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Establishment of *Fagus sylvatica* and *Fraxinus excelsior* in an old-growth beech forest

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Abstract. Distribution of tree seedlings, forest architecture, light conditions, ground vegetation and humus conditions were studied in a 45 m x 100 m area including multiple gaps in an old-growth beech forest. Gaps were created after some beech trees had been felled in severe storms in February 1990. A group of adult ash trees is found near the study site. The data were analyzed by Correspondence Analysis. Young seedlings (< 4 yr), of both *Fraxinus* (a sun species) and *Fagus* (a shade species), were most abundant under the crown of beech trees in semi-shade conditions, and where beech litter did not accumulate. Differences in the dissemination of *Fraxinus* and *Fagus* explained differences in the establishment of the two species. In contrast, older seedlings of beech established before the storms were more numerous in the gaps, suggesting a change in the ecological requirements of beech seedlings in the course of time.

Keywords: Forest architecture; Gap; Humus; Light; Vegetation history; Windthrow.

Nomenclature: Rameau et al. (1989) for plants; Anon. (1992) for soil horizons.

Introduction

Successful establishment of tree seedlings is fundamental for the regeneration of forest ecosystems (Ponge et al. 1994). This process is determined by seed rain quality (Hofgaard 1993), predation (Weissen 1986) and environmental conditions of the regeneration niche (e.g. Dimbleby 1953; Grubb 1977; Bemier & Ponge 1994). Study of old-growth forests can provide information on the natural distribution of these conditions in the absence of silvicultural practices. Moreover, such forests can be considered as natural experimental sites where the combined action of environmental factors can be followed in time by synchronic analysis (Walter 1991). Nevertheless, investigations in natural forests may be complicated by the fact that environmental conditions are seemingly affected both by forest architecture (Oldeman 1990) and by site conditions (Bemier & Ponge 1993), thus making causal relationships unclear. The chosen site is unique in that it has escaped silviculture for centuries. Our aim was to determine the relationships between environmental conditions and re-generation processes of two tree species, *Fagus sylvatica* and *Fraxinus excelsior* in storm gaps by describing distribution patterns of tree seedlings (< 0.5 m in height), forest architecture, ground vegetation, thickness of litter layers and distance from seed producers. The data were analysed with multivariate analysis without an a priori assumption on causes and effects.

Study area and history of the site

The selected site at La Tillaie (33 ha) is located in the Fontainebleau Forest (50 km south of Paris). It has not been subjected to silvicultural practice since the 17th century, and only extensively pastured from the 15th to the 17th century (Lemée 1990). *Fagus sylvatica* has progressively replaced *Quercus petraea* since the end of the Middle Ages until a nearly pure beech forest had developed with natural cycles of death and replacement of *Fagus* (Lemée et al. 1991). The regeneration of beech in this site has occurred both through autogenic and exogenic processes (Lemée 1989). Mature trees decline over a period of 60 yr on average before they die (Lemée et al. 1991) and during that time the fall of main branches creates opportunities for the maturation of young beech trees. Saplings (50 cm to 5 m high) growing in shade conditions thus ensure the regeneration of this ecosystem, usually in areas where beech trees were deeply rooted and less subject to windthrow (pers. obs. in other old-growth beech forests). Generally, sapling growth was unsuccessful – young trees died when reaching the lower branches of parent trees – until adult trees (more than 30 m high) declined. Numerous gaps in the canopy cover had also been created by infrequent storms. The most recent gaps were formed in 1990, 1967 and during the 1930s (Lemée et al. 1991). Generally, these gaps were small (Bachacou et al. 1979). Some of these

small openings might be closed by crown enlargement of neighbouring trees (Koop & Hilgen 1987) or, when wider, by the development of seedlings (< 50 cm high) which thrive in open conditions (Pontailier 1979). Multiple windthrow gaps may delay the regeneration of the beech forest ecosystem because of limited seed dispersal to their centre, which may lead to the establishment and development of other tree species, such as *Fraxinus excelsior* and *Ilex aquifolium* (Lemee 1985). The present study was carried out during the summer of 1992 in a zone of beech windthrow gaps formed in February 1990 and situated in the vicinity of some seed-producing ash trees. The joint establishment of beech and ash seedlings could be followed in time, both before and after the 1990 storms. Only dead standing trees created small openings in the canopy before these storms. The 45 m x 100 m area also included unaffected zones with adult beeches (5-40 m high). Fig. 1 indicates the crown projection and height of all trees (living and dead) present in the study area. This area partly overlaps 'Plot 1' used by van Baren & Hilgen (1984) and Koop & Hilgen (1987) for their studies on forest architecture in the same biological reserve.

The seed production of beech varied considerably from year to year, but that of ash did not (Lemee 1985). Here it should be noticed that 1989 (the year preceding the storms) was a mast year. No mast year occurred from that time until 1994.

Shrub and ground vegetation did not cover the whole surface at the time of sampling, even in open conditions. Shrub species were *Ruscus aculeatus* and *Ilex aquifolium*, the former occurring mainly as dense carpets in shady conditions. Ground vegetation mainly included *Melica uniflora* and *Phytolacca decandra*, but also *Brachypodium sylvaticum*, *Galeopsis tetrahit*, *Festuca heterophylla*, *Pteridium aquilinum* and *Carex* spp. All of these were favoured by sunny conditions.

Soil in this area consists of a thin layer of sandy soil overlying limestone bedrock; it is leached and acid but without any podzolization (Bouchon et al. 1973). The humus was an acid mull, with both epigeic and endogeic earthworm species (Delhay & Ponge 1993; Ponge & Delhay 1995) and there is strong activity of white-rot fungi. Mull humus conditions combined with the absence of dense ground vegetation were said to be favourable for the establishment of beech (Watt & Tansley 1932; Le Tacon & Oswald 1978; Weissen et al. 1986).

Material and Methods

The study area was divided into 720 square units, 2.5 m x 2.5 m each. At the centre of each unit, the thickness of three litter horizons (OL, OF and OH when present) was recorded, together with tint, value and chroma of the A horizon at 5 cm depth, according to the Munsell code (Anon. 1990). The presence of white-rot fungi in the litter was recorded. The opportunity for light to reach the surface was checked by visual observations in seven directions, except north (this direction being considered as never sunny). Other parameters (Table 1) were taken from the vegetation map, which was made directly in the field. Crown projection and height of the trees, shrub and ground vegetation and fallen wood were mapped, together with tree seedlings, the age of which was determined as well. For each square unit, the distance to the western side of the study area was measured. This was considered indicative of the distance to the group of ash trees that produced seed. In total there were 60 variates. Table 1 indicates-how these were numbered and measured or estimated.

Correspondence Analysis was performed on a data matrix with 720 square units and 59 parameters. The distance to the western side of the study area was excluded from the analysis, because it was only used to interpret the factorial axes. All variates were transformed so that their mean value = 10 and their variance = 1. This ensured that distance to the origin of the axes (centre of gravity) did not depend on the nature of the data (presence-absence, countings or measurements), but only on the contribution of each measurement to the factorial axes. In addition each transformed variate was associated with a new variate, created by complementing the former to 20 (giving mean and variance equal to 10 and 1, respectively). The creation of a pair of positive and negative poles around each variate was proposed by Benzecri (1973) in case variables differed much in mean and variance but are of equal importance to describe the studied phenomenon.

The significance of some of the effects brought about by Correspondence Analysis was tested with one-way ANOVA (Sokal & Rohlf 1981).

Results

Fig. 2 presents the correspondence between the position of the 720 plots in the diagram of axes 1 and 2, and some of the variates (Table 2). The position of variate 27 (degree of opening) at the farthest distance from the origin along axis 1, together with other variates describing the presence/absence of trees (Table 2), indicate that the most prominent feature in this site is the contrast between closed canopy and gaps. The variate most negatively related to canopy opening was the density of 3-yr-old beech seedlings (11) which increased from

open to closed environments (Table 3). 2-yr-old beech seedlings (10) showed a similar trend, while 1-yr-old seedlings were totally absent. *Melica uniflora* (2) and > 4-yr-old beech seedlings (12) – dating from before the 1990 storms – followed an opposite trend. They were more abundant in the gaps created by these recent storms than under the tree crowns (Table 3). A similar but less pronounced response was shown by ash seedlings, but with a lesser degree of association with canopy opening (Table 3).

The association between the tallest trees (33) and the density of saplings (35, 2) suggests that the development of saplings under full-grown trees was a common way of regeneration for beech in this site.

Axis 2 distinguished two groups within the group of below-canopy squares (Fig. 2), indicated by ‘west side’ and ‘east side’. The distance to the west side of the study area (60) was most closely related to this axis (Table 2). Closely associated with this separation were the high pole stage (31) and full-grown trees (33), respectively associated with ‘west side’ and ‘east side’. Full-grown trees of the east side were associated with beech saplings (28) as mentioned above and the pole stage of the ‘west side’ with ash seedlings of varying age (13, 14, 15, 16, see Table 4) and *Ruscus aculeatus* (1). We may note that height classes of trees were spread along axis 2 (Table 2). From the positive to the negative side sap-lings (28) were followed by trees from 5 to 10 m high (29), then from 10 to 20 m high (30), and finally from 20 to 30 m high (31). The complete sequence can be followed by going back to the positive side, with adult trees from 30 to 40 m high (32) followed by those over 40 m high (33) which were found at about the same places as saplings (28), indicating their co-occurrence.

Along axis 3 (Fig. 3) there is differentiation within the below-canopy group of square units, one group corresponding to the establishment of ash seedlings (13, 14, 15, 16) in half-sunny places (Table 5) where light mostly comes from the east (51), and the southeast (47), with thin OL (53) and OF (54) horizons (Table 6), and the other group corresponding to little light from the east and southeast, thicker OL and OF horizons. It seems that these different environmental conditions at the ground surface are associated with different architectural patterns of the trees. Half-sunny places, with a thin litter cover and higher densities of ash seedlings are located under full-grown trees (33). These relatively favourable humus and light conditions can be associated with the senescence of beech trees (a lower foliage production creating small openings in the canopy). This has been demonstrated for humus and earthworm communities in a previous study (Delhaye & Ponge 1993; Ponge & Delhaye 1995). Humus and light conditions under the canopy seem to have little influence on the establishment of beech very much, except 4-yr-old seedlings which are 17 significantly more numerous under more sunny conditions (Table 5), and 2-yr-old seedlings which are significantly more numerous when the OF horizon is of a

medium thickness (Table 6).

Discussion

Evidently, certain variates are highly correlated, for example tree height and stem diameter classes. This is reflected in the results, more particularly in the hierarchy of the first axes (Ramsey 1986). However, these redundancies are the result of natural processes (i.e. ecological interactions in an old-growth forest, the subject of our study) rather than a deliberate organization of the data prior to the study. Thus we chose to interpret the shape of the data cloud in the subspace delineated by the first three axes, while concluding that the following axes reflect variation in less important, secondary processes. Although the first three axes extracted only a small part of the total variance (5.0, 4.6 and 4.1 % respectively), this was considered significant, given the large number of variates used in the analysis ($59 \times 2 = 118$ variates, with 59 degrees of freedom).

It has been stated by Watt (1925) that regeneration of beech occurs mainly in small gaps, given that (1) most seedlings are present under the crowns of the trees that produced seed and (2) light is necessary for optimal development. Thus the best conditions for regeneration occur when a tree falls in the winter following a summer favourable for beechnut production. In our site, we observed that 1989 (i.e. just before the 1990 storms), was a mast year. We did not notice that 3-yr-old seedlings (i.e. germinated just before the storms) were more numerous in the gaps opened after the 1990 storms; we even observed the contrary (Table 3). Thus the growth of beech seedlings does not seem to be hampered by the presence of a canopy cover at least in the first three years of their life. Four-yr-old or older seedlings were more numerous in the gaps, contrary to younger seedlings (Table 3, Fig. 2). Although based on very low densities, this result suggests that gaps create more favourable conditions for the development of beech seedlings – as was demonstrated by Pontailleur (1979) at the same site. Our results could, nevertheless, indicate that this does not apply to very young seedlings. Watt (1923) observed in the field that direct light stimulated the growth of 5-yr-old *Fagus sylvatica* seedlings much more than that of 2-yr-old ones; this is supported by our results. In contrast, Logan (1973) demonstrated experimentally that the growth of American beech (*F. grandifolia*) seedlings was better in semi-shade conditions, whatever their age. Further establishment of beech within the gaps created in 1990 will depend upon a year of good seed production and can not be described in our study.

Beech saplings can develop under the canopy of adult trees, as was pointed out by Faille et al. (1984),

Koop & Hilgen (1987), Lemée (1987) and Lemée et al. (1991). This process is independent of the existence of a gap phase for the renewal of the forest ecosystem. Thus, there are two kinds of events that may affect the development of such a forest ecosystem, described as ‘silvatic mosaics’ in a late ‘pre-equilibrium’ or early ‘equilibrium’ stage according to the nomenclature of Oldeman (1990): storms may abruptly shorten the life of a tree or a group of trees and create a single or multiple gap, in contrast to tree decline, that commonly occurs progressively between 240 and 300 yr in the investigated site, according to Lemée et al. (1991). This combination of events is responsible for the present architecture of this forested area but it should be mentioned that the renewal of the beech ecosystem may occur without a need for gaps. Such phenomena were also observed in *Fagus crenata* forests in Japan (Peters et al. 1992). Less clear is the process observed by Remmert (1991) in some German beech (*Fagus sylvatica*) forests, which involves a succession of three different tree species for the renewal of the beech forest ecosystem. This author indicated that a shortcut in this scheme often allows the direct regeneration of beech. Thus the first step of regeneration he described belongs to a class of unpredictable events (such as the establishment of ash within the present beech ecosystem) rather than to steady state mechanisms allowing the forest ecosystem to renew itself by its own means.

The appearance of adult ash trees in the vicinity of the west side of the area is associated with large-surface multiple gaps that occurred in the periphery of the biological reserve of La Tillaie during the 1930s (Lemée 1989; Lemée et al. 1991), giving an opportunity for previously absent shade-intolerant species, such as ash, to establish themselves deep into the reserve. Only a part of this zone is included in the study area which explains both the existence of a west-to-east decrease in the establishment of ash (Table 4) and the gradient from pole stage to full-grown beech trees (Table 2).

Watt (1925) was the first to find differences in the distribution of *Fraxinus* and *Fagus* seedlings in a forest dominated by *Fagus sylvatica*, but our data did not indicate similar differences in the distribution of these two tree species. Watt observed gaps with many ash seedlings while beech seedlings were present under beech trees and grew better at the border of the canopy; thus they surrounded a carpet of ash seedlings. In our study the establishment of ash was mainly under the beech canopy (Table 3, Fig. 2), with a preference for semi-shade conditions (Table 5). This may be due to poorer soil conditions in the gaps, at least before the development of ground vegetation, as observed in the same site by Ponge & Delhay (1995). The stricter requirements of *Fraxinus* regarding humus quality (Rameau et al. 1989; Lemée 1985) lead to a preference of this species for places with thinner litter layers (Table 6, Fig. 3). A similar discrimination of the thickness of litter layers during

the establishment of two co-occurring species was observed in a spruce-fir ecosystem (Knapp & Smith 1982). If the fate of ash seedlings growing under a dense canopy of beech is uncertain, we may question whether ash will replace beech in those places where the only beechnuts were those shed before the last storm. The wide gaps produced by the multiple windthrows, will certainly increase the probability that ash individuals reach the canopy before beech could fill the gaps by crown enlargement or regeneration. Again, it is clear that gaps should not be considered as a stabilizing agent of the beech forest ecosystem, even if water and light conditions in the gaps are more favourable for the development of beech seedlings (Pontailier 1979; Fardjah et al. 1980).

Conclusion

Despite apparent complexity, the distribution of tree seedlings in the old-growth forest studied can be explained (even if not fully understood) by the creation of gaps during two periods of severe windthrow (1990, 1930s), now replaced by a dense cover of growing beech. Storms in 1967 did not affect the study area, according to Bouchon et al. (1973) who mapped the felled trees. Other events, such as the increased influx of light under the crowns of remaining trees, are a consequence of the last storm. Our analysis cannot answer the question whether light or humus conditions are the decisive factor in the establishment of ash under a beech canopy, since both seem tightly connected.

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Legends of figures

Fig. 1. Projection of tree and sapling crowns in the study area. Small dashed lines indicate the connection of a tree base with the corresponding crown when this tree base was outside the crown projection.

Fig. 2. Diagram of axes 1 and 2 of the Correspondence Analysis of 720 square units. All units and seven variates regarding *Fagus* and *Fraxinus* seedling densities are represented. B2, B3, B4 = *Fagus* saplings of 2 yr, 3 yr and > 4-yr, respectively; A1 = *Fraxinus* seedlings; A2, A3, A4 = *Fraxinus* saplings of 2 yr, 3 yr and > 4-yr, respectively.

Fig. 3. Diagram of axes 1 and 3 of the Correspondence Analysis of 720 square units. See Fig. 2 for details.

Table 1. List of the 60 variates used in data analysis. Coding indications for variates 1-9, 34, 41-45, 56: 0/1/2= absent/present/abundant; for variate 27, 0/1/2 = closed/half-open/open; for variates 46-52, 0/1 = no/yes; for variates 53-55: cm = thickness in cm; for variates 57-59 Munsell = Munsell coding; for variate 60, m = distance in m; for all other variates, N = total number of individuals.

No.	Variate		Coding
1	<i>Ruscus aculeatus</i>		0/1/2
2	<i>Melica uniflora</i>		0/1/2
3	<i>Pteridium aquilinum</i>		0/1
4	<i>Galeopsis tetrahit</i>		0/1
5	<i>Festuca heterophylla</i>		0/1/2
6	<i>Brachypodium sylvaticum</i>		0/1/2
7	<i>Ilex aquifolium</i>		0/1
8	<i>Phytolacca decandra</i>		0/1/2
9	<i>Carex</i> spp.		0/1/2
10	<i>Fagus sylvatica</i>	2 yr	N
11		3 yr	N
12		4 yr	N
13	<i>Fraxinus excelsior</i>	1 yr	N
14		2 yr	N
15		3 yr	N
16		4 yr	N
17	<i>Prunus avium</i> seedlings		N
18	<i>Quercus petraea</i> seedlings		N
19	<i>Carpinus betulus</i> seedlings		N
20	<i>Populus tremula</i> seedlings		N
21	<i>Betula pendula</i> seedlings		N
22	<i>Acer pseudoplatanus</i> seedlings		N
23	<i>Sorbus aucuparia</i> seedlings		N
24	<i>Solanum dulcamara</i> seedlings		N
25	<i>Mespilus germanica</i> seedlings		N
26	<i>Salix aurita</i> seedlings		N
27	Degree of canopy opening		0/1/2
28	Height class	0.5–5 m	N
29		5–10m	N
30		11–20m	N
31		21–30m	N
32		31–40 m	N
33		>40m	N
34	Trunks of living trees		0/1
35	Trunk diameter class	10 cm	N
36		10–30 cm	N
37		31–40 cm	N
38		41–60 cm	N
39		61–80 cm	N
40		81–110cm	N
41	Dead branches on the ground		0/1
42	Dead trunks on the ground		0/1
43	Uprooted tree stumps		0/1
44	Whole tree crown on the ground		0/1
45	Standing dead trunk		0/1
46	Canopy aperture in direction	S	0/1
47		SE	0/1
48		SW	0/1
49		W	0/1
50		NW	0/1
51		E	0/1
52		NE	0/1
53	OL horizon		cm
54	OF horizon		cm
55	OH horizon		cm
56	White-rot fungi		0/1
57	Colour tint of the A horizon		Munsell
58	Colour value of the A horizon		Munsell
59	Colour chroma of the A horizon		Munsell
60	Distance to the western side (additional)		m

Table 2. Position of the 60 variates along the first three axes of a Correspondence Analysis (the coordinates may be interpreted as contributions to the axes, see text for explanation). The coordinates of the 60 conjugate variates were omitted, because they were symmetrical around the origin.

Variate	Axis 1	Axis 2	Axis 3	Variate	Axis 1	Axis 2	Axis 3
1	0.38	-5.20	2.86	31	0.76	-5.54	1.59
2	-3.39	-0.09	-0.85	32	2.82	0.31	3.57
3	-1.54	0.21	-1.26	33	4.72	3.37	-3.11
4	0.55	-2.12	-3.22	34	4.76	1.39	2.61
5	0.70	-0.50	0.21	35	3.79	3.84	-0.97
6	-0.36	-0.13	-1.34	36	1.77	-0.27	1.24
7	0.90	-0.38	-0.67	37	1.21	-0.59	1.29
8	-2.45	3.27	-2.73	38	1.35	0.25	1.30
9	-0.73	0.92	-1.34	39	1.32	-0.32	2.05
10	3.34	0.76	-0.47	40	1.66	0.90	1.52
11	4.80	-0.52	-1.71	41	-3.44	-2.16	1.53
12	-2.28	1.13	-1.87	42	-3.22	0.33	-0.45
13	1.76	-5.14	-3.74	43	-2.14	1.04	-1.65
14	2.12	-5.50	-3.70	44	1.65	2.89	0.71
15	1.90	-4.12	-5.12	45	1.40	-0.01	0.83
16	-0.53	-2.30	-4.53	46	-2.13	1.66	0.47
17	1.60	-0.54	-1.43	47	0.68	0.42	-2.85
18	0.18	-1.17	0.58	48	-0.33	4.72	-2.69
19	-0.63	-0.73	-0.38	49	-2.40	-0.62	-0.56
20	-1.38	-0.40	-1.12	50	-1.92	-2.46	2.07
21	0.24	-1.10	-0.42	51	2.49	1.48	-2.80
22	1.07	-1.64	-2.37	52	-3.35	1.42	-2.42
23	0.72	-1.01	0.34	53	-0.53	-2.04	2.59
24	-0.97	-0.15	-0.67	54	0.09	0.69	2.66
25	0.68	0.15	0.18	55	-1.02	0.48	0.47
26	0.99	-0.78	-3.09	56	1.18	-0.22	1.90
27	-6.76	2.03	-1.85	57	0.61	-0.06	-0.05
28	3.92	3.73	-1.67	58	0.29	-1.53	-0.54
29	1.24	1.64	0.19	59	-0.70	-0.38	-0.44
30	1.21	-0.46	-0.84	60 (add.)	0.53	-6.48	0.43

Table 3. Influence of the degree of canopy opening on the distribution of *Fagus* and *Fraxinus* seedlings. Densities expressed as number of individuals per 100 m². Means differing significantly at the 0.05 level are indicated by distinct letters (Newman-Keuls a posteriori test). *, **, *** = significance threshold levels at 0.05, 0.01 and 0.001 respectively.

		Canopy	Border	Gap	P (F > F _{obs})	
<i>Fagus sylvatica</i>	2 yr	1.8 a	0.8 b	0.6 b	0.002	**
	3 yr	13.8 a	7.7 b	3.9 c	0.0000	***
	4 yr	0.5 b	1.5 a	1.6 a	0.0005	***
<i>Fraxinus excelsior</i>	1 yr	10.0 a	7.3 ab	5.3 b	0.004	**
	2yr	4.5 a	3.5 a	1.7 b	0.003	**
	3 yr	1.7 a	0.9 b	0.7 b	0.03	*
	4yr	0.7	1.3	1.3	0.06	

Table 4. Influence of the distance to the west side of the study area (distance to adult *Fraxinus* trees) on the distribution of *Fagus* and *Fraxinus* seedlings. Otherwise as for Table 3.

		0–35 m	35–67.5 m	67.5–100 m	P (F > Fobs)	
<i>Fagus sylvatica</i>	2 yr	0.7 b	1.6 a	1.8 a	0.02	*
	3 yr	13.4 a	8.9 b	8.0 b	0.008	**
	4 yr	0.5 b	1.3 a	1.2 a	0.04	*
<i>Fraxinus excelsior</i>	1 yr	21.4 a	5.8b	1.2c	0.0000	***
	2yr	9.7 a	1.9b	0.3 c	0.0000	***
	3yr	3.1 a	0.8b	0.1b	0.0000	***
	4 yr	1.7 a	0.9b	0.2c	0.0001	***

Table 5. Influence of the number of directions from where light reaches the ground surface on the distribution of *Fagus* and *Fraxinus* seedlings under the canopy. Otherwise as for Table 3.

		0	1	2	≥ 3	P (F > Fobs)	
<i>Fagus sylvatica</i>	2 yr	1.3	1.9	2.3	1.3	0.46	
	3 yr	10.4	14.6	15.8	11.9	0.24	
	≥ 4 yr	0.2 b	0.3 b	0.4b	1.5 a	0.006	**
<i>Fraxinus excelsior</i>	1 yr	7.8 b	7.5 b	14.8 a	7.7 b	0.003	**
	2 yr	5.8	3.9	5.7	2.5	0.07	
	3 yr	1.1	1.2	2.6	0.8	0.14	
	≥ 4 yr	0.7	0.5	0.8	0.8	0.89	

Table 6. Influence of the thickness of the OF horizon on the distribution of *Fagus* and *Fraxinus* seedlings under the canopy. Otherwise as for Table3.

		0–1 cm	1.5–2 cm	>2cm	P(F>Fobs)	
<i>Fagus sylvatica</i>	2 yr	1.0 b	2.7 a	1.3b	0.009	**
	3 yr	13.6	14.8	12.0	0.53	
	≥ 4 yr	0.8	0.4	0.4	0.40	
<i>Fraxinus excelsior</i>	1 yr	13.5 a	8.9 b	8.2b	0.04	*
	2 yr	7.2 a	3.9 b	2.9b	0.004	**
	3 yr	2.7	1.7	0.8	0.06	
	≥ 4 yr	1.3 a	0.6ab	0.0b	0.01	*

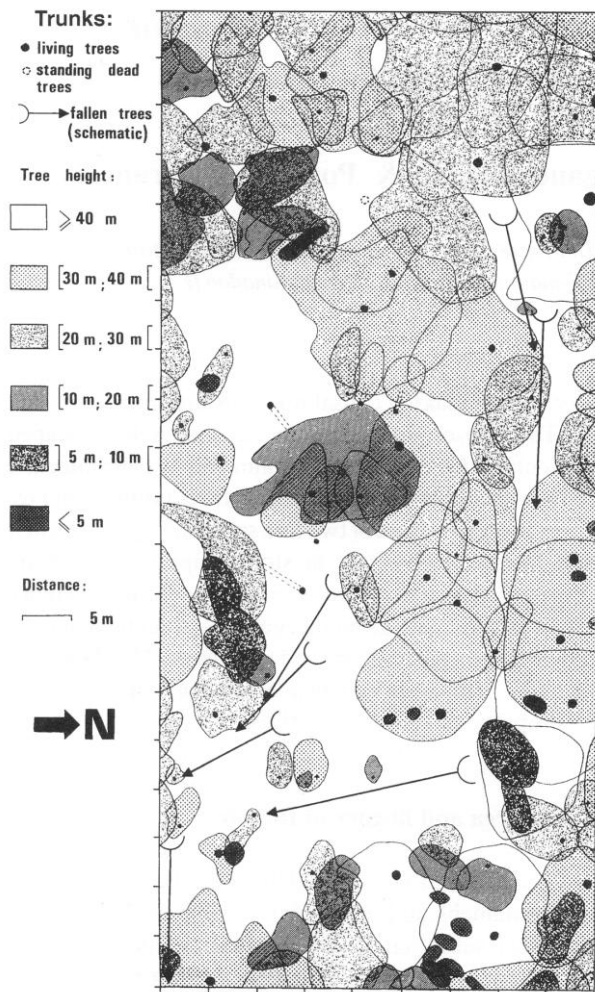


Fig. 1

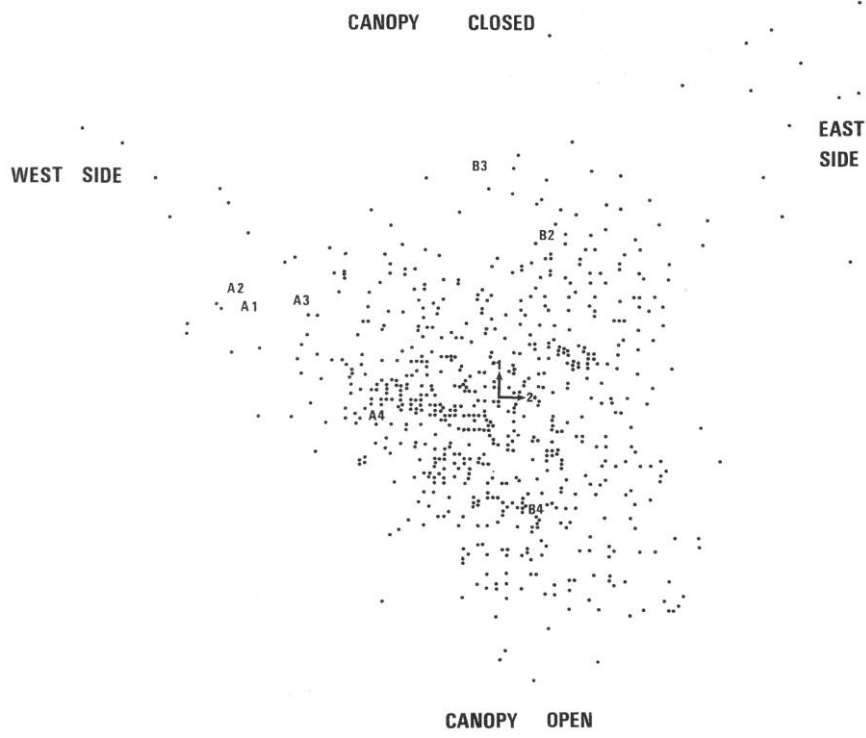


Fig. 2

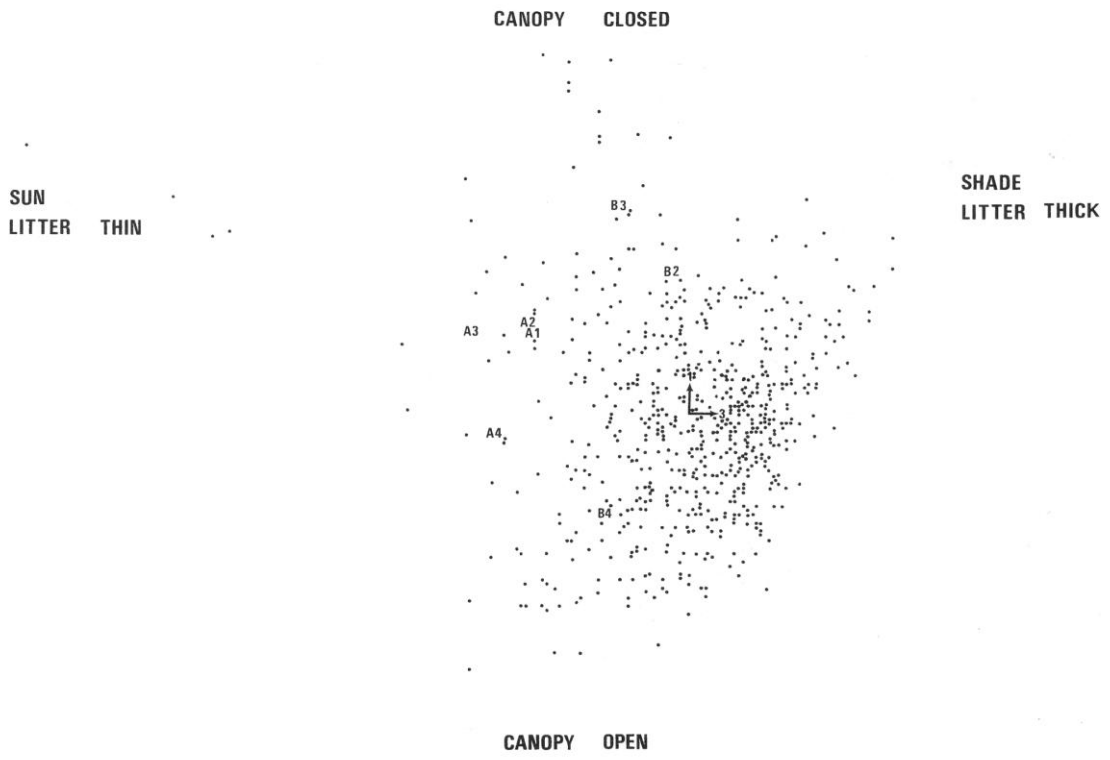


Fig. 3