

PETR PYŠEK

Na Dlážďence 2096, 182 00 Praha 8, Czechoslovakia

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## Sprout Demography and Intraclonal Competition in *Lycium barbarum*, a Clonal Shrub, during an Early Phase of Revegetation

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### Keywords

*Lycium barbarum*, Clonal shrub, Post-fire revegetation, Population of sprouts, Demography, Growth analysis, Intraclonal competition

### Abstract

PYŠEK P. (1991): Sprout demography and intraclonal competition in *Lycium barbarum*, a clonal shrub, during an early phase of revegetation. — *Folia Geobot. Phytotax.*, Praha, 26: 141—169. — A demographic study of post-fire revegetation in a clonal shrub *Lycium barbarum* is presented. Spontaneous development of the sprout population was estimated using both nondestructive and destructive methods and compared to the data from experimentally thinned plots. Relationships between growth parameters (height, biomass, leaf area) and their changes in the course of development are analysed. Description of the seasonal dynamics of the sprout population is given. Intraclonal competition among individual sprouts was observed. Results of the growth analysis are presented for populations of different age.

### INTRODUCTION

Shrubs represent an ecologically important group of plants which may occur in a wide range of habitats. The clonal habit is typical of many shrubs. It may be favoured in extreme habitats where the chances of successful seedling establishment are low (SILVERTOWN 1982). Unfortunately demographic studies on clonal shrubs are few (see HARPER 1977, further more e.g. ABRAHAMSON 1975, WEST et al. 1979, VASEK 1980, AULD 1987, HUENNEKE 1987), mostly because of complicated modular construction (WHITE 1979, BEGON et al. 1986), the different age structure of individual organs and generally difficult identification of single genets in clonal plants (KAYS et HARPER 1974, HARPER 1981, BELL 1984, WATKINSON et WHITE 1985, COOK 1985). In addition, slow growth and a long life span make shrubs notoriously difficult subjects for experimental cultivation for the purposes of studying life cycles and testing hypotheses.

This paper presents a demographic study of the revegetation in a clonal shrub *Lycium barbarum* following the first year after burning. It addresses following questions:

1. How do the relationships between growth parameters (height, biomass, leafiness) vary as the population grows? Is it possible to use any easily measurable growth parameter for nondestructive running observation?

2. What are the mutual relationships among modular units? Which is the appropriate modular level for demographic studies at an early stage of development?

## STUDY SITE

The field work was carried out in the town of Plzeň (lat. 49.46 N, long. 13.24 E), West Bohemia. The mean annual temperature of the area is 7.8 °C, annual precipitation is 495 mm (according to a 50-year average, VESECKÝ et al. 1961). The study site was located along the railway line, 350 m distant from the central railway station, on the right bank of the Radbuza river. *Lycium barbarum* predominated on the exposed (35–40°) south-facing slope. The shrub layer at the locality consisted of *Lonicera tatarica*, *Symphoricarpos rivularis*, *Clematis vitalba*, *Rosa subcanina*, *Berberis vulgaris* and *Rubus* sp. div. Among trees, *Fraxinus excelsior* and *Robinia pseudoacacia* should be mentioned. Herbs occurred only rarely in the undergrowth of the dense *Lycium barbarum* stands (*Ballota nigra*, *Impatiens parviflora*, *Poa nemoralis*, *Urtica dioica* and *Chelidonium majus*).

The area of 20 × 50 m covered by *Lycium barbarum* was completely burned in May 1988. Analyses of soil samples are presented in Table 1. The increase in the content of Cl<sup>-</sup>, SO<sub>4</sub><sup>2-</sup>, Ca<sup>2+</sup> and K<sup>+</sup> is apparent when burnt down places (samples no. 6, 7, 8) are compared with the old stand of *Lycium barbarum* growing in the vicinity (no. 4, 5). The soil was clayey-sandy, loose, drying up, with a high content of ash in the surface layer.

## STUDY SPECIES

*Lycium barbarum* (Solanaceae) is an adventive species (neophyte) in Czechoslovakia. It is a native of China, widely naturalized in Europe (CHAPMAN et al. 1987). Its occurrence is due to plantation in hedges and vineyards and subsequent escape from cultivation (DOSTÁL 1954). It is frequently naturalized in vineyards and on walls and waste ground, along railway lines and in fringe habitats.

Large monospecific thickets of *Lycium barbarum* are formed by older leafless branches covered with horizontal and overhanging upper branches which bear leaves. Stems are up to 2.5–3 m, arching, greyish-white, often spiny (SCHROEDER 1964, CHAPMAN et al. 1987).

The species spreads clonally through the horizontal root system, with clumps of sprouts growing from the root buds (Fig. 1). The individual sprouts bear alternate, shortly petiolate leaves, up to 10 cm, varying from very narrowly elliptical to narrowly lanceolate in form. No seedling recruitment was observed at the locality. Slight predation by aphids occurred at the locality throughout the year. Extensive stands of *Lycium barbarum* were infested by mildew after growth finished at the end of the vegetational period.

The species may serve as an example of modularity apparent at more than one level (HARPER 1977, 1978, WHITE 1979, BEGON et al. 1986, HUTCHINGS 1986a). One can thus recognize modules (a) at the level of clumps of sprouts growing close together from the more or less horizontal root and/or (b) at the level of individual sprouts. For roots lying relatively deep in the soil (more than 10 cm in some cases), sprouts can be rather distant from each other when they reach the ground surface. Moreover, the clumps are often situated close to each other. The sprouts of different clumps can thus grow nearer to each other than those belonging to the same clump. For the resulting problems linked with the identification of clumps in the field, the sprouts are more convenient units and these are the focus of the present study.

Table 1. Soil analyses. Samples were taken on July 25, 1989. The values are given in mg · l<sup>-1</sup>

No.	Description of the sampling site	KCL-eluante	Colorimetry		Titration		Adsorption	
			NO <sub>3</sub> <sup>-</sup>	PO <sub>4</sub> <sup>3-</sup>	SO <sub>4</sub> <sup>2-</sup>	Cl <sup>-</sup>	Ca <sup>2+</sup>	K <sup>+</sup>
		pH						
1	Unburned stand of <i>Robinia pseudacacia</i> , <i>Sambucus nigra</i>	5.39	34.2	0.78	113.83	18.08	45.49	26.1
2	<i>Impatiens parviflora</i> , <i>Cheledonium majus</i>	5.65	35.4	0.93	36.02	33.68	32.26	18.5
3	Unburned foot of the slope	5.30	22.6	0.35	58.6	25.17	24.24	32.2
4	with <i>Lycium barbarum</i>	4.95	19.80	1.15	55.23	37.94	26.45	31.9
5	Old stand of <i>Lycium</i>	4.88	8.12	0.30	14.41	25.17	15.23	3.8
6	Area of plots A, B (burned)	6.72	38.63	0.45	69.16	24.46	36.47	31.1
7	Area of plot T (burned)	4.95	14.3	0.45	72.05	74.46	78.74	45.3
8	The most burned area	5.01	37.0	0.97	221.91	129.77	336.47	61.9

## METHODS

The study plots for detailed observation were located in May 1988, immediately after burning. The following treatment regimes were applied:

a) The plot  $0.5 \times 0.5$  m was designed for running observation (plot R) in the course of the vegetational period. Sprouts were recorded as they emerged. I numbered all individual sprouts with plastic tags fastened around the stem with a wire (HUTCHINGS 1986a). It was necessary to transpose tags to the upper parts of stems during each measurement in order to keep interference with growing sprouts to a minimum. Otherwise, tags must be looked for with difficulty in the lower parts of the stand. Measurements of sprout height were made on the plot weekly at the beginning of revegetation and monthly during the second half of the vegetational period. The plot was harvested on September 16.



Fig. 1. Clump arrangement in *Lycium barbarum*. Soil surface is indicated by a dashed line. Del. J. PŘŠKOVÁ.

Table 2. Survey of the plots according to the treatment applied

Plot	Area (m)	Treatment	No. of replicates	Running observations	Date of harvest	Age at the time of harvesting	Way of analysis
a) R	0.5 × 0.5	--	1	Yes (height measurement)	16. 9.	87 days	Height, number of leaves, biomass, root diameter
b) T	0.5 × 0.5	Experimental thinning	1	Yes (height measurement)	16. 9.	87 days	Height, number of leaves, biomass
c) A	0.5 × 0.5	--	1	No	1. 7.	30 days	Height, number of leaves, biomass, leaf area
B	0.5 × 0.5	--	1	No	14. 8.	74 days	Height, number of leaves, biomass, leaf area, stem basal diameter
d)	1.0 × 1.0	Experimental thinning	5	No	16. 9.	87 days	Total biomass of a clump
e)	0.5 × 0.5	--	2	No	16. 9.	87 days	Total biomass produced in the plot

b) The density of eight sprouts per 0.25 m<sup>2</sup> was experimentally maintained in the thinned plot (T) by regularly removing newly emerged sprouts. One sprout from each clump present in the plot was retained. The running observation was conducted as in the case of plot R.

c) Two quadrat plots 0.25 m<sup>2</sup> were harvested, the first (plot A) on July 1 (after 30 days of population development), and the second (plot B) on September 14 (74 days old population).

Harvested sprouts were divided according to clumps. For each individual sprout the following characteristics were recorded: height, biomass, (separately for stems, leaves, and branches), leaf area, number of leaves, and basal diameter of stem. For estimation of biomass, plant material was dried up for 48 hours at 85 °C. The leaf area assessment was made by the drawing method (RYCHNOVSKÁ et al. 1987).

d) To estimate the maximum biomass produced by a single clump, the sprouts belonging to the other clumps were removed from its vicinity on five plots of 1 m<sup>2</sup>. Variation in the density of clumps and sprouts was also estimated.

e) In addition, two plots of 0.5 × 0.5 m were harvested on September 16 for estimation of the total biomass per plot.

For summarization of the treatments applied see Table 2.

Parameters of growth analysis were calculated from the data obtained (HARPER 1977, MOORE et CHAPMAN 1986, RYCHNOVSKÁ et al. 1987).

The data were analysed using linear regression according to SOKAL et ROHLF (1981). Where necessary, logarithmic transformation was used for calculation.

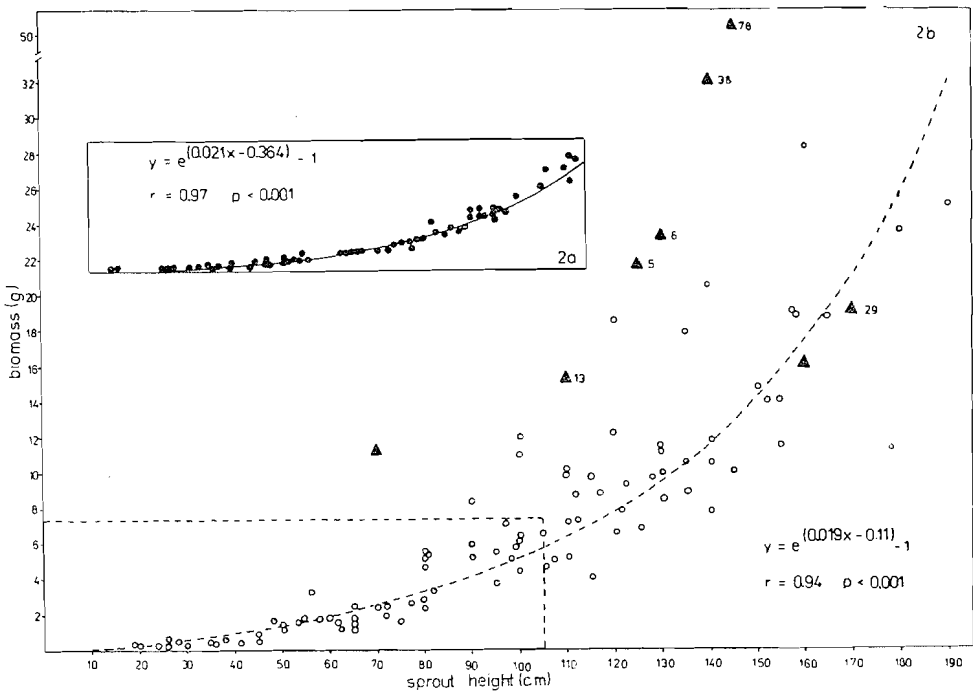


Fig. 2. Sprout biomass plotted against sprout height.

a) 30 days old population (plot A) — full circles

b) 74—87 days old population (plots B, R) — empty circles

Sprouts of the thinned plot (T) — triangles. Numbers indicate percentage proportion of the biomass of branches. Area delimited by the frame on Fig. 2a corresponds to that indicated by the dashed line on Fig. 2b.

RESULTS

Parameters of growth

A close relationship between sprout biomass and sprout height was found in the 30 day old population changing from linear to a J-shaped with increasing sprout height (Fig. 2a). Small morphological diversification within the rapidly growing

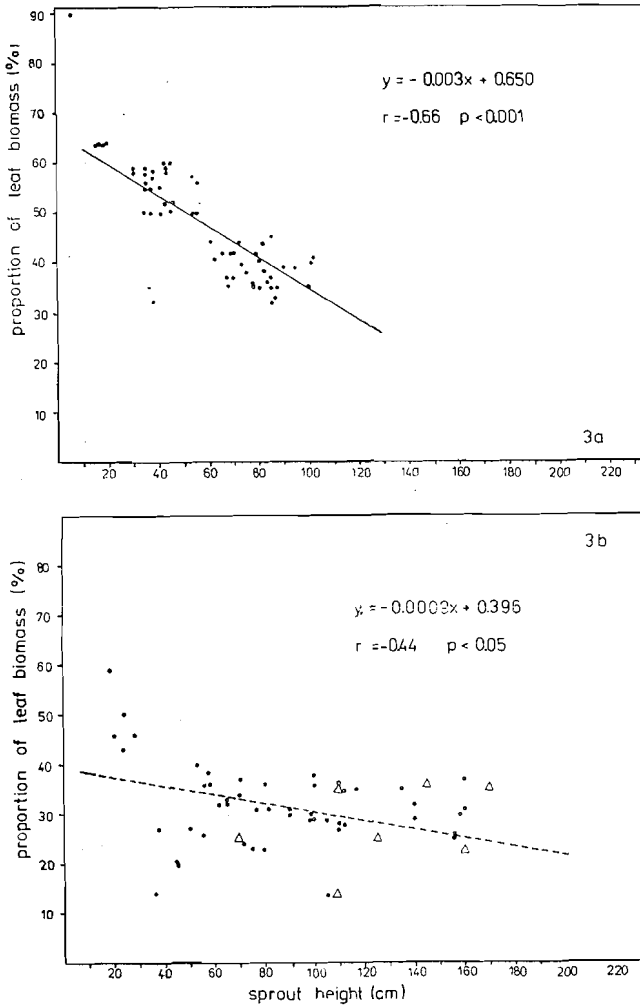


Fig. 3. Proportion of leaf biomass in relation to sprout height.  
 a) 30 days old population (plot A)  
 b) 74 days old population (plot B). Plot T (not included in statistical analysis) — triangles.

Table 3. Performance of sprouts in the experimentally thinned plot T.  
 (+branching from the base of the sprout; 5a - horizontal branch of the sprout 5 laying on the ground surface)

No. of sprout	Height (cm)		No. of leaves		Biomass (g)			Branches					
	24.6.	1.7.	8.7.	22.7.	22.9.	16.9. (harvest)	Total	Stem leaves	Leaves	Stem	Total	Biomass (g)	% of the total sprout biomass
1+	27	60	82	100	105	125	70	(40)	4.44	17.31	21.75	1.15	5.2
2+	25	52	79	110	155	170	131	(57)	6.73	12.33	19.06	5.59	29.3
3	26	58	85	115	125	130	183	(30)	3.45	20.24	23.69	1.43	6.1
4+	28	61	92	120	120	140	235	(34)	8.70	23.37	32.06	12.10	37.7
5+	30	65	95	130	140	145	375	(30)	17.53	18.09	50.65	39.84	78.6
5a	21	49	74	125	140	160	105	(0)	3.31	11.72	15.26	1.99	13.0
6	15	32	58	90	105	110	112	(55)	5.56	9.70	11.39	1.99	13.0
7	-	27	38	55	60	70	33	(33)	2.93	8.46	16.03	1.99	13.0
8	-	21	52	110	140	160	60	(60)	3.67	12.36	16.03	1.99	13.0
Total							1 304	(339)	66.32	189.90	246.22	62.10	25.2



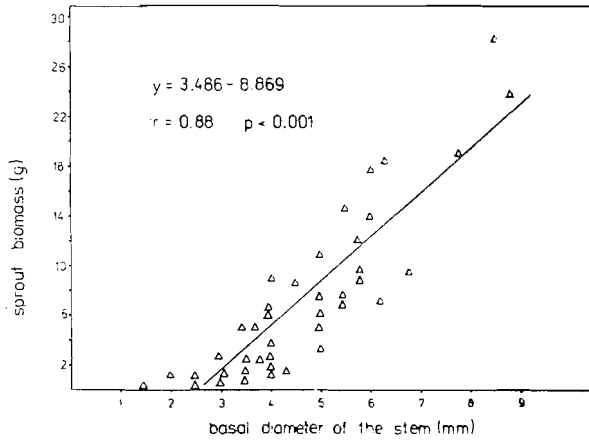


Fig. 4. Sprout biomass plotted against basal diameter of the stem (74 days old population, plot B).

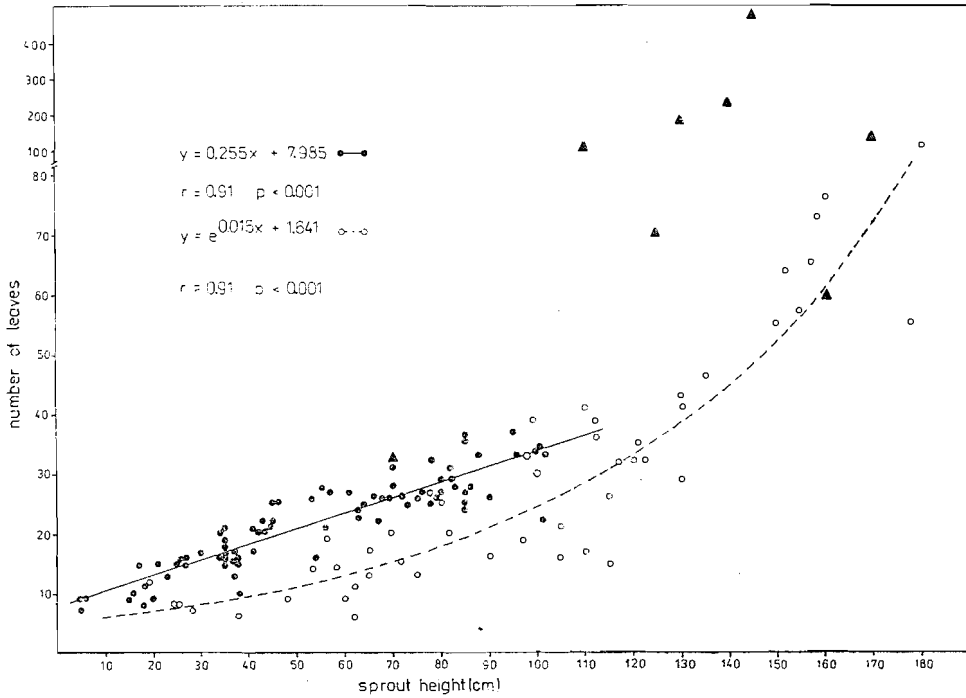


Fig. 5. Number of leaves plotted against sprout height. 30 days old population (plot A) — full circles, 74 days old population (plot B) — empty circles. Plot T — triangles. Note the different scale in the upper part of the figure.

population is reflected by lesser variance of data, increasing variance which is apparent in plot B (Fig. 2b), can be explained by branching and turning to wood. Sprouts of the same height may possess a different biomass and pattern of branching. The influence of branching is conspicuous in sprouts from the thinned plot T; branches may represent up to 78% of total sprout biomass (Table 3). Less obvious correlation between biomass and height has thus been found in plot T.

Changes in the leaf proportion of sprout biomass correspond to the allometric rule (WALLER 1986). 30 days old sprouts have thus relatively more biomass located in leaves than those of the same height harvested at the end of the vegetational period, which have already turned to wood (Fig. 3).

Sprout biomass shows a linear relationship to the basal diameter of the stem (Fig. 4). However, an allometric relationship better fitted by the power function may be expected in the further development.

The number of leaves increased with sprout height (Fig. 5). For the leaves falling from the lower parts of the stem, the number of leaves is fewer in older sprouts than in younger ones of comparable height. Linear relationship between the number of leaves and sprout height was found in smaller sprouts up to approximately 120 cm regardless of population age. However, the curve shows a rapid J-shaped

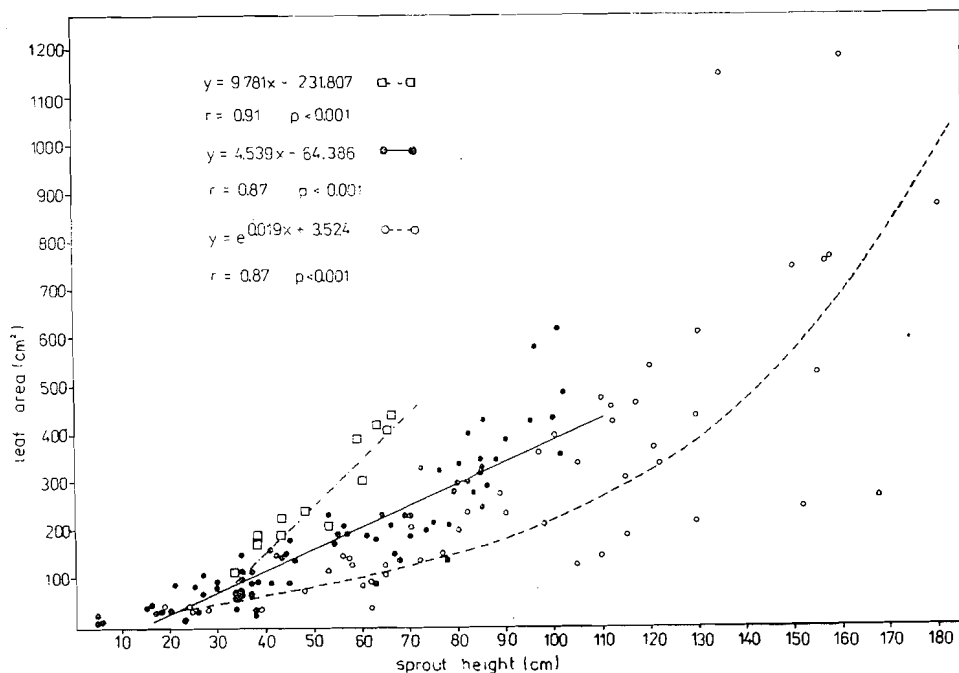


Fig. 6. Leaf area of the sprout plotted against sprout height. Solitary sprouts (30 days old) — squares, 30 days old population (plot A) — full circles, 74 days old population (plot B) — empty circles.

increase in taller sprouts. This is due to the large number of new leaves emerging on branches. A conspicuous increase in the number of leaves per sprout which was observed in plot T is due to the same reason (see Table 3).

The increase with sprout height is also apparent when the leaf area of the sprout is taken into account (Fig. 6). The steepest increase was observed in young solitary sprouts.

The increase of the total leaf area with increasing height is due rather to the increase in the number of leaves than to the enlargement of individual leaves (Fig. 7). Distinct increase with increasing height in the mean leaf area was observed only in the 30 days old population. The highest, vigorously branched sprouts in the older population showed even decrease in the mean leaf area because the leaves located on branches are usually smaller than those growing on stems.

The leaves become thicker during development, which is seen from the changes of the specific leaf area (Fig. 8) expressed as the ratio between leaf area and leaf biomass (RYCHNOVSKÁ et al. 1987). However, regardless of sprout size, generally smaller specific leaf area was recorded in the older population than in the younger one. This indicates a closer relationship of specific leaf area to the age of the sprout rather than to its size. The mean value calculated for one sprout was  $284.8 \text{ cm}^2 \text{ g}^{-1}$  in plot A and  $158.6 \text{ cm}^2 \text{ g}^{-1}$  in plot B, respectively.

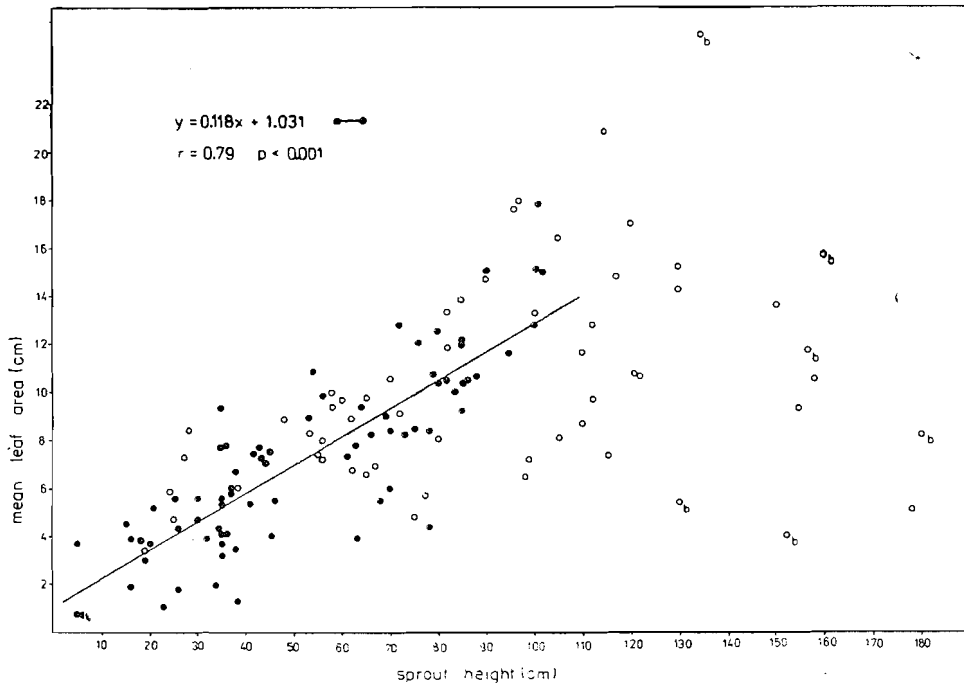


Fig. 7. Mean leaf area plotted against sprout height. 30 days old population (plot A) — full circles. 74 days old population (plot B) — empty circles, b — intensively branched sprouts.

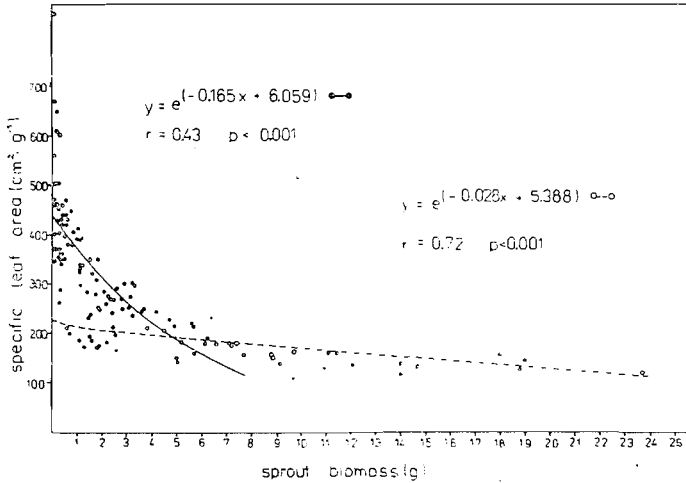


Fig. 8. Specific leaf area plotted against sprout biomass. 30 days old population (plot A) — full circles, 74 days old population (plot B) — empty circles.

### Seasonal dynamics

Unfortunately, the time interval between the burning and the start of revegetation can only be estimated because the exact date of the stand damage is not known. Revegetation did not start simultaneously on the whole area; there was a time delay up to three weeks (from the beginning of June to the beginning of its third decade). This was probably due to the different degree of damage. It can be roughly estimated that the revegetation process started within 2–5 weeks after the fire.

The initial rapid growth in height (up to 4.6 cm · day<sup>-1</sup>, see Fig. 9) was attended by the intense enlargement of leaf area (compare with Fig. 5a). In comparison to both these parameters, the increase in biomass was slow (Fig. 2a) up to the height of 40–50 cm (which corresponds to approximately 10 days of growth in the most rapidly growing sprouts). A conspicuous increase in biomass then appeared which continued until the carrying capacity of the given environment was reached (see chapter Stand structure). After approximately 30 days of development (at the height of dominant sprouts 90–120 cm) all the stems regardless of height turned to wood and the growth in height slowed down (Fig. 9). Maximum value of LAI was reached at this point of development. This was 6.12 m<sup>2</sup> m<sup>-2</sup> in plot A and 6.32 m<sup>2</sup> m<sup>-2</sup> in plot B, respectively. Further emergence of new leaves, especially on branches, was compensated by the leaves falling off stems and so the total leaf area remains stable from now on.

Branching of the highest sprouts started within the next developmental phase, e.g. from the age of 30 days on. Sprouts were bowed by their own weight and

branches grew upwards from their horizontally oriented terminal parts (“Champagnat” pattern of branching sensu HALLÉ et al. 1978). In plot R, branching occurred in the six most vigorous sprouts which had all reached a considerable height and biomass (I/2, IV/1, VIII/3, XIII/1, 2, 7 in Table 4). In the second half of August (after approximately 50 days of growth) the onset of flowering was recorded in several vigorously growing sprouts. However, the number of flowers per sprout was very low as compared with the unburned stand.

Mortality of sprouts was 14.8%. Sprouts which have lost all leaves in the course of the vegetational period were considered dead.

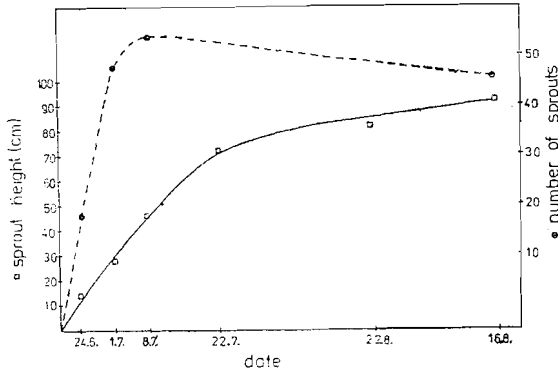


Fig. 9. Changes in the mean sprout height and in the number of sprouts during the vegetational period (plot R).

The differences between growth characteristics calculated for the initial developmental phase (i.e. before the stems turned to wood) and those obtained in the second half of the vegetational period are presented in Table 5. NAR and RGR values were 10 times greater in the early phase of population growth. The total productivity expressed as CGR remained roughly stable throughout the vegetational period. However, if calculated separately for leaves and stems, respectively, seasonal differences in biomass allocation can be seen: The leaf growth rate decreased and, on the contrary, the stem growth rate increased obviously within the second half of the vegetational period.

Fig. 10 illustrates differences in the growth of cohorts in plot R. A cohort was defined as a set of sprouts commencing growth within a certain time interval (HUTCHINGS 1986a). All sprouts present in the plot emerged within 18 days and were divided into three cohorts. Members of the first cohort retained their advantage during the whole vegetational period and, moreover, the distinction became even more profound. Members of later cohorts showed less height increment which is expressed in terms of  $\text{cm} \cdot \text{day}^{-1}$  in Fig. 10. Differences among individual cohorts are presented in Table 6. The first cohort, which comprised 1/3 of the total number of sprouts represented 55.9% of the total biomass produced (Fig. 11).

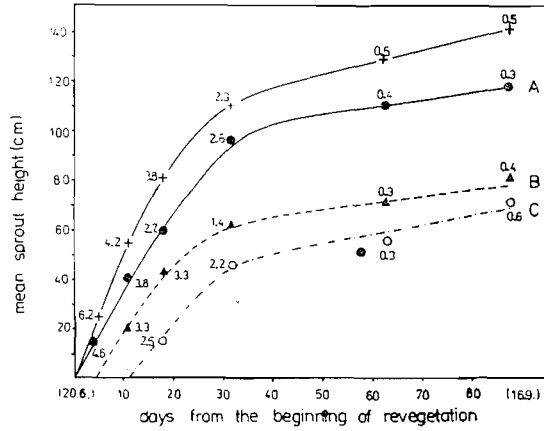


Fig. 10. Performance of cohorts (plot R) expressed as an increase in the mean sprout height in the course of the vegetational period (compare with Table 6). Numbers indicate the rate of the growth in height (cm · day<sup>-1</sup>) calculated for the time interval between observations. Cohorts are designated according to the date of emergence: A 21. – 24. 6., B 25. 6. – 1. 7., C 2. 7. – 8. 7. For comparison, data from the thinned plot T are added (+).

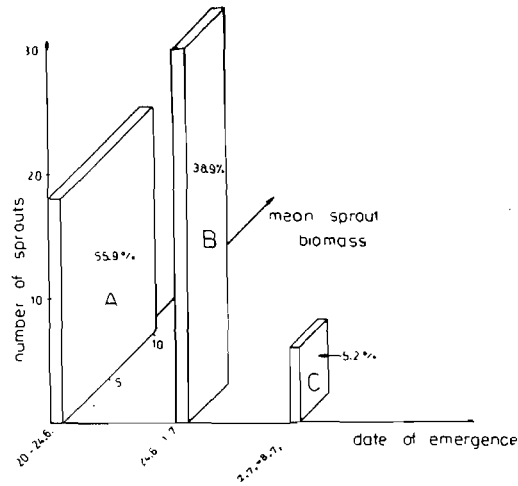


Fig. 11. Comparison of individual cohorts. Percentage share of the total population biomass is expressed by relative extent of the area. Mean sprout biomass (g) is given on the third axis. Cohorts are designated according to the date of emergence as follows: A 21. – 24. 6., B 25. 6. – 1. 7., C 2. 7. – 8. 7.

Table 4. Performance of sprouts in the plot R (harvested at the population age of 87 days)

Clump no.	Sprout no.	Biomass (g)										Allocation into branches
		24. 6.	1. 7.	8. 7.	22. 7.	22. 9.	16. 9. (harvest)	Number of leaves	Leaves	Stem	Total	
R I	1	17	49	80	100	100	100	23	3.62	7.42	11.04	3.9%
	2	21	55	88	105	120	165	62	4.98	13.70	18.68	
	3	12	40	69	102	110	110	23	2.76	7.37	10.13	
	4	—	17	49	105	130	130	33	2.43	8.76	11.19	
R II	1	—	13	—	75	80	80	18	0.53	1.75	2.28	—
	2	—	20	42	25	35	36	7	0.06	0.44	0.44	
	3	—	—	12	25	35	36	7	0.06	0.38	0.44	
	4	—	—	27	90	100	135	35	3.00	7.41	10.41	
R III	1	—	21	49	105	120	128	43	3.15	6.37	9.52	—
	2	—	21	49	105	120	128	43	3.15	6.37	9.52	
	3	—	13	45	50	55	55	7	0.47	1.32	1.79	
	4	—	—	15	25	25	25	0	—	0.33	0.33	
R IV	1	—	18	38	40	40	40	3	0.06	1.08	1.14	—
	2	—	21	22	40	40	40	0	—	0.42	0.42	
	3	—	12	34	90	90	100	34	2.53	9.12	11.95	
	4	—	—	14	40	50	72	8	0.44	1.40	1.84	
R V	1	—	18	40	80	130	140	43	1.33	6.24	7.57	—
	2	—	35	65	95	110	135	32	2.77	5.87	8.64	
	3	—	—	11	40	45	45	4	0.12	0.47	0.59	
	4	—	—	10	80	90	140	44	3.32	7.02	10.34	
R VI	1	—	32	48	60	70	70	19	0.80	1.59	2.39	—
	2	—	49	81	120	120	140	40	2.53	9.07	11.60	
	3	19	49	80	90	90	90	28	1.78	4.09	5.87	
	4	20	51	84	110	130	130	43	3.27	8.10	11.37	
R VII	1	—	7	36	90	95	107	37	1.48	3.87	6.28	—
	2	—	32	57	95	130	130	43	2.58	5.60	8.18	
		6	20	44	80	95	100	34	1.20	2.94	4.14	

Table 4. (Continuation)

Clump no.	Sprout no.	24. 6.	1. 7.	8. 7.	22. 7.	22. 8.	16. 9. (harvest)	Biomass (g)				Allocation into branches
								Number of leaves	Leaves	Stem	Total	
R VIII	1	—	31	52	80	95	95	28	1.82	3.56	5.38	4.8 %
	2	—	—	21	40	45	45	7	0.19	0.74	0.93	
	3	30	62	93	115	120	120	38	5.42	13.17	18.59	
	4	—	22	25	30	30	30	0	—	0.31	0.31	
	5	—	30	51	80	80	80	37	1.66	3.00	4.66	
	6	—	20	38	55	55	55	17	0.67	1.27	1.94	
	7	—	27	52	100	105	125	45	1.75	4.92	6.67	
	8	9	38	61	105	130	145	42	2.29	7.59	9.88	
	9	—	31	52	80	80	80	24	1.86	3.66	5.52	
	10	—	12	15	15	15	15	—	—	—	—	
R IX	1	18	45	73	100	110	110	42	3.23	6.65	9.88	7.9 %
	2	—	7	15	—	—	—	—	—	—	—	
R X	1	10	35	58	83	85	120	41	1.52	4.94	6.46	3.1 %
	2	—	21	40	55	60	65	15	0.85	1.73	2.58	
	3	—	15	29	35	35	35	0	—	0.46	0.46	
R XI	1	14	36	55	70	75	81	31	1.90	3.48	5.38	18.1 %
	2	4	25	40	45	50	50	15	0.38	1.02	1.40	
	3	—	18	23	25	25	28	0	—	0.35	0.35	
R XII	1	4	20	34	50	50	50	13	0.32	1.03	1.35	7.9 %
	2	—	12	18	20	20	20	6	0.12	0.14	0.26	
R XIII	1	12	38	70	120	135	155	38	3.90	11.40	15.30	3.1 %
	2	9	35	70	125	180	190	43	6.05	18.99	25.04	
	3	7	29	58	90	90	90	22	2.57	8.75	11.32	
	4	—	15	37	70	75	80	27	1.38	3.77	5.15	
	5	—	20	46	80	80	80	26	1.64	3.07	4.71	
	6	—	—	20	50	50	75	95	34	0.94	3.68	
	7	19	47	82	120	130	140	48	6.00	14.39	20.39	



Table 5. Growth characteristics

Time interval number of days	June 1 — July 1	July 1 — August 14
	30	44
NAR (net assimilation rate)	$3.06 \times 10^{-3}$	$3.20 \times 10^{-4}$
LAR (leaf area ratio)	67.8	70.9
RGR (relative growth rate)	0.207	0.023
CGR (crop growth rate)	17.00	19.92
	7.16	4.17
	9.84	15.75
		Total
		Leaves
		Stems

Table 6. Differences among cohorts observed in plot R (harvested at the population age of 87 days)

Cohort	Date of emergence	Number of sprouts	Number of leaves		Biomass (g)		Mean height of the sprout (cm)	
			Total	Per sprout	Total	Per sprout		
					Total	% from the total yield		
A	21. — 24. 6.	18	677	37.6	188.98	10.49	55.9	117.5
B	25. 6. — 1. 7.	30	613	20.4	130.93	4.36	38.9	79.8
C	2. 7. — 8. 7.	6	97	16.1	17.71	2.95	5.2	70.3

## Competition among sprouts

The comparison of plot R with plot T where a low density of sprouts was maintained may serve as a comparison of an overcrowded sprout population (total 54 sprouts  $\cdot$  0.25 m<sup>-2</sup>) with one not influenced by density dependent processes (8 sprouts  $\cdot$  0.25 m<sup>-2</sup>).

Sprouts which did not suffer from interference possessed conspicuously different habit and showed more rapid growth. Intensive branching started as early as 1–2 weeks after the revegetation. Branching at the very basis of sprouts was found in some cases. This resulted in rapid occupation of an open space. The growth in height was also faster, even in comparison to the first cohort in plot R. (Fig. 10). However, the final height of sprouts in plot T did not surpass the height recorded in dominant sprouts of plot R. The greater mean value presented on Fig. 10 is due to the absence of suppressed sprouts in plot T which lower the mean value obtained from plot R. Nevertheless, great differences between plots T and R in total biomass (Fig. 2b, Table 3 vs. Table 4) and number of leaves per sprout (Fig. 5) were found. In addition, only the sprouts in plot T showed a normal course of flowering which began in August and was similar to that observed in unburned stands.

The above results indicate that competition for light has taken place within the population of sprouts during revegetation. Due to the rapid development of the stand, the lower layers are overshadowed in a short time. Sprouts suffering from lack of light lose their leaves and eventually may die. Further developmental processes (branching, flowering) are presumably conditioned by reaching the upper layers of the stand.

## Stand structure

The number of sprouts per 1 m<sup>2</sup> varied from 188 to 336 in a fully covered stand (87 days old), the mean value was 252.4 ( $n = 20$ ).

Frequency distribution of biomass is presented in Fig. 12a. To express the distinction from normal distribution, skew  $g_1$  was used (HUTCHINGS 1986b). Skew indicates whether the distribution is negatively ( $g_1 < 0$ ) or positively skewed ( $g_1 > 0$ ) or whether the distribution is symmetrically bell-shaped ( $g_1 = 0$ ). Frequency distribution of sprout biomass is positively skewed and  $g_1$  value increased from 1.40 on June 1 to 4.80 on August 14.

Frequency distribution of sprout height is approximately symmetrical at the beginning and becomes negatively skewed in the course of the vegetational period (Fig. 12b). Some of the suppressed sprouts undergo rapid height extension towards the light and so grow closer to the height of their neighbours. However, these sprouts increase very little in weight (cf. OGDEN 1970, HARPER 1977). Changes in the height distribution in the course of the vegetational period are illustrated in Fig. 13. More or less apparent bimodality of height distribution can be seen in both plots (B and R, Figs. 12b and 13).<sup>1)</sup>

<sup>1)</sup> However, one must keep in mind the limited generality of conclusions drawn from the mutual comparison of plots resulting from a low number of replicates.

The structure of the stand at the level of clumps is presented in Fig. 14 where the position of individual clumps in the plot B was mapped (corresponding data see in Table 8). Different symbols were used according to biomass estimated. The dominant clumps are not distributed evenly in the plot. They are concentrated on the edge of the slope close to the pathway from where the shrub probably spread down the slope. The number of clumps per 1 m<sup>2</sup> was relatively stable (40–56, mean value 46.4, n = 20). This holds true for the covered stands of *Lycium barbarum* whereas more sparse distribution was found at the periphery of the area occupied.

Linear relationship between clump biomass and root diameter can be seen in Fig. 15.

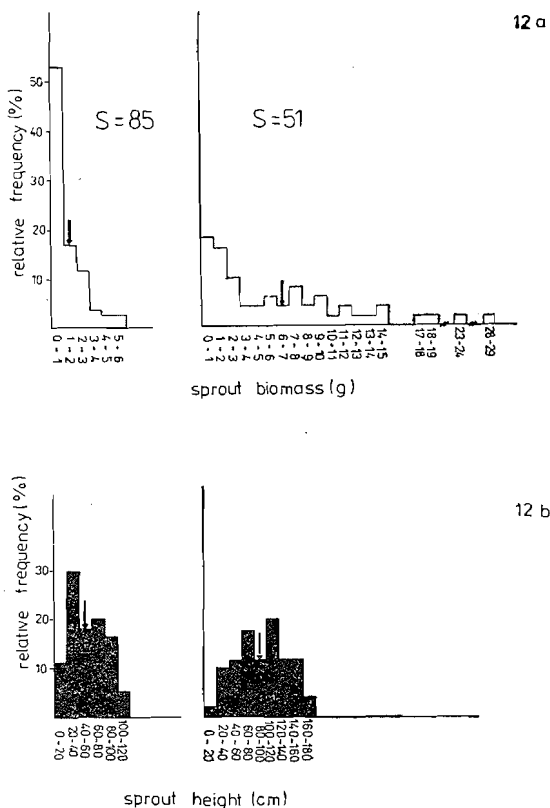


Fig. 12a. Frequency distribution of sprout biomass. Left: 30 days old population (plot A) — variance  $s^2 = 2.506$ , standard deviation  $s = 1.583$ , skew  $g_1 = 1.40$ . Right: 74 days old population (plot B) —  $s^2 = 41.639$ ,  $s = 6.45$ ,  $g_1 = 4.80$ .  
 Fig. 12b. Frequency distribution of sprout height. Left: 30 days old population —  $s^2 = 691.9$ ,  $s = 26.30$ ,  $g_1 = 0.12$ . Right: 74 days old population —  $s^2 = 2786.4$ ,  $s = 52.78$ ,  $g_1 = -1.51$ . Mean values are shown by arrows.

The stand structure expressed as percentual proportion of individual clumps on the total biomass of the harvested plot is presented on Fig. 16. Regardless of the age of the stand which is 30, 74, and 87 days (Table 7–9), respectively, there are usually 1–3 dominant clumps, each of them forming on average 15–20% of total biomass of the plot. Maximum biomass produced by a clump was 70.73 g in plot B,

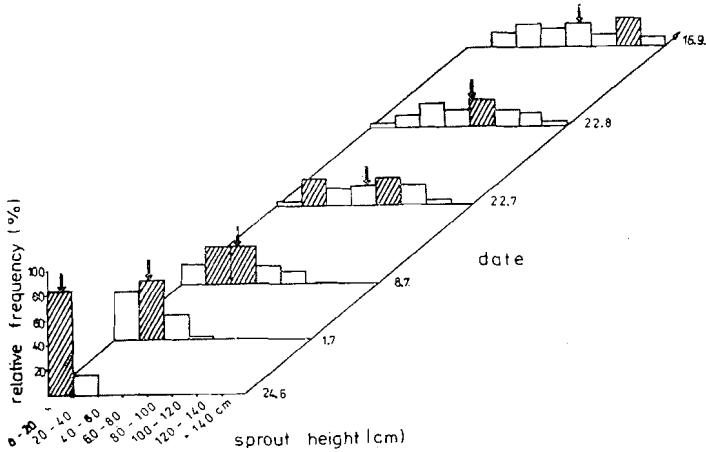


Fig. 13. Changes in the frequency distribution of sprout height in the course of vegetational period (plot R). Prevailing height classes are indicated by hatching. Mean sprout height is shown by a black arrow.

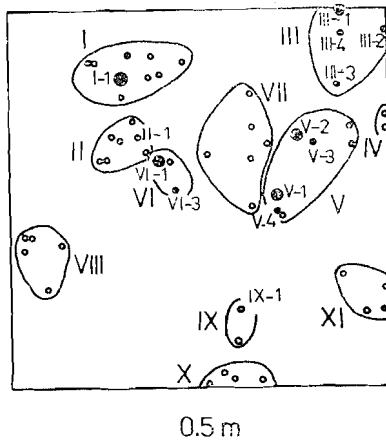


Fig. 14. Distribution of sprouts in the plot B. Sprouts of the same clump are delimited by the line. Numbers of clumps and sprouts correspond to Table 4. Different symbols are used to indicate sprouts according to the biomass produced: small circles -- up to 15 g, large circles -- more than 15 g. Black circles indicate members of the first cohort (emerged on June 6).

Table 7. Performance of clumps in the plot A (harvested at the population age of 30 days). Raw data table containing information of each sprout is available on request

A	Number of sprouts	Number of leaves		Biomass (g)						Leaf area (cm <sup>2</sup> )	
		Total	Per sprout	leaves		stems		total		Total	Per sprout
				Total	Per sprout	Total	Per sprout	Total	Per sprout		
I	8	182	22.7	3.32	0.41	4.18	0.52	7.50	0.93	1 177.9	147.2
II	4	79	19.7	1.00	0.25	0.83	0.21	1.83	0.45	439.3	109.8
III	4	90	22.5	3.01	0.75	4.61	1.15	7.62	1.90	823.3	205.8
IV	6	133	22.1	6.33	1.06	8.29	1.38	14.62	2.44	1 610.0	251.6
V	5	118	23.6	4.32	0.86	6.32	1.26	10.64	2.13	1 221.6	244.2
VI	5	111	18.5	2.60	0.43	2.67	0.45	5.27	0.88	817.5	136.2
VII	6	119	19.8	2.33	0.39	2.10	0.35	4.43	0.74	308.8	61.5
VIII	6	102	17.0	1.48	0.25	1.34	0.22	2.82	0.47	545.1	90.8
IX	10	241	24.1	11.32	1.32	17.78	1.78	29.10	2.91	2 909.0	290.9
X	11	195	17.7	5.61	0.51	7.48	0.68	13.09	1.19	1 667.1	151.5
XI	9	187	20.8	6.43	0.71	10.05	1.11	16.48	1.83	1 691.6	211.4
XII	10	257	25.7	5.98	0.60	8.18	0.82	14.16	2.13	2 131.5	213.1
Plot-1	85	1 814	21.3	53.73	0.64	73.83	0.88	127.56	1.50	1.53 m <sup>2</sup>	182.2
m <sup>-2</sup>	340	7 256		214.9		295.3		510.2		6.12 m <sup>2</sup>	

Table 8. Performance of clumps in the plot B (harvested at the population age of 74 days). Raw data table containing information on each sprout present is available on request

B	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	Biomass (g)						Leaf area (cm <sup>2</sup> )					
												Number of leaves		leaves		stems		total		Per sprout	Allocation into branches	Total	Per sprout
												Total	Per sprout	Total	Per sprout	Total	Per sprout	Total	Per sprout				
	9	275	30.5	21.55	2.39	49.18	5.46	70.73	7.86	3.2 %	3 038.6	379.8											
	7	180	25.7	9.39	1.34	27.17	3.88	36.56	5.22		1 264.7	210.7											
	4	190	47.5	19.18	4.80	40.89	10.22	60.05	15.01	4.1 %	2 781.2	695.3											
	2	16	8.0	0.26	0.13	0.30	0.15	0.56	0.28		84.6	42.3											
	7	241	34.4	22.42	3.20	45.88	6.55	68.30	9.76	5.1 %	3 629.0	518.4											
	3	120	40.0	7.27	2.42	21.89	7.30	29.16	9.72	11.7 %	1 027.0	342.3											
	6	125	20.8	5.83	0.97	16.12	2.69	21.95	3.66		1 043.4	173.9											
	5	89	17.8	5.50	1.10	15.53	3.11	21.03	4.21		993.6	248.4											
	2	88	44.0	1.96	0.98	13.18	6.59	15.14	7.57	9.3 %	296.5	148.2											
	4	76	19.0	2.08	0.52	7.17	1.79	9.25	2.31		793.3	198.3											
	4	83	20.8	4.13	1.03	9.84	2.46	13.97	3.49		844.6	211.1											
Plot-1	53	1 483	28.0	99.57	1.88	247.15	4.66	346.72	6.79		1.58 m <sup>2</sup>	315.9											
m <sup>-2</sup>	212	5 932		398.3		988.6		1 386.9			6.32 m <sup>2</sup>												

and 82.59 g in plot R. Those clumps which were experimentally protected against the influence of neighbours did not exceed these values (mean biomass 70.45 g; n = 5).<sup>2)</sup>

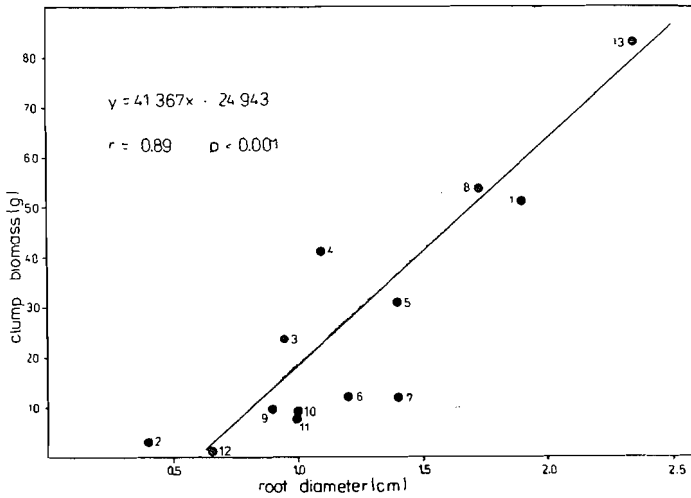


Fig. 15. Clump biomass plotted against root diameter (plot R). Numbers of clumps correspond to the Table 11.

Table 9. Performance of clumps in the plot R (harvested at the population age of 87 days)

	Number of sprouts	Number of leaves	Biomass (g)			Allocation into branches
			leaves	stems	total	
I	5	141	13.79	37.25	51.04	1.5 %
II	2	25	0.59	2.13	2.72	
III	6	88	6.68	16.93	23.61	6.5 %
IV	6	165	10.81	30.12	40.93	
V	4	130	8.38	22.84	31.22	
VI	2	80	3.91	7.28	11.19	1.7 %
VII	2	77	3.78	8.54	12.32	
VIII	10	238	15.66	38.22	53.88	
IX	2	43	3.23	6.65	9.88	
X	3	56	2.37	7.13	9.50	6.8 %
XI	3	46	2.28	4.85	7.13	
XII	2	19	0.44	1.17	1.61	
XIII	7	280	22.48	60.11	82.59	
Plot-1	54	1 387	94.40	243.22	337.62	2.9 %
m <sup>-2</sup>	208	5 548	377.6	972.9	1 350.5	

<sup>2)</sup> These results must be treated with caution, however, because replicate plots are lacking.

Regarding total biomass produced, there is very good accordance in the values obtained from both plots which were harvested at the end of the vegetational period: 1386.9 and 1350.5 gm<sup>2</sup>, respectively. This is despite the localization of sampled plots in different parts of the slope, time delay in the start of the revegetation (June 3 vs. June 21) and the different age of harvested populations. One can thus consider the value obtained to correspond to the carrying capacity of the environment. This is confirmed by additional samplings which were used for the estimation of total biomass only (1330.3 gm<sup>2</sup> and 1411.2 gm<sup>2</sup>).

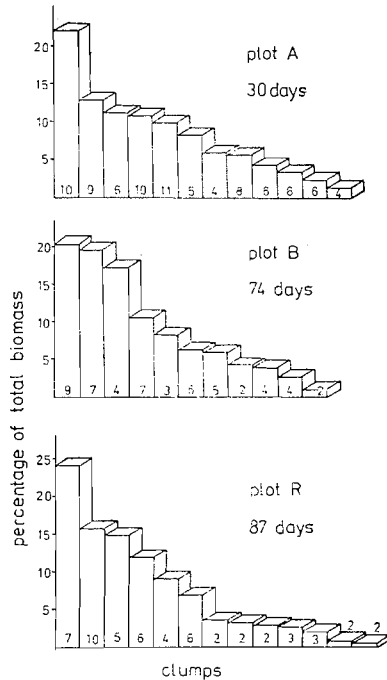


Fig. 16. Performance of clumps expressed as their share of total biomass produced in the plot. Numbers in bars represent the numbers of sprouts present in the clump.

## CONCLUSIONS AND DISCUSSION

Conclusion 1: Sprout height is a parameter convenient for nondestructive measurement of the population growth in the early developmental phase when sprouts do not branch. It is more or less closely correlated with other growth characteristics (biomass, leaf area). Branching caused greater variance in data and weaker correlation of all parameters observed. Biomass is thus considered the more appropriate characteristic for estimation of branched sprouts. However, these results indicate that the nondestructive estimation of further population development is problematic.

An indirect method to estimate the aerial biomass based on its correlation with



height was proposed by FITZGERALD (1983) for several single-stemmed woody plants. The use of the method is restricted to young unbranched shoots, however (e.g. *Populus tremuloides*).

Integration of plant demography with sampling methods of productivity analysis seems to be very useful (FLOWER-ELLIS 1980). Nowadays it represents a new level of demographic-productivity analysis and provides valuable information on proportional biomass allocation (WHITE 1984). This allocation changes as the plant grows. My results are in accordance with those of SVEINBJÖRNSSON (1978) who has found in *Betula pubescens* subsp. *tortuosa* decrease of proportional leaf biomass from about 50% of total plant dry weight for the smallest plants to about 10% of total plant dry weight for 1 m tall plants, after which the proportion remains stable. In general, taller plants are forced to allocate proportionally more resources to supportive stems and so usually grow only as tall as necessary to compete (WALLER 1986). There is evidence given by MØDVE (1987) that burning has no effect on allocation of resources in some cases.

Conclusion 2: Competition for light took place among sprouts. Both growth rate and branching were reduced by interference from neighbours, which resulted in the reduction of biomass produced per sprout. Some features of sprout population development and its changes in the course of the vegetational period are similar to the behaviour of populations of genetically different individuals. A single sprout is the most convenient module for the demographic study in *Lycium barbarum* because it can be easily defined, counted and measured.

The typical response to the presence of neighbours is reduction in size which is almost invariably expressed in terms of biomass (HARPER 1977, WHITE 1984). Change in morphology due to interference — especially the intensive branching in spatially unlimited conditions — have been described both for herbs (NEW 1961) and trees (WHITE 1984). As a consequence of competition for light, more rapid growth in height was reported (GIVNISH 1982). Size hierarchies can also be caused by interference from neighbouring plants. It may be more likely to occur for light, since dominant plants (or sprouts) may capture a disproportionate share of incoming solar radiation (MITCHELL-OLDS 1987). However, as emphasized by HUTCHINGS (1986b), the sole existence of size hierarchy in itself is not evidence that competition has taken place. It is very dangerous to measure competition simply by looking for correlated sizes of neighbours, since competition cannot be measured when the effects of competition and local site quality are confounded (MITCHELL-OLDS 1987). As discussed by HARPER (1981), one of the ways to show competition is to remove individuals and show that those that remain benefit from the removal. In the case of *Lycium barbarum*, release from density stress caused conspicuous morphological changes and vigorous growth of sprouts that remained. The reasons for considering light to be a decisive factor are as follows:

1. Sprouts are genetically uniform, so differences in the individual ability to capture resources are minimized.
2. The root system is common to a great extent which diminishes differences resulting from local site quality.

The structural differentiation of the population is thus conditioned mostly by relationships in the above ground space.

The situation described represents competition on the level of individual organs or apical meristems, respectively (WHITE 1984, SILANDER 1985). Competition for light is in fact the interference among individual leaves which leads to the mutual shading of parts of the same genet ("narcissistic competition" sensu HARPER 1981).

This study does not provide sufficient data to evaluate conceivable competition among clumps. Individual clumps vary considerably in total biomass and number and size of sprouts. It seems that an individual clump is capable of producing only a limited biomass in a given time interval. Clumps experimentally freed from the interference of neighbours did not produce more biomass than did the most vigorous ones growing in fully developed stands. However, studies dealing with competition among ramets and with problems of intraspecific regulation of growth have been conducted exclusively on herbs so far (KAYS et HARPER 1974, HARPER 1985, COOK 1985, ERIKSSON 1986).

The final wave of herbaceous reiteration in the top canopy of a tree has been compared to a population of herbs by HALLÉ et al. (1978), WHITE (1979). The advantage of an early emergence of sprouts and the gradual exaggeration of differences in the course of development of the sprout population in *Lycium barbarum* corresponds to the results obtained from investigations of herbaceous populations (ROSS et HARPER 1972 quoted by HARPER 1977, WALLER 1986). Frequency distribution of both biomass and height of sprouts is similar to that known for populations of genetically independent individuals (OGDEN 1970, HARPER 1977, HUTCHINGS 1986b). The bimodality typical of height distribution of sprouts in *Lycium barbarum* is suggested as more usual in circumstances where competition took place (FORD et NEWBOULD 1970 quoted by HUTCHINGS 1986b).

Conclusion 3: The capability of rapid revegetation and the high growth rate enable *Lycium barbarum* to go through the critical herbaceous period in the development of a woody plant quickly. Due to these characters as well as due to the clonal habit of growth, *Lycium barbarum* is thus capable of successful occupation of frequently disturbed sites.

Fire is an important mode of ecological disturbance (RYKIEL 1985). Clonal character of growth is typical of species of fire-disturbed habitats (COOK 1985, KOOP 1987). Burning of above ground biomass stimulates vegetative growth from specialized underground organs (KOMAREK 1983, CRAWLEY 1986). There is a large body of literature on post-fire resprouting from root buds (PELTON 1963 quoted by HARPER 1977, CRAWLEY 1986, KEELEY et ZEDLER 1978 quoted by AULD 1987, BROWN et DEBYLE 1987) or lignotubers (AULD 1987, KOOP 1987). This type of revegetation after burning was observed even in normally nonsprouting species (DRISCOLL 1963). In general, low seed production is typical of clonal shrubs and seedling recruitment appears to be a rare event (SILVERTOWN 1982, HUENNEKE 1987). From the point of view of life strategy, *Lycium barbarum* belongs rather to the "phalanx" type (CLEGG 1978 quoted by HARPER 1981, LOVETT-DOUST 1981, BELL 1984, SILANDER 1985).

The effects of fire bring about improvement of habitat conditions which makes the site suitable for subsequent occupation. Breakdown of plant litter, breaking dormancy in many species and the release of nutrients from accumulated standing dead biomass are the main consequences of fire (CRAWLEY 1986). Despite these

favourable circumstances, *Lycium barbarum* formed exclusively monospecific stands at the locality investigated. Only rarely were seedlings of *Robinia pseudo-acacia* recorded.

CGR values calculated for *Lycium barbarum* is 2–4 times higher than those reported by RYCHNOVSKÁ et al. (1985) for meadow communities. A comparable value was recorded only in the stands of *Glyceria maxima*. Similarly, the biomass produced by *Lycium barbarum* in 70–85 days is comparable with the whole year's yield of the most productive fertilized meadows (RYCHNOVSKÁ et al. 1985). However, one must keep in mind that such high productivity is restricted to an early phase of development in *Lycium barbarum*.

Provided the population is growing exponentially, the RGR value can be formally identified with the intrinsic rate of natural increase of a population (HARPER 1977). However, even the value calculated on the base of data obtained on June 1 (30 days old population) was influenced by interference from neighbouring sprouts. In general, rapid growth is typical of root suckers since they can use a previously established root system (KOOP 1987).

#### Acknowledgements

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#### SUMMARY

1. The dependence of sprout biomass, number of leaves and leaf area on sprout height was closer in the 30 days old sprout population than in the 74 days old one. Increasing variance in data in the course of the vegetational period is due to the sprouts branching and turning to wood. Sprout height is thus a convenient parameter for nondestructive measurement of population growth only until branching occurs.

2. Initial rapid growth in height is attended by the intense enlargement of leaf area. Maximum value of LAI (6.12–6.32 m<sup>2</sup>m<sup>-2</sup>) was reached after approximately 30 days of growth. Total biomass harvested at the end of the vegetational period varied from 1330.3 to 1411.2 g m<sup>-2</sup>. Maximum biomass produced by a single sprout was 28.18 g, the corresponding value for a single clump was 82.59 g. Number of sprouts per 1 m<sup>2</sup> varied from 188 to 336; number of clumps per 1 m<sup>2</sup> was 40–56. Mortality of sprouts was 14.8%.

3. NAR and RGR values were 10 times greater in the early phase of population growth than in the second half of the vegetational period. CGR remained stable throughout the vegetational season. However, if calculated separately, the leaf growth rate decreased from 7.16 to 4.17 g m<sup>-2</sup> day<sup>-1</sup> and, on the other hand, the stem growth rate increased from 9.84 to 15.57 g m<sup>-2</sup> day<sup>-1</sup>.

4. Competition for light took place within the population of sprouts during revegetation. Growth rate and branching were reduced by interference from neighbours which resulted in the reduction of sprout biomass. Maximum sprout biomass produced in the experimentally thinned plot, where the sprouts were freed from competition, was 50.65 g.

5. The frequency distribution of sprout biomass and sprout height is similar to that known for populations of genetically independent individuals. The frequency distribution of sprout biomass was positively skewed and  $g_1$  values increased from 1.40 in June to 4.80 in August. The frequency distribution of sprout height was approximately symmetrical at the beginning and became negatively skewed ( $g_1 = -1.51$ ) in the course of the vegetational period.

6. Owing to the high growth rate and clonal spreading, *Lycium barbarum* is capable of successful occupation of frequently disturbed sites.

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