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AN INTERPRETATION OF THE DISTRIBUTION OF *EPILOBIUM HIRSUTUM* AND *LYTHRUM SALICARIA* IN RELATION TO THEIR PHYSIOLOGICAL ECOLOGY

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Abstract

Results of some experimental investigations of the comparative biology of *Epilobium hirsutum* and *Lythrum salicaria* are discussed in relation to their different patterns of ecological and geographical distribution.

The two species show profound differences in their germination characteristics in respect of light, temperature and pH. *Epilobium* showed a very high germination percentage at temperature below 10°C while in *Lythrum* it was negligible below 20°C. Further low temperature had a depressing effect on the post-germination growth of *Lythrum*. Q10 of growth was far higher in the case of *Lythrum* as compared to that of *Epilobium*.

Lythrum was more tolerant of moderate shade in respect of dry weight production than *Epilobium*. This was due to an increase of leaf area to compensate for the decreased light intensity. Under short day conditions there was a greater suppression of post-germination growth in *Lythrum* than in *Epilobium*. Also *Lythrum* did not respond to any photoperiod other than a critical photoperiod of 13 hours for extension growth and flowering.

Response to a range of nutrient dilutions was also remarkably different in the two species. In *Lythrum* growth was comparatively better in the weaker nutrient solutions as compared to *Epilobium* whereas *Lythrum* responded to every nutrient stringency by an adaptive increase of root/shoot ratio, *Epilobium* failed to show such a plastic response. Uptake of major nutrients *viz*; N.P.K. and Ca in *Lythurm* was comparatively higher than *Epilobium* under nutrient stress. Further, in *Epilobium* unlike *Lythrum* any deficiency of potassium supply results in physiological disorders and suppression of flower and fruit production.

Under high temperature conditions *Lythrum* was found to be more successful than *Epilobium* in inter-specific as well as intra-specific competition in the nutrient rich and poor soils. *Epilobium* when given the seasonal advantage of growth at a low temperature of autumn and spring in a base rich soil, out-competed *Lythrum* in the following summer.

Introduction

The ecological and geographical distribution of plants is one of the most complex of the problems of plant ecology. The descriptive side of these problems has received considerable attention but far less experimental work has been attempted. The two species investigated, *Epilobium hirsutum* and *Lythrum salicaria* are both pioneer plants of fen communities. *Epilobium hirsutum* has a narrow ecological amplitude, distribution being strictly confined to base rich fens in England and most of nothern Europe (Clapham, Tutin & Warburg, 1952; Post, 1932; Raven, 1962; Ellis; 1965). *Lythrum salicaria* primarily a fen plant has a rather wider ecological amplitude. It has an extensive geographical distribution extending from cold northern Europe to warm Central and Southern Europe, where it is a dominant plant in the communities (Clapham. Tutin & Warburg, 1952; Perring & Walters, 1962; Pearsall, 1918; Hulten, 1950). It is more tolerant of both low pH and low nutrient supply. It even extends to the southern hemisphere in Australia (Black, 1929).

Their occurrence as dominant species in different plant communities in different parts of the world has always intrigued ecologists. In this paper results of work on comparative biology of *Epilobium hirsutum* and *Lythrum salicaria* (Shamsi, 1970) are reviewed and discussed in an attempt to offer an eco-physiological explanation for their different distribution patterns.

Materials and Methods

Seeds of both the species were collected from plants growing in wheat fen Broads, Norfolk England in September, 1966 and stored dry in a refrigerator. Seeds were germinated on the surface of a suitable substratum in Petri dishes illuminated at 800 ft. candles from a bank of flourescent tubes. Germination was scored in terms of number of seeds with emerged hypocotyls.

In the experiments concerned with the growth of the species in relation to light intensity and photoperiod, the plants were grown in 36 cm, pots in a mixture of sand and peat. Experiment concerning effect of different temperature regimes on growth was conducted in Fison's phytotrons. Seedlings of both the species were grown in the Long Ashton nutrient solution (Hewitt, 1952) in blackened plastic boxes of 600 ml. capacity, culture solution being replaced after every two days. Ten seedlings per box per species and ten boxes of each species per treatment were used.

For experiments on mineral nutrition, plants of both the species were grown in 50 litre capacity 4'X2' wooden tanks lined internally by thick black polythene. Separate tanks were used for each species. Seedlings were transplanted 1" apart in the perforated tops of the tanks. Long Ashton nutrient solution (Hewitt. 1952) was used depending upon the requirements of the particular experiment. An inter-linked system of glass and Polyvinyl tubings (with microholes in the polyvinyl tubings) was passed through the tanks arranged in two rows for aeration of culture solutions. The solutions were regularly aerated for 6 hours every day and in each tank the solution renewed after every three weeks.

Harvests of plants in various experiments were taken periodically using 15-20 replicates per treatment per species depending upon the situation. The harvested plants were washed in distilled water, separated into individual plant parts placed in clean filter paper and then dried in a ventilated oven at 80°C and weighed after cooling in a desiccator.

A lay-out of randomized blocks was used in the experiments concerned with photoperiod, light intensity and temperature. However, in the experiments concerned with mineral nutrition, huge size of tanks did not allow the laying out of randomized blocks.

Experimental Results

GERMINATION AND SEEDLING BEHAVIOUR

The two species showed profound differences in their germination characteristics, especially in regard to temperature and soil type. While *Lythrum* is tolerant of acidic

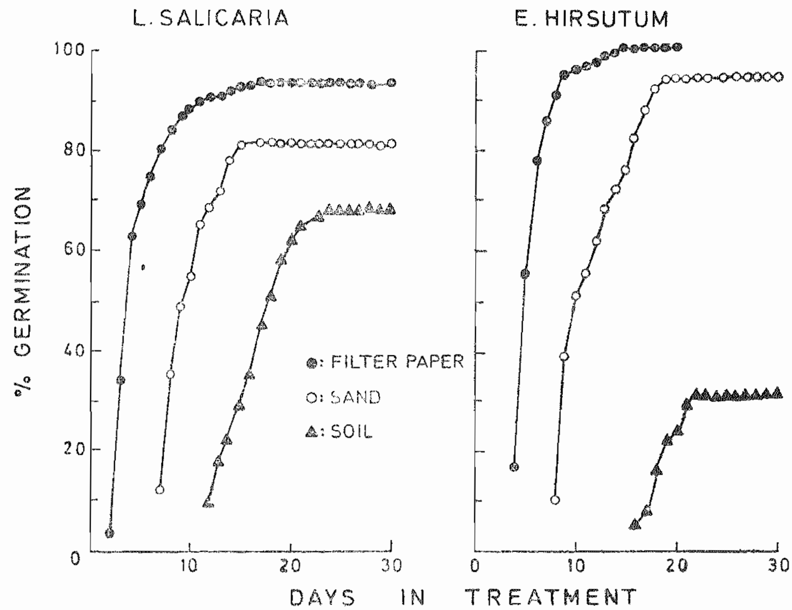

Fig. 1. Effect of different media on the germinability of *Lythrum salicaria* and *Epilobium hirsutum* in light at 20°C.

and poor nutrient status soils, response in *Epilobium* as regards germination is very low (Fig. 1). In both species there was an absolute light requirement for germination at low temperatures. Combination of light and low temperature promotes germination in *Epilobium*, to the extent of 90% germination at 10°C while in *Lythrum* below 20°C germination is negligible (Fig. 2). In the dark, germination increased with a rise in temperature

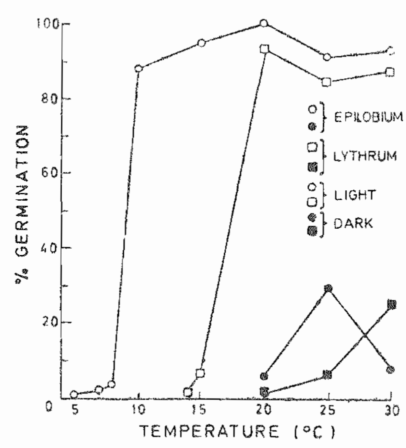

Fig. 2. Effect of different temperatures on germination of *Epilobium hirsutum* and *Lythrum salicaria* in light and dark.

in *Lythrum* but there was no such relationship in *Epilobium* (Fig. 2). Because of their specific temperature requirements in Britian *Epilobium* seeds can germinate in autumn or early spring but that of *Lythrum* only in summer. Field experiments confirmed this hypothesis. Light requirements of germination are especially advantageous as seeds are of light weight and contain only a little stored food reserve. Further, from survival view-point it is important that they germinate under conditions where photosynthesis occurs soon after germination.

Germination having been successfully accomplished in any environmental condition, the successful establishment of seedlings depends upon the biology, growth commitments, growth habit and growth rate of the species in relation to competitors in the particular environment.

Daylight Levels and Growth

Plants were grown at three levels of daylight referred to as 100%, 70% and 40% daylight. Natural illumination was supplemented by artificial light with a fixed photoperiod of 16 hrs. Two levels lower than that of full daylight were controlled by using terylene netting screens. The illumination in the three treatments was measured photometrically, using an "EEL" light master photometer and found to be 2020 ± 45; 1400 ± 31 and 780 ± 18ft. candles, respectively.

Of the two species, *Lythrum* was found to be more tolerant of moderate shade than *Epilobium*. Fig. 3 shows that relatively there is a greater reduction in dry weight gain with

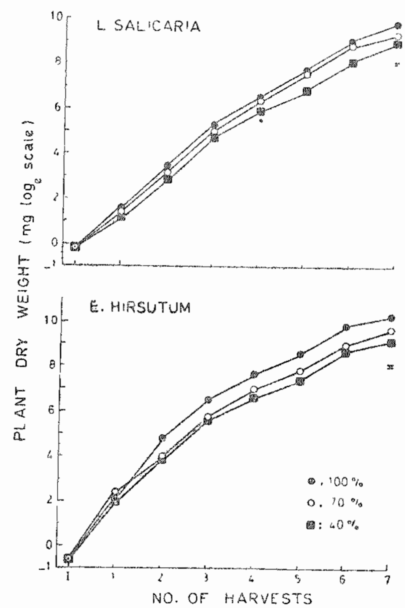

Fig. 3. Effect of different daylight levels on increase of plant dry weight with time in *Lythrum salicaria* and *Epilobium hirsutum*. (I—initial harvest) I, fiducial limits at P=0.05 apply to each point except intial.

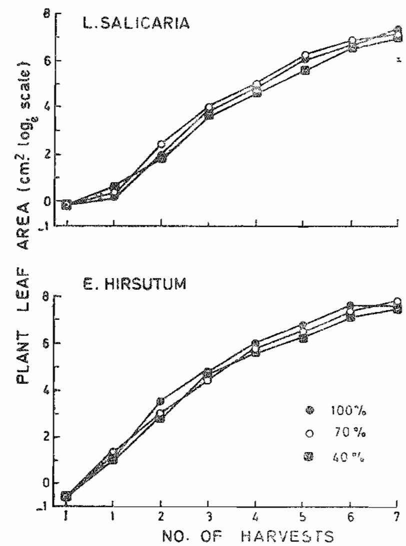

Fig. 4. Effect of different daylight levels on increase of plant dry weight with time in *Lythrum salicaria* and *Epilobium hitsutum*. (I—initial harvest) 1, fiducial limits at P—0.05 apply to each point except initial.

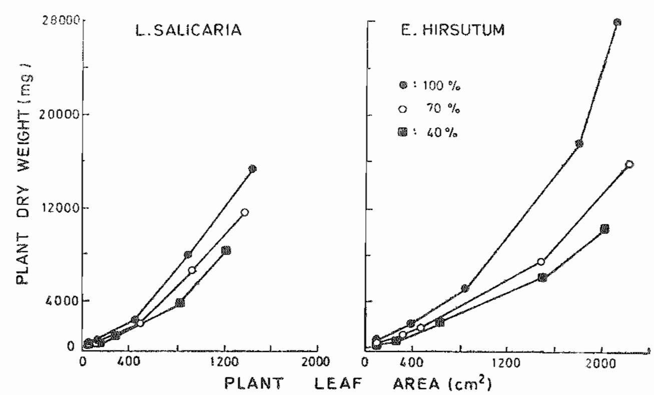

Fig. 5. Effect of daylight levels on relation between plant leaf area and dry weight in *Lythrum salicaria* and *Epilobium hirsutum* (harvests three to seven inclusive).

the decrease in light intensity in *Epilobium* as compared to that in *Lythrum*. Also in *Lythrum* moderate light intensity plants (70%daylight) showed a relatively higher leaf area compared with 100% dalyight plants for most part of the growth period (Fig. 4). Fig. 5 gives a correlation of the increase in leaf area with the gain in plant dry weight. While similar leaf areas are obtained in *Lythrum* with very small difference in the dry weights in 70% and 100% light plants in *Epilobium* the difference is such that the dry weight in 100% light plants is almost twice that of the 70% light plants for similar leaf areas. It may be mentioned that in *Lythrum* there is something of a "compensating mechanism" (Whitehead, 1962) in response to decreased light intensity, while *Epilo ium* has no such mechanism. In the case of *Lythrum*, with decrease of light intensity, there occurs an increase of leaf area. This works as an adapative "compensating mechanism" *i. e.*, the increased amount of photosynthetic tissue (leaf area is sufficient to compensate for the reduced rate of biochemical processes of photosynthesis, so that over a wide range of light intensities carbon assimilation (dry weight) per individual over time is the same, (also in Blackman & Butter, 1946 and Myerscough & Whitehead, 1967). This better growth of *Lythrum* at moderate 70%) daylight level is in accordance with the observations of Pearsall (1918) that *Lythrum* occurs in shade in "closed cairs" while *Epilobium* is mostly confined to open habitats.

This operation of "compensating mechanism" to reduced light intensity is not without effect on other aspects of the individual's biology. In other words although plants at each light intensity can be said to be equally photosynthetically efficient, they are not equally biologically efficient. In economic terms the individuals at low light intensity require a larger investment of capital (*i.e.*, photosynthetic apparatus of leaves) to give a particular rate of return (*i.e.*, production of fruits and seeds) and are thus biologically less efficient than plants growing in full light intensity. Though it has been claimed earlier, that both are equally efficient in terms of carbon assimilation, yet the reduced biological efficiency is manifested in a greatly lowered reproductive rate, a reduction in the number of rhizomes, flowers, fruits and seeds in both the species (Tables 1 & 2). However, despite the reduction in reproductive potential with increasing shade, there

TABLE 1 Mean number of rhizomes, flowers and fruits per plant developed at various levels of daylight in *Epilobium hirsutum* and *Lythrum salicaria* after 14 weeks in the treatments.

	Daylight levels		
Plants	100%	70%	40%
(a) *Epilobium hirsutum*			
Rhizomes	10.5 (±0.93)	9.6 (±0.62)	4.8 (±0.39)
Flowers	450.5 (±19.53)	168.1 (±12.88)	65.0 (±5.38)
Fruits (capsules)	585.6 (±23.97)	145.2 (±9.71)	120.8 (±5.91)
(b) *Lythrum salicaria*			
Rhizomes	—	—	—
Flowers	975.8 (±39.76)	580.6 (±27.5)	440.4 (±17.8)
Fruits (capsules)	520.4 (±37.95)	150.6 (±13.37)	92.0 (±5.38)

TABLE 2 Mean dry weight of fruits and seeds at various daylight levels in *Epilobium hirstum* and *Lyrthrum salicaria* after 16 weeks in the treatments.

Plants	Daylight levels			
	100%	70%	40%	L.S.D. (P=.05)
Mean dry weight per 50 fruits (mg)				
Lythrum salicaria	381.2	297.6	278.2	14.268
Epilobium hirsutum	1708.5	1625.8	1031.5	18.377
(b) Mean Seed dry weight per 50 fruits (mg)				
Lythrum salicaria	210.66	148.82	132.24	27.798
Epilobium hirsutum	1075.00	946.25	685.18	36.949
(c) Mean dry weight per 100 seeds (mg)				
Lythrum salicaria	5.46	5.31	5.26	0.3126
Epilobium hirsutum	16.27	15.98	14.76	1.6432

is no reduction in individual seed weight (Table 2C). Thus the essential characters of the seed, necessary for its successful germination are maintained at the expense of the seed number. It is, however, emphasized that *Lythrum* is endowed with the most important pre-requisites essential for the successful competition of a species in shade *i.e.*, a genotype which allow phenotypic flexibility to compensate for the reduction in light intensity and an efficient perennation system in the form of root-stocks, allowing persistence of individual and clone into conditions unsuitable for seedling establishment.

Effect of Daylength on Growth

Daylength appears to affect plant form in these species. Seeds of both the species were germinated and seedlings grown on the two lots-one in a daylength of 9 hours and the other in one of 16 hours light in specially prepared black polythene chambers. All other conditions were the same for both treatments.

Seeds of both the species showed germination under short photoperiod and while the post germination growth of *Lythrum* was greatly suppressed, *Epilobium* developed into large rosette form with considerable leaf area and dry weight (Table 3). Short-day plants of both the species were also tested for their critical photoperiod. In *Lythrum* there was no growth response to any photoperiod except the critical photoperiod of 13

TABLE 3. Dry weight and leaf areas in *Epilobium hirsutum* and *Lythrum salicaria* after 10 weeks of treatment in 16hr. photoperiod and 9hr. photoperiod.

Plants	PHOTOPERIODS			
	16 hrs.		9 hrs.	
	Leaf area (cm^2)	Dry weight (mg)	Leaf area (cm^2)	Dry weight (mg)
E. hisutrum	1953.0	19071.8	449.5	1999.0
L. salicaria	1178.4	7969.2	27.0	126.0

hours. There is a critical photoperiod of 14 hours in the case of *Epilobium* in respect of its growth form and flowering, unlike *Lythrum* all increments of light either of intensity or duration during the short-day treatment resulted in a greater amount of carbon fixation. This is of great ecological significance as it passes from minimum to maximum duration of photoperiods during its lite-cycle in nature.

Growth in Different Temperature Regimes

Seedlings of both the species were grown in Fison's Phytotrons to study their growth response at 8 and 18°C temperature regimes. All other conditions were similar in both the phytotrons, *i.e.*, 80% relative humidity, 16-hour photoperiod and 1200 ft.candles light intensity. The temperature levels selected could have releavance to the autumn winter-spring growth cycle of the species in Britian.

Results of growth after 12 weeks of treatment are summarised in Table 4. It can be seen that Q10 of growth is far higher in the case of *Lythrum* compared with that of

TABLE 4. Growth responses of *Epilobium hirsutum* and *Lythrum salicaria* to temperature regimes of 8°C and 18°C after 12 weeks of treatment.

Plant	Temperature regimes 18°C		8°C	
	Leaf area (cm^2)	Dry weight (mg)	Leaf area (cm^2)	Dry weight (mg)
Epilobium hirsutum	825.0	4393.6	264.0	2437.7
Lythrum salicaria	898.6	5673.9	21.5	234.8

	Initial values *Lythrum salicaria*	*Epilobium hirsutum*
Dry weight (mg)	8.23	8.74
Leaf area (cm^2)	3.20	2.83

Epilobium. There is a marked difference in the two species in their growth response to low temperature. The contrast is such that in the case of *Lythrum* (unlike *Epilobium* there is a little increase in dry weight and leaf area over the respective initial values. Growth at 18° C is much better in the case of *Lythrum* plants as compared to their counterparts in *Epilobium*.

In Britian short-days and low temperatures occur together in nature while long days are accompanied by high temperatures. In *Epilobium* ability to germinate at low temperature is complemented by an efficient growth of the seedling into a dwarf rosette under low temperature and short day conditions This may be an imprortant factor in its establishment and competition with other plants. On the other hand *Lythrum* can flourish only in summer when the days are longer and the temperature is high. These different responses may underline the differences in their ecological distribution in the British Isles. *Epilobium* is common throughout the cold northern regions while *Lythrum* is less frequent in Scotland and absent from most of the north (Clapham, Tutin & Warburg, 1952); on the contrary it is widespread and dominant along the warm west coast of Ireland. The general tendency of *Lythrum* to increase in frequency from north to the south temperate regions in central and southern Europe and as far as the sub-tropics in Australia (Black, 1929) whilst *Epilobium* tends to spread northwards (northern-most Europe to Sweden, and north America) from temperate areas, is a reflection of the temperature control operating their geographical distribution.

Growth in Different Dilution of a Standard Nutrient Solution

Plants of both the species were grown in the standard culture solution and its five successive dilutions referred to as S, S/10, S/50, S/100, S/200, and S/300.

In both the species there were similar large successive decreases of performance with increased dilution in respect of the gain of dry weight with time (Fig. 6). As the solu-

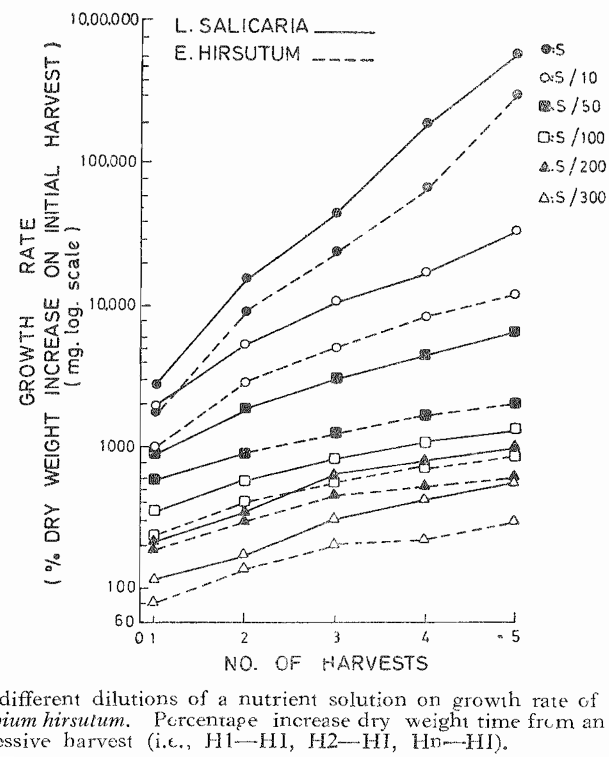

Fig. 6. Effect of different dilutions of a nutrient solution on growth rate of *Lythrum salicaria* and *Epilobium hirsutum*. Percentage increase dry weight time from an initial harvest to each successive harvest (i.e., H1—H1, H2—H1, Hn—H1).

tion became weaker, reduction in the dry weight gain is relatively greater in *Epilobium* than in *Lythrum*. Also, unlike *Epilobium* most of the *Lythrum* plants at S/10 level developed flowers after a prolonged treatment. This satisfactory growth of *Lythrum* in weaker solution (especially at S/10 level) is a reflection of low nutrient requirements of this plant. Plants grown in the standard solution and in its different dilution were analysed for the uptake of nitrogen, phosphorus, potassium and calcium. The determinations were made dwith the Technicon Auto-analyser using the standard methods of Steckel & Flanner (1965) for nitrogen, potassium and calcuim and that of Varley (1966) for phosphorus.

Results presented in Fig. 7, shows that *Epilobium* is not only a plant of high nutrient requirements but also its uptake of these major nutrients is more severely curtailed under nutrient stringency than that of *Lythrum*. On the contrary, *Lythrum* has a dual advantage of low nutrient requirements and high uptake capacity under stringent conditions. Thus in terms of logistics of supply and demand *Lythrum* would have a natural advantage over *Epilobium* in the event of competition. In addition *Lythrum* responded to nurtient

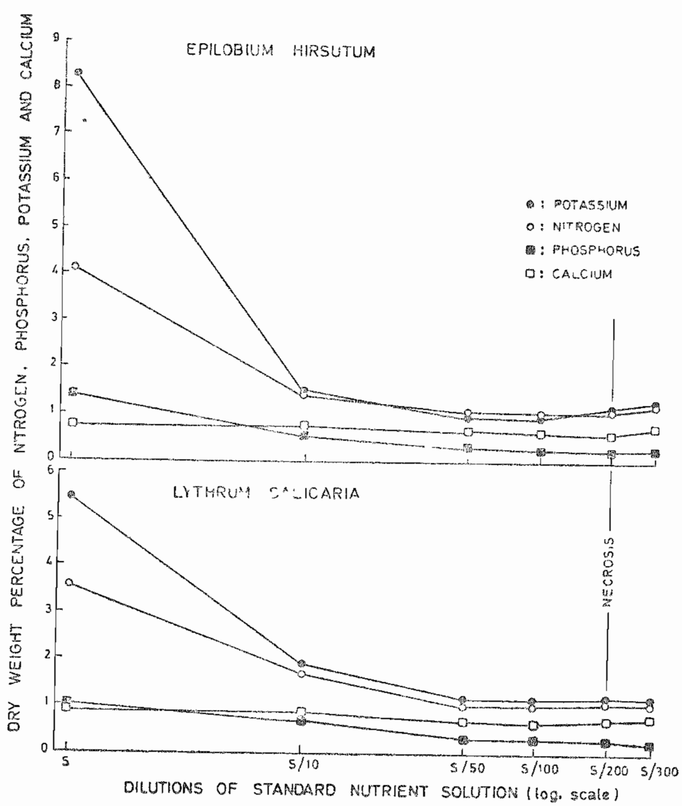

Fig. 7. Effect of different dilutions of a standard nutrient solution on the uptake of Potassium, Nitrogen, Phosphorus and Calcium in *Epilobium hirsutum* and *Lythrum salicaria* (N. P. K and Ca represented as dry weight percentage per plant.)

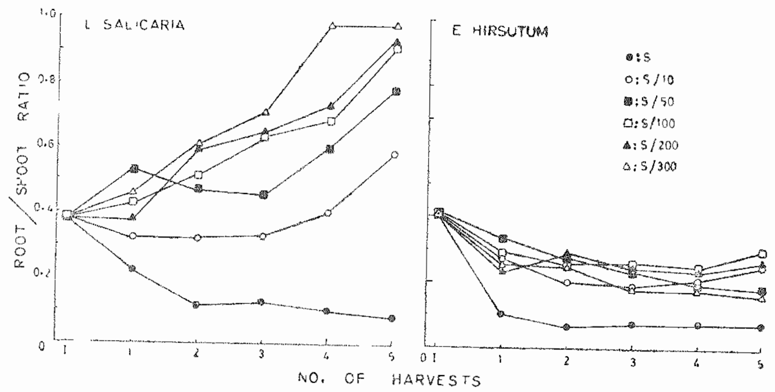

Fig. 8. Effect of different dilutions of a nutrient solution on root shoot ratio in *Lythrum salicaria* and *Epilobium hirsutum*.

stringency by phenotypic plastic response in terms of increased root in porportion to shoot (Fig. 8). In other words as the nutrient stress becomes greater a proportionately larger root system capable of exploiting larger volumes of soil is produced. On the other hand *Epilobium* does not show any marked tendency to increase the root/shoot ratio in response to nutrient stringency. The confinement of *Epilobium* to base rich fens and the silted banks of dykes and its complete exclusion from less fertile sites speaks of its high demands on the nutrient content of the soil and its narrow ecological amplitude. While *Lythrum*, although dominant in fens is tolerant of a variety of habitats such as acidic bogs, marshes and carrs of low nutrient status as well as rich well aerated soil. This is indicative of its wider ecological amplitude.

Due to the simpler plant structure in *Lythrum* and the ability to complete its life-cycle in a short period of time it seems that in the course of coevolution this species has adapted to nutrient poor situations combined with a low rate demand on the nutrient supplying power of the system, a greater efficiency of uptake and the changes in its morphological balance. Most probably, the selective processes caused an overall decline in the plant size with a corresponding increase in the competitive ability which seems to be of survival value.

The results of chemical analysis in the previous experiments on the uptake of N.P.K., and Ca suggested that the stringencies of these individual nutrients might be an important factor in the establishment of these species in nutrient poor soils. The two species were further investigated for their response to stringencies of N.P and K. This was observed by comparing their growth in the standard solution; the same solution with a series of decreasing nitrogen levels as N/10, N/50, N/100 and N/200 and O/N. In the same way two other series of decreasing levels of phosporus and potassium referred to as P/10, P/50, P/100, P/200 and O/P and K/10, K/50, K/100 K/200, O/K respectively were obtained. Throughout, the standard solution is referred to as "S".

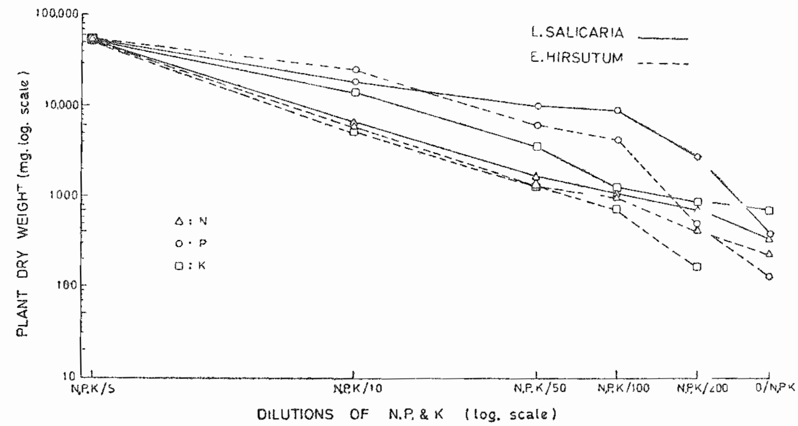

Fig. 9. Effect of different levels of Phosphorus, Nitrogen and Potassium on growth of *Lythrum salicaria* and *Epilobium hirsutum*. (Total plant dry weight after 10 weeks in the treatments.)

The results of dry weight gain after 10 weeks of growth in different treatments are shown collectively in Fig. 9.

Relatively speaking the performance of *Lythrum* is much better as compared to that of *Epilobium*. In *Lythrum* there is a "normal" reduction of growth with a corresponding decrease in the availability of N,P and K. On the other hand, in *Epilobium*, although growth was less affected by phosphorus deficiency, as in the *Lythrum*, nitrogen and potassium deficiencies had a greater depressing effect on the dry weight gain. Potassium deficiency was also accompanied by physiological disorders such as necrosis and root malformation even at K/10 level. The reproductive growth was also differently affected in the two species. In *Lythrum*, flowering occurred in all the 3 deficient series, though much less in the higher deficiencies of nitrogen and potassium. On the contrary in *Epilobium*, flowering and rhizome production occurred upto P/100 and N/10 levels of phosphorus and nitrogen deficiency series but in the potassium deficiency series even at the K/10 level of potassium deficiency there was a complete supression of flower formation and rhizome production. It can be postulated that the deficiency of potassium would play a critical and decisive role in determining the establishment and growth of the two species in low nutrient status soils.

In increasing stringency of major nutrient elements there is a corresponding reduction in the level of reproduction and yield. This has long term effects on the survival and continuation of these plants in nature since a lower potential contribution made to the populations and hence to population dynamics.

COMPETITION

The profound difference in the growth of the two species with respect to light, temperature and nutrients, could have great impact on their competition abilities and survival capacities in nature. An experiment was set up in the glass house to study inter specific as well as intra-specific competition both in low and high nutrient levels. Plants were grown in water culture in a standard solution (s) and a S/20 dilution in wooden tanks at a constant temperature of 25°C. in 2' × 1' wooden tanks and 1000 seedlings of each

TABLE 5. Competition and survival in high and low nutrient regimes at a constant temperature of 25°C. Total number of surviving plants, biomass and mean dry weight perplant in *Ep lobium hirsutum* and *Lythrum salicaria*.

(Initial number at transplantation time= 1000 seedlings in pure stands and 500± 500 1000 in mixed stands)

Plants	Stand	Total Survivors	%Survival	Biomass/ unit area (gm)	Wt./Plant. (gm)
Standard solution					
Lythrum salicaraia	Pure	93	9.3	731.25	7.86
Lythrum salicaria	Mixed	54	10.8	522.00	9.67
Epilobium hirsutum	Mixed	1	0.2	24.00	24.00
Epilobium hirsutum	Pure	4	0.4	144.00	36.00
S/20 Dilution					
Lythrum salicaria	Pure	478	47.8	144.15	0.3016
Lythrum salicaria	Mixed	378	77.6	137.53	0.3554
Epilobium hirsutum	Mixed	—	—	—	—
Epilobium hirsutum	Pure	185	18.5	46.25	0.2500

species were transplanted 1/2 in. apart seperately and mixed together. In all there were three categories of plants in each treatment, *i.e.*, pure *Lythrum* unit pure *Epilobium* unit and a mixed unit. The results of comparative performance of the two species are summarised in Table 5.

In the standard solution performance of *Lythurm* is much better in terms of survival and biomass per unit area as compared to *Epilobium* when these species are grown separately. In the mixed unit only one plant located on the periphery of the tank managed to survive. Dry weight per plant is higher in *Epilobium* because of low survival rate. However, in some of the large surviving *Lythrum* plants the dry wt. per plant, was as high as 43.47 g. In the S/20 dilution both the survival and biomass per unit area was much less in the case of *Epilobium* than in *Lythrum*. In the mixed stand *Lythrum* succeeded in completely eliminating *Epilobium*.

FIELD EXPERIMENTS

Effect of fertilizer on density survival at a high temperature on wet soils

This experiment was carried out in the summer of 1968 at Silwood Park. Berks around margin of a swamp receiving drainage from springs coming of nutrient poor

Bagshot sands (Druce, 1897). Six plots each 10" square were marked out at 9" intervals in two rows after clearing the natural vegetation of the site. One row of three plots was sprinkled with Fison's Topgrow 8" fertilizer at the rate of 2 oz. per plot. This fertilizer is rich, in N,P.K. present in a 3:2:3 ratio. A number of 1024 seedlings were planted 1/2 in. apart in each plot separately and mixed together, so that in the fertilizer treated and non-treated series there was one pure plot of each species and one with the two species mixed together. Soil pH was 5.2 ±0·2. The results of the performance of the two species after six months growth in the two treatments are summarised in Table 6. In the inter-specific competition performance of *Lythrum* in the acidic and nutrient poor soil

TABLE 6. Total survival, biomass per plot and mean-dry weight per plant in *Epilobium hirsutum* and *Lythrum salicaria* in plots with and without fertilizer treatment (summer, 1968).

(Initial number at transplanation time = 1024 seedlings in pure plots and 512 ± 512 = 1024 in mixed plots.

	Without Fertilizer				With Fertilizer			
Plots	Pure	Mixed	Pure	Mixed	Pure	Mixed	Pure	Mixed
Plants	L.S.	L.S.	E.H.	E.H.	L.S.	L.S.	E.H.	E.H.
Total survivors	492	348	359	—	550	439	465	—
% survival	48.05	67.97	35.06	—	35.71	85.74	45.41	—
Biomass/unit area (gm)	942.0	487'0	225.4	—	1705.0	1485.0	697.5	—
Dry wt./plant (gm)	1.915	1.399	0.628	—	3.10	3.38	1.50	—

LS —*Lythrum salicaria*

EH—*Epilobium hirsutum*

was much better than the *Epilobium* both in terms of survival and biomass. In the intra-specific competition *Lythrum* completely eliminated *Epilobium* both in treated and non-treated plots.

Effect of low temperature and over-wintering on competition and survival on nutrient rich soil.

Since *Epilobium* failed to grow in the acidic and nutrient poor soil the above experiment was repeated at wheat-fen Broad, Norfolk, a natural habitat of this species with its nutrient rich and alkaline soil (Buttery, Williams & Lambert, 1965).

A site was selected near the bank of a dyke in the Home Marsh adjoining the river Yare. Six 16 in, square plots were prepared and transplanted with 1024 seedlings per plot as in the previous experiment. There were two replicates of pure plots of each species and two mixed plots. Plantation was completed on 21 October, 1968 and plants were harvested on 20 September, 1969.

TABLE 7. The effect of low temperature and ower wintering on growth, competi' tion and survival in high temperature of the following summer (October 1968 to September, 1967). Total survival, biomass and mean dry weight per plant in pure and mixed plots of *Epilobium hirsutum* and *Lythrum salicaria*.

(Initial number at transplantation time = 1024 seedlings in pure plots and 512+ 512± 1024 in mixed plots).

Plots	Pure		Mixed	
Plants	*L. salicaria*	*E. hirsutum*	*E.hirsutum*	*L. salicaria*
Total survivors	66	17	29	58
% survival	6.44	1.66	2.84	5.68
Biomass/plot (gm)	57.55	67.10	85.60	16.20
Dry weight/plant (gm)	0.872	3.941	2.952	0.276
Average ht./plant (cm.)	20.60	68,60	56.20	11.20

Results are summarised in Table 7. Better performance of *Epilobium* both in the mixed and pure plots shows that when *Epilobium* was given the seasonal advantage of growth at the low temperature of autumn or early spring, it exerts a strong suppressive influence on the growth of *Lythrum* in the following summer. The survival of *Lythrum* in terms of numbers is much higher than that of *Epilobium*, both in the pure and mixed plots. On the other hand, the biomass per unit area, dry weight perplant and average height per plant are markedly higher in case of *Epilobium* than in *Lythrum* both in pure and mixed plots.

These results are suggestive of the fact that *Epilobium* made good growth immediately after transplantation in the autumn of 1968, even when the temperatures were quite low and established itself as small rosette plants by the end of its first season of growth. In the second growing season, in 1969, *Epilobium* had the dual advantage of making an early start in the low temperature of February and of exploiting the stored food material (in its rhizomes) from the previous year's growth. On the other hand, *Lythrum* started its growth in the second season very late (almost ten weeks later) and there did not seem to be any large amount of surplus stored food material from the previous year's growth to boost its growth in the second year.

These esults are a clear evidence of the suppression of *Lythrum's* growth by *Epilobium* in the mixed plots. Although the number of survivors in *Lythrum* was twice that of *Epilobium* but the biomass in the *Epilobium* was five times higher and the dry weight per plant more than ten times higher. This may explain the success and dominance of *Epilobium* in British climatic conditions.

Another experiment on the germination of the two species at low temperature was also carried out at wheat-fen Broad alongwith the previous experiment. Approximately, 30,000 seeds of each species (by weight *i.e.*, 1.9 gm. of *Lythrum* and 5.5. gm. of

Epilobium were uniformly scattered in their respective 3ft. square plots and covered with a thin layer of wet soil. The setting up was completed on 19 October, 1968.

Although there was a flush of seedling emergence in both species in the begining but a great reduction in their number with the passage of time. Comparatively reduction was greater in the number of *Epilobium* seedlings than that of *Lythrum*. At the time of last observation in September, 1969, there were 27 seedlings of *Epilobium* and 487 seedlings of *Lythrum*. All the *Lythrum* seedlings were growing uniformly, 5 to 7 cm in height with upto five pair of small leaves. However, most of the surving *Epilobium* seedlings had grown into small plants 19-24 cm in height with upto nine pairs of broad well developed leaves; there was no flowering but most of these plants had developed two to three long slender rhizomes.

Observations on the germinating seedlings were made periodically. *Epilobium* seeds started germination at the end of February when the temperature was still very low (4.4 °C) and the peak of germination was reached in May with the average maximum temperature of 16.8°C. *Lythrum* on the other hand did not start germination till the end of May and maximum germination was in June when average maximum temperature was 19.5°C. The results show that the seeds collected for over two years readily germinated in the spring of 1969. Also temperature significantly affected germination in two species.

Conclusion

Germination characteristics, the pattern of development and the timing of its phases, plant form and reaction to temperature, light and the chemical nature of the substrate have been discussed to give a greater understanding of various aspects of biology of the species in an effort to explain the mechanism of competition and distribution in nature.

Since *Epilobium* showed a very high percentage germination at below 10°C. and *Lythrum* only at 20°C. obviously in Britian the *Epilobium* seeds can germinate in autumn or early spring while *Lythrum* seeds only in summer.

Further germination and successful seedling growth of *Lythrum* both in alkaline and acidic nutrient rich and poor soils is an attribute important in its occurence in a wide variety of habitats. In the case of *Epilobium* successful germination and seedling establishment could take place in moist, rich and alkaline soils thus restricting the species to sites with sufficient moisture. However, both the species can persist for long periods in suitable sites because of efficient dormancy mechanisms and also seeds are viable for several years.

Of the two species, *Lythrum* was found to be more tolerant of moderate shade than *Epilobium* a difference of greater importance in the ecological distribution of the two species. Pearsall (1918) had reported an increase in the frequency, growth and flowering of *Lythrum* with the increase in light intensity in the "closed carr" Esthwaite Water, England.

The behaviour of the two species in respect of germination and growth to temperature and photoperiod seems to be complementry. In *Epilobium*, the ability to germinate at low temperature is accompanied by an efficient growth of the seedling into a dwarf rosette at low temperature and short-day conditions. In the case of *Lythrum*, the requirement of high temperatures for germination is accompanied by a rapid growth at this temperature and complete suppression of growth at low temperature and short-day conditions. Since in Britian short days and low temperatures occur together, the plants of *Epilobium* would be able to over-winter as green rosettes.

As regards the nutrient relations of the two species, experiments showed that *Epilobium* is not only a plant of high nutrient requirement but its uptake of the major nutrients like potassium, nitrogen and phosphrous is more severely curtailed under nutrient stringency than that of *Lythrum*. On the contrary, *Lythrum* is not only a plant of low nutrient requirements and high uptake capacity under stringent conditions but also responded to any nutrient stringency by a phenotypic plastic response in terms of increased root proportionately to shoot. Of the various nutrients investigated it was found that the deficiency of potassium would play a decisive and crucial role in the establishment and growth of the two species in nature.

These differences in the biology of the two species have a great impact on their competitive abilities. Laboratory and field experiments showed *Lythrum* was highly successful in the inter-specific as well as intra-specific competition both in the high and low nutrient levels under high temperature conditions. On the other hand autumn/ winter established plants of *Epilobium* on nutrient rich alkaline soils out-competed *Lythrum* in the following summer in the inter-specific competition. It can be concluded that *Epilobium* is a good colonizer under the most suitable conditions of soil and temperature. It takes advantage of seasonal growth for its establishment, has a tendency to avoid compeition with *Lythrum* and spreads in territory due to rhizomatous habit of growth. *Lythrum*, on the contrary is not only an aggressive colonizer in favourable circumstances of soil and temperature, especially the latter, but also an efficient competitor even in nutrient poor soils if given a chance to become established.

It is emphasised that the different patterns of ecological and geographical distribution of the two species may be explained on the basis of their different response to various environmental factors. Greater frequency of *Epilobium* from central Europe towards the cold northen regions and in British Isles where it forms larg monospecific stands in contrast to that of *Lythrum* which increases in abundance from north to southern Europe is a reflection of the temperature control of their geographical distribution. Clapham has emphasized that plant distribution and hence the ecosystem are of frightening complexicty ; that environmental control is multifactorial ; that various factors may act and interact in various ways-addittively or compensatingly as major factors or only as triggers and that we are as yet unaware of the causes of the most significant forms of vegetation patterns and distribution. In natural habitats, the observed distribution and inter-relationship of competing species are the outcome of a long period of progressive adjustment to the prevailing environmental conditions. It is, therefore, desirable to analyse this complex enviornment into component parts and to experiment with a factor varying its intensity and keeping other factors constant as far as possible. Nevertheless one of the factors often appears to have predominating influence. In this investigation, it is certain that temperature is a primary factor governing the ecological and geographical distributino of the two species, whereas light and nutrient factors are of secondary nature affecting the localized distribution of the species in the same climatic region.

Lastly it may be added that research in comparative eco-physiology is beginning to discover some of the underlying causes of plant distribution. The need for such environmental biological research has been stressed by a number of workers, (Clapham, 1956; Poore, 1964 ;Watt, 1964; Buttery & Lambert, 1965, Myerscough & Whitehead, 1966, 1967).

References

Black, J.M. 1929. Flora of South Australia. Adelaide.

Blackman, G.E. and A.J. Rutter, 1946. Physiological and Ecological studies in the analysis of Plant Environments.

I. The light factor and distribution of the Bluebell (*Scilla non-scripta*) in woodland communities. Ann. Bot. N.S., 10, 361-390.

Buttery, B.R., W.T. Williams and T.M. Lambert. 1965. Competition between *Glyceria maxima* and *Phragmites* in the region of surlingham Broad. II. The fen gradient. J. Ecol., 53, 183-196.

Clapham, A.R. 1956 Autecological Studies and the Biological flora for the British Isles. J. Ecol.' 44, 1-11.

Clapham, A.R., T.G. Tutin and E.F. Warburg., 1952. The flora of British Isles. Cambridge.

Druce, G.C. 1897. The Flora of Berkshire. Oxford.

Ellis, E.A. 1965. The Broads. The New Naturalist. Collins. London.

Hewitt, F.J. 1952. Sand and water culture method used in the study of plant nutrition. C.A.B. Pub. England.

Hulten, E. 1950. Atlas of the distribution of vascular plants in N.W. Europe. Stockholm.

Myerscough, P.J. and F.H. Whitehead, 1966. Comparative Biology of *Tussilago farfara* L., *Chamaenerion angustifolium* (L); Scop; *Epilobium montanum* L. and *Epilobium adenocaulon* Hausskn. I. General Biology and Germination. New Phytol; 65, 192-21.

Myerscough, P.J. and F.H Whitehead. 1967. Comparative Biology of *Tussilago farfara* L., *Chamaenerion angustifolium* (L) Scop; *Epilobium montanum* L'. and *Epjlobium adenocaulon* Hausskn. Growth and Ecology. New Phytol. 66, 785-823.

Pearsall, W.H. 1918. The aquatic and marsh vegetation of Esthwait Water. J. Ecol., 6, 63-74.

Perring, F.H. and S.M. Walters, 1962. Atlas of the British Flora. London.

Poore, M.E.D. 1964. Integration in the Plant Community. J.Ecol., 52; 213-226.

Post, G.E. 1932. Flora of Syria, Palestine and Sinai (Revised by J.E. Dinsmore) Bierut.

Raven. P.H. 1962. The genus *Epilobium* in the Himalayan region. Bull. Br. Mus. Nat. Hist. E. Botany., **2**: 325.

Shamsi, S.R.A. 1970. Comparative Biology of *Epilobium hirsutum* and *Lythrum salicaria*. Ph.D. Thesis, University of London.

Steckel, J.B. and R.L. Flannery. 1965. Automatic determination of Phosphorus, Potassiun, Calcium and Magnesium in Wet digestion solution of plant tissue. Technicon Symposium "Automation in Analytical Chemistry" New York. N.Y.

Varley, J.A. 1966. Automatic Methods for the determination of Nitrogen, Phosphorus and Potassium in plant material. Analyst, **91**: 119-125.

Watt, A.S. 1964. The Community and the individual. J. Ecol., **52**: 203-212.

Whitehead, F.H. 1962. Experimental Studies of the effect of Wind on plant growth and anatomy. II. *Helianthus annus*. New Phytol., **61**: 59-62.