THE EARLY STAGES OF SPONTANEOUS FOREST REGENERATION ON POOR SOILS AND CONTINENTAL SAND DUNES IN NORTHERN BELGIUM

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Abstract

Spontaneous natural regeneration under variable conditions on sandy soils and continental sand dunes were analysed in 5 locations in N.E. Belgium.
The number of seedlings varies between 14.000 and 522.000/ha. The most prominent invading species are red oak, pedunculate oak and Scots pine.
Two principal types of regeneration are recognized : homogeneous groups of oak or pine and mixtures, predominantly composed by the same species. Pioneers such as birch, willow, white poplar and wild black cherry do not play an important role.
Social differentiation sets in quite early and is mainly provoked by age differences. Therefore early silvicultural intervention is advisable. The growth relationships between the species indicate that Scots pine is not in danger of spontaneous elemination by other species. Because of the density and variability of spontaneous forest regeneration, the conversion of pure pine stands into mixed forest, using group regeneration to this end, poses no real technical problems.

INTRODUCTION

Spontaneous establishment of hardwoods and conifers on the poor sandy soils and continental sand dunes of N. Belgium occurs under the cover of artificial stands of Scots pine (Pinus silvestris L.) and Corsican pine (Pinus nigra Arn. calabrica Schn.) as well as in heather and grassland or on

completely denuded soil after clearcutting or forest fires. Such colonizations indicate a potential for natural afforestation and regeneration, that can be put to good use in the conversion of unsuitable stands or to create more stable forest communities.
To study these regenerations circular sample plots, with a radius of 1 or 3 m, were laid out in 5 locations and 2 different regions.

Birch-pedunculate oak forest region of Antwerp

(Querco roboris - Betuletum R. Tx.)

W = " Withoefse Heide " / Kalmthout

Regeneration in forest clearings, where the soil is already covered with heather-vegetation.

C = Provincial Domain " Vrieselhof " / Oelegem

Regenerations under the cover of a semi-natural mixed oak forest, enriched with poplar (Populus x euramericana) and red oak (Quercus rubra L.)

K = Recreation area/Kasterlee

Reclaimed continantal dunes, covered with 40-50 yrs old artificial stands of Scots pine of normal density, attaining an average top-height of 18-20 m.
In these homogeneous stands a mixed understory of oak, red oak and maple developped, prior to more recent invasions by different species. These poor sites are continually trampled by countless visitors.

Birch-sessile (and pedunculate) oak forest region of Limburg

(Querco sessiliflorae - Betuletum R. Tx.)

B = Continental dune reserve " De Brand "/ Hechtel
Regeneration under a fairly dense cover of 35-50 yrs old artificial pine stands and under the low-reaching crown of isolated oaks, birches and pines on naked dunes.

P = State forest " Pijnven "/Hechtel

Regeneration on continental sand dunes under the cover of 60 yrs old artificial pine stands with an understory of oak and maple on the more productive sites.

Z = Communal Forest / Zutendaal (Used as reference)

Older, consolidated regenerations on superficial sandy soils in a typical heather region.
Under extreme ecological and evolutive conditions, a wide range of situations is available :

a. Artificial stands of Scots pine (14-55 yrs)

b. Dense artificial stands of Corsican pine (22-55 yrs)

c. Naturally regenerated pine forest (50-60 yrs)

d. Replanted burned area.

Humus podsols prevail in both regions, but the soils are fairly deep and well-aerated at Kalmthout (W), Oelegem (O) and Kasterlee (K).
Hechtel (B and P) is a region with continental sand dunes, partially still moving.
At Zutendaal (Z) the soil is superficial with a nearly inpenetrable hardpan at 30-60 cm.

Phreatic water reserve : At about 1 m at Oelegem, Kalmthout and Kasterlee.
At 5-15 m or more at Hechtel and Zutendaal.

Annual rainfall : 713-867 mm.

Mean annual temperature : 9.3-10.1°C.

Aridity index de Martonne : 38 - 44.

To indicate tree species the following symbols are used :

P	Pinus silvestris L.
PN	Pinus nigra Arn. calabrica Schn.
Q	Quercus robur L. and Quercus petraea Liebl.
Pr	Prunus serotina L.
S	Sorbus aucuparia L.
B	Betula pendulata Roth
Qr	Quercus rubra L.

THE DENSITY OF REGENERATION

The number of seedlings is high (Tab. 1), extreme conditions, poor soils and the absence of silvicultural interventions taken into account. Densities correspond to an equivalent of 60 000 - 520 000 seedlings pro ha :

Kalmthout	W	76 000 - 161 000/ha
Oelegem	O	194 000 - 522 000/ha
Hechtel	B	59 400 - 423 000/ha

Even on moving sand dunes up to 839 oak seedlings pro are were found in a single case under an isolated Scots pine with a very deep and dense crown.

All regeneration groups are consolidated, but differences in age and ageclass distribution (Tab. 3 ; Tab. 7) implicate the interference of external influences, that undoubtly, reduced the number of early invaders. It is reasonable to assume that far higher numbers of seedlings, than are present to-day, participated, at one time or another, in colonizing the site. Age-distributions further prove that regeneration is not an accidental phenomen.
This thesis is confirmed by the situation in the older regeneration groups and nuclei, however small.
Some regenerations at Zutendaal are even older than the artificial stands of

Tab. 1 : Average number of seedlings/are and their distribution in %

Species		L / NP / A	W	O	K	B	P
		L	W	O	K	B	P
		NP	5	4	5	6	3
		A	1 - 6	1 - 4	1 - 11	1 - 8	1 - 9
N/are	P		492	-	85	25	217
	Q		-	1783	362	144	94
	Qr		549	1273	1599	-	578
	B		76	-	-	-	-
	Pr		6	16	190	62	286
	S		-	8	3	4	-
Total			1123	3080	2269	235	1175
In %	P		43.8	-	3.7	10.8	18.5
	Q		-	57.9	16.0	61.2	8.0
	Qr		48.9	41.3	70.5	-	49.2
	B		6.8	-	-	-	-
	Pr		0.5	0.5	8.4	26.4	24.3
	S		-	0.3	1.4	1.6	-
Total			100	100	100	100	100

L = location   NP = number of plots   A = age of seedlings/yrs.

corsican pine in which they occur (Plot 1 and 2; burned-out area of plot 12). Sometimes, seedlings already invaded young artificial stands shortly after their creation. Seedlings, spontaneously establishing 7 to 29 years after artificial reforestation, still survive as components of 20 years or older.

The most prominent invader is red oak, with a maximal average of 1599 remaining seedlings/are at Kasterlee and absolute maxima of 3151/are at Oelegem and 3174/are at Kasterlee. Of real importance are also the regenerations of Scots pine with a maximal average of 492 seedlings/are at Oelegem and absolute maxima of 1132/are at Withoefse Heide/Kalmthout and 1528/are at Pijnven/Hechtel.
Indigenous oak did not establish at Withoefse Heide/Kalmthout, but in all other locations, eventually, reached high densities : 5220/are not at Oelegem; 1712/are at Kasterlee; 258/are at " De Brand "/Hechtel and 1283/are at Pijnven/Hechtel. Indigenous oak reached an average maximal density of 1283/are at Oelegem.

Tab. 2 Number of seedlings (N/are) and species in regeneration groups under cover at Zutendaal

Nr. of plot		1	2	3	4	5	6	7	8	9	10	11	12
Cover	Tree species	PN	PN	PN	PN	P	P	P	P	P	P	P	PN
	Age in years	13	15	24	54	23	25	25	29	36	54	55	4/5
	N/ha	12.800	7.600	3.000	800	2.700	3.800	3.800	1.375	1.425	1.063	650	7.935
	Height in m	6.4	7.5	12.0	21.0	12.3	13.3	12.5	12.5	14.5	17.7	14.9	-
	Mean diametre/cm	6.3	7.3	13.5	27.1	11.6	11.1	10.4	14.5	16.0	21.1	23.1	-
	Basal area /m²/ha	45.2	34.0	43.9	48.2	29.9	33.3	34.9	21.7	30.2	37.8	26.9	
Principal regeneration species (N/are)	Pinus silvestris L.	-	-	-	98.6	-	15.7	-	-	-	-	40.8	0.6
	Quercus robur L.	14.3	12.0	12.5	7.1	16.7	2.8	8.3	8.5	19.9	13.4	37.5	10.0
	Quercus rubra L.	2.4	11.0	17.5	10.0	-	1.9	8.3	68.0	5.0	18.8	13.5	8.1
	Quercus palustris L.	-	-	-	-	-	-	-	-	-	-	-	0.7
	Betula pendula Roth	4.8	4.0	-	35.7	-	9.7	-	6.5	8.8	3.3	13.1	8.5
	Castanea sativa Mill	-	1.0	-	-	-	-	-	-	-	-	0.7	
	Total	21.5	28.0	30.0	151.4	16.7	30.1	16.6	83.0	33.7	35.5	105.6	27.9
Secondary regeneration species (N/are)	Populus tremula L.	-	-	-	-	-	-	-	-	-	-	-	21.5
	Prunus serotina L.	-	7.0	90.0	32.8	991.6	416.3	16.7	3.2	-	56.4	3.9	3.9
	Sorbus aucuparia Cr. L.	4.8	9.0	2.5	61.4	158.3	28.2	129.1	24.0	55.7	51.4	41.8	12.7
	Rhamnus frangula L.	26.2	35.0	17.5	8.5	8.3	-	4.2	5.7	2.3	3.1	5.5	7.1
	Total	31.0	51.0	110.0	102.7	1158.2	444.5	150.0	32.9	58.0	110.9	51.2	45.2
Grand total N/are		52.5	79.0	140.0	254.1	1174.9	474.6	166.6	115.9	91.7	146.4	156.8	73.1
Age distribution in years		5/24	1/18	1/7	1/6	1/16	1/13	1/6	1/19	1/23	1/25	1/21	1/21

Mixed regenerations are the rule. The differences between the atlantic western region (W,K and O) and the more continental eastern region (B and P) are relevant, especially with regard to the presence of oak in the regeneration groups.
Pioneers, such as birch, seem to be rather unimportant. Secondary species, particularly Prunus serotina, Rhamnus frangula and Sorbus aucuparia only participate in the absence of oak regeneration.

THE PROCESS OF ESTABLISHMENT

The actual regeneration period (RP = age difference between the oldest and the youngest seedlings), all species, present in a single plot ,included, covers 2 to 11 years (Tab. 3). The real invasion, probably, took more time as must be reckoned with repeated destruction of early settlers.

Tab. 3 Minimal (Rm) and maximal (RM) duration in years of the actual regeneration period. Minimal (Lm and maximal (LM) age of seedlings in years. (First number refers to Rm, second to RM)

Location	Species	Rm	RM	Lm	LM
Kalmthout W	P. silvestris	2	6	2/2	3/6
	Q. rubra	2	5	1/1	3/5
	Total	4	6	1/1	3/6
Oelegem O	Q.petraea/robur	3	3	1/1	3/3
	Q. rubra	3	4	1/1	3/4
	Total	3	4	1/1	3/4
Kasterlee K	Q. petraea	8	8	1/3	10/10
	Q. rubra	6	10	1/1	6/10
	P. silvestris	11	11	1/1	11/11
	Total	11	11	1/1	6/11
Hechtel B De Brand	Q. petraea/robur	2	8	1/1	2/8
	P. silvestris	2	8	1/1	2/8
	Total	2	8	1/1	2/8
Hechtel P Pijnven	Q. petraea/robur	4	4	2/2	5/5
	Q. rubra	5	8	1/1	5/8
	P. silvestris	6	6	1/1	6/6
	Total	6	8	1/1	5/8

The actual balance between invasion and destruction over a much longer period of time as can be deduced from present age differences within the same regeneration unit.

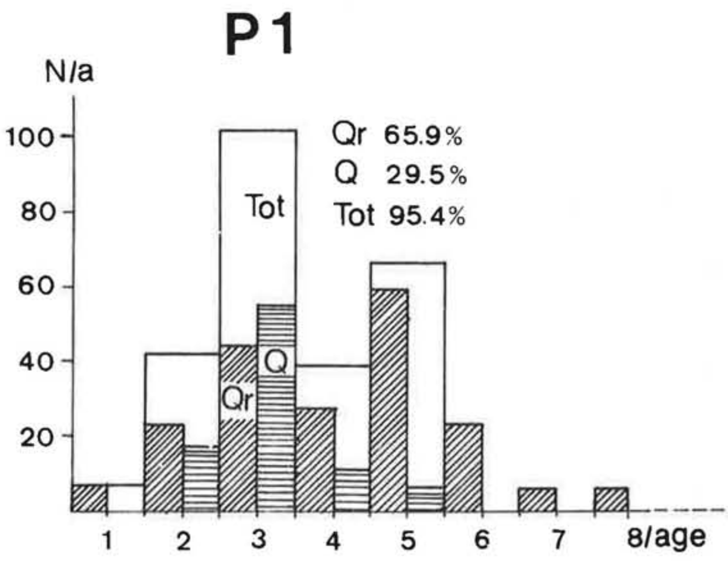
Hardwoods, with a RP of 2-10 years for red oak and 2-8 yrs for indigenous oak seem to establish a little more quickly than pine with a RP of 2-11 yrs.

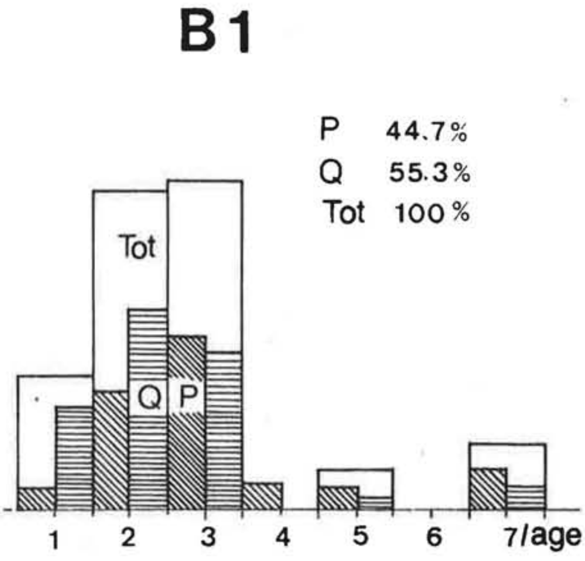
In all groups 1-year old seedlings are present and, in most cases, also all ages between Lm and LM. Both phenomena point to the continuity of establishment and to the fact that most regenerations have not yet attained a terminal state. Actual occupations may still suffer severe reductions in the number of seedlings and of species. In some instances they represent but a pre-regeneration phase. As a whole, they confirm the considerable length of the regeneration period, more amply illustrated by the situation in the older groups (Tab.2).

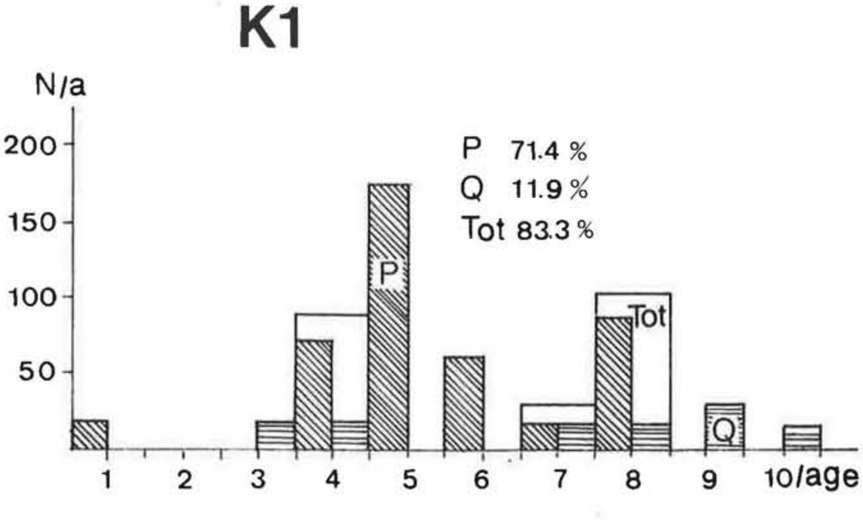
As to the succession of species, no clear lines are descernible. There is no indication that some species act as real pioneers and modify the site to such a degree as to make it more favourable for the invasion by more tolerant or more demanding species.
On the other hand, it is observed that powerful bursts of regeneration, covering but a few years, have rapid culmination of the number of invading seedlings as a direct consequence (Fig.1a, 1b).
These observations apply to regeneration groups as a whole and to species separately.
In most cases the bulk of surviving regeneration is concentrated in a single year as illustrated by the existence of clearly dominant age-classes, representing 27 to 85 % of all seedlings.
Such determining years mostly occur during the first third of the regeneration period. They are recognizable by the strikingly high number of seedlings, still present and belonging to that particular year. (Tab. 4).

Tab.4 Dominant age-classes (D.A.C.) and their share in the total number of seedlings (N%) still present.

Plot	RP	D.A.C.	N%	Plot	RP	D.C.A.	N%
W1	5	2	62.2	O1	3	2	85.4
W2	6	4	31.8	O2	3	2	73.8
W3	6	3	31.1	O3	4	2	52.5
W4	6	2	37.8	O4	3	2	66.7
W5	4	2	52.8				
				K1	11	5	35.7
B1	8	3	36.2	K2	7	2	46.8
B2	4	1	72.9	K3	6	2	52.0
B3	5	1	52.3	K4	10	2	42.7
B4	6	1	74.4	K5	6	2	61.5
B5	2	1	85.0				
				P1	8	3	36.4
B6	3	1	74.4	P2	5	3	35.8
				P3	9	3	27.1







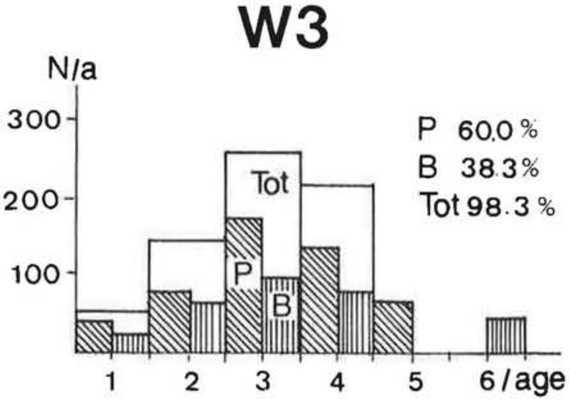
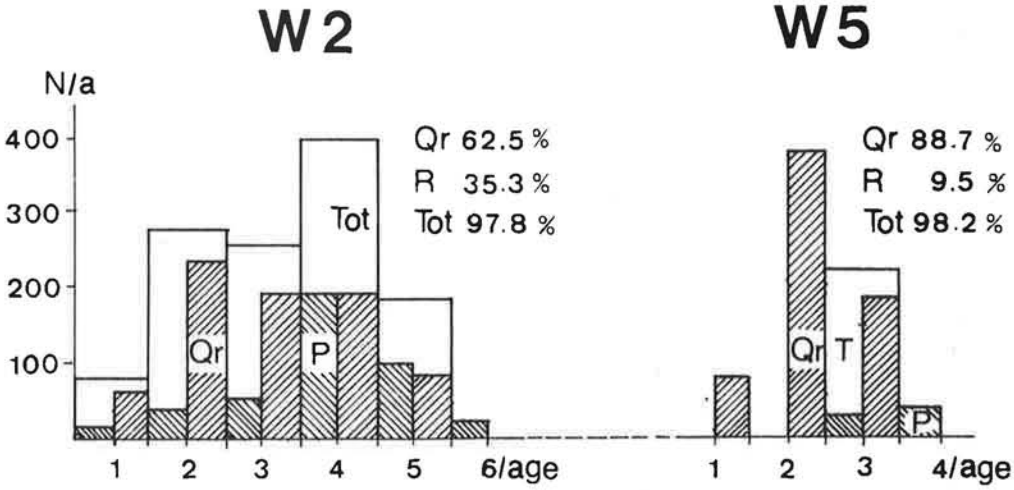
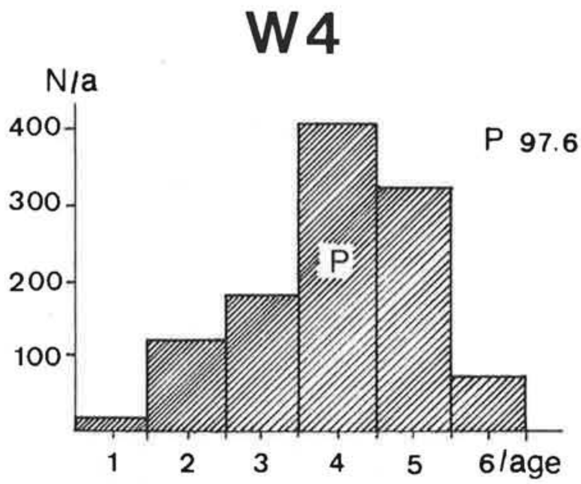
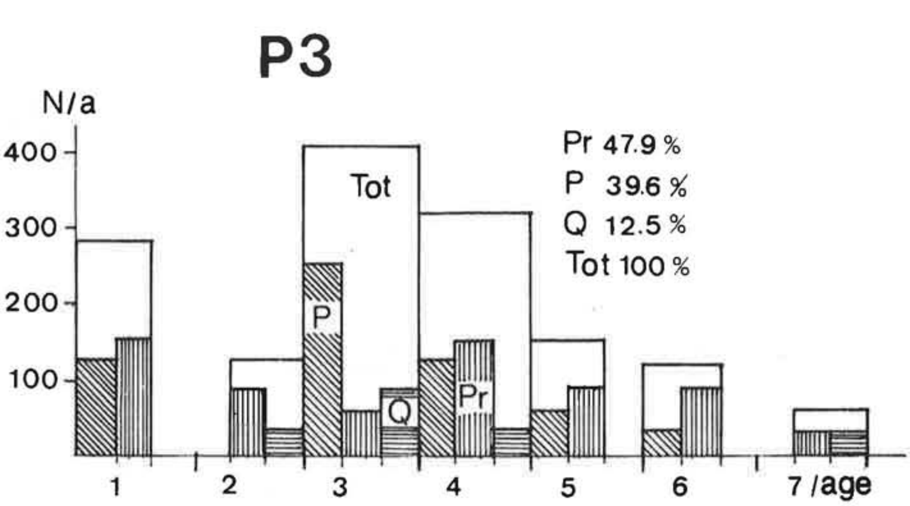


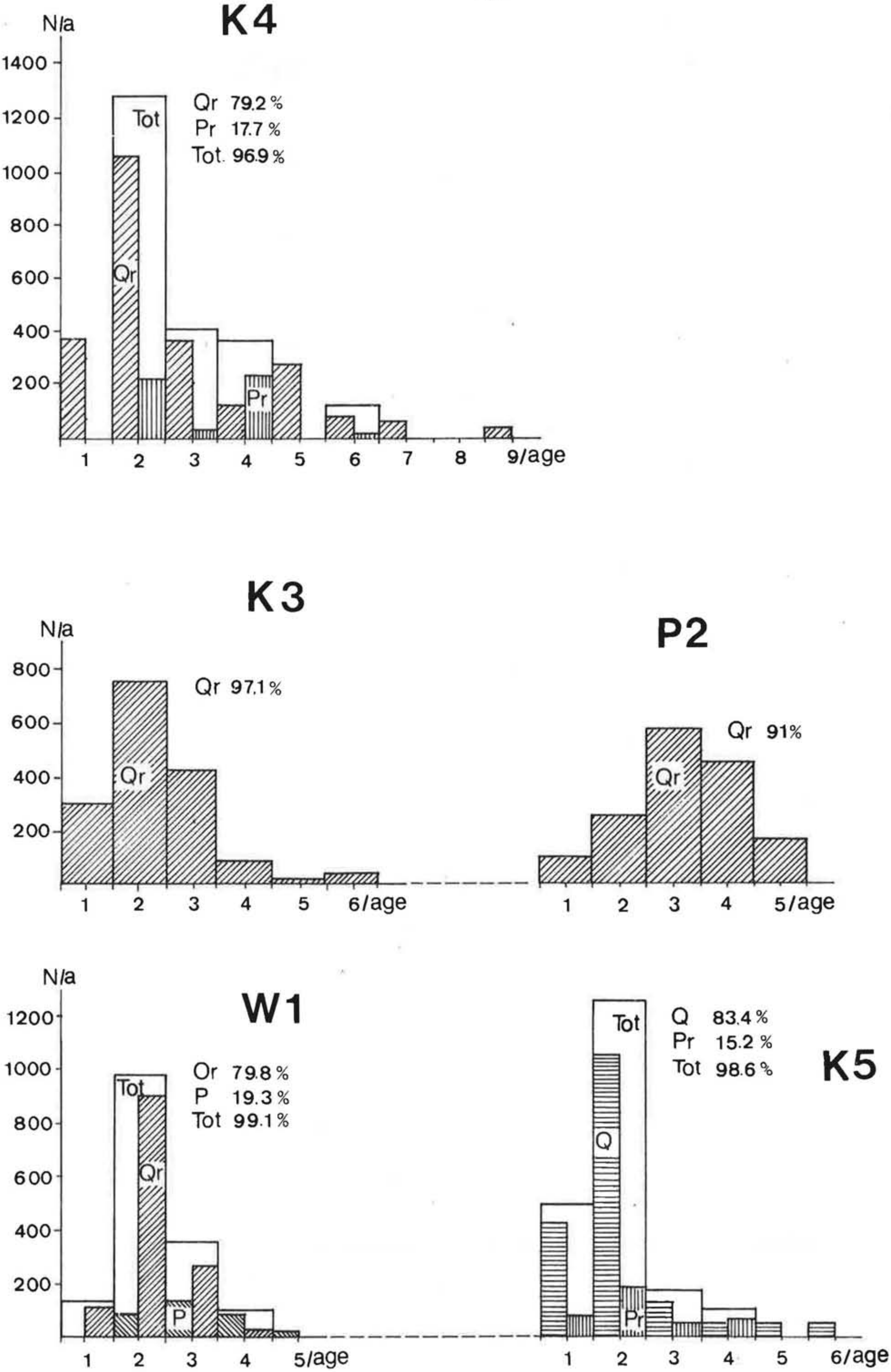
Fig.1 a Species composition (age-classes, number of seedlings pro are)
P = Scots pine Qr = red oak Q = indigenous oak
Pr = cherry B = birch T = Total


W2
W5
N/a
400
300
200
100
Qr 62.5 %
R 35.3 %
Tot 97.8 %
Tot
Qr
P
1
2
3
4
5
6/age
Qr 88.7 %
R 9.5 %
Tot 98.2 %
Qr
T
P
1
2
3
4/age

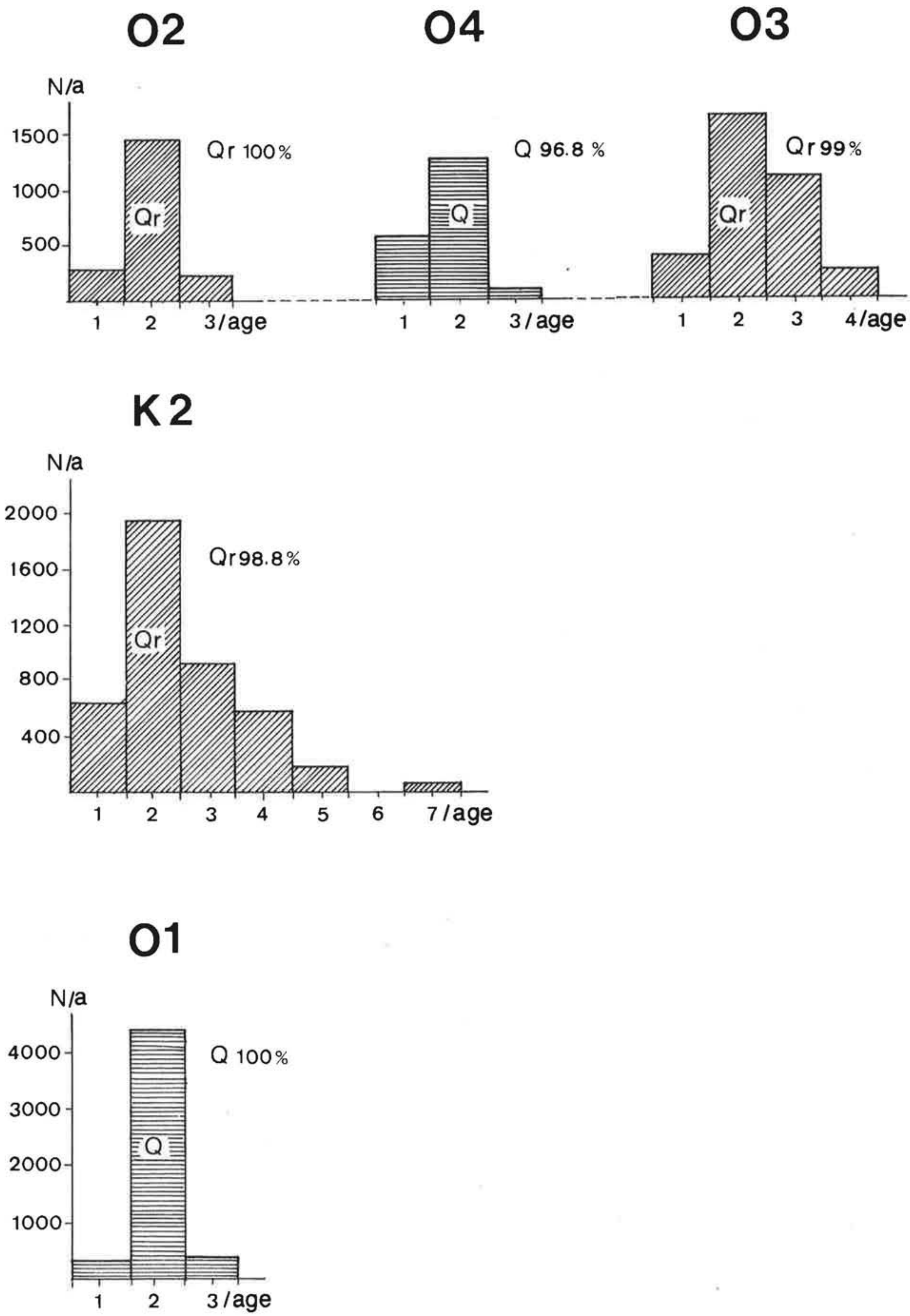

W4
N/a
400
300
200
100
P 97.6 %
P
1
2
3
4
5
6/age


P3
N/a
400
300
200
100
Pr 47.9 %
P 39.6 %
Q 12.5 %
Tot 100 %
Tot
P
Q
Pr
1
2
3
4
5
6
7 /age

b


K4
N/a
Qr 79.2 %
Pr 17.7 %
Tot. 96.9 %
Tot
Qr
Pr
9/age
K3
N/a
Qr 97.1 %
Qr
6/age
P2
Qr 91%
Qr
5/age
W1
N/a
Or 79.8 %
P 19.3 %
Tot 99.1 %
Tot
Qr
P
5/age
K5
Q 83.4 %
Pr 15.2 %
Tot 98.6 %
Tot
Q
Pr
6/age

c



O2
N/a
1500
1000
500
Qr 100%
Qr
1
2
3/age
O4
Q 96.8 %
Q
1
2
3/age
O3
Qr 99%
Qr
1
2
3
4/age
K2
N/a
2000
1600
1200
800
400
Qr98.8%
Qr
1
2
3
4
5
6
7/age
O1
N/a
4000
3000
2000
1000
Q 100%
Q
1
2
3/age

d

They do not necessarily correspond with maximal establishment, but in any case, with maximal survival, probably due to good conditions for establishment in a given year.
In a general way, concentration is favoured either by relative homogeneity or by the high regeneration potential of oak, both red oak and indigenous oak.

REGENERATION TYPES

Two principal types of regeneration are recognizable : Homogeneous regeneration with dominance of oak, pine and, exceptionally, wild blak cherry and mixed regeneration, in which oak is always present. (Tab. 5).

Tab. 5 Regeneration types

a. Homogeneous regeneration or groups, dominated by a single species (DS = dominant species)

Dominants species	Plot	Number of seedlings/are	DS in %
Red oak	0 2	1942	100.0
	0 3	3152	100.0
	K 2	4174	98.8
	K 3	1401	97.1
	P 2	1528	90.6
	W 5	1132	88.7
	K 4	2419	79.2
Indigenous oak	0 1	5220	100.0
	0 4	1910	96.8
	B 4	259	89.0
	K 5	1712	84.6
	B 5	110	78.0
	B 3	117	77.0
	B 2	170	50.0
Scots pine	W 4	1132	97.6
	K 4	424	71.4
	W 3	509	60.0
Black cherry	B 6	127	75.6

b. Mixed regeneration groups

Type	Plot		P	Q	Qr	P+Q	P+Qr	Q+Qr
P+Qr	W 1	N/are	311		1287		1598	
		In %	19.3		79.8		99.1	
	W 2	N/are	439		778		1217	
		In %	35.3		62.5		97.8	
P+Q	K 1	N/are	424	99		523		
		In %	71.4	16.7		88.1		
	B1	N/are	109	135		244		
		In %	44.7	53.3		98.0		
Q+Qr	P1	N/are		92	205			297
		In %		29.5	65.9			95.4

Early succession species or species, considered as such (birch, willow, white poplar, wild black cherry and buckthorn) either fail completely or do not play an important role in the early stages of invasion in both areas. Under certain circumstances, so-called climax species such as pedunculate oak and sessile oak are early or very first settlers.
All regeneration nuclei are dominated by hardwoods, a rather puzzling, although promising fact in areas, where pure artificial stands of conifers prevail. Regenerations, with the exception of those at Oelegem (O) are not a replica of the composition of the stands under which they have established.
Most remarkable are the great differences in density, age-class distribution, composition, structuration and development between groups, growing within a short distance (10m or less) of each other (Especially at Kalmthout, Kasterlee and Pijnven).
These phenomens lead to the rejection of the uniqueness of a succession, linked to a given site. It permits the speculative assumption that micro-ecological site conditions, the life history ad hoc of the species and their potential for seed production and dispersal are of primordial importance. The high variability of regeneration is clearly illustrated. It tends to disappear with the sheer passing of time, due to the homogenizing effect of the reduction of the number of individuals, combined with increasing space requirements of the survivors at any later moment.

This variability also points to the possibilities of alternative development, both spontaneous or induced by silvicultural treatment. The high density of most spontaneous regenerations under cover further proves the feasibility of planned conversion of predominantly homogeneous, artificial pine stands, which, in their actual state, pose serious problems to forest management. The differences in composition of numerous small regeneration nuclei, often not surpassing the space corresponding to the crown projection of a single adult tree, create good conditions for spatial variation, the choice of species and the use of conversion technics, that have not yet been sufficiently explored.
At the same time, it should, nevertheless, be kept in mind, that the greater part of the groups under observation represent but the juvenile phases of a spontaneous invasion process, that takes time and is not yet finished. This conclusion is based on the phenomens and the length of the regeneration period in the older and more advanced groups at Zutendaal (Tab. 6), which demonstrate three facts :

- The duration of the regeneration period varies between 6 and 25 years, with an average of 16.3 years.
- In most regeneration groups (11 out of 12) 1-year old seedlings are present in fairly high numbers, proving the continuity of establishment.
- The post-regeneration period (last quarter of actual RP) is responsible for 10 to 80% of all seedlings present to-day.

In the older regenerations also, no indisputable line of succession is discernible. Secondary species such as buckthorn, wild black cherry and mountain ash are relatively important as far as their numbers are concerned. They do, however, not act as pioneers and establish after or simultaneously with the principal climax-species (oak, pine, birch).

Tab.6 Distribution in % of seedlings over the three phases of the regeneration period at Zutendaal (Pre-regeneration = first quarter of RP; principal regeneration phase = second and third quarter of RP; post-regeneration = last quarter of RP.

Plot	1-yr.old seedlings in % of N	Pre - regeneration		Principal regeneration		Post-regeneration	
		Age-class	N %	Age-class	N %	Age-class	N %
1	-	> 18	4.5	10 - 18	50.0	< 10	45.5
2	51.9	> 14	6.4	5 - 14	36.6	< 5	57.0
3	39.3	> 6	3.6	3 - 6	42.8	< 3	53.6
4	32.0	> 5	0.6	2 - 5	67.4	< 2	32.0
5	16.6	> 12	4.0	5 - 12	61.6	< 5	34.4
6	47.6	> 10	3.8	4 - 10	16.2	< 4	80.0
7	70.0	> 5	2.5	2 - 5	27.5	< 2	70.0
8	24.9	> 14	4.4	6 - 14	35.1	< 6	60.5
9	30.5	> 14	3.0	5 - 14	48.9	< 5	48.1
10	14.4	> 12	2.6	5 - 12	18.4	< 5	79.0
11	18.2	> 13	13.1	5 - 13	32.1	< 5	54.8
12	8.3	> 15	3.8	6 - 15	58.6	< 6	37.6

STRATIFICATION

Inegalities between the components of a regeneration group are caused by specific differences, genetic variation and unequal space requirements. They are basic to structural development and, ultimately, have social differentiation as a consequence. Their impact can be magnified by individual or collective age-differences. In the course of development, internal causes for diversity blend, with the effects of external influences.
Diversity is maximal during the early phases of regeneration :

- High number of components, both species and individuals.
- Large amplitude of genetically determined morphological and physiological characteristics.
- High degree of adaptation to micro-ecological site-conditions.
- Limited exposure to external influences and exogenous selection (1st degree natural selection), whereas internal selection (2nd degree natural selection) is not yet active.

Stratification can be observed quite early if due attention is paid to relative differences in growth. It is of practical importance as soon as absolute differences in height are easy to distinguish.

Stratification models

Differences in growth and, consequently, in size lead to a temporary structural equilibrium with static, dynamic and functional aspects. These differences, more detectable with the passing of time, develop quite early. In the first phases of development, they are directly connected with age-differences. For this reason, simple norms, such as class-distribution (height and age) and conventionally defined social strata can be used to identify structural situations and to evaluate their impact on subsequent community.

In the early phases of regeneration of the principal species (pine and oak) height-classes correspond with age-classes. (Tab. 7).

The absolute differences increase and the relative differences decrease with the progression of age or development

Tab. 7 Height-class distribution and average age (in yrs) pro class of the dominant species in the regeneration groups W and K.

Plot	Spec.	h-class /cm	N	Age / yrs	t-value
W1	Qr	0 - 16	38	1.9	2.553*
		16 - 32	46	2.2	2.648*
		32 - 48	7	2.7	
W3	P	0 - 16	3	1.3	1.205
		16 - 32	20	2.8	1.504
		32 - 48	7	3.9	3.395**
		48 - 64	4	4.8	0.533
		64 - 80	2	5.0	
W4	P	0 - 16	5	2.0	2.761*
		16 - 32	23	3.0	6.684***
		32 - 48	22	4.2	3.335**
		48 - 64	16	4.6	3.761**
		64 - 80	8	5.1	2.021
		80 -	6	5.7	
W5	Qr	0 - 16	14	1.6	3.618***
		16 - 32	26	2.3	2.249*
		32 - 48	7	2.9	

Plot	Spec.	h-class /cm	N	Age /yrs	t-value
K2	Qr	0 - 16	230	2.1	10.909***
		16 - 32	58	3.4	5.823***
		32 - 48	4	6.1	1.477
		48 -	3	6.7	
K3	Qr	0 - 16	92	2.3	5.283***
		16 - 32	7	4.1	
K4	Qr	0 - 16	47	1.9	6.846***
		16 - 32	21	3.6	2.784*
		32 - 48	4	5.5	1.766
		48 -	4	7.3	
K5	Q	0 - 16	99	1.7	4.822***
		16 - 32	19	2.6	3.079**
		32 - 48	2	5.5	
		48 -	1	6.0	

The top-height of a group (h_T) (= average height of the highest seedlings, representing 5 % of the total number of seedlings in the group) can also be used to recognize three conventional strata :

D	dominant stratum	$h_D > 2/3.h_T$
M	intermediary or medium stratum	$2/3.h_T > h_M \quad 1/3.h_T$
L	Lower stratum	$1/3.h_T > h_L$

In the groups under observation, the dominant stratum comprises 5.6 to 13.6% of the total number of seedlings (Tab. 8). Such a share, considered as normal in older stands, indicates the progress of stratification in these regeneration groups.
The differentiation is less advanced in the dominated sub-population : The repartition between M and L is in full course. The intermediary stratum M is strongly represented with 18 to 50% of the total number or more than would be normal in older stands. Inversely, the lower stratum L is moderately represented with 37 to 64% of the total number of seedlings : It is slowly building up.

The mixture ' P + Qr ' (W1; Tab. 8) reveals the concentration of pine in the dominant stratum, correlated with a slight advance in age, and of red oak in the lower stratum. Such a structural situation is, more or less, a direct consequence of internal social distribution within each species separately :

Procentual distribution of seedlings within each population

Stratum	Pine in %	Red oak in %	Total in %
D	45.4	3.3	11.4
M	45.4	39.6	41.2
L	9.2	57.1	47.4

Pine takes an early advance as a candidate for permanent dominance by a slight difference in both age and height. The stratification, in the group as a whole, seems normal as far as D is concerned, but differentiation between M and L. is still going on. Internal differentiation within the younger red oak population is already outspoken, but only in the initial phase within the older pine population. For this reason and also because the absolute difference in height between dominant pine and oak is rather small, the increase of the relative importance of red oak in the upper stratum may be expected. Early intervention can allow to create a mixed stand of pine and red oak, in which both species are given equal functional importance.

A more subtle situation exists in the mixture ' P + Q ' (B1; Tab. 8), with pine dominating numerically, but with an advance in age, height and differentiation for oak :

Procentual distribution of seedlings within each population

Stratum	Pine in %	Oak in %	Total in %
D	21.4	7.9	13.6
M	35.7	13.2	22.7
L	42.9	78.9	63.7

Tab.8 Characteristics of stratification

h = average height/cm L = age/yrs N = number of seedlings

Plot	Stratum	Characte-ristic	P	Q	Qr	B	Pr	Total stratum
W1	D > 36 cm	N% → h L	76.9 45.5 3.8		23.1 40.7 3.0			↓ 11.4% 44.4 3.6
	M 18-36cm	N% → k	21.2 23.4 2.5		76.6 23.5 2.3	2.1 30.0 2.0		↓ 41.2% 23.6 2.3
	L < 18 cm	N% → h L	3.7 14.0 2.0		96.3 13.2 1.9			↓ 47.4% 13.4 1.9
B1	D > 26 cm	N% → h L	66.7 32.3 4.0	33.3 41.3 7.0				↓ 13.6% 35.3 5.0
	M 14-26 cm	N% → h L	66.7 17.8 2.8	33.3 15.0 2.8				↓ 22.7% 16.9 2.8
	L < 14 cm	N% → h L	28.6 9.2 2.1	71.4 10.1 2.0				↓ 63.7% 9.9 2.0
K5	D > 28 cm	N% → h L		37.5 39.0 5.7			62.5 39.0 3.4	↓ 5.6% 39.0 4.3
	M 15-28 cm	N% → h L		86.0 17.6 2.4			14.0 20.2 2.5	↓ 30.1% 18.0 2.4
	L < 15 cm	N% → h L		88.0 10.3 1.7			12.0 11.5 1.6	↓ 64.3% 10.5 1.7
P1	D > 51 cm	N% → h L			100.0 64.4 6.3			↓ 12.5% 64.4 6.3
	M 24-51 cm	N% → h L	6.8 28.7 3.3	22.7 27.5 3.5	70.5 33.3 4.3			↓ 50.0% 31.7 4.0
	L > 24 cm	N% → h L	3.2 13.0 3.0	48.4 15.3 2.9	48.4 17.4 2.7			↓ 37.5% 16.2 2.8

The numerical dominance of pine in the upper layer and its potential for structuration are all the more impressive, because pine-seedlings are much younger as the oak-seedlings, belonging to the same stratum, which were the first invaders (t = 3.550***). In the dominant stratum the difference in height between pine and oak is still significant (t = 2.934*), but it is indicated to reckon with the progressive emergency of pine, taken its capacity for growth under cover and under fairly poor conditions of access to light radiation into account.

A disturbing element in some regeneration groups is the wild black cherry (Pr), which is able to suppress, at least temporarily, more valuable species.
In the mixture ' Q + Pr ' (K5; Tab.8) oak is clearly underrepresented in the dominant stratum : only 2.5% of all oak-seedlings are relatively dominant, against 5.6 % of all seedlings, oak included. Cherry, although much younger than oak in the upper layer, attains the same height and is numerically superior.
Oak, on the other hand, represents nearly 85% of seedlings in the lowest stratum, against only 35% of all seedlings, whatever their social position. The negative effect of black cherry on actual structuration and quality of the dominant stratum is evident. Oak-regeneration is here in a precarious position and the prospects for improvement are restricted, because only 42, mostly dominated oak-seedlings pro are are present.

Finally, the mixture ' Q + Qr ' (P1; Tab. 8) is clearly dominated by red oak, the first surviving invader and sole component of the upper stratum. No forecast can be made about future developments, but the lead of red oak, due to differences in numbers, age and height-growth (10.22 cm annually against 8.70 cm for oak) may continually increase, significantly reducing the possibilities of indigenous oak ever to gain dominant status without help.

The importance of age and time

The analysis of differentiation proves the importance of even the slightest age-differences in the juvenile phases of development (Tab. 9).
Significant differences in age exist between the strata in all regeneration units. They also determine stratification within populations, made up by a single species, with the exception of the pine-population in B1 as far as the relation D/M is concerned.
Therefore the moment of invasion of individuals and species, as well as the sequence of establishment are of primordial importance in the early phases of stand formation. Age-differences determine course and direction of early differentiation and social development. They create opportunities to gain, at least temporarily, dominant status. They work against later migrants. They stress the importance of the local life history of species, as well as the significance of early selection and stand treatment as a means to direct development and functional structuration.

The importance of the time-factor is also illustrated in this context, by the positive correlation between age and height of the seedlings, whatever their age or social position (Tab. 10). This relationship surpasses the importance of differences in local site conditions. It confirms that differences of only 1 year often are sufficient to create and provisionally to maintain significant differences in seedling-height and thus in social position (Tab. 11).

Tab. 9. Relative importance of age differences between strata
Average age in years

Perc.	Ref.	Tot.		P		Q		Qr	
		Age/yrs	t-value	Age/yrs	t-value	Age/yrs	t-value	Age/yrs	t-value
W1[a]	D/M	3.6/2.3	7.043***	3.8/2.5	4.995***			3.0/2.3	2.606*
K5[b]		4.3/2.4	4.777***			5.7/2.4	6.795***		
B1[b]		5.0/2.8	4.337***	4.0/2.8	3.677	7.0/2.8	4.400**		
P1[a]		6.3/4.0	6.103***					6.3/3.7	5.268***
W1[a]	M/L	2.3/1.9	3.600***	2.5/2.0	0.682			2.3/1.9	3.697***
K5[a]		2.4/1.7	6.222***			2.4/1.7	5.793***		
B1[a]		2.8/2.0	3.911***	2.8/2.1	2.404*	2.8/2.0	2.320*		
P1[a]		4.0/2.8	3.647***			3.8/2.9	2.467*	3.7/2.6	2.529*

a. No age-differences between species belonging to the same stratum

b. Age differences between species belonging to the same stratum

K5[b]	Q/Pr	5.7/3.4	t = 4.244***
B1[b]	Q/P	7.0/4.0	t = 3.550**

Tab.10. Correlation between height (h/cm = y) and age (L/yrs = x).

Perc.	Spec.	N	Equation	r	F - value
W	Qr P(1)	91 22	y = 4.70 + 6.38x y = 10.67 + 14.80x	0.47 0.85	26.000*** 50.98***
W2	Qr P(1)	55 31	y = 0.75 + 5.14x y = 12.50 + 11.21x	0.83 0.79	121.44*** 48.07***
W3	B P(1)	23 36	y = 12.64 + 11.42x y = -5.54 + 11.69x	0.75 0.83	27.30*** 77.46***
W4	P	80	y =-16.0 + 14.62x	0.83	167.33***
W5	Qr	47	y = 21.63 + 0.69x	0.19	1.76
K1	Q P(1)	7 30	y = 6.00 + 9.50x y = 6.07 + 11.33x	0.93 0.89	32.95** 115.75***
K2	Qb	295	y = 2.11 + 4.89	0.73	329.58***
K3	Qr	99	y = 2.49 + 3.46 x	0.75	122.32***
K4	Pr(1) Qr	17 76	y =-6.10 x 10.12x y = 6.43 + 3.90x	0.85 0.62	42.84*** 47.80***
K5	Pr(1) Q	22 121	y = -2.65 + 10.17x y = 4.44 + 4.37x	0.83 0.69	39.90*** 110.76***
01	Q	164	y = 7.22 + 1.57x	0.24	9.89**
02	Qr	61	y = 6.44 + 1.82x	0.31	6.48*
03	Qr	99	y = 5.49 + 2.31x	0.49	30.10***
04	Q	60	y = 8.93 + 0.99x	0.19	2.12
B1	Q P(1)	38 31	y = 7.39 + 1.89x y = 16.39 + 12.5x	0.45 0.94	9.23** 229.45***
B2	Q	48	y = 1.81 + 3.82x	0.59	24.72***
B3	Q	50	y = 5.60 + 2.29x	0.45	12.15**
B4	Q	73	y = 4.28 + 3.00x	0.62	44.98**
B5	Q	31	y = 7.29 + 1.19x	0.18	1.01
P1	Q Qr(1)	26 58	y = 1.69 + 5.94x y = 0.06 + 8.47x	0.64 0.77	16.59*** 83.67***
P2	Qr	48	y = 5.83 + 2.88x	0.59	25.25***
P3	Pr P(1)	23 19	y = 4.86 + 10.42x y = 3.89 + 10.95x	0.95 0.95	186.41*** 93.19***

(1) = Quickest growing species.

Tab. 11. Difference in height between consecutive age-class

Perc.	Spec.	Pop. age	Refe-rence	h - cm	t-value	Perc.	Species	Pop. Age	Refe-rence	h/cm	t-value
W1	Qr	1/4	1/2	10.9/17.7	9.236***	K2	Qr	1/8	1/2	10.1/11.7	3.526***
			2/3	17.7/22.8	4.502***				2/3	11.7/14.9	6.187***
W2	Qr	1/5	2/3	10.2/15.7	6.012***				3/4	14.9/20.0	4.694***
			3/4	15.7/21.7	3.393**				4/5	20.0/27.2	2.967**
W3	B	1/6	2/3	27.8/49.9	3.536**	K3	Qr	1/6	1/2	6.6/9.7	3.034**
			3/4	49.9/68.8	4.338**				2/3	9.7/11.9	3.537***
W5	Qr	1/3	1/2	11.0/23.1	10.707***				3/4	11.9/16.8	3.528***
			2/3	23.1/32.1	5.029***	K4	Qr	1/10	1/2	9.3/12.5	2.347*
03	Qr	1/4	1/2	7.7/10.2	2.631*	K5	Q	1/6	1/2	10.3/12.4	2.831**
			2/3	10.2/12.3	3.433***				2/3	12.4/76.6	4.033***
B1	Q	1/8	2/3	10.5/12.6	2.233*	P1	Q	2/5	2/3	12.4/19.7	2.505*
B3	Q	1/3	2/3	9.0/14.0	2.659*				3/4	19.7/29.3	2.686*
B4	Q	1/3	1/2	7.4/9.7	4.214***		Qr	1/8	5/6	37.7/54.1	2.993**
B6	Pr	1/3	1/2	8.0/18.4	10.521***	P2	Qr	1/5	4/5	16.6/22.2	2.168*
K1	P	1/11	4/5	36.8/48.0	3.771**	P3	P	1/6	1/3	8.3/27.0	5.887***
			5/6	48.0/65.0	9.025***				3/4	27.0/40.5	3.390**

Early differentiation during the early phases of forest regeneration is no more than 2 to 3 years after the first invasions, to be reckoned with by silvicultural practice and stand treatment.

The importance of species

Although early differentiation is mainly induced by age differences, the impact of the fundamental differences between species on community development is not neglectable.
The level of annual height-increment and the correlation between height and age (Tab. 10) allow to characterize pine, wild black cherry and birch as relatively fast growing and agressive species, whereas indigenous oak and red oak are slower growing and less agressive.

Average annual height-increment in cm

Species	Min.	Plot	Max.	Plot
B	10.12	K4	10.42	P3
P	10.95	P3	14.80	W1
Pr	10.12	K4	10.42	P3
Q	1.19	B5	9.50	K1
Qr	0.69	W5	8.47	W1

In all mixtures pine, wild black cherry and birch provisionally dominate indigenous oak and red oak in the absence of age-differences in favour of oak. Pine can, eventually, hold wild black cherry in check (P3), but is often surpassed in height and relatively dominated by birch (W3). Because of the relative dominance of oak in the mixture ' Q + Qr ' the following classification seems acceptable :

B > P > Pr > Q > Qr

In a number of cases, the differences in height between even-aged seedlings of different species are rather significant :

Plot	Seedling type	Species	Height in cm	t-value
W1	S2	P/Qr	20.4/17.7	2.987**
	S3		31.0/22.8	2.087*
W2	S2	P/Qr	13.0/10.2	3.720**
	S4		30.8/21.7	2.708*
	S5		42.7/26.8	3.595***
W3	S3	B/P	49.9/26.0	7.263***
	S4		68.8/37.3	7.395***
B1	S3	P/Q	18.2/12.6	2.518*
B3	S1	Q/Pr	8.4/4.9	4.495***
P1	S2	Qr/Q	22.0/12.4	2.298*
	S3		25.2/19.7	2.802**

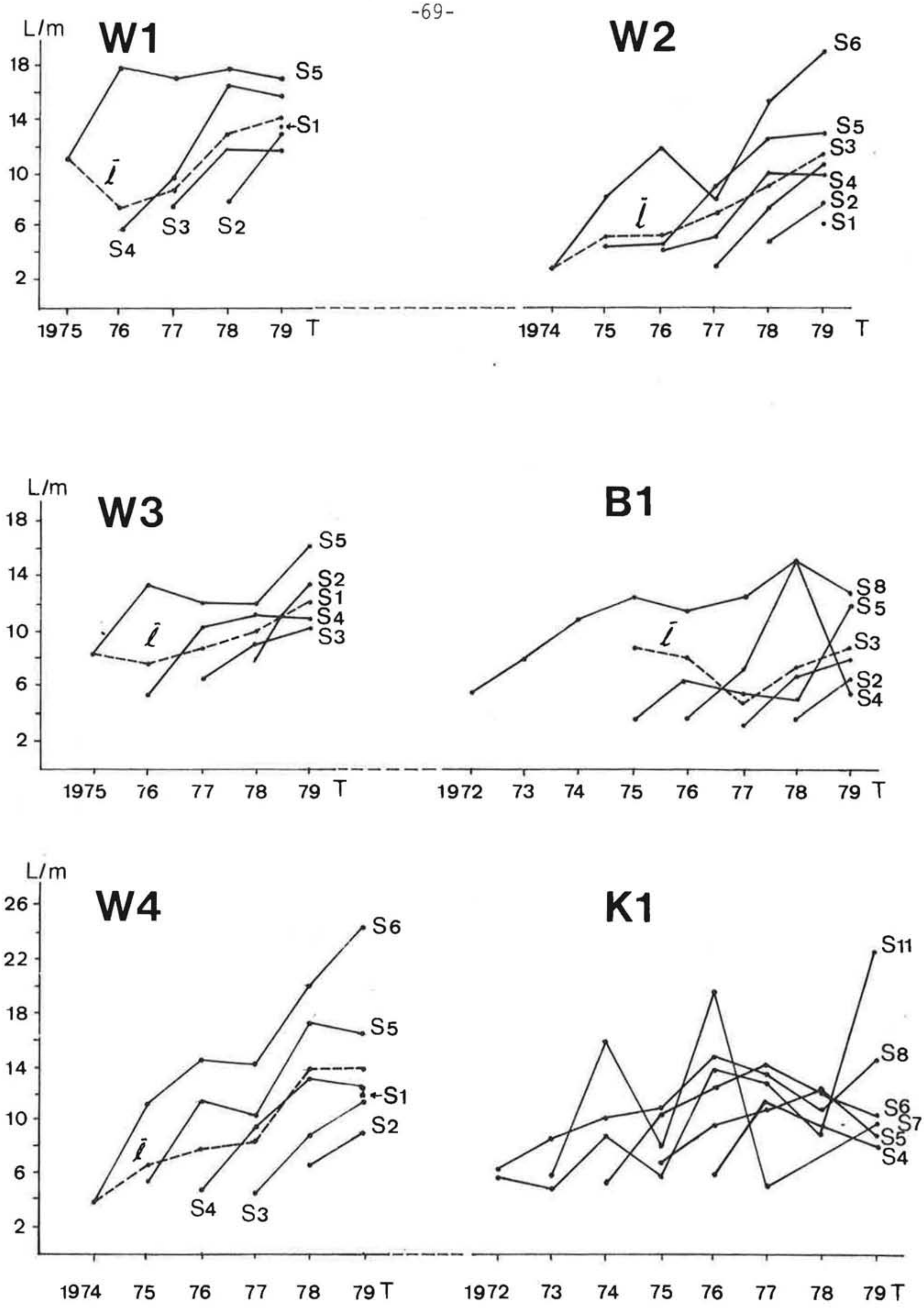


Fig 2: Average annual growth / cm of seedlings of a different age.

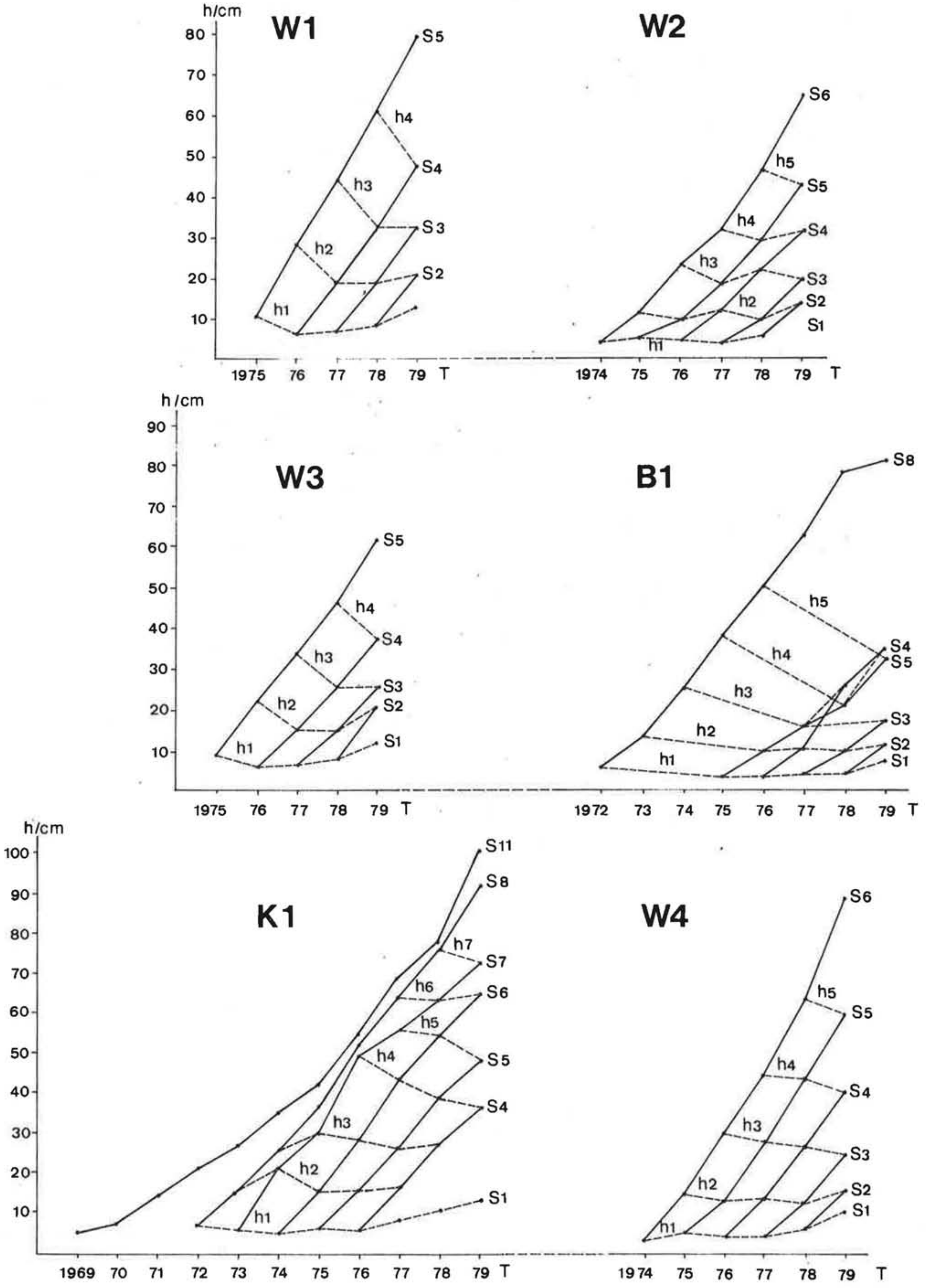


Fig 3: Analogous height / cm of seedlings of a different age.

From a practical point of view, keeping the necessity of conversion of many pure pine stands in mind, it is important to notice that pine is not in danger of elimination. Pine grows faster than most other species, birch and, occasionally, wild black cherry excepted.
Birch can only temporarily check pine-growth if he is the first invader. The growth-relations between pine and oaks prove, on the other hand, the technical possibility of indirect conversion of pure pine stands.

THE HEIGHT-GROWTH OF PINE

Retrospective analysis of annual height-growth of pine poses no problems. It proves that pine grows very good in different mixtures, justifying its choice as a principal species. It also makes evolutive tendencies more conspicuous (Fig. 2 ; Fig. 3).

Within any pine-population, the slighest differences in age between individuals are of primordial importance. The first invaders quickly gain and, at least provisionally, maintain a dominant position.
The differences in total height and annual increment between early invaders and retarded settlers, increase with the passing of time. This phenomen is most evident in more advanced developmental stages, as well as with increasing differences in age : The leading shoot of dominant individuals becomes progressively more important, compared with the leaders of younger, dominated or suppressed individuals. This means that dominant elements tend to dominate more with the passing of time (Fig. 2).

The negative effect of older dominants on height growth of younger individuals is demonstrated by the gradual decrease of analogous height (= height reached after an equal period of time since establishment by seedlings of unequal age, but belonging to the same group or unit) with descending age-class (Fig. 3). This is further proof of the incresing dominance of early invaders with the passing of time and the increase of age-differences, the main reason being their relative superiority in actual height-growth. As a consequence, social promotion of late invaders is quite exceptional. However, these conclusion only apply to the comparison between dominant and clearly dominated individuals or between the upper and the lower strata. As a matter of fact, the difference in height between age-classes, belonging to the intermediate or lower stratum disappear nearly completely. These lower strata tend to homogeneization, not to be observed in the upper stratum, where continual differentiation is the rule.

Within the pine-population differentiation begins early and, in some cases, immediately after first crown contact.

A difference in age of only 1 year can be sufficient for social differentiation, particularly during the very first phases of establishment (Tab. 12). Differences of 3 years or more provoke definitive differences in height, increment, social position and potential value. Occasionally, differentiation in height between seedlings of consecutive age-classes does not occur at first contact and may be postponed for up to 4 or 5 years.

A fairly clear pattern of establishment and early development in spontaneous pine regenerations on sand dunes can be deduced from these facts :

Tab. 12. Differences in height between pine-seedlings belonging to consecutive age-classes

Plot	Reference	Actual Height of seedlings/cm	t-value	Age /yrs at differentiation	Height/cm at differentiation	t-value
K	S5/S4	48.0/36.8	3.776***	2/1	16.2/6.0	7.780***
	S6/S5	65/0/48.0	5.682***	2/1	16.0/6.3	5.464***
	S8/S6	91.3/65.0	2.385*	3/1	25.7/5.5	4.791**
W1	S3/S2	31.0/20.4	2.081	2/1	19.1/7.8	3.732**
	S4/S3	47.2/31.0	3.269**	2/1	15.2/6.2	3.827**
W2	S3/S2	19.3/13.0	2.884*	2/1	8.8/5.0	1.658
	S4/S3	30.8/19.3	2.002	2/1	11.1/1.0	3.927**
	S5/S4	42.7/30.8	2.420	2/1	9.3/4.1	8.972***
	S6/S5	64.5/42.7	2.230	2/1	11.0/4.0	4.414**
W3	S2/S1	21.0/11.7	3.183*	2/1	21.0/11.7	3.183*
	S3/S2	26.0/21.0	1.601	2/1	15.2/8.0	5.658***
	S4/S3	37.3/26.0	3.210**	2/1	15.1/16.1	5.064***
	S5/S4	62.0/37.3	4.229***	2/1	21.6/5.0	6.540***
W4	S3/S2	25.2/15.9	4.060***	2/1	12.0/9.3	2.706*
	S4/S3	40.3/25.2	6.118***	2/1	12.8/12.0	0.580
	S5/S4	60.2/40.3	5.600***	2/1	16.2/12.8	2.328*
	S6/S5	88.4/60.2	4.165***	2/1	24.4/16.2	2.964**

1. Early settlers do not pave the way for later invaders by favourably modifying their immediate environment.
2. First invaders easily gain dominant status in the early stages of development.
3. If they establish simultaneously and in sufficient numbers, early invaders are able to consolidate their position for a number of years until internal competition between individuals of roughly the same age engenders secondary stratification within the dominant stratum.
4. If early invaders do not establish or survive in sufficient numbers, later colonists can reach a position of relative dominance, provided that differences in age and growth between early and later invaders are not too important.
5. Later settlers, usually, build poorly differentiated sub-populations. Their promotion to dominance is exceptional and depends mostly upon eventual destruction of early dominants.

This pattern, typical for homogeneous regenerations, can be profoundly modified by mixture.

CONCLUSIONS

Spontaneous natural regeneration under forest cover, on denuded soil and even on moving continental dunes occurs frequently on the poor sandy soils of N.E. Belgium. It is a continual process and by no means an accidental phenomen. The most common invading tree species are red oak, Scots pine and pedunculate oak.
The regeneration periods are of medium length and age-differences between surviving seedlings seldom exceed 11-12 years. Hardwoods establish more quickly than conifers. No distinct or unique succession line is observed. Differentiation into real height-classes, corresponding with age-classes, begins shortly after the first invasions. The oldest seedlings are rapidly concentrated in the dominant stratum.
Age-differences are the main reason for differentiation. Differences of 1 year can be sufficient to create and to temporarily maintain marked differences in social position.
Because of the positive correlation between age and height and on account of the early manifestation of stratification and social differentiation, which have functional consequences, silvicultural treatment must start early and pay attention to the smallest variations in micro-ecological conditions.