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# **Influence of site conditions on the survival of *Fagus sylvatica* seedlings in an old-growth beech forest**

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**Abstract** : Following a full mast production in autumn 1995 in the old growth beech forest of la Tillaie, France, cupules, live and dead yearling seedlings were counted in September 1996 in 40 plots, embracing a wide range of ecological conditions. The influence of geomorphology and forest stage on mast production and on seedling establishment and survival was studied. Maximum seedling abundance did not occur in areas with the largest cupule abundance, but this result was not statistically significant. The presence of a shallow sandstone table under Fontainebleau sand, where beech is far from its optimum, influenced positively the production of mast but negatively influenced seedling survival. Contrary to all expectations, the early biostatic rather than the late biostatic phase seemed to be the best stage for beech regeneration. Gaps also provide good environmental conditions for seedling establishment. Humus and light conditions, water availability and competition between beech individuals may explain the results. Light was the main factor influencing mast production in mature stages, and drought was an important factor causing seedling mortality. This study points out the importance of seedling survival for regeneration patterns in beech forests.

**Keywords** : Forest regeneration, Forest stage, Geomorphology, Humus form.

**Nomenclature** : Oldeman (1990) for stages of the forest cycle and Brêthes et al. (1995) for humus forms.

## Introduction

Difficulties in the regeneration of *Fagus sylvatica* L. (beechwood) are well known. In the 19<sup>th</sup> century, plantation of seedlings and saplings was required due to regeneration failure of the beechwood in Normandy (Silvy-Leligeois 1949).

Quantity and quality of the seed rain are important factors in the regeneration process, but not the most prominent ones (Le Tacon et al. 1976; Weissen 1978; Lemée 1987). Regeneration failure often occurs in spite of a full mast year because of high seed mortality, due to predation, fungal diseases and harsh climatic conditions such as frost and drought (Watt 1923; Le Tacon et al. 1976; Weissen 1978, 1986). Also, light quality and quantity (Logan 1973; Lemée 1978; Peltier et al. 1997; Ponge & Ferdy 1997), water availability (Pontailier 1979) and humus form (Harley 1949; Weissen, 1986) may influence the survival of seedlings and saplings. Lastly, competition between beech and other plant species (Becker 1981; Nakashizuka 1987; Peters et al. 1992; Yamamoto et al. 1995) and competition between beech trees of varying age (Nakashizuka 1983, 1984) have been mentioned as important factors for the establishment success of beech seedlings.

In this paper, we focus on the initial phase of beech regeneration only. The purpose of our study is to determine how environmental factors, especially humus form and stage of development of the beech ecosystem, influence establishment and survival of beech seedlings during this first year. The study site in the Biological Reserve of La Tillaie (Fontainebleau forest, France) has been free of management since the beginning of the 16<sup>th</sup> century (Lemée 1990). This old-growth forest, where European beech (*Fagus sylvatica* L.) invaded an old grazed oak forest at least four centuries ago (Lemée 1990), provides an opportunity to study natural regeneration of beech (Pontailier 1979; Peltier et al. 1997; Ponge & Ferdy 1997). Moreover, 1995 was a full mast year, which was followed by the establishment of a significant number of seedlings in 1996, the year this study was conducted.

## Study site

The Biological Reserve of La Tillaie (33.74 ha) is located at the centre of the Fontainebleau forest, 50 km south-east of Paris. This old-growth forest is characterized by a strong heterogeneity of

soil conditions (geomorphology and humus forms) and stages of development of the beech ecosystem due to gap dynamics (Lemée 1978; Lemée 1990).

The soil is derived from fine Fontainebleau sand with a low clay content (<5%), overlying limestone or sandstone. Thickness of the sand layer and nature of the underlying rock (limestone or sandstone) vary, and Ponge & Delhaye (1995) demonstrated a close relationship between geomorphology, soil type and humus form. In shallow sand overlying limestone, the soil is leached and acidic and associated with an oligomull humus form. Podzols or podzolic soils are always found in deep sand overlying limestone, with an associated dysmull humus form (Ponge & Delhaye 1995). In the shallow sand overlying sandstone, the soil type is principally ochrous podzolic with a dysmoder humus form. The humus form is linked to soil biological activity, especially that of earthworms (Ponge & Delhaye 1995).

Concurrently with geomorphology, the distribution of vegetation is heterogeneous (Lemée 1978, 1990). All major successional stages of the beech ecosystem which occurred in this old growth forest were included in the study. The appearance of gaps [zero-events sensu Oldeman (1990)] follows the fall of main branches or uprooting of old trees by storms. Small gaps created by the fall of branches are often closed by the expansion of neighbouring trees' crowns (Faille et al. 1984), which prevents regeneration of the beech (Oldeman 1990). When large gaps are created by severe storms like in 1930, in 1968, and in 1990 (Peltier et al. 1997), the success of beech regeneration depends on the vegetation which became established after the gap creation (Faille et al. 1984). The innovation phase (establishment of beech seedlings and growth of saplings) occurs when large gaps are not colonized by light-demanding species like blackberry or bracken fern (Faille et al. 1984). These social species, which form a dense and permanent cover, create environmental conditions unfavourable for seedling survival and so prevent the regeneration of beech. The aggradation phase (phase of intense growth) is characterized by natural thinning in the population of young trees (Nakashizuka 1984). The high mortality is caused by a strong competition between individuals for available space (Lemée 1987). In the following phase, the biostatic phase, trees reach reproductive maturity. In the early biostatic phase, trees keep on growing and their height growth normally ceases in the late biostatic phase. In the degradation phase, senescent trees stop fruiting.

## Material and Methods

The study was conducted on 40 plots (7m x 7m) previously chosen for studying plant-soil relationships (Ponge et al. 1999). The 40 selected plots covered all geomorphological types and stages of the forest cycle (Table 1).

Seeds dispersed in autumn 1995 and seedlings germinated in spring 1996 were sampled on the 40 plots during the first half of September 1996. Ten sampling points were randomly chosen on each plot. At each sampling point, yearling seedlings were counted in 2m x 2m quadrats and cupules (fruit-walls) were counted in 0.25m<sup>2</sup> subquadrats at the centre of each quadrat. Cupule counts were used to estimate the seed production (Oswald 1981). We distinguished between dead and live seedlings. Death of seedlings was mostly caused by summer drought or predation of cotyledons by herbivores.

To distinguish the influence of the forest cycle upon the distribution of cupules, live and dead seedlings from that of soil conditions, data were analysed with respect to either forest stage or geomorphology as sources of variation. The different forest stages were pooled in four groups (gap and degradation phase, aggradation phase, early biostatic phase and late biostatic phase). The gap and degradation phases were pooled because no seeds were produced in these stages. Despite its abovementioned influence on regeneration, ground vegetation in gaps was not taken into account because the number of plots was insufficient to warrant separate analysis. Three geomorphological categories were considered (sandstone, thick sand cover on limestone and thin sand cover on limestone).

Because of heterogeneity of the studied site, average values were compared between groups by t-tests (Sokal & Rohlf 1995). All plots were taken into account for studying the influence of the stage of forest dynamics, except gaps closed by lateral encroachment (plots R and Z), with mixed characteristics. The influence of geomorphology was assessed only on plots with mature trees (biostatic phases and gaps closed by lateral encroachment). Relationships between cupule numbers and the total number of seedlings (live + dead seedlings) and between live seedling numbers and the total number of seedlings were analysed by linear regressions (Sokal & Rohlf 1995), estimating germination percentage and seedling survival percentage respectively.

## Results

The average density of cupules in the early and late biostatic phases was significantly higher than in the gap and degradation phases and in the aggradation phase (Table 2). The early biostatic phase had a significantly higher total density of seedlings than the late biostatic phase whereas densities of cupules were not significantly different. The density of live seedlings was highest in the early biostatic phase, where it was significantly different from that in the aggradation and gap and degradation phases. Differences in the density of dead seedlings were not significant between the gap and degradation phase, the aggradation phase and the late biostatic phase on one hand and between the late biostatic phase and the early biostatic phase on the other hand.

The low number of plots did not allow statistical analyses of the effect of geomorphology on the distribution of cupules, live and dead seedlings on plots. Nevertheless the density of cupules was highest on sandstone, whereas the density of live seedlings was highest on thin sand cover overlying limestone (Fig. 1). The density of dead seedlings seemed to be lowest on thin sand cover overlying limestone.

The correlation between cupule number and the total number of seedlings was not significant for any forest stage or geomorphological category (Table 3) thus we could not use a regression of the total number of seedlings on cupule number to estimate the germination percentage. Comparison of linear regressions for the number of live seedlings on the total number of seedlings (all significant at the 0.01 threshold level) showed that forest stage and geomorphology influenced seedling survival (Fig. 2, Table 4). Seedling survival percentage, represented by the slope of the linear regression, was significantly higher in the early biostatic phase than in the gap and degradation phases. Seedling survival percentage in the latter stage was significantly higher than in the aggradation and late biostatic phases, which were not significantly different from one another. Seedling survival percentage was significantly higher on thin sand cover overlying limestone than on the two other geomorphological substrates, on which differences in survival percentage were not significant.

## Discussion

The age of trees in a beech population clearly influences mast production. Mast production was similar and higher in the two biostatic phases (early and late) and similar and lower in the gap and degradation, and the aggradation phase. The two main environmental factors influencing mast production are light and water availability (Becker et al. 1977). Density of cupules was higher on sandstone than on the other geomorphological substrates. On sandstone, where the humus form (dysmoder) is unfavourable to the establishment of beech seedlings (Weissen 1986), the beech population is less dense and trees are smaller than on other substrates (Ponge et al. 1999), and thus tree crowns normally do not touch one another. Trees produce more fruits in this open crown population as compared to the population on limestone where the humus form is more favourable for the establishment of beech (Ponge & Delhaye 1995). Moreover, the presence of a shallow sandstone table offered more water to the root system of beech.

Although the total density of seedlings followed cupule density in the different forest stages, there was no statistically significant correlation between these parameters. The same absence of correlation has been observed by several authors working on beech forest regeneration. It often has been noted that regeneration failure occurred despite a full mast year (Watt 1923; Le Tacon et al. 1976; Weissen 1978). Several factors can explain this phenomenon. Predation by birds, rodents and big mammals, which can ruin a whole mast, is mentioned as the main factor explaining regeneration failure despite a good mast production. It is hard to predict the germination percentage of a whole mast, even when seeds are protected from predation (Weissen, 1978). Frost and drought also cause seed mortality, and the percentage of viable seeds varies from year to year. Watt (1923) showed that seeds required a film of water to germinate. Protection of the seed from desiccation can be afforded by litter or earthworm casts which create a moist environment. Whereas mast production was less important on thin sand cover overlying limestone than on sandstone, beech seedlings were more abundant in the first case. On this geomorphological substrate, beech seeds are buried and litter is degraded more rapidly due to a higher earthworm activity (Ponge & Delhaye 1995; Ponge et al. 1999), which prevents damping-off and protects seeds from frost and drought, as after ploughing (Weissen 1986; Le Tacon et al. 1976). We have no explanation for the results that the total number of seedlings was lower in the late than in the early biostatic phase despite the density of cupules did not differ.

Beech is known to be a shade-tolerant species. Seedlings can survive for 5 years in 2% daylight, but the optimal light level for seedling establishment is much higher than this (Watt 1923). To survive suppression by shade, beech seedlings change their growth rate and leaf morphology (Peters 1997; Pontailier 1979). The root system of young seedlings in sunny places is more strongly developed and leaves are more resistant to desiccation than those of seedlings growing in shade (Pontailier 1979). Pontailier (1979) showed that seedling mortality in gaps was constantly low, contrary to that in the late biostatic phase. Our results on seedling survival are similar. In the aggradation phase, the accumulation of organic matter and the high uptake of nutrients by actively growing beech can easily explain the low survival percentage of beech seedlings (Ponge & Delhay 1995). On the other hand, processes by which the survival of beech seedlings is negatively influenced in the late biostatic phase and positively in the early biostatic phase remains to be understood. On thin sand cover overlying limestone, seedlings occurred more densely than on other geomorphological substrates and their survival percentage was highest; both sandstone and thick sand cover on limestone disfavoured the survival of seedlings. The negative influence of acid soils on survival and growth of beech seedlings is well known (Harley 1949). This thus explains their poor performance on thick sand cover overlying limestone and sandstone where associated humus forms are dysmull and dysmoder respectively, contrary to thin sand cover overlying limestone with associated oligomull humus form (Ponge & Delhay 1995).

The present study shows the complexity of the relationships between plants and environmental conditions. The success of beech regeneration depends more on conditions of seedling establishment than on mast production, as was observed in coniferous forests (Ponge et al. 1998). Thin sand cover overlying limestone with an associated oligomull humus form was the most favourable condition for natural regeneration of beech, as was the early biostatic phase. The latter result contrasts with all expectations, but can explain the presence of a small population of slender young trees growing in the understorey. Fall of main branches from canopy trees may allow the suppressed saplings to reach the canopy. In the absence of storms opening wide gaps in the canopy, these individuals may help to renew the beech ecosystem, as claimed by Peltier et al. (1997).

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## LEGENDS OF FIGURES

**Fig. 1.** Distribution of cupules, live seedlings and dead seedlings according to geomorphology. Bars represent means of 10 sampling points with standard errors.

**Fig. 2.** Linear regression of the density of total versus live seedlings.  $R^2$  = coefficient of determination.

**Table 1.** List of the 40 plots selected in La Tillaie, characterized by forest stage and geomorphology.

Geomorphology	Forest stage	Plots
Thin sand cover on limestone	Gap	A, D, K', O, Q, S
	Gap closed by lateral encroachment	R
	Aggradation phase	B, E, I, J, M, M', N, N", U, AJ
	Early biostatic phase	C, F, L, N'
	Late biostatic phase	K, P, AE
	Degradation phase	T
Thick sand cover on limestone	Gap	W, AB, AD
	Gap closed by lateral encroachment	Z
	Aggradation phase	V, X, AA, AC
	Late biostatic phase	Y
Sandstone	Gap	G, AH
	Aggradation phase	AF
	Early biostatic phase	H, AG
	Late biostatic phase	AI

**Table 2.** Influence of forest stage on the distribution of cupules, live and dead seedlings. Means were compared by t-test. Differences significant at the 0.05 threshold level are in bold type.

	Cupules		Live seedlings		Dead seedlings		Total seedlings	
	t	P	t	P	t	P	t	P
Gap + degradation phase/Aggradation phase	0.52	0.610	0.25	0.805	1.01	0.324	0.03	0.978
Gap + degradation phase/Early biostatic phase	7.07	<b>&lt;0.001</b>	3.63	<b>0.002</b>	4.35	<b>&lt;0.001</b>	4.20	<b>&lt;0.001</b>
Gap + degradation phase/Late biostatic phase	3.26	<b>0.005</b>	1.59	0.132	1.93	0.072	2.17	<b>0.046</b>
Aggradation phase/Early biostatic phase	7.90	<b>&lt;0.001</b>	4.12	<b>&lt;0.001</b>	2.07	0.053	4.60	<b>&lt;0.001</b>
Aggradation phase/Late biostatic phase	3.56	<b>0.002</b>	1.86	0.079	1.03	0.316	2.16	<b>0.044</b>
Early biostatic phase/Late biostatic phase	0.58	0.577	2.11	0.064	0.59	0.567	2.36	<b>0.043</b>

**Table 3.** Correlation coefficients ( $r$ ) between total number of seedlings and cupules, and  $P$ -values for  $t$ -test of departure from zero.

	$n$	$r$	$P$
Forest stage:			
Gap + degradation phase	12	0.363	0.246
Aggradation phase	15	0.079	0.780
Early biostatic phase	5	0.070	0.911
Late biostatic phase	6	0.084	0.874
Geomorphology:			
Thin sand cover on limestone	25	0.150	0.474
Thick sand cover on limestone	9	0.601	0.087
Sandstone	6	0.306	0.555

**Table 4.** Influence of forest stage and geomorphology on seedling survival percentage. The survival percentage was estimated by the slope of the linear regression line of live seedlings on total seedlings. Pair-wise comparisons were tested by *F*-test. Homogeneous groups (means not significantly different at the  $P < 0.005$  level) share the same letter. All coefficients of determination were significant at the 0.01 level.

	<i>n</i>	Slope	Y-intercept	$R^2$
Forest stage:				
Gap + degradation phase	12	0.9037 <sup>b</sup>	0.0035	0.9613
Aggradation phase	15	0.7778 <sup>c</sup>	0.0039	0.8479
Early biostatic phase	5	0.9929 <sup>a</sup>	-0.1108	0.9812
Late biostatic phase	6	0.8130 <sup>c</sup>	-0.0023	0.8045
Geomorphology:				
Thin sand cover on limestone	25	0.9718 <sup>a</sup>	-0.0289	0.9914
Thick sand cover on limestone	9	0.5901 <sup>b</sup>	-0.0616	0.7010
Sandstone	6	0.7781 <sup>b</sup>	-0.0266	0.7836



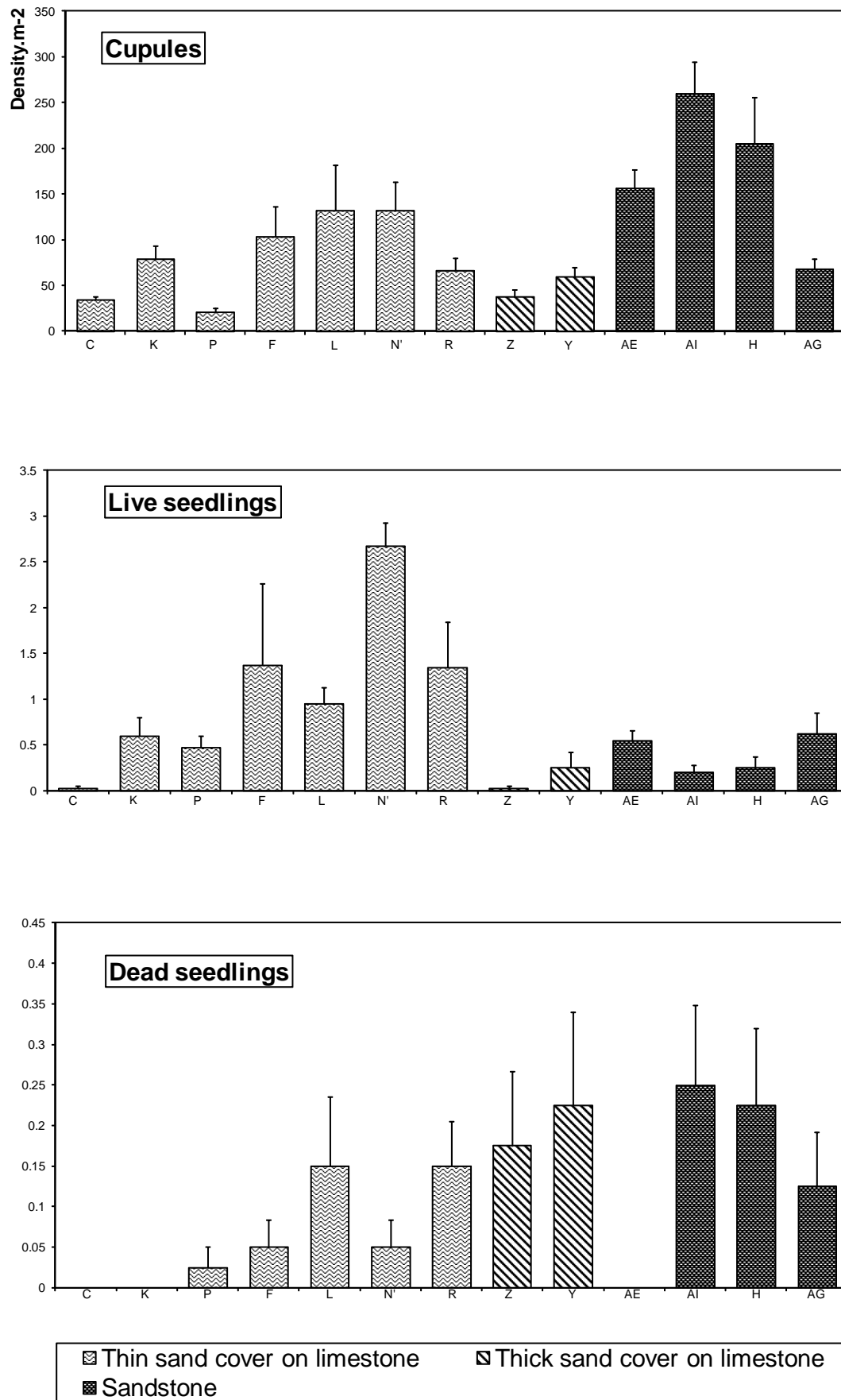


Fig. 1

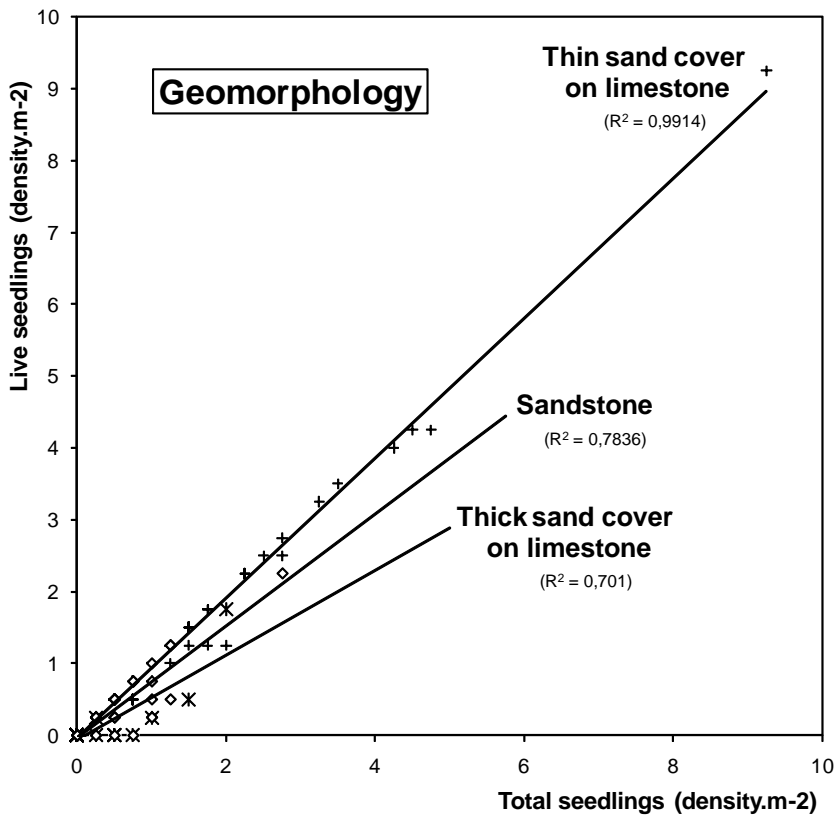
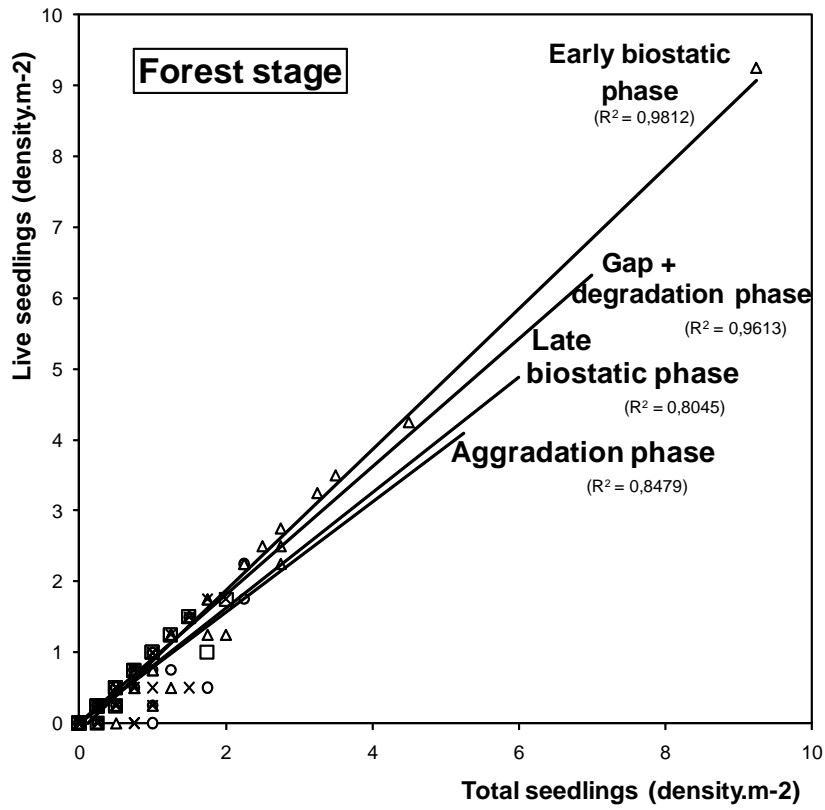


Fig. 2