TRENDS OF DEVELOPMENT IN THE EARLY STAGES OF MIXED NATURAL REGENERATIONS OF ASH AND SYCOMORE

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1. I N T R O D U C T I O N

Early regeneration-phases of ash (Fraxinus excelsior L.) and sycomore (Acer pseudoplatanus L.) were studied in the experimental forest 'Aalmoeseneie ', of the State University of Ghent, where mixed regenerations under cover arose spontaneously in the spring of 1977*.

Six sample plots of 5 m x 10 m (I to VI) werd laid out. In the four corners and the centre of each plot, 5 squares (A, B, ... E) of 1 m x 1 m each were distinguished and further subdivided into basic units of 25 cm x 25 cm (1 to 16). A total of 6 sample plots, 30 squares and 480 basic units was thus analysed. (Fig. 1). The basic idea behind this procedure was to avoid disproportions between the area covered by basic research units and the dimensions of the seedlings; further to create an opportunity for changing space levels, according to the growth of the seedlings and spatial variations. A total of 9 surveys were made between june 1977 (first year; 1st. growing season) and october 1978 (second year; 2nd growing season).

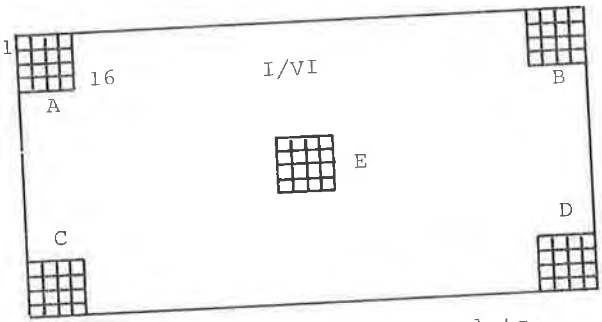

Fig. 1. Disposition of sample plots.

The regeneration occurred under the cover of fairly dense oak - stands with a low proportion of sycomore :

Sample plot	Number of stems/ha	Basal area m2/ha	% of Basal area			
			Oak	Ash	Sycom.	Other spec.
I.II	530	32	26	20	8	46
III.IV	530	24	42	16	3	39
V.VI	464	32	28	14	4	54

During summer an average of no more than 2,86 % of light radiation in the open reaches the forest soil, partly because of a well-developed secondary shrub-stratum.

* The ' Aalmoeseneie, is a semi-natural forest on sandy-loamy soil near Ghent at an elevation of 11 to 21 m above sea level. Annual temperature reaches 9,6° C and precipitation 865 mm. Oak (Quercus robur L.) is the most important species next to beech. The age of the dominant tree varies between 50 and 80 years.

2. INITIAL REGENERATION DENSITY

In the formation of a regeneration group the number of seedlings continually increases toward a culmination point over a period of variable length. After this point the number of seedlings steadily decreases (Fig. 2) The actual number of seedlings at any moment is the result of opposite phenomens : continual establishment and, subsequently, uninterrupted disappearance of seedlings due to external influences (1st. degree selection) and internal competition (2nd degree selection). The rate of establishment and destruction, the length of the regeneration period, the relative importance of primary and secondary natural selection, as well as of interspecific and intraspecific competition determine the pattern of spatial distribution and redistribution of species. All these phenomens, acting simultaneously, affect the structuration of the forest. They create opportunities, but also set the limits for silvicultural interventions.

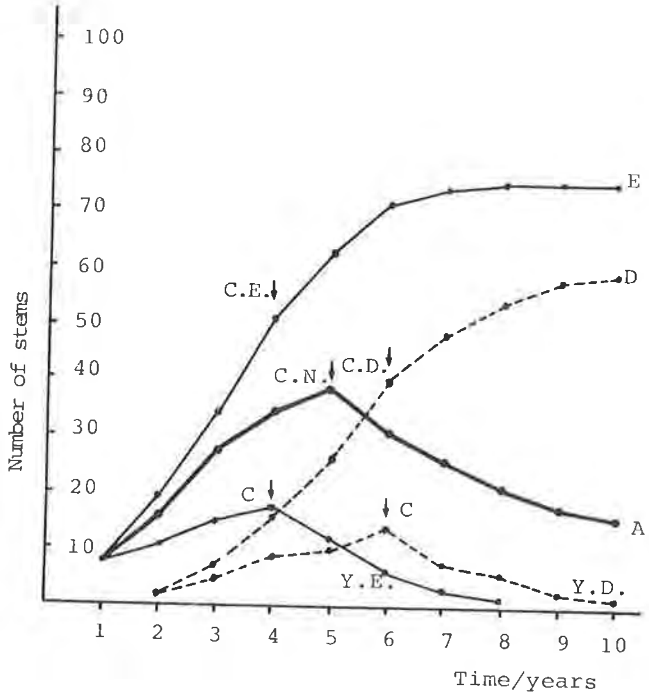

Fig. 2. Evolution of number of seedlings
E = Cumulative establishment
D = Cumulative destruction
A = Actual number of seedlings
Y = Yearly E and D
C = Culmination

Establishment occurred very quickly at Gontrode. A first assessment in june 1977 (Tab.1) revealed the presence of an average of 18.687 seedlings/are as the result of a single burst of regeneration, comprising an average of 13.470 ashes (72,1 %), 4,840 sycomores (25,9 %), 287 oaks (1,5 %) and 90 other species (0,5 %) pro are. The real initial number of seedlings might have been higher as the first and most critical period of establishment - the transition to autonomous life of the seedlings - was already over at the moment of the first survey (june, 1977).

Tab.1 : Number of seedlings/m^2 at different stages (month year)

	Plot	6.77 N_1	7.77	8.77	9.77	10.77 N_2	7.78 N_3	8.78	9.78	10.78 N_4
Ash	I	162.6	133.8	106.4	89.4	77.8	20.0	9.0	8.4	5.0
	II	153.2	142.0	117.4	104.8	101.0	28.3	17.0	14.5	7.0
	III	172.4	158.6	141.8	134.2	116.2	62.2	46.0	43.4	29.2
	IV	137.8	117.4	102.2	92.2	85.4	34.8	24.8	24.3	13.3
	V	55.2	53.8	48.0	46.2	42.2	19.8	15.0	13.4	11.8
	VI	127.0	123.4	113.0	107.0	98.0	51.0	39.2	31.0	26.0
	$\bar{N}$	134.7	121.5	104.8	95.6	86.8	36.0	25.2	22.5	15.4
Sycomore	I	114.8	112.2	112.2	108.0	107.8	91.8	88.3	85.8	82.0
	II	83.6	79.4	77.4	77.0	77.6	63.5	57.8	57.0	54.8
	III	8.0	8.0	7.6	7.8	7.0	6.8	7.2	7.8	7.2
	IV	33.6	27.8	28.2	27.6	27.6	29.3	29.3	29.5	28.0
	V	35.4	34.2	35.2	33.8	34.2	35.6	35.0	36.2	34.4
	VI	15.0	13.8	14.0	13.0	13.4	13.2	13.6	14.2	13.4
	$\bar{N}$	48.4	45.9	45.8	44.5	44.6	40.0	38.5	38.4	36.6
Oak	I	1.6	1.6	4.0	2.8	3.4	4.3	3.8	3.3	3.3
	II	3.8	3.4	4.0	4.0	4.2	4.3	4.3	4.3	4.8
	III	4.6	5.6	7.8	7.8	7.2	5.8	5.6	5.2	4.8
	IV	6.4	11.2	12.8	9.8	10.8	8.0	6.5	5.5	5.0
	V	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
	VI	0.6	0.6	0.8	0.8	1.0	0.4	0.4	0.4	0.6
	$\bar{N}$	2.9	3.9	4.9	4.2	4.5	3.8	3.5	3.1	3.1
Other species	I	0.2	1.4	1.4	1.0	0.8	0.3	0.5	0.5	0.5
	II	0.0	1.2	2.8	2.8	2.4	2.8	3.0	2.5	2.5
	III	0.2	1.0	1.2	1.2	1.0	1.2	1.0	0.8	0.6
	IV	3.0	3.0	3.4	2.8	2.4	2.3	2.0	2.3	1.8
	V	1.2	3.0	2.0	2.2	2.0	2.4	2.4	2.4	1.6
	VI	0.8	0.4	1.4	1.2	1.6	0.8	0.8	0.8	0.6
	$\bar{N}$	0.9	1.7	2.0	1.9	1.7	1.6	1.6	1.5	1.3
Total	I	279.2	250.0	224.0	201.2	189.8	116.3	101.5	98.0	90.8
	II	240.6	226.0	201.6	188.6	185.2	98.8	82.0	78.3	69.0
	III	185.2	173.2	158.4	151.0	131.4	76.0	59.8	57.2	41.8
	IV	180.8	159.4	146.5	132.4	126.6	74.3	62.5	61.5	48.0
	V	92.0	91.2	85.4	82.2	78.6	58.0	52.6	52.2	48.0
	VI	143.4	138.2	129.2	122.0	114.0	65.4	54.0	46.4	40.6
	$\bar{N}$	186.9	173.0	157.5	146.2	137.6	81.4	68.7	65.6	56.4

Tab. 2 Variation on the level of squares and sample plots of the number of seedlings/m2 in june 1977 (N1) and october 1978 (N4).

Level	Plot	Species		Max.		Min.		Average A	s	s% of A
Squares (A - E)	I	Ash	N1	197	A	124	D	162.6	32.88	20.2
			N4	15	B	0	D	4.0	3.28	82.0
		Sycom.	N1	154	A	64	B	114.8	43.35	36.9
			N4	137	A	0	E	65.6	49.21	75.0
	II	Ash	N1	301	B	41	E	153.2	94.53	61.7
			N4	19	B	0	E	5.6	5.20	92.9
		Sycom.	N1	109	C	53	B	83.6	23.15	27.7
			N4	72	D	0	C	43.8	28.27	64.5
	III	Ash	N1	224	D	110	C	172.4	47.47	27.5
			N4	64	A	3	E	29.4	23.92	81.4
		Sycom.	N1	12	E	5	A	8.0	2.87	35.9
			N4	10	E	5	C	7.2	1.92	26.7
	IV	Ash	N1	210	D	72	C	137.8	50.79	36.9
			N4	26	D	0	E	10.6	10.16	95.8
		Sycom.	N1	55	B	13	D	33.6	19.38	57.7
			N4	57	B	0	E	22.5	22.48	99.9
	V	Ash	N1	75	C	28	E	55.2	24.42	44.2
			N4	34	B	0	D	11.8	11.01	93.3
		Sycom.	N1	65	B	12	D	35.4	5.39	15.2
			N4	61	B	8	D	34.4	21.55	62.6
	VI	Ash	N1	250	E	73	A	127.0	72.08	56.8
			N4	87	E	6	C	26.0	24.26	47.2
		Sycom.	N1	34	D	1	A	15.0	14.27	95.1
			N4	38	C	1	A	23.8	4.90	24.8
Plots	Ash		N1	172	III	55	V	134.7	42.26	31.4
			N4	29	III	5	I	15.4	9.12	59.3
	Sycomore		N1	114	I	8	III	48.4	42.83	88.5
			N4	82	I	7	III	36.6	27.83	76.1
	Grand Total		N1	279	I	92	V	185.2	67.15	36.3
			N4	91	I	41	VI	56.4	19.73	35.0

Tab. 3. Initial (june 77) and final (october 78) composition of regeneration groups (in %)

Plot	Initial composition			Final composition		
	Ash	Sycomore	other species	Ash	Sycomore	other species
I	58.24	41.12	0.64	5.51	90.36	4.13
II	63.67	34.75	1.58	10.14	79.35	10.51
III	93.09	4.32	2.59	69.86	17.22	12.92
IV	76.22	18.58	5.20	27.60	58.33	14.07
V	60.000	38.48	1.52	24.58	71.67	3.75
VI	88.56	10.46	0.98	64.04	33.00	2.96
Total	72.07	25.90	2.03	27.28	64.99	7.73

Tab. 4. Ratio of number of seedlings ash/sycomore on the level of squares and sample plots. ($N_{Ash}/ N_{Syc.}$).

Plot / Sq	Initial situation (1st assessment)						Final situation (End of observation period)					
	A	B	C	D	E	Tot.	A	B	C	D	E	Tot.
I	0.85	3.08	1.33	1.68	1.24	1.42	0.02	0.25	0.03	0.00	-	0.06
II	1.69	5.68	1.11	1.58	0.59	1.83	0.15	0.32	-	0.01	0.00	0.13
III	41.60	37.33	1.57	18.10	11.58	21.55	9.14	4.83	2.40	4.88	0.30	4.06
IV	5.00	2.47	1.38	16.15	6.82	5.84	0.30	0.26	0.19	5.20	-	0.47
V	1.87	1.12	1.67	2.42	1.65	1.56	0.30	0.56	0.29	0.00	0.00	0.34
VI	73.00	20.80	8.89	3.76	9.62	8.47	10.00	6.00	0.10	0.48	3.22	1.94

The density of occupation shows great variation on different levels. (Tab. 2).

On the level of sample plots the total number of seedlings at first count varies between 92 and 279 m2, 55 to 172 / m^2 for ash and 8 to 114/m^2 for sycomore. On the level of squares the variations are greater : 28 to 301 m^2 for ash and 1 to 154/m^2 for sycomore. On the level of basic units the seedling-density even varies between 0 and 704/m^2.

The composition of the regeneration is also different (Tab.3). In all groups ash dominates by numbers, but the ratio ash/sycomore is subject to considerable variation in space and time (Tab. 4). The variation within the sycomore-population is greater than within the ash-population, indicating a more uniform covering of available space by ash, whereas sycomore-regeneration is more dispersed and locally concentrated.

The considerable density of regeneration as a whole and of the main species separately, is indicative for the high degree of regeneration pressure, considering the low level of light radiation. No direct relationship seems to exist between density and composition of the regeneration groups and the characteristics of the covering stands. The densities of ash and sycomore regenerations are not correlated. There is no evidence of a complementary relationship between both species in the early stages of establishment.

The variation in density and composition of regeneration nuclei within a restricted space does however not permit to qualify the regenerations, their pattern and establishment, as accidental. Spatial variation is to be interpreted in function of the dimensions of the seedlings and only microecological analysis on an suitable scale could furnish definitive proof in one sense or the other. From a silvicultural point of view the accidental character of these acute bursts of regeneration is considered as hypothetical.

The high degree of spatial variation in the primary regeneration stages, on the other hand, creates opportunities for alternative choice regarding intervention and potential composition of the future stand. In this respect even the number of oak-seedlings, with an average of 28.700/ha and a maximal density of 64.000/ha, is not neglectable.

3. EARLY DEVELOPMENTAL TRENDS

The number of seedlings reaches or has already past the culmination point at the moment of the first survey, a few weeks after establishment started. Between this moment (june 1977) and the end of the observation period (october 1978) an evolution with distinct features takes place (Tab. 1) :

- General and quick reduction of the number of seedlings.
- Unequal resistance of the species to reduction.
- Low level of additional regeneration
- High degree of spatial variation of all phenomens.

3.1. Reduction of numbers

At the end of the 2nd growing season and within less than 18 months after establishment began, the total number of seedlings is reduced from between 92/m2 (V) and 279/m2 (I) to between 41/m2 (VI) and 91 m2 (I) (Tab. 1). This reduction, corresponding to an average loss of 69,8 %, however varying between 47,8 % (V) and 77.4 % (III), is not to be considered as exceptional. (Tab. 5).

Tab. 5. Periodical survival rate (Actual number of seedlings/ Initial number of seedlings in %).

Species	Plot	N_2/N_1	N_3/N_1	$N_4/N1$	N_3/N_2	$N_4/N3$
Ash	I	47.8	12.3	3.1	25.7	25.0
	II	65.9	18.4	4.6	28.0	24.8
	III	67.4	36.1	16.9	53.5	46.9
	IV	62.3	25.2	9.6	40.5	38.1
	V	76.4	35.9	21.4	46.9	59.6
	VI	77.2	40.2	20.5	52.0	51.0
	Tot.	63.4	26.7	11.4	41.5	42.8
Sycomore	I	93.9	79.9	71.4	85.1	89.4
	II	92.8	76.0	65.5	81.8	86.2
	III	87.5	85.0	90.0	97.1	105.9
	IV	82.1	87.2	83.3	106.0	95.7
	V	96.6	100.6	97.2	104.0	96.6
	VI	89.3	88.0	89.3	98.5	101.5
	Tot.	92.1	82.6	75.6	89.7	91.6
All species	I	68.0	41.6	32.5	61.2	78.1
	II	77.0	41.0	28.7	53.3	69.9
	III	71.0	41.0	22.6	57.8	55.0
	IV	70.0	41.1	26.5	58.6	64.6
	V	85.4	63.0	52.2	73.8	82.8
	VI	79.5	45.6	28.3	57.4	62.1
	Tot.	73.6	43.6	30.2	59.2	69.2

N_1 = Initial number of seedlings 1977
N_2 = Final number of seedlings 1977
N_3 = Initial number of seedlings 1978
N_4 = Final number of seedlings 1978.

At the end of the 1st growing season, nearly 74 % of all seedlings survive (N2/N1 ; Tab. 5). The most important reduction occurs during winter when nearly 41 % (N3/N2) of all seedlings, still present at the end of the 1st growing season, disappear, reducing the number of seedlings to about 44 % of the initial number (N3/N1). During the 2nd vegetation period another reduction to about 70 % of all seedlings surviving winter occurs (N4/N3). It leads to a survival rate of 30 % at the end of the 2nd season in comparison to the initial situation (N4/N1). The observed development is clearly characterized by intense numerical reduction during winter, stressing the importance of external influences.

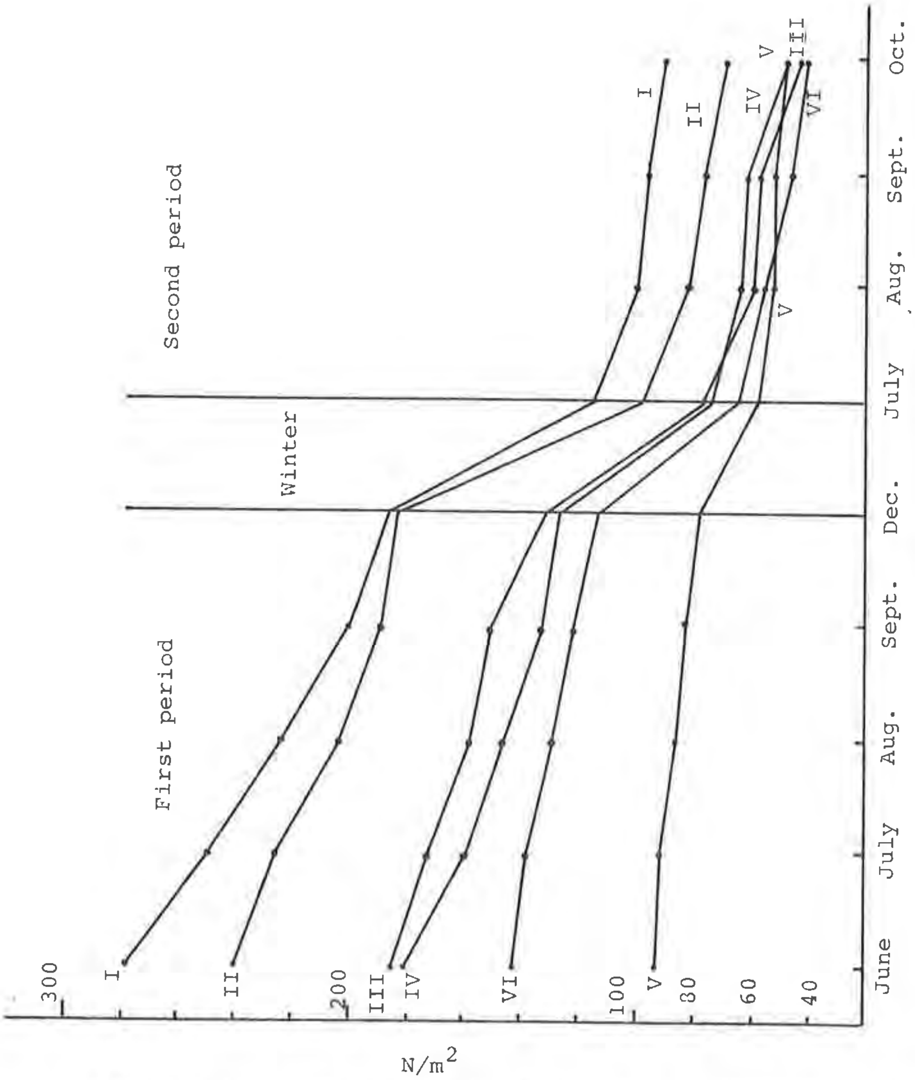

Fig.3. Evolution of number of seedlings (N/m2) in squares I - VI

Furthermore, the intensity of reductions, absolutely and relatively, increases with initial regeneration density. As a consequence the density levels of all plots come within a closer range after a relatively short time (Fig. 3). The ratio between plot I (maximal initial density) and plot V (lowest initial density) p.ex. diminishes from 3,03 at the start to 1.89 at the end of the observation period. The tendency toward egalization is visible in regenerations as a whole, but also applies to species, considered separately (Fig. 4).

3.2. Unequal resistance of species

The difference in resistance to reduction of the species and their unequal potential for survival is of direct importance (Tab. 1). Ash suffers most; the reduction of the number of sycomore seedlings is rather limited; the regeneration density of oak and other accessory species often seems to increase slightly in the course of the first two seasons.

Only 11.4 % of ash seedlings survive at the end of the 2nd vegetation period, although still representing 15.4 seedlings/m2 (Tab. 1). Spatial variations are important : On the level of sample plots, the rate of survival varies between 3.1 % and 21.4 % or between densities of 5/m2 and 29/m2. On the level of squares this trend is no less evident (Tab. 6): In 7 out of a total of 30 squares ash has disappeared completely although its initial regeneration density reached 28 to

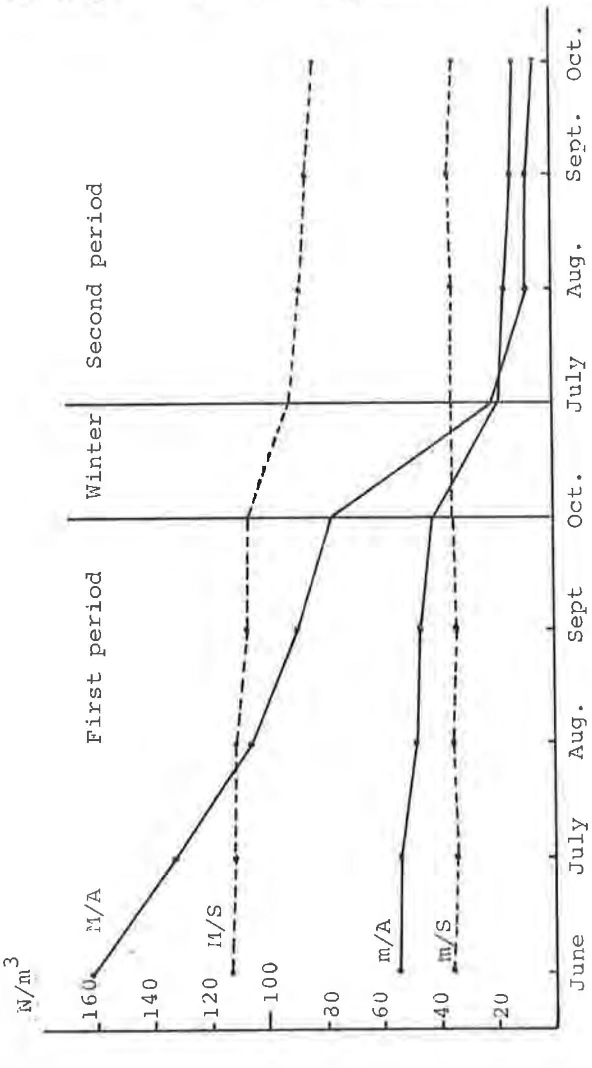

Fig.4. Evolution of number of seedlings (N/m^2) for Ash (A) and sycomore (S) in plots with maximal (M) and minimal (m) initial density.

170 seedlings/m2 ; in 10 more squares relative density (N4/N1) has been reduced to less than 10 %.

Reduction of ash is a little more than average at the end of the 1st vegetation period with 36.5 % against 26.4 % for total regeneration. (Tab. 5). It greatly varies in space, even at short distances and within the same plot (between 67.9 % in V.E. and 6.9 % in V.B.)(Tab. 6). It is fairly mild during the 1st growing season, but high during winter when it reaches 58,5 % on the level of sample plots, lowering initial density of occupation to about 26.7 %. The same rate of reduction is maintained during the 2nd vegetation period (57.2 % on the level of sample plots). It ultimately lowers density to 11.4 % in comparison to initial establishment. (N4/N1).

For ash, there is no evidence of any correlation between initial density (N1) and either density at a later stage, rate of survival or type of development.

The other components of the regeneration groups, especially sycomore and oak, behave differently and possess a higher potential for early survival.

The number of sycomore seedlings decreases only with an average of 7.9 % (plots) (Tab. 5) to 10.3 % (squares) (Tab. 6) during the 1st vegetation period (N2/N1), with 10.3 % (plots) to 7.0 % (squares) during winter (N3/N2) and again with 8.4 % (plots) to 2.5 % (squares) in the course of the 2nd growing season. On the level of sample plots the number of seedlings is thus reduced over two vegetation periods with no more than 24,4 % from an average of 48,4/m2 to 36,6/m2 (Tab. 1). Only in 3 squares with an initial density for sycomore of 17/m2, 109 m2 and 144/m2, this species has completely disappeared, but in 7 squares more than 90 % of sycomore-seedlings survive and in 5 squares their number even increased.

For oak normal reduction is compensated by new establishment, increasing the average number of seedlings from 2,9/m2 initially to 3.1/m2 at the end of the observation period. A wide rage of spatial variation exists on the level of sample plots, with densities from 0,2 to 6.4/m2 initially and 0.2 to 5.0/m2 at the end of the 1nd year.

From a total of 9 assessments, executed over a period of two growing seasons a general picture of the developmental trends in the early stages of regeneration can be deduced :

1. For the totality of all species, a general pattern of reduction is distinguishable on the level of sample plots (Fig. 3) :

   1st growing season : fairly mild reduction
   1st winter : intensification of reduction
   2nd growing season : reduction on about the same level as during 1st. season.

This kind of development demonstrates the importance of external influences and the relatively restricted signification of internal competition.

2. The general pattern of reduction is determined by the initial dominance in numbers of ash, as neither sycomore (Fig. 4) nor oak separately (Fig. 5) follow this general pattern of reduction (Fig. 6).
3. As a consequence, the composition of the regeneration groups and the relationship between species is already profoundly modified in the early phases of development (Tab. 4).

In a general way oak is able to maintain and even to improve its position relatively and absolutely. The relationship ash/sycomore, as indicated by the ratio of the number of seedlings ash/sycomore, changes considerably :

Plot	Start	End
I	1.42	0.06
II	1.83	0.13
III	21.55	4.06
IV	4.10	0.47
V	1.56	0.34
VI	8.47	1.94
Tot.	2.78	0.42

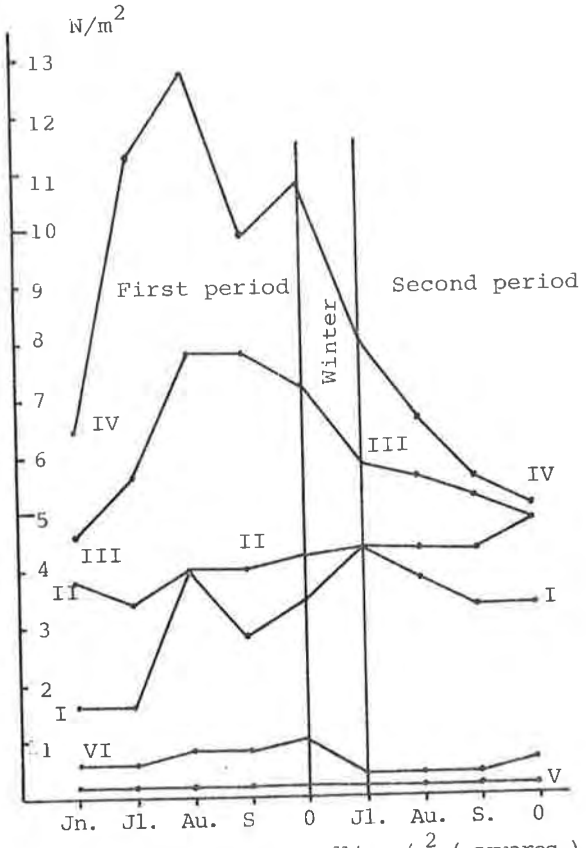

Fig. 5. Number of oak-seedlings/m^2 (squares)

Ash, dominating in numbers at the moment of establishment (72.07 %), becomes secondary (28.28 %) to sycomore (64.99 %) at the end of the 2nd growing year. The changes are still more important on the level of squares (Tab.4). From a silvicultural point of view, the difference in pattern of behavior between ash and sycomore is significant. Their relationship changes rapidly and profoundly : Syçomore-regeneration consolidates early, whereas ash suffers severe reduction in numbers. Both species prove their early tolerance by establishing under a dense cover, but sycomore undoubtly is the more tolerant and resistant. It suffers no competition from ash. On the other hand, there is no indication that the quick decrease in the

Tab. 6. Number of seedlings and rate of survival on the level of squares (in %)

Plot	Square	Ash N/m^2		Ash Survival rate N_F / N_I					Sycomore N/m^2		Sycomore Survival rate N_F/N_I				
		N_1	N_4	N_2/N_1	N_3/N_1	N_4/N_1	N_3/N_2	N_4/N_3	N_1	N_4	N_2/N_1	N_3/N_1	N_4/N_1	N_3/N_2	N_4/N_3
I	A	131	3	40.4	12.2	2.3	30.2	18.8	154	137	103.8	104.5	88.9	100.6	85.1
	B	197	15	57.3	19.3	7.6	39.6	39.5	64	59	85.9	96.9	92.1	112.7	95.2
	C	183	2	42.6	8.2	1.1	19.2	13.3	138	77	91.3	63.0	55.8	69.0	86.5
	D	124	0	35.4	8.9	0	25.0	0	74	55	91.9	77.0	74.3	83.8	96.5
	E	178	-	56.7	-	-	-	-	144	-	90.2	-	-	-	-
II	A	124	8	65.7	21.4	5.7	32.6	26.7	83	54	86.7	74.7	65.0	86.1	87.1
	B	301	19	74.7	23.9	6.3	32.0	26.4	53	60	101.8	124.5	113.2	122.2	90.9
	C	121	-	66.1	-	-	-	-	109	-	91.7	-	-	-	-
	D	163	1	53.3	4.3	0.6	8.0	14.3	103	72	95.1	77.7	69.9	81.6	90.0
	E	41	0	51.2	9.8	0	19.0	0	70	33	91.4	65.7	47.1	71.9	71.7
III	A	208	64	83.6	51.4	30.7	61.5	59.8	5	7	120.0	140.0	140.0	116.7	100.0
	B	224	29	64.3	34.4	12.9	53.5	37.7	6	6	100.0	100.0	100.0	100.0	100.0
	C	110	12	57.2	31.8	10.9	55.6	34.3	7	5	42.8	57.1	71.4	133.3	125.0
	D	181	39	66.8	40.3	20.9	60.3	52.1	10	8	100.0	70.0	80.0	70.0	114.3
	E	139	3	56.8	13.7	2.1	24.1	15.8	12	10	83.3	83.3	83.3	100.0	100.0
IV	A	155	7	53.5	14.2	4.5	26.5	31.8	31	23	87.1	77.4	74.2	88.9	95.8
	B	136	15	63.2	30.1	11.0	47.7	36.6	55	57	105.4	109.1	103.6	103.4	95.0
	C	72	5	51.3	11.1	6.9	21.6	62.5	52	27	69.2	53.8	51.9	77.8	96.4
	D	210	26	75.2	32.4	12.3	43.0	38.2	13	5	69.2	38.5	38.4	55.6	100.0
	E	116	-	56.0	-	-	-	-	17	-	47.0	-	-	-	-

Tab. 6 . (continued)

Plot	Square	Ash							Sycomore						
		N/m^2		Survival rate N_F / N_I					N/m^2		Survival rate N_F / N_I				
		N_1	N_4	N_2/N_1	N_3/N_1	N_4/N_1	N_3/N_2	N_4/N_3	N_1	N_4	N_2/N_1	N_3/N_1	N_4/N_1	N_3/N_2	N_4/N_3
V	A	71	13	81.7	33.8	18.3	41.2	54.2	38	44	97.3	118.4	115.7	121.6	97.8
	B	73	34	93.1	61.6	46.5	66.2	75.6	65	61	98.4	98.5	93.8	100.0	95.3
	C	75	12	82.6	33.3	16.0	40.3	48.0	45	42	95.5	93.3	93.3	97.7	100.0
	D	29	0	48.2	3.4	0	7.1	0	12	8	75.0	66.7	66.6	88.9	100.0
	E	28	0	32.1	14.3	0	44.4	0	17	17	105.8	111.8	100.0	105.6	89.5
VI	A	73	10	61.6	26.0	13.7	42.2	56.6	1	1	100.0	100.0	100.0	100.0	100.0
	B	104	12	80.7	32.7	11.5	40.5	35.3	5	2	100.0	40.0	40.0	40.0	100.0
	C	80	6	67.5	25.0	7.5	37.0	30.0	9	58	88.8	55.6	64.6	62.5	120.0
	D	128	15	71.8	32.0	11.7	44.6	36.6	34	31	85.3	88.2	91.1	103.4	103.3
	E	250	87	86.0	56.4	34.8	65.6	61.7	26	27	92.3	107.7	103.8	116.7	96.4
Mean		134.7	15.8	63.6	25.4	11.0	37.9	33.4	48.4	39.7	89.7	84.9	82.1	93.0	97.5

N_1 : Initial number of seedlings 1977
N_2 : Final number of seedlings 1977
N_3 : Initial number of seedlings 1978
N_4 : Final number of seedlings 1978.

number of ash-seedlings is caused by internal competition, especially by any inhibitive effect of sycomore on ash.

Additional regeneration during the 2nd year is relatively unimportant. For ash it is observed in 16 squares out of 30 (52 %), averaging 1.1. seedlings/m2 with a maximum of 5/m2.

For sycomore it occurs in 20 squares (60 %) with an average of 3.5/m2 and a maximum of 15/m2. The net result is an over-all increase with 2.9 seedlings (ash + sycomore) / m2, fairly low although not negligible.

3.3. S p a t i a l v a r i a t i o n

Spatial variation related to time, species and rate of change is considerable. In the initial stages of establishment spatial differences are greater within the sycomore-population as within the ash-population. (Tab. 2). The degree of change, as indicated by the survival rate, is subject to important spatial differences, in the ash-regeneration and relatively restricted variation in the sycomore-regeneration. (Tab. 5 ; Tab. 6). As a whole, however, spatial variation in total regeneration density does not change very much, because increasing spatial variation in ash-density is compensated by decreasing spatial variation in sycomore-density (Tab. 2), even though spatial variations in regeneration density remain higher for sycomore as for ash.

These phenomens indicate a better consolidation of sycomore, with significant differences in density at a fairly high level, and the general decline of ash, with relatively less important variations in density, but at an extremely low level.

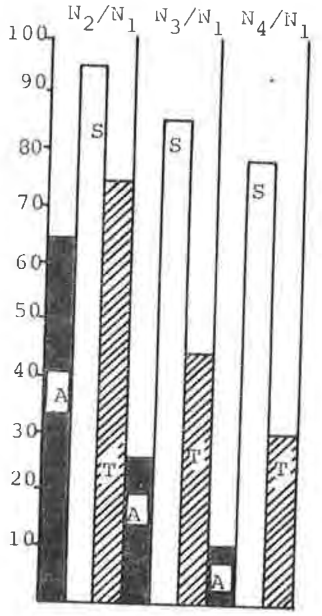

Fig. 6. Relative number of seedlings (T = Total , A = Ash ; S = sycomore)

N_1 = June 1st. per.

N_2 = Oct. 1st. per.

N_3 = July 2nd. per.

N_4 = Oct. 2nd. per.

As a direct consequence the pattern of mixture changes profoundly in the course of early development and, even at the level of squares, modifications are evident.

At the origin ash is the dominant species (Tab. 3; Tab. 4 ; Tab. 6) : In 93 % of all squares ash surpasses sycomore in number of seedlings ; sycomore even represents less than 10% of the total number of seedlings in 7 squares (33 %).

At the end of the observation period the general picture and the pattern of mixture have changes profoundly :

- 3 squares (10.0 %) are devoid of regeneration.
- In 4 squares (13.3 %) a homogeneous sycomore regeneration has developed.
- In 15 squares (50.0 %) sycomore now dominates (In 3 squares ash-regeneration has become practically non-existant).
- In 8 squares (26.7 %) ash still dominates in numbers, but at a remarquably low level.

Not in a single case has ash improved, even maintained its position, so that a regeneration, initially dominated by ash (72 %), has developed, within a short time, into a regeneration dominated by sycomore (65%) (Tab.3). At the same time general group development favours the relative expansion of oak and its associates : they represent at the end 3,1/m2 7,73 % of the number of seedlings or 4.4/m2 of which are oak, against 2.03 % at initial establishment.

This is not so unimportant, because, from a pragmatic point of view, absolute numbers should also be kept in mind when planning silvicultural intervention.

N/ha (average)

	Initially	Finally
Ash	1.347.000	154.000
Sycomore	484.000	366.000
Oak	29.999	31.000
Other species	9.000	13.000

These absolute numbers do not only demonstrate the degree of change occurring in natural regenerations within a limited space, but illustrate, above all other things, the characteristics of spontaneous development and, consequently, the opportunities of well-conceived silvicultural intervention.

At least three trends of development are distinguishable on a level not exceeding the space, covered by the crown projection of an adult tree. From a choice of basic situations the creation of either mixed or homogeneous stands, dominated by ash or by sycomore, is theoretically possible. The presence of oak and its early resistance, even do not exclude the formation of oak stands, with ash and sycomore, in variable combination, as accessory species.

4. REGENERATION TYPES

Spatial differences in regeneration density for both ash and sycomore, variations in initial composition and early developmental tendencies on the level of squares of 1 m2, allow to distinguish three fundamental regeneration types : the ash-type (A-type), the sycomore type (S-type) and the mixed type (AS-type). Their presence during the early phases of establishment, does not imply their permanence. They are typical for a mosaic-pattern of spatial dispersal. Their occurrence next to each other at short distances, could be indicative for possible future developments on a larger level of space.

To characterize their state of development, the following parameters are used :

- N : number of seedlings/m2 at indicated moment.
- AR : Absolute reduction = decrease in number of seedlings/ m2 during a given period.
- RR : Relative reduction = decrease in number of seedlings at the end of a period (F_n in % of number of seedlings at the start (I_n) of that same period.
- R% : Procentual repartition of decrease in number of seedlings.

4.1. The A-type

The A-type is characterized by the dominance in numbers of ash from the start of the first till the end of the second growing season : The ratio N_{ash}/N_{syc} : although gradually decreasing, remains higher than 1 (Tab.4).

9 squares are representative for this type, to be divided into a sub-type with high initial regeneration density for ash (= 181 to 250/m2 ; III A,B,D ; IV D; VI E) and a sub-type with low initial density for ash (= 70 to 110/m2; III C ; VI A,B,C).

4.1.1. The high density A-subtype

The average initial density attains 233/m2 (ash = 215 ; sycomore = 12; oak and others = 6). It means that 35 to 50 cm2 of space is available for each seedling (average = 42.92 cm2), corresponding with a crown diameter of 6,1 to 7,1 cm (average= 6,61 cm) and a potential seedling length of no less than 6 cm.

Under such conditions primary selection and internal competition could start early.

At the end of the 2nd growing season nearly 4/5 of the initial number of ash-seedlings has disappeared (215 ―― $49/m^2$), whereas sycomore, by the maintenance of its initial number of seedlings, improves its position relatively well. The distribution of space has also changed : at the end of the 2nd year an average of 166,67 cm2/seedling is available, corresponding with a potential average crown diameter of about 13 cm.

The initial and final situation give no clue to the intensity of internal competition as far as the distribution of space is concerned. The decrease in number of ash-seedlings, absolutely and relatively, is in fact, most important during winter, when external influences prevail (Tab. 7 ; Fig. 7a). During the 2nd growing season the intensity of reduction (RR) is still increasing, although the number of ash-seedlings has already been reduced by 58 %. This constatation proves that the consolidation-crisis for ash really starts after the first vegetation period.

Tab. 7. Evolution of density in A-regeneration groups with a high (H) or low (L) level of initial density

Sub-type	Species	Para-meter	1.Per. I_1		F_1 I_w	Winter	2.Per. F_w I_2		F_2	Tot.
H	Ash	N	215		162		93		49	
		AR		53		69		44		166
		RR		24.7		42.6		47.3		
		R%		31.9		41.6		26.5		100
	Sycm.	N	12		11		11		11	
		AR		1		-		-		1
		RR		8.3		-		-		
		R%		100.0		-		-		100.0
L	Ash	N	92		62		27		10	
		AR		30		35		17		82
		RR		32.6		56.5		63.0		
		R%		36.6		42.7		20.7		100
	Syc.	N	6		4		3		4	
		AR		2		1		-		3
		RR		33.3		25.0				
		R%								

Tab.8. Evolution of density in S-regeneration groups

Sub-type	Species	Para-meter	1.Seas I_1		F/I	Winter	2.Seas F/I		F	Tot.
H	Ash	N	131		53		16		6	
		AR		78		37		10		125
		RR		59.5		69.8		62.5		
		R%		62.4		29.6		8.0		
	Syc.	N	154		160		161		162	
		AR	-	-	-	-	-	-	-	-
		RR	-	-	-	-	-	-	-	-
		R%	-	-	-	-	-	-	-	-
L	Ash	N	41		21		4		0	
		AR		20		17		4		41
		RR		48.8		81.0		100.0		
		R%		48.8		41.5		9.7		100
	Syc.	N	70		64		46		36	
		AR		6.6		18		10		34
		RR		8.6		28.1		21.7		
		R%		17.6		53.0		29.4		

4.1.2. The low density A-subtype

With an initial average of 98 seedlings/m2 (ash = 92 ; sycomore = 6) 102 cm2 of space is available for each seedling, corresponding to an average crown diameter of 10,2 cm. At the end of the observation period available space has increased to 714 cm2/seedling corresponding with a potential average crown diameter of 26,97 cm.

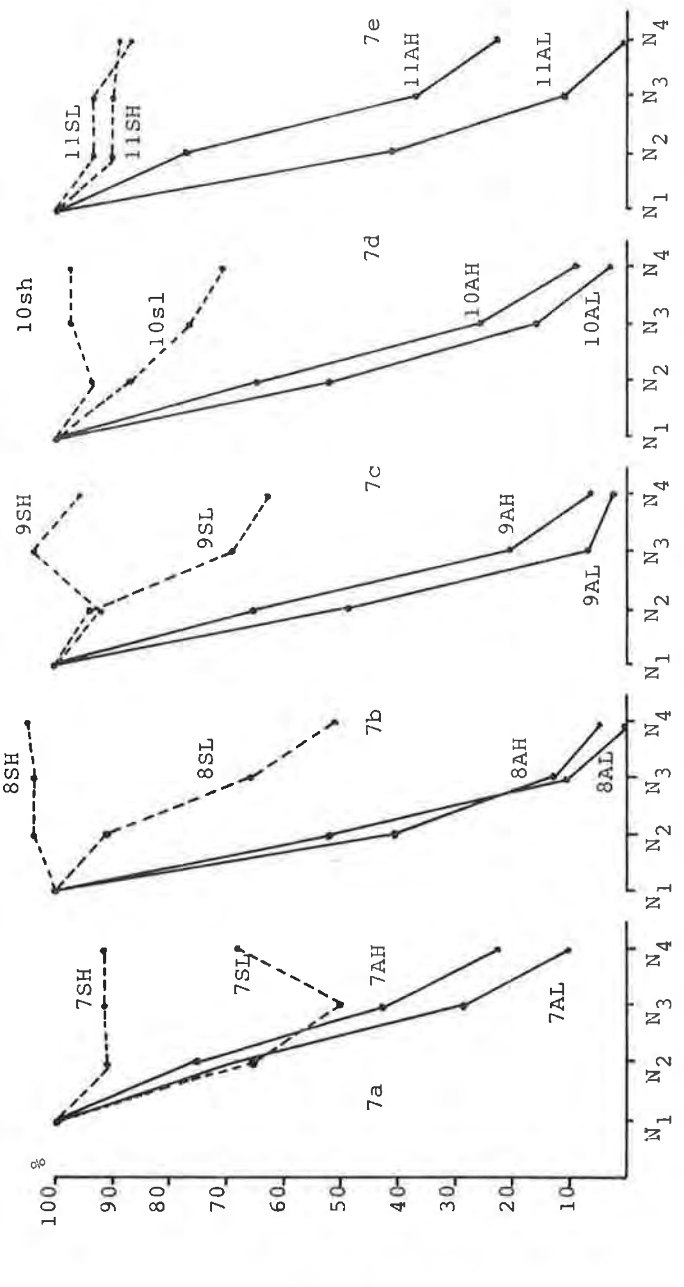

Fig. 7 = Average relative number of seedlings (% of initial number)

A = ash ; S = sycomore

L/H : low/high initial density

$N_1/N_2/N_3/N_4$ = cfr. Fig. 6

It is evident that crown contact between the seedlings is reduced from the start and is limited during the very first years. Internal competition does not start during this period.

Nevertheless, development follows the same pattern as in the groups with high density. Relative reduction is even greater at any moment and final density much lower, proving the restricted importance of internal competition : Local conditions for establishment and growth seem to be more significant. (Tab. 7 ; Fig. 7a).

4.1.3. Comments

The general trends of development of A-type regeneration groups proves the primordial importance of establishment conditions and the reduced effect of internal competition during the first two years. The initial density of regeneration is indicative for the local readiness of the site to receive and support seedlings. In the more dense groups the decrease in number of seedlings is relatively less important than in groups with a lower initial density. This constatation also applies to all reduction periods, considered separately. Otherwise, general developmental trends seem to be quite independant from initial regeneration density.

In all cases the decrease in numbers of sycomore is feeble, gradually increasing the relative importance of this species.

In both subtypes reduction is minimal, absolutely and relatively, during the first growing season; it is maximal, absolutely, during winter and, relatively, in the course of the 2nd growing season.

The real developmental crisis in nearly homogeneous ash-regenerations occurs after the first winter. Their eventual consolidation requires protective measures during the first growing season and not the regulation of internal competition, nor the redistribution of space.

4.2. T h e S - t y p e

The S-type, characterized by numerical dominance of sycomore from the start, occurs only in 2 cases (Tab. 8; Fig. 7 b).

IA = very dense regeneration with 286 seedlings/m2 of which 154 or 54 % are sycomore.

II E = regeneration of lower density with 111 seedlings/m2 of which 70 or 63 % are sycomore.

The most striking phenomen in the case of more dense regeneration group is the less severe reduction of the total number of seedlings : After 2 growing season the number of ash-sycomore seedlings still represents 59 % of the initial number in IA, against only 33 % in II E, although, quite evidently, absolute reduction is higher in the dense group.

This fact again illustrates the restricted importance of early internal competition. It also confirms the view, that high initial density of establishment is indicative for the local readiness of the site to support regeneration, linked with a higher potentiality for survival of early settlers on the better locations.

High initial density does not affect sycomore negatively, but ash also suffers less in the group with higher density. In IA the initial numerical density of sycomore nearly remains unchanged, taking an additional regeneration of 15/m2 during the second year into account. Although ash is reduced to 4.6% of its initial numerical density, it is still present in IA after 2 years, reckoning with an additional regeneration of 3/m2 during the 2nd year, but it has completely disappeared. in II E.

On the other hand the strongest reductions in the number of ash-seedlings occurs during the 1st growing season in the dense group and about equally during the first vegetation period and the following winter in the less dense group. The numerical reduction of sycomore-seedlings, only occurring in the less dense group, is most important during winter.

These findings confirm earlier statements, that initial numerical density is not a measure for the degree of internal competition to be expected. On the contrary it seems more indicative for better opportunities for establishment, growth and survival. Dense regeneration nuclei become, in fact, relatively more dense in the course of time in comparison with less dense regeneration nuclei, where the relative rate of survival is lower and additional establishments are less frequent.

In the groups of the S-type, ash and sycomore also behave differently. Sycomore, apparently the more tolerant species, consolidates more quickly in an early stage and also better with increasing initial total regeneration density.

Ash-seedlings disappear early. Their relative disappearance is accelerated by the presence of a dense sycomore-population. Their survival rate, however limited, is better where local conditions favour more dense regenerations.

The confrontation of the developmental trends in de A-type and S-type, seems to indicate that interspecific competition has a stronger effect on ash than intraspecific competition.

4.3. The AS-type

In the AS-type ash and sycomore establish simultaneously. In most units ash dominates numerically immediately after establishment, but in about 2/3 of all groups this relation is reversed in the course of development. Three subtypes of regeneration are distinguishable :

AS-Subtype with high density of ash regeneration
(= 150/m2) ; I,B,C; II B,D; IV A)

AS-Subtype with medium density of ash regeneration
(= 120 - 150 m2 ; ID ; II A; III E; IV B ; VI D).

AS-Subtype with low density of ash regeneration
(75 m2 ; IV C; VA, B, C, D, E).

IE and II C are not considered here, because all seedlings disappeared in the course of the 2nd vegetation period.

4.3.1. AS-Subtype with high initial density of ash

Within this subtype a further distinction could be made between groups with a high and low initial riation between the number of ash- and sycomore-seedlings ($N_A/N_S > 2$; $N_A/N_S < 2$).

In both cases a quick reversal of dominance is observed. Sycomore already dominates numerically at the end of the 1st. vegetation period (Tab.9 ; Fig. 7c).

The number of ash-seedlings is severly reduced within a short time, more intensily in contact with a dense sycomore-population (reduction to 2/m2 and 1.2 % of initial establishment at the end of the 2nd. vegetation period) then in the case of outspoken initial numerical dominance of ash (reduction to 14/m2 and 6.4 % of initial establishment). In the first case the initial share of ash in the mixture is reduced from 58,8 % to 2,6 %; in the second case the share of ash still amounts to 23 %, down from 81.6 % initially. The difference in development indicates the precedence of interspecific or intraspecific competition, as far as ash is concerned.

The changes, occurring within the S-population, are more complex. In a general way sycomore suffers only a mild numerical decrease and improves its position in the mixture accordingly. Decrease, in its absolute and relative aspects, is minimal when the own initial number of seedlings is low, but due to the relatively mild reduction of the ash-population in the presence of low sycomore-density, the ultimate dominance of sycomore is less pronounced. On the other hand, when the initial density of sycomore is higher, the numerical decrease of sycomore is also more important, both absolutely and relatively. Its ultimate dominance, however, will be more accentuated, because ash suffers severely from interspecific competition with increasing sycomore-density.

In nearly all cases the most important numerical decrease, both relatively and absolutely, for ash and for sycomore, occurs during the transition between the vegetation periods, stressing the importance of external influences.

The sycomore population, however, does not follow this rule when its own initial number of seedlings is low and practically does not change over a period of nearly 2 years. At this stage sycomore seems to be fairly resistant to interspecific competition and external influences and to suffer slightly from intraspecific competition of the density of its own population is high.

4.3.2. Subtype with medium initial density of ash.

Essentially the same phenomens occur as in the previous subtype (Tab. 10, Fig. 7 d). The number of ash-seedlings is quickly reduced, more severely if the initial number of sycomore-seedlings is high. Sycomore becomes more dominant because of the slower decrease of its numbers of seedlings. A decrease even does not occur if the initial density of the sycomore population is low. Its ultimate relative dominance, however, is more outspoken when its initial density is higher (93 % of

Tab. 9. Evolution of density in AS-regeneration with high initial regeneration density for ash.

Situation	Spec.	Par.	I.Seas. I		I.Seas. F/I	Winter	2.Seas F/I		2.Seas F	Tot.
N_A N_3 (initially)	Ash	N	218		140		44		14	
		AR		78		96		30		204
		RR		35.8		68.6		68.2		
		R%		38.2		47.1		14.7		100
N_A/N_S 2	Syc.	N	49		45		51		47	
		AR		4		–		4		2
		RR		8.2				7.8		
		R%		–		–		–		
$N_A \pm = N_S$ (initially)	Ash	N	173		83		11		2	
		AR		90		72		9		171
		RR		52.0		86.7		81.8		
		R%		52.6		42.1		5.3		100
N_A/N_S 2	Syc.	N	121		112		84		75	
		AR		9		28		9		46
		RR		7.4		25.0		10.7		
		R%		19.6		60.8		19.6		

Tab.10. Development of density in AS-regeneration with medium initial regeneration density for ash.

Situation	Spec.	Par.	I.Seas. I		I.Seas. F/I	Winter	2.Seas. F/I		2.Seas. F	Tot.
N_A/N_S 2 initially	Ash	N	134		86		34		11	
		AR		48		52		23		123
		RR		35.8		60.5		67.6		
		R%		39.0		42.3		18.7		
	Syc.	N	34		32		33		33	
		AR								
		RR								
		R%								
N_A/N_S 2	Ash	N	132		68		20		4	
		AR		64		48		16		128
		RR		48.5		70.6		80.0		100
		R%		50.0		37.5		12.5		
	Syc.	N	79		70		60		55	
		AR		9		10		5		24
		RR		11.4		14.3		16.7		
		R%		37.5		41.7		20.8		100

Tab. 11. Evolution of density in AS-regeneration with low initial regeneration density for ash.

Situation	Spec.	Par.	I.Seas. I		I.Seas. F/I	Winter	2.Seas. F/I		2.Seas. F	Tot.
	Ash	N	73		56		26		16	
		AR		17		30		10		57
		RR		23.3		53.6		38.5		
		R%		29.8		52.6		17.6		100
	Syc.	N	50		45		45		44	
		AR		5		-		1		6
		RR		10.0		-		2.2		
		R%		83.3		-		16.7		100
Ash $30/m^2$	Ash	N	29		12		3		0	
		AR		17		9		3		29
		RR		58.6		75.0		100.0		
		R%		58.6		31.0		10.4		
	Syc.	N	15		14		14		13	
		AR		1		-		1		2
		RR		6.7		-		7.1		
		R%		50.0		-		50.0		100

total number against 75 % if initial density is lower), because in that case, ash suffers more from interspecific competition than sycomore from intraspecific competition.

The most important absolute decrease in numbers of ash-seedlings occurs during the 1st. growing season in groups with a dense sycomore-population. In the other case the most important decrease, absolutely and relatively, for ash and for sycomore, takes place during the transition from the 1st to the 2nd vegetation period.

The comparison of two equivalent ash populations in confrontation with sycomore-populations of high and low density confirms the importance, at this stage, of external influences and interspecific competition for ash and of intraspecific competition for sycomore.

4.3.3. Subtype with low initial regeneration density of ash

When initial density is low for the regeneration as a whole and for each of the main species separately, the number of sycomore seedlings practically does not change. (Tab. 11, Fig. 7e). Ash, on the other hand, is able to maintain itself in the mixture only if its own initial regeneration density is sufficient, quite independently of the density of the sycomore-population. An initial density for ash of 30/m2 is marginal. There seems to be no marginal limit for sycomore.

Competition can not be important in nuclei with low density, as available space for each seedling and corresponding potential crown diameter reach high values :

		Available space/cM^2	Crown diameter/cm
Low density	Initially	81,30	9,10
	Finally	166,67	13,03
Marginal density	Initially	277,27	15,22
	Finally	769,23	27,99

In the marginal groups the most severe reductions occur already during the 1st growing season, in the others especially during winter.

The local readiness of the site to receive and to support ash-regeneration determines the course of development.

4.3.4. Comments

The AS-type quickly develops into a homogeneous sycomore group or in regenerations with an outspoken dominance of sycomore. This development occurs independantly from the initial density of the ash-population or its relative importance in the mixture. Ash suffers most from external influences during winter, poor micro-conditions for establishment and interspecific competition. The numerical decrease of ash is directly related to the increasing density of the sycomore-population. A higher degree of ash-survival occurs if the density of the sycomore population is low, proviced initial ash-density is not marginal.

Sycomore easily maintains its original numerical density and gradually becomes more dominant. Even in the case where its own high initial density provokes fairly severe intraspecific competition, its relative position steadily improves because the degree of intraspecific competition is always lower than the degree of interspecific competition, that apparently does not harm sycomore, but which makes ash suffer severely even at fairly low levels of sycomore-density.

Contrary to ash, disappearing quickly in marginal situations, sycomore can hold its ground, even in nuclei, with extremely low density.

5. CONCLUSIONS

The observation in the Almoeseneie at Gontrode indicate that, under certain circumstances, a dry summer period does not seem to affect negatively subsequent forest regeneration. Even under a dense cover and at a fairly low level of light radiation, mixed regenerations of ash-sycomore-oak are able to establish. The high density of the groups is indicative for the pressure that can go out from a single burst of regeneration. Equally important is the high degree of spatial variation in initial density and composition of spontaneous regenerations arising without any kind of previous stand perturbation, neither spontaneous nor induced by human intervention. From an ecological point of view it is highly significant that the respective initial regeneration densities of the dominant species, ash and sycomore, are not correlated. There is no sound indication that these species function complementary to each other in colonizing the site.

The first stages of development of the regeneration groups are characterized by a quick and general reduction of the number of seedlings and unequal resistance of the species to reductive influences. At the end of the second vegetation period the rate of reduction reaches 70 %. The fact that most reductions occur during winter is of great silvicultural consequence. It indicates the importance of external influences during early regeneration stages.

Equally important is the constatation that the positive correlation between regeneration density and reduction ratio is the start of a movement toward egalization.

Ash suffers most from reductions. At the end of the 2nd vegetation period its average survival ratio reaches only 11%. The corresponding survival rate of sycomore is considerably higher (76%) and for oak even an increase in occupational density is observed. As a consequences the relationship between species is rapidly changing during the early phases of development, shifting numerical dominance from ash to sycomore. The fact that these modifications are not the result of internal competition and that spatial variations in function of species, time and rate of change are important from the start and remain considerable during early development, stresses the need for a differentiated silvicultural approach to the treatment of regeneration groups to be based on the recognition of ecological diversity on the smallest possible space level.

From a choice of basic situations silvicultural treatment can progress, early and wilfully, toward a choice of stand types and patterns of mixture.

Available space in each of three distinguishable regeneration types, warrants optimal conditions for crown development. It proves the need for direct interventions to check external influences and regulate the primary patterns of mixture.

In nearly all regeneration units, the primordial importance of establishment conditions and the reduced importance of internal competition during the establishment and consolidation period is evident. High initial density is indicative for the readiness of the site to support regeneration, for a better potentiality for establishment, growth and survival and, consequently for greater opportunities for silvicultural choice.

As far as the relationship between species is concerned it seems reasonable to conclude that ash suffers most from interspecific competition, sycomore more, however, slightly, from intraspecific competition.

To maintain itself in the mixture after two vegetation periods, ash must be able to establish in sufficient initial numbers (at least 30/m2), especially if sycomore-regeneration reaches a high level of density.

In all cases development favors sycomore. If establishment of ash is poor, the original mixed ash-sycomore-regeneration quickly, develops into a nearly homogeneous sycomore group.

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