Mean topsoil water content after a dry spell was negatively correlated with the diffuse site factor (DSF). The mean density of accumulated seedlings of the most abundant seedling species (*Hedera*) was positively correlated with the topsoil water content. Densities of other species showed no strong correlations with either topsoil water content or DSF. The probable factors controlling recruitment are discussed.

Key words: diffuse site factor; experimental scrub; invasive species; mortality; seedling densities; soil water content.

INTRODUCTION

In central and western Europe, most fleshy-fruited species are tall-shrubs or vines (Tutin *et al.* 1964–1980). The abundance and extent of fruiting of these species are highest in hedges, scrublands and along forest edges (Ellenberg 1988). Snow and Snow (1988) reported that in southern England about 14 passerine birds, mainly thrushes and warblers, feed on fruits of these species and disperse the seeds. The frugivorous birds prefer dense and tall scrub for perching and deposit seeds in highest densities at such sites (Izhaki *et al.* 1991; Debussche & Isenmann 1994; Kollmann & Pirl 1995), which often leads to intensive recruitment of fleshy-fruited species beneath tall shrubs and isolated trees (Debussche *et al.* 1982; Milton *et al.* 1997). In addition to height (McDonnell 1986), several other properties of shrubs determine the extent to which seed-dispersing birds are attracted: for example, aspects of crown architecture (Denslow & Moermond 1982), and abundance and attractiveness of fruit (Sorensen 1981; Sallabanks 1993). However, the resulting distribution of seedlings is also controlled by spatial and species-

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Received 9 March 1998.
Accepted 24 August 1998.

specific differences in seed predation, germination and establishment, which lead to a 'regeneration window' under intermediate scrub cover (Kollmann 1995). Competition with adult shrubs is important during establishment of seedlings (Putz & Canham 1992), and recruitment is often absent in deeply shaded sites (Kollmann & Reiner 1996). Competition among seedlings, on the other hand, has rarely been observed, since in most cases seedling densities are low. The net effect of established scrub on seedling recruitment is a species-specific balance of facilitation and inhibition (cf. Berkowitz *et al.* 1995).

In the present study we determine whether or not the number and identity of seedlings recruited under different European, tall-shrub species is controlled by under-canopy conditions of the shrubs in an experimental setting. There seem to be only a few published studies which address this question explicitly (cf. Herrera *et al.* 1994). Little is known about under-canopy conditions of European tall shrubs (Küppers 1992), but for related woody vegetation some information exists about variation in microclimate, soil moisture and soil nutrient contents which result from specifics of the canopy, litter fall or transpiration (Joffre & Rambal 1993; Burton & Bazzaz 1995; Milton *et al.* 1997; Moro *et al.* 1997). In addition to the above-mentioned processes, during seed dispersal it is likely that under-canopy conditions affect recruitment of fleshy-fruited species, and that effects may vary among species since differences in light, water and nutrient demands of shrub seedlings are significant (Grubb *et al.* 1996; Kollmann & Reiner 1996).

Effects of under-canopy conditions of shrubs on recruitment are testable, in a strict sense, only in a fully experimental design with transplanted seedlings, excluding variation in seed rain, predation and germination, since the total effect of the different processes might be zero in a field site, or results could be due to variation in height and distribution of adult shrubs rather than reflecting species-specific differences. For the present study, we chose an experimental scrub plot which at least had the advantage of similarity in age and height of shrubs, and a random distribution of species. However, this study was not designed to investigate spatial differences in seed rain, seed predation or germination within the scrub plot, and its conditions may deviate to some extent from fully natural shrub communities.

The study focuses on the following questions: (i) in an experimental plot of even-aged shrubs, which of the species planted recruit most abundantly as seedlings and which non-planted fleshy-fruited species invade the plot; (ii) are there differences between the shrub species in the number and identity of seedlings recruited under them; (iii) can these differences be explained, at least partially, by differences in mortality rates under the various species, and under conspecific versus heterospecific shrubs; and (iv) can mortality be related to species-specific differences in penetration of photosynthetically active radiation, cover by leaf litter, or degree of drying of the topsoil during rainless spells?

METHODS

Experimental site and shrub species

We conducted this study from April to September 1995 in the Cambridge University Botanic Garden. The experimental site was about 500 m^2 (36 m × 14 m). The soil of the plot originated from river gravel deposits and had a long history of cultivation. The top horizon of stony silty loam was 0.3–0.4 m deep (pH 7.4–7.9, in water), with a sharp transition to a yellowish-brown layer of compact stony sandy clay.

The site had been established in October 1986 by planting seedlings (10–30 cm) of nine broad-leaved dicotyledonous shrubs of the coniferous shrub *Juniperus communis* and of the tree *Sorbus aria.* We grew the individuals from seed, and planted 180 of them randomly in 10 rows 1.3 m apart with 2 m between plants in each row. The seeds were collected mostly from sites in southern England. Where possible, we used more than one provenance and 10 seedlings per provenance. The provenances are numbered I, II and III; they are not further mentioned but explain the unequal numbers of replicates (cf. Table 2). *Cornus sanguinea* I, *Crataegus monogyna* I, *Ligustrum vulgare* I and *Viburnum lantana* I were obtained from EFG Nurseries (Bronington, Shropshire, UK); *Cornus* II, *Juniperus*, *Rosa canina* and *Viburnum opulus* I from Banff and Buchan Nurseries (Banff, Scotland; seeds collected on the European continent); *Crataegus* II, *Ligustrum* II, *Prunus spinosa* and *Rhamnus catharticus* from an ancient chalk earthwork (Devil's Ditch, Cambridgeshire, UK, National Grid reference TL 583645); *Euonymus europaeus* and *Viburnum lantana* II from derelict arable land on chalk (Crookhorn Wood, Kent, UK, TQ 677627); *Crataegus* III, *Ligustrum* III and *Sorbus* from a similar site at Pulpit Hill, Buckinghamshire (SP 830048); and *Viburnum opulus* II from coppiced woodland on chalky boulder-clay soil (Buff Wood, Cambridgeshire, UK, TL 285502). Nomenclature follows *Flora Europaea* (Tutin *et al.* 1964–1980); only generic names are used later except for the two species of *Viburnum*, the only genus with more than one species. Further information on habitats and reproduction of the shrub species are given in Lee *et al.* (1991).

Fifteen of the 180 seedlings died in the first years or were poorly developed; they were consequently excluded. Therefore, 165 shrubs were analyzed in total; the final sample size for each species is given in Table 2. Due to the low number of replicates in some species, we had to include the edge plants in the analyses. All individuals of all species except *Crataegus* and *Sorbus*, and several individuals of these two taxa, fruited in 1994 and 1995, but the exact amount of fruit was not recorded, either in 1995 or in previous years. In May 1995, we measured the maximum height of all shrub individuals with a metal pole to the nearest 5 cm.

Area surrounding the experimental plot

The plot is approximately 20 m from the northern boundary of the Botanic Garden; beyond the boundary is dense housing with small gardens containing mostly exotic species. Away from the boundary, there are dense hedges of *Cotoneaster lacteus* and *Thuja plicata* var. *atrovirens* about 2.5 m tall and approximately 2 m away on two sides of the plot. Of the area within 100 m of the plot, about one-quarter has been occupied for the last 10 years by experimental beds containing mostly herbaceous plants; the other three-quarters have consisted of exotic trees (not fleshy-fruited) set in lawns. Shrub beds have covered less than 5% of the area; they contain exotics, and the fleshy-fruited are mostly *Berberis* or *Cotoneaster*. Just one or two small individuals of species planted in our plot, plus potential fleshy-fruited invaders (*Arum maculatum, Bryonia dioica, Malus sylvestris, Prunus cerasifera, Solanum dulcamara*) occur within 100 m; there are extensive hedges of *Crataegus monogyna* but these are trimmed tightly and carry few fruit. On the boundary of the garden grows a vigorous plant of the native climber *Hedera helix* with abundant fruit. Apart from this species, fleshy-fruited plants outside the experimental plot could contribute only a small number of seedlings in our plot. Of the area within 1 km of the plot about half is composed of schools and housing, and half of the Botanic Garden has few shrubs of the study species.

Permanent plots

In March 1995, a permanent plot (1 m × 1 m) was established beneath each of the 165 experimental shrubs, with the base of the original stem in the center of the plot. We divided the plot into four equal square subplots for practical reasons. In these plots, seedlings (<15 cm) of all fleshy-fruited plants and other woody species were recorded and labeled in the first week of the month from April to September 1995. We differentiated between first-year and older seedlings; no seedling >15 cm occurred in the experimental site. The percentage cover of herbs, mosses and leaf litter was estimated for each plot in April 1995 to the nearest 5%; the cover of herbs and mosses is not mentioned further since it was generally $<5\%$.

We kept records in a standard meteorological station about 100 m from the experimental plot. The records for temperature and precipitation of 1995 and of the previous 4 years are compared in Fig. 1, which shows that the summer of 1995 was unusually hot and dry.

Soil water content

After several weeks of exceptionally dry and hot weather (cf. Fig. 1), we determined soil water content beneath each shrub on 24–26 July 1995. Four soil samples per plot were taken with a cork-borer (2.4 cm diameter, 9 cm length, i.e. 40 cm^3), one in the center of each subplot, respectively. Soil water content of the soil samples was calculated as percentage of dry weight (2 days, 105°C). Mean values per plot were used for further calculations.

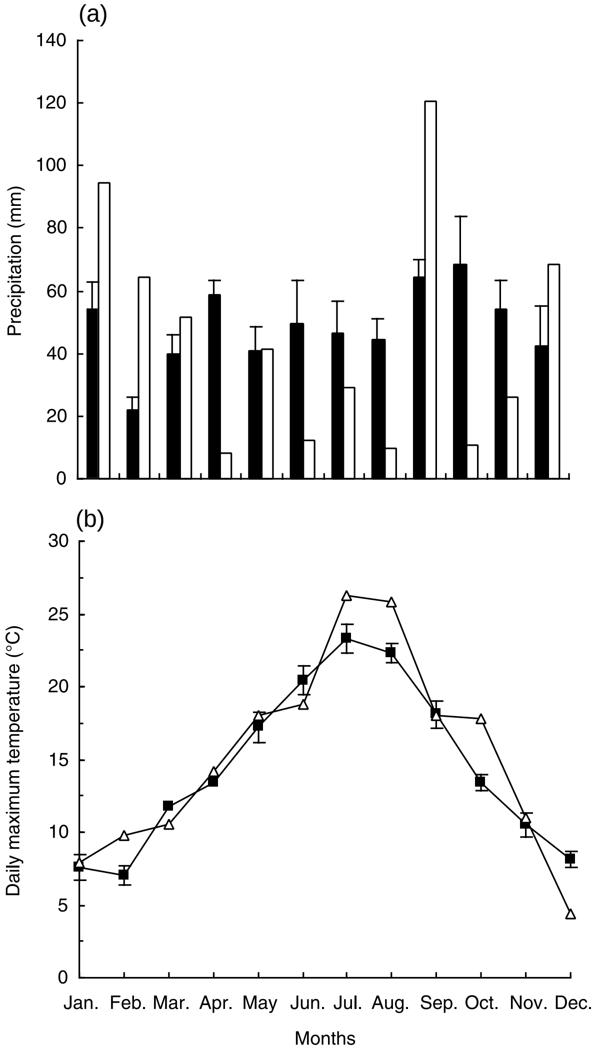

Fig. 1. Comparison of the monthly climatic data for 1995 with means of the previous 4 years (+SE) in the Cambridge University Botanic Garden: (a) precipitation; ■, 1991–1994 (554 mm); □, 1995 (537 mm); and (b) daily maximum temperature; –■–, 1991–1994 (14.4°C); –△–, 1995 (15.2°C).

Diffuse site factor

Relative photosynthetically active radiation at the height of the seedlings was measured in the four subplots beneath each shrub on a totally overcast day in mid June 1995, with a quantum sensor (Skye Instruments Ltd, Llandrindod Wells, UK). We used the same type of sensor to record irradiance in the open area next to the scrub at the same time to calculate the diffuse site factor (DSF) *sensu* Anderson (1964a). Mean values per shrub were calculated on the basis of four readings.

Statistical analyses

The statistical analyses followed Zar (1996). Since most data had non-normal distributions even after transformation, we applied mainly the non-parametric Kruskal–Wallis test and Spearman rank correlation, but did use regression analysis on log-transformed data. The specific statistical tests are mentioned in the results section. Because the data were not normally distributed, we have generally quoted median values (plus 25–75th percentiles) rather than means.

RESULTS

Total number of seedlings and overall mortality

During the period of observation, 3124 seedlings of 18 fleshy-fruited species were recorded with marked differences in abundance (Table 1). Of these seedlings, 28% germinated in 1995; frequencies of species among first-year and older seedlings were dissimilar (Spearman rank correlation: $r_s = 0.21$, $P > 0.05$). Recruitment of fleshy-fruited species was prevalent, and only 87 seedlings of woody species with wind-dispersed seeds were observed, all native or naturalized for many years (*Acer pseudoplatanus* 75, *Fraxinus excelsior* 11, *Carpinus betulus* 1); these species were excluded from further analyses. Seedlings of all planted species were found with the exception of *Euonymus* and *Sorbus*, both of which produced few fruits in most years. However, the number of seedlings of a given species was not correlated with the number of individuals planted in the experiment ($r_s = 0.52$, $P > 0.05$). Seedlings of nine non-planted fleshy-fruited species were observed, and they accounted for 44% of all seedlings. Of these, 76% were of *Hedera*; no seedling of *Berberis* was found, and only 60 of *Cotoneaster*. Thus, the various exotic shrubs within 100 m of the plot were not effective invaders. Strikingly high was the percentage of species with long-lasting or evergreen leaves (63% individuals), mainly *Hedera, Viburnum lantana, Ligustrum* and *Ilex aquifolium*.

Mortality of seedlings was markedly different among the 18 species (Table 1). Considering the rates of mortality for the species with more than 50 seedlings, there were significant differences

Table 1 Total number and mortality of seedlings of fleshy-fruited species in the experimental scrub where 165 permanent plots (1 m × 1 m) were checked monthly from April to September 1995

	All seedlings		First-year seedlings	
Species	Number	Mortality (%)	Number	Mortality (%)
*Hedera helix**†	1039	26	34	65
Viburnum lantana†	604	35	102	82
Rhamnus catharticus	349	50	111	76
Rosa canina	349	69	231	78
Ligustrum vulgare†	162	26	15	67
Cornus sanguinea	138	60	68	84
*Solanum dulcamara**	114	94	101	90
*Ilex aquifolium**†	90	63	41	68
Viburnum opulus	75	89	62	76
Cotoneaster spp.*†	60	67	37	60
Crataegus monogyna	39	69	22	73
*Sambucus nigra**	38	97	37	78
Prunus spinosa	31	45	14	57
*Rubus fruticosus**	12	58	5	(5)
*Arum maculatum**	9	(0)	—	
*Taxus baccata**†	6	(3)	4	(3)
Juniperus communis†	3	(2)	2	(2)
*Ribes uva-crispa**	1	(1)	—	
Unknown seedlings	4	(4)	4	(4)
Sum	3124	44	885	78

For species with less than 10 seedlings percentage of mortality was not calculated, but the number of dead seedlings is given in parentheses.

*Invasive species, not planted in the scrub. †Species with at least partly winter-green leaves.

between the species (Kruskal–Wallis test: $H = 62.7$, d.f. $= 9$, $P < 0.001$). Mortality of seedlings of all ages taken together was highest for *Solanum* and *Viburnum opulus* (94%, 89%) and lowest for *Hedera* and *Ligustrum* (both 26%). There was a significant negative correlation between percentage mortality and total number of seedlings (linear regression: seedlings $= 687 - 7.4$ mortality; $r^2 = 0.36$, $P = 0.029$, $n = 13$, species with > 12 seedlings), suggesting that abundance was partly controlled by differential mortality. However, this result did not hold true for the first-year seedlings and mortality of these seedlings in 1995 ($P > 0.05$). Mortality resulted mostly from desiccation during the exceptionally dry and hot summer, with some additional effects of fungal attack; no sign of herbivory was observed.

Host-specific density of seedlings and mortality

The density of seedlings was significantly different among the 11 'host' species of the experimental scrub (Table 2). The median values for total densities of seedlings of 18 fleshy-fruited species differed under the different 'hosts', being highest under *Crataegus*, *Viburnum opulus* and *Rosa* (24–20 m^{-2}); intermediate under *Sorbus, Rhamnus, Cornus*, *Ligustrum* and *Juniperus* (17–12 m^{-2}); and lowest under *Euonymus*, *Viburnum lantana* and *Prunus* (10–9 m^{-2}). These differences in recruitment were similar for non-planted species (e.g. *Hedera, Solanum*). The number of seedlings per plot of all species and of the non-planted species were strongly correlated (Spearman rank: $r_s = 0.82$,

Table 2 Mean number and rates of mortality of seedlings beneath the experimental plants (*n*, number of replicates)

Species	*n*	Seedlings (m^{-2})	Mortality (%)	Non-planted spp. (m^{-2})	No. seedlings
Crataegus monogyna	26	24 (14–38)	49 (32–68)	9 (3–14)	39
Viburnum opulus	20	20 (11–26)	47 (32–61)	8 (6–15)	75
Rosa canina	10	20 (10–25)	46 (33–60)	5 (4–12)	349
Sorbus aria	8	17 (10–20)	45 (35–53)	8 (6–10)	0
Rhamnus catharticus	10	16 (11–24)	41 (25–73)	5 (3–9)	349
Cornus sanguinea	20	14 (9–25)	53 (30–68)	8 (5–15)	138
Ligustrum vulgare	28	13 (10–24)	45 (30–59)	6 (5–11)	162
Juniperus communis	10	12 (11–14)	56 (47–82)	4 (3–5)	3
Euonymus europaeus	6	10 (7–22)	52 (27–70)	4 (3–7)	0
Viburnum lantana	18	9 (4–20)	42 (21–57)	4 (2–8)	604
Prunus spinosa	9	9 (7–14)	50 (33–72)	6 (3–7)	31
H		20.4*	3.8^{NS}	19.4*	

The third and fourth columns give median values (25–75th percentiles) for seedlings of all fleshy-fruited species, the fifth column gives these values for densities of seedlings of non-planted species which invaded the experiment. In the sixth column, the total numbers of seedlings of the various species are given for the whole site (cf. Table 1). Kruskal–Wallis test: $^{*}P < 0.05$, $^{NS}P > 0.05$.

$P < 0.001$, $n = 165$ plots). The different seedling densities might therefore reflect host-specific effects on the number of seeds reaching the ground, or the proportion surviving and germinating. No significant correlation was found between shrub-specific densities of seedlings and total number of seedlings of this host species within the site ($r_s = 0.17$, $P > 0.05$, $n = 11$; cf., Table 2, column 3 *vs* 6).

No significant difference in median mortality of all seedlings, of non-planted species or of first-year seedlings was observed among host shrubs (Kruskal–Wallis test: $P > 0.05$; Table 2). However, mortality of all seedlings was slightly higher under *Juniperus* and *Cornus* (56%, 53%) and lower under *Viburnum lantana* and *Rhamnus* (42%, 41%). There was no significant correlation between mortality and density of any of the three seedling fractions ($r_s = -0.15, -0.09, -0.32$, $P > 0.05$, $n = 11$), indicating that mortality was not density-dependent.

Mortality of all seedlings of a given species was higher under conspecific shrubs (Fig. 2), but these differences were significant only in *Cornus* (Chi-squared contingency tables: $\chi^2 = 3.8$, $P = 0.05$), *Crataegus* ($\chi^2 = 13.9$, $P < 0.001$), *Rosa* ($\chi^2 = 15.9$, $P < 0.001$) and *Viburnum lantana* ($\chi^2 = 5.4$, $P = 0.02$). This result was not explained by differences in seedling densities, since densities were not higher under conspecific shrubs than under hosts belonging to other species (Mann–Whitney test: $P > 0.05$); exceptions were *Crataegus* (0.92 ± 0.28 seedlings m^{-2} *vs* 0.10 ± 0.03; means ± SE; $T = 3118$, $P < 0.001$) and *Rhamnus* (6.20 ± 2.16 *vs* 1.83 ± 0.19; $T = 1161$, $P = 0.023$). The number of first-year seedlings was too low for us to do the same analysis for this fraction.

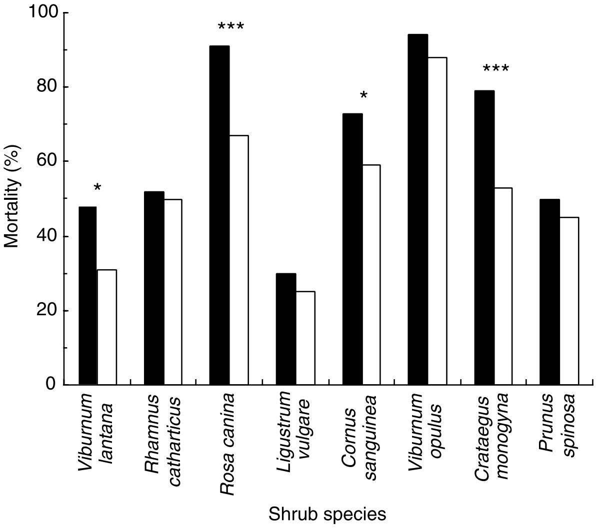

Fig. 2. Mortality of seedlings under conspecific shrubs versus 'hosts' belonging to other species. Differences are tested with Chi-squared contingency tables ($^{***}P < 0.001$, $^{*}P < 0.05$): ■, conspecific; □, heterospecific.

Factors affecting density and mortality of seedlings

The height of the experimental shrubs, leaf litter cover, DSF and topsoil water content beneath the shrubs all differed among species (Table 3). However, there was no significant difference in cover of litter when we excluded *Rhamnus*, which had a remarkably sparse litter layer, since among the other species variation in litter was more or less within the error of estimation. Significant positive correlations were found between topsoil water content and cover of leaf litter, and between water content and shrub height (Spearman rank: $r_s = 0.34$, $r_s = 0.21$, $P < 0.001$, $n = 165$); a negative correlation occurred between water content and DSF ($r_s = -0.46$, $P < 0.001$, $n = 165$). However, when we used median values of water content and DSF for each species, the significance of the negative correlation disappeared ($r_s = -0.43$, $P > 0.05$, $n = 11$; Fig. 3).

The four factors were tested for possible effects on seedling densities and mortalities. The total number of seedlings per plot correlated positively with soil water content ($r_s = 0.21$, $P = 0.008$, $n = 165$), and DSF ($r_s = 0.15$, $P = 0.048$, $n = 165$); the same was true for the relationship between the number of surviving seedlings and soil water ($r_s = 0.20$, $P = 0.01$, $n = 165$) but not DSF ($r_s = 0.14$, $P = 0.07$, $n = 165$). Diffuse site factor and shrub height were also correlated with the number of first-year seedlings ($r_s = 0.24$, $P = 0.002$; $r_s = 0.22$, $P = 0.006$; $n = 165$). Multiple linear regressions after log transformation showed that only a small percentage of the variation in total seedling number ($r^2 = 0.05$, $P = 0.02$), surviving seedlings

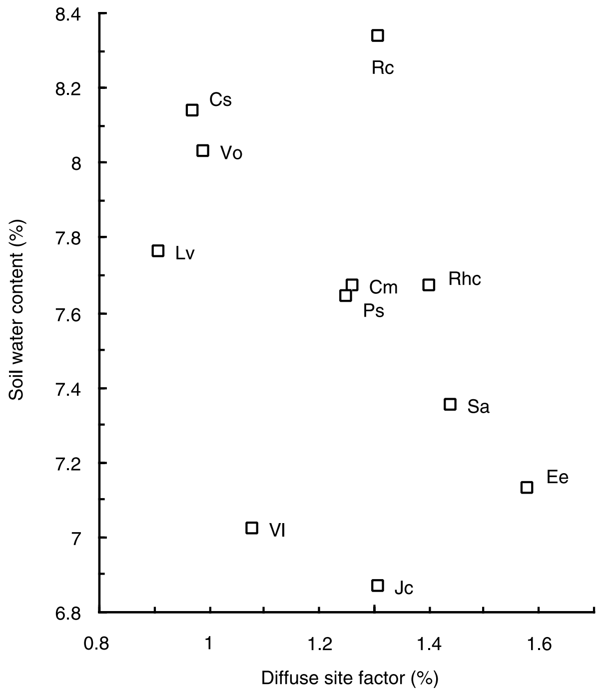

Fig. 3. The relationship between mean soil water content after drought and median diffuse site factor (Spearman rank: $r_s = -0.43$, $P > 0.01$, $n = 11$): Cm, *Crataegus*; Cs, *Cornus*; Ee, *Euonymus*; Jc, *Juniperus*; Lv, *Ligustrum*; Ps, *Prunus*; Rc, *Rosa*; Rhc, *Rhamnus*; Sa, *Sorbus*; Vl, *Viburnum lantana*; Vo, *Viburnum opulus*.

Table 3 Heights of shrubs, leaf litter, diffuse site factor (DSF) and soil water content during drought under the experimental shrubs (median, 25–75th percentile); rank order of species follows light availability

Species	*n*	Height (m)	Leaf litter (%)	DSF (%)	Soil water (%)
Euonymus europaeus	6	2.9 (2.4–3.5)	18 (10–25)	1.58 (1.24–2.45)	7.13 (6.65–7.20)
Sorbus aria	8	3.7 (3.5–3.8)	25 (5–62)	1.44 (1.10–2.23)	7.35 (7.03–7.51)
Rhamnus catharticus	10	2.8 (2.6–3.0)	2.5 (0–5)	1.40 (1.12–2.12)	7.67 (7.03–7.78)
Rosa canina	10	3.2 (2.8–3.8)	25 (25–25)	1.31 (0.88–3.49)	8.34 (8.00–8.99)
Juniperus communis	10	2.5 (2.0–2.7)	50 (25–50)	1.31 (1.06–1.98)	6.87 (6.67–7.09)
Crataegus monogyna	26	3.6 (3.2–4.2)	25 (10–50)	1.26 (0.94–1.98)	7.67 (7.20–8.17)
Prunus spinosa	9	3.8 (2.6–3.9)	25 (4–56)	1.25 (0.69–1.75)	7.64 (7.28–8.03)
Viburnum lantana	18	2.5 (2.4–3.0)	12 (0–25)	1.08 (0.68–2.25)	7.02 (6.28–7.75)
Viburnum opulus	20	3.2 (2.6–3.3)	25 (5–69)	0.99 (0.71–1.66)	8.03 (7.20–8.47)
Cornus sanguinea	20	3.6 (3.2–4.0)	25 (5–25)	0.97 (0.83–1.32)	8.14 (7.56–8.65)
Ligustrum vulgare	28	3.1 (2.8–3.3)	25 (18–75)	0.91 (0.72–1.23)	7.76 (7.20–8.09)
H		64.8***	19.0*	18.5*	35.3***

Kruskal–Wallis test: ***$P < 0.001$, *$P < 0.05$.

($r^2 = 0.05$, $P = 0.04$), and first-year seedlings ($r^2 = 0.14$, $P < 0.001$) were explained by the above factors. Again all correlations disappeared if tested with mean values for the 11 host species. Although we suspected drought to be the main factor for mortality of seedlings, no significant correlation was observed between any of the site factors and percentage mortality ($P > 0.05$).

Seedlings of the most abundant species (> 100 seedlings: *Cornus, Hedera, Ligustrum, Rhamnus, Rosa, Solanum, Viburnum lantana*) were tested individually for correlations between mean seedling density per host shrub and soil water content or irradiance. However, the only significant result was for *Hedera* where recruitment was positively correlated with soil water content during a dry spell (linear regression: $r^2 = 0.65$, $P = 0.003$, $n = 11$ species; Fig. 4).

DISCUSSION

Control of seedling abundance in the experimental scrub

The differences between the fleshy-fruited species in total abundance of seedlings (Table 1) are difficult to explain as they are likely to depend on differential seed input, as well as on differences in tolerance of the seedlings. For fleshy-fruited species there were only very small sources of seed of the study species within a distance of 1 km, and of all non-planted invaders except *Hedera*, so we assume that the main differences in seed input are correlated with the fruit crops of the planted individuals. As to tolerance, it is notable that (leaving aside species not planted) two of the three most abundant species among the seedlings (*Viburnum lantana* and *Rhamnus*, not *Rosa*) proved to be notably shade-tolerant in previous experiments (Grubb *et al.* 1996). The abundance of species which are at least partly winter-green, above all *Hedera* and *Viburnum lantana*, was conspicuous. This tactic is surely an advantage in a strongly shaded environment, since it provides additional photosynthetic yields in spring and autumn (Ellenberg 1988).

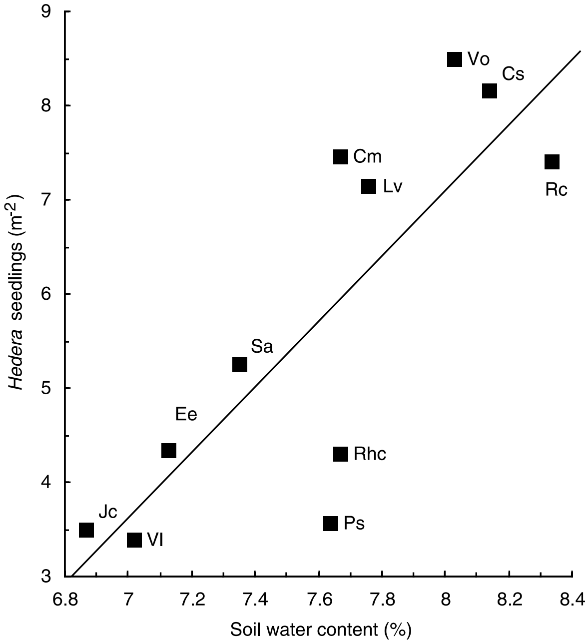

Fig. 4. Median densities of *Hedera helix* seedlings beneath 11 'host' species as a function of median soil water content after drought (abbreviations as in Fig. 3). $y = -20 + 3.5x$, $r^2 = 0.65$, $P = 0.003$.

The number of seedlings of non-planted fleshy-fruited species was somewhat surprising, since increase in diversity in dense scrublands and hedges is believed to be a rather slow process (Dowdeswell 1987; Reif & Aulig 1990), whereas the less shaded conditions beneath fruit trees in abandoned orchards allow more rapid recruitment (Debussche *et al.* 1982; Milton *et al.* 1997). One reason for our result is probably that the surroundings of the experimental scrub in the Cambridge University Botanic Garden were favorable for frugivorous birds because of the dense cover provided by hedges and the diversity of perching structures; *Turdus merula* L., *Erithacus rubecula* L. and *Sylvia atricapilla* L. were frequently observed.

The differences in abundance between non-planted species probably reflect not only the availability of fruits but also their attractiveness for birds (cf. Sorensen 1981; Debussche & Isenmann 1989; Fuentes 1994). Not only was there a large source of *Hedera* fruits near to the plot, but this species plays a prominent role for birds in late winter, and is consequently widely dispersed (Kollmann 1994). However, the other non-planted species are also believed to be attractive to birds due to specifics of their pulp composition (*Sambucus nigra, Solanum dulcamara*; cf. Herrera 1987; Snow & Snow 1988). *Hedera* is also a common marker of secondary forest in Great Britain

(Rodwell 1991); perhaps the explanation is that rapid arrival by bird-dispersal enables it to become abundant before taller-growing and potentially suppressive shade-tolerant herbs invade.

Control of host-specific seedling density by physical factors

In our experimental plot, we found shrub-specific differences in total seedling densities beneath the various tall-shrub species, and these differences hold true for non-planted species. These results were not explicable by differential mortality in the one year when we measured it, and did not reflect species-specific variation in the height of shrubs or extent of cover by leaf litter. Moreover, seedling density was correlated only weakly with DSF. Very interestingly, there was a much stronger correlation between seedling density and soil water content during a dry spell, and in the case of the most abundant species (*Hedera*) the differences in abundance under various host species were strongly correlated with the extent to which the hosts failed to desiccate the soil (Fig. 4). We suggest the effect of soil water content was prominent in *Hedera* because it is much more shade-tolerant than the other species observed (Ellenberg 1988), and thus the light factor may be less decisive. However, the soil water content explained only a modest amount of the variation for most species, and this result may arise from a balance between enhanced germination and survival under the more deeply shading species during a dry spell, and greater survival under the less shading species during moist weather; a clear example of seed-seedling conflicts *sensu* Schupp (1995).

The negative correlation between the degree of soil drying and depth of shade is based on a very simple method of light measurement. Adequate characterization of the light climate beneath different plants is notoriously difficult. Under a collection of individuals of one species at a particular site, instantaneous measurements of DSF under overcast conditions may be strongly correlated with the total site factor for the whole range of weather conditions (Parent & Messier 1996), but the complexities of canopy form and light penetration are such that a close correlation is unlikely when comparing different species (Anderson 1964b; Eber 1972). We accept that our measurements may have failed to capture the *magnitude* of change in the penetration of light over all weather conditions. However, it is virtually certain that the *direction* of change has been established.

A negative correlation between degree of soil drying and the degree of shade could, in theory, arise from greater evaporation at the soil surface where a greater proportion of daylight is incident. However, there is much evidence from a variety of plant community types that the topsoil is dried during rainless spells mainly by uptake into the roots, and not by direct evaporation from the soil surface (Slavíková 1958; Robberecht *et al.* 1983; Vitousek & Denslow 1986; Becker *et al.* 1988; Veenendaal *et al.* 1996). The tendency found in our study is in accordance with the model of Tilman (1988) in which exhaustion of a soil resource is negatively related to interception of light, when different species are compared. His model is based on differences between species in allocation of dry mass to roots as opposed to leaves, and thus potentially to root length density in the soil. However, the placement of roots in the soil profile may be as important as the total amount in the profile in determining the degree of drying of the top 10 cm, which is what we studied, as it is what affects young seedlings. Breshears *et al.* (1997) have shown how *Juniperus monosperma* is especially effective in drying the uppermost soil layers. Possibly, *Juniperus communis* and the shrub species in other genera allowing high penetration of light behave in a similar way.

Key (1979) found that soil beneath *Crataegus* scrub in Cambridgeshire was significantly drier than that under adjacent chalk grassland; Burton and Bazzaz (1995) reported a similar result in eastern USA. In Key's study, the amounts of available nitrogen and phosphorus were markedly higher under scrub than outside, but that is not true for our experimental scrub in the Botanic Garden (P. J. Grubb, unpubl. obs.). Nutrient deficiency is unlikely to limit seedling recruitment under the experimental shrubs because the experimental plot of this study was established on relatively fertile soil of former allotment gardens. On the contrary, high nutrient supply is often detrimental for the growth and survival of shrub seedlings in deep shade (Grubb *et al.* 1996). Moreover, preliminary experiments showed that differences in soil fertility under host shrubs did not explain the different seedling densities (P. J. Grubb, unpubl. obs.).

A serious problem of our study is that the results might be affected by edge effects since we were forced to include edge individuals (42 of 165 shrubs). All measured environmental factors and both seedling densities and mortalities changed for shrub plants along the edges (Mann–Whitney test: $P < 0.05$). The height of shrubs, soil water content and litter cover were significantly lower, whereas mean DSF was higher; mean number of seedlings was lower and mortality higher. However, the proportion of edge plants was not significantly different among the shrub species (Chi-squared contingency tables: $\chi^2 = 3.4$, $P = 0.97$), and the basic findings of this study remained robust when we analyzed shrub-specific recruitment and microenviroment after excluding edge plants.

Control of host-specific seedling density by biological factors

Although the significant differences between host species in seedling density were correlated with soil water content during a dry spell, and to a much lesser extent with DSF, only a small percentage of the total variation was explained by these physical factors. Thus, we suspect that biological effects on seed rain, seed predation, germination and survival are important for the observed patterns in seedling densities, and determine effectiveness of seed dispersal (Schupp 1993). We covered only some of these processes in the present study; most of them also need to be checked under field conditions. However, results from field studies in similar habitats (Kollmann 1994) suggest that no significant spatial pattern in seed predation is to be expected in the rather homogeneous experimental scrub plot, although the attractiveness of the various seed species is certainly different (Kollmann *et al.* 1998).

The supposed spatial patterns in seed rain were most likely caused by differential attractiveness of shrub species for birds, since quality and quantity of the fruit crop were different among the shrub species investigated (cf. Sorensen 1981; Herrera 1987; Lee *et al.* 1991). Moreover, the shrubs investigated exhibited marked differences in architecture, but these differences and their consequences are only partly understood (Küppers 1985; Snow & Snow 1988). The higher a shrub is, the more attractive it is for many frugivorous birds (McDonnell 1986), which perhaps explains low seedling densities under *Euonymus* and *Viburnum lantana*. Moreover, most branches of *Euonymus*, and similarly of *Sorbus*, have a strong vertical component, whereas *Cornus, Crataegus* and *Rhamnus* are rich in more or less horizontal branches and twigs which are likely to be attractive to perching birds. *Prunus* develops a very dense and spiny crown which may be difficult to penetrate, especially for larger passerines such as thrushes. This effect is seen all the more clearly in the case of *Juniperus* which produces extraordinarily dense and very spiny pillar-shaped crowns. The mean diameter of branches could also be decisive for perching birds (cf. Reid 1989). Much more work needs to be carried out in this field, for example, by analysis of crown architecture of shrubs and by close observation of the preferences of frugivorous birds for perching sites (Denslow & Moermond 1982; Winkler & Leisler 1986). Monitoring of seed dispersal into even-aged scrub will certainly also be important, since seed rain is an indicator of the habitat selection of birds (Kollmann & Pirl 1995).

The higher mortality of seedlings under conspecific adults is an intriguing result of this study which might be discussed within the framework of the Janzen-Connell hypothesis (cf. Streng *et al.* 1989), although we need more information on physical site factors and biotic effects under field conditions to investigate this question. In the experimental setting, the higher mortality under conspecifics was certainly not caused by differential shading, since mean irradiance was not significantly lower under species with a strong effect of conspecific adults (median DSF 1.26%) than in species with no significant effect (median DSF 0.98%; Mann–Whitney test: $P > 0.05$). Also the soil water content in a dry spell was not significantly different among the two groups ($P > 0.05$). We suggest that the higher mortality under conspecifics might be due to shrub-specific nutrient demands, autopathic effects or shrub-specific pathogens, since in a previous experiment we observed that seedlings of *Crataegus* (but not of other shrubs) grew less well and had higher mortality on soil from *Crataegus* scrub than on soil from adjacent grassland (Grubb *et al.* 1996).

Conclusions and possible application to the field situation

The study revealed some answers to the questions set out in the Introduction: (i) in an experimental plot of even-aged shrubs, there are marked differences among the species which become established most abundantly as seedlings; (ii) there are significant differences between the shrub species in the number and identity of seedlings recruited under them; (iii) these differences can be partially explained by differences in mortality under the various species; furthermore, mortality is higher under conspecific shrub; (iv) mortality was not correlated with species-specific differences in DSF, cover of leaf litter, and topsoil water content during a rainless spell.

The results on differential recruitment of fleshy-fruited species in the experimental scrub have a potential bearing on nature conservation, since shrubs are often planted to enhance biodiversity in degraded landscapes (Dowdeswell 1987; Reif & Aulig 1990; Robinson & Handel 1993). High recruitment of additional species could be an argument for choosing particular shrub species, since this process leads to a more natural community structure (Kollmann 1994).

Unfortunately, the present study covered only 1 year and was performed in a single plot. However, the seedlings observed are an accumulated product of several years' seed input, since only a third of the investigated seedlings emerged in 1995. The effects of shrub canopies might vary depending on site-specific factors, and it is not clear how far the observed differences would hold true in natural scrublands where additional factors might be more decisive. It is therefore encouraging that the results of an extensive field survey beneath established fleshy-fruited shrubs (1–3 m in height and diameter) on abandoned calcareous grassland in south-west Germany were in agreement with the findings of our garden experiment in the UK (J. Kollmann, unpubl. obs.). At the German site the average density of seedlings and the number of fleshy-fruited species under about 200 shrubs was highest beneath *Crataegus*, intermediate in *Rosa* and *Cornus* and low in *Prunus* (see also Kollmann 1994). Markedly higher densities of bird-dispersed seeds and subsequent recruitment under *Crataegus monogyna* compared with *Rosa canina* were also observed by Herrera (1984) in Spain where *Crataegus* shrubs were much more attractive for frugivorous birds than *Rosa*.

Clearly, in order to understand shrub-specific effects on recruitment, additional work is needed on differential attractiveness of shrub canopies for birds, on seed rain, seed predation, under-canopy effects on germination, and on deleterious effects of conspecific hosts.

ACKNOWLEDGEMENTS

Alex Goodall planted and maintained the bed of shrubs. Glyn D. Jones assisted with measuring the heights of shrubs and the DSF beneath them. Peter L. Marks, Max Debussche and the referees of the journal improved previous versions of the manuscript with critical comments. J. K. is obliged to the Reinhold-Tüxen-Gesellschaft (Hannover) for financial support for a postdoctoral stay at Cambridge University.

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