

## Monitoring of natural regeneration in a mixed deciduous forest

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### Abstract

Monitoring of natural regeneration in a dense semi-natural mixed hardwood forest on the base of ash, beech, oak and sycamore occurred over 3 years in the Aelmoeseneie experimental forest, Belgium. 40 permanent plots (4 m × 5 m) were selected in three various humus types, located in an ash stand and in an oak - beech stand. In all plots abundance and top height of all broadleaved regenerated species were determined at the end of the growing seasons 1995 and 1998. In addition, the seedlings which appeared in the plots during 1996 and 1997 were identified and followed up.

This study proves that in the investigated sites natural regeneration is drastically poor and diversity is low, in particular where the humus layer is more acidic (mull moder) and the litter layer is thick. No regeneration phase older than the seedling stage ( $h < 40$  cm) is developed on the different humus types. On average, total number of seedlings in 1995 amounts to 38 units/are in the ash stand and to 63 units/are in the oak - beech stand. Survival rate over a 3-year period is 37% and 42% respectively in the ash and oak - beech stands. Total ingrowth during the growing seasons 1996 and 1997 is virtually poor, indicating 16 and 8 units/are respectively in above mentioned stands. Survival rate of occurring seedlings, as well as the ingrowth of new seedlings are notably different ( $P < 0.05$ ) according to the soil conditions of the ash stand. Generally, the low presence of seedlings and the lack of regeneration older than the seedling stage reveal that the regeneration development encounters with a critical problem. The continuation of this process would likely result in a progressive succession by the invasive and the unwanted tree species.

### 1. Introduction

Plant monitoring studies underline the importance of the young stages of the life cycle. The seed, seedling and juvenile phases prove to be the most vulnerable stages in virtually all monitoring studies (Silvertown, 1982; Pinero *et al.*, 1984). Processes during these age stages are clearly crucial for the understanding of patterns, dynamics and succession in plant communities (Grubb, 1977; Fenner, 1987; Schupp, 1990). By monitoring of natural regeneration the process of the forest succession can be demonstrated. On the other hand, succession takes place if the sum of the demographic processes at a site, i.e. deaths and establishments of plant individuals, results in a directional change with time of the relative abundance of species (Grubb, 1985). Accordingly, the mechanistic explanations of species replacement during succession may be derived from the specific characters, which generate differences between the species

involved in the rate of mortality of established individuals and/or the rate of establishment of new individuals, under existing environmental conditions (e.g. Connell and Slatyer, 1977; Noble and Slatyer, 1980; Peet and Christensen, 1980; van der Valk, 1981; Pickett *et al.* 1987).

Most recruitments of tree individuals in a closed canopy forest occur in gaps (Watt, 1947; Bray, 1956; Whitmore, 1975, 1978; Platt and Strong, 1989). It is predicted that trees established in the canopy persist until their death from senescence or external disturbances, and hinder further establishment (cf. the inhibition model of Connell and Slatyer, 1977). The "regeneration niche" (Grubb, 1977) of the species present will determine the probabilities for individuals of different species to reach the gap at the right time and grow to maturity in it and, hence, influence the relative abundance between species. Clearly, knowledge of processes during seed, seedling and juvenile stages is critical in exposing causal mechanisms of the replacement of species during a succession, and only long-term monitoring of plant individuals and manipulating experiments can increase it (Peet and Christensen, 1980; Martinez-Ramos *et al.* 1989).

By monitoring the process of regeneration development, the dimensions of forest decline and of forest degradation can also be indicated at the present time and be anticipated in the future. Van Miegroet (1991) states that, generally, forest degradation has developed into a problem with global dimensions. It is often the result of historical evolution, leading to use or abuse of the forest by man. Sometimes, its origins can be traced to purely natural causes and to minor or major catastrophes, not directly involving bad human conduct. Totally, it implies a certain amount of unwelcome change in the forest. The reduction of the number of species, textural decline due to an abnormal decrease in the number of trees and structural modifications, are usually recognized as the main physical and visual characteristics of forest degradation. Considerable loss of material production and productivity, exceeding the probability of recovery within a reasonable time, is nearly always considered as the ultimate parameter for degradation. Homogeneous, even-aged and structurally uniform forests, especially the man-made forests of this type, are generally considered as most susceptible to the impact of exogenous disturbance and, consequently, to degradation. Generally, long term would be required to re-establish the original composition and structure of the degraded forests, whereas complete rehabilitation is not impossible, but highly improbable (Whitmore, 1975; Knight, 1975).

Generally, in our research, monitoring of natural regeneration can clearly show the condition of the species at different growth stages within the ash and oak - beech stands. This way, the dynamical and the future processes (evolution, decline and retrogradation) of these stands can be evaluated.

## **2. Materials & methods**

At the end of September 1995, in a 1.8 ha-dense semi-natural deciduous broadleaved forest, consisting of an ash stand and an oak - beech stand, 40 permanent plots of 4 m × 5 m were selected. For the plots selected in this research, Zahedi (1998) presented that, according to the phytosociological classification of Noirfalise (1984) and humus quality indication (Rogister, 1985), three main humus types could be classified on the basis of the vegetation groups: group (1) with typical mull, group (2) with acid mull, group (3) with mull moder humus characteristics.

In addition, in the ash stand, along with the rich-nutrient vegetation elements, favourable conditions were created for microbial activity and increased decomposition rate. It presented conditions connected with typical and acid mull humus. Whilst, the oak - beech stand, with a lower pH value, was made up of acidophile species, indicating conditions related with moder humus. In this way, the sample plots were determined on the basis of the most important chemical and morphological properties (total N, total C, C/N ratio, moisture index and thickness of each horizon) of the humus layers. Table 1 gives some characteristics of the humus types in the two present stands.

Table 1. *Soil acidity (pH) and Carbon/Nitrogen ratio of humus layers, depth of forest floor and field layer density at three humus types, located in the ash and oak - beech stands*

Humus type	Stand	pH (acidity)	C/N ratio	Depth of forest floor (cm)	Field layer density
Typical mull	Ash	5.3-6.5	8-12	0-2	Dense
Acid mull	Ash	4.4-5.2	16-22	3-5	Scattered to dense
Mull moder	Oak - Beech	3.8-4.3	18-28	6-15	Poor

In Sep. 1995 in total 401 seedlings were growing in these plots on the three humus types. All existing seedlings within these plots were identified and tagged and then their number and total height registered. In late September 1998 the second survey within the confines of these plots was carried out and survival rate of seedlings in each humus type and stand was assessed. Likewise, all naturally regenerated seedlings, which appeared and survived in the plots during 1996 and 1997, were recorded (at the end of growing season 1997) and compared among the humus types and also the stands.

Statistical tests were performed using analysis of variance (ANOVA). The comparison of means was conducted by Tukey's test and T-test at 5% probability level.

### 3. Results

#### 3.1. Total height of seedlings

At the end of Sep. 1995, from the 401 naturally regenerated seedlings no individuals higher than 40 cm could be found. Seedlings age apparently ranged between 2 and 5 years. In the ash stand, 22 and 16 seedlings/are on average were noticed respectively to the height class of 10-20 cm and 20-40 cm (Fig. 1), whereas in the oak - beech stand these values were respectively 36 and 27 seedlings/are. In total 58 seedlings/are demonstrated a height between 10 cm and 20 cm, and 43 seedlings/are between 20 cm and 40 cm.

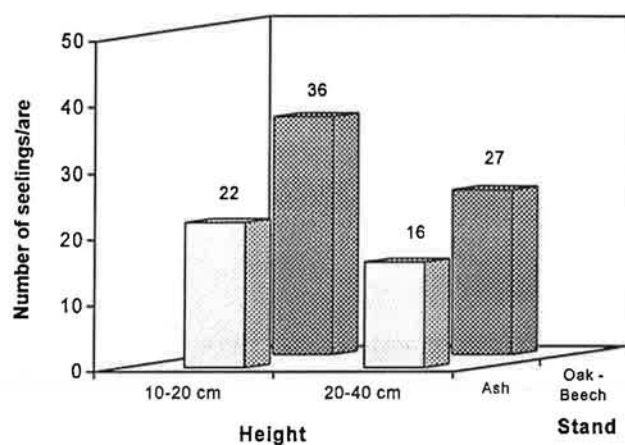


Figure 1. No. of seedlings (per are), over two height classes, in the investigated stands, measured in Sep. 1995.

### 3.2. Regeneration density

In late Sep. 1995, 151 seedlings were present in the ash stand and 250 seedlings in the oak - beech stand (Table 2). The number of seedlings appearing on the different humus types is also displayed in the same table.

Table 2. Number of seedlings in plots of 20 m<sup>2</sup> in the 2 stands and on the 3 humus types, registered in late Sep. 1995

Humus type	Ash			Oak - Beech		Total
	Typical mull	Acid mull	Mull moder	Acid mull	Mull moder	
Number of plots	9	6	5	7	13	40
Sum of seedlings, measured in plots	59	67	25	140	110	401
Sum of seedlings, measured in all plots of each stand		151		250		401
Mean number of seedlings, occurred on humus type/are	36	56	25	100	42	50
Mean number of seedlings, occurred in all plots of each stand/are		38		63		50

Records indicated that the mean seedling density in the ash stand amounted to 38/are (Table 3). This number was 33/are on typical mull, 56/are on acid mull and 25/are on mull moder. Analysis of variance (ANOVA), however, showed that the mean seedlings density did not differ among these three humus types (d. f. = 2, P = 0.413).

In the oak - beech stand, the mean seedling density on acid mull and mull moder was 100/are and 42/are, respectively. These numbers, however, did not display marked differences at the two humus types (t = 1.884, d. f. = 18, P = 0.076).

The mean seedlings density in the two stands was 50 units/are. It averaged 38 seedlings/are in the ash stand and 63 seedlings/are in the oak - beech stand. The comparison of means, using t-test, demonstrated that this characteristic did not differ substantially between the two stands ( $t = 1.129$ , d. f. = 38,  $P = 0.266$ ).

By pooling the data of the two stands, the mean seedlings number varied from 33 units/are and 37 units/are, respectively on typical mull and mull moder, to 80 units/are on acid mull. There was no appreciable difference in the number of seedlings occurring on the three humus types (d. f. = 2,  $P = 0.083$ ).

Table 3. Differences in seedling density (mean  $\pm$  se) (in are), grown on different humus types in the ash and oak - beech stands

Stand	Humus type	(Mean $\pm$ se)/are	P value (ANOVA)	T-test
Ash	Typical mull	33 $\pm$ 12	0.413 <sup>ns</sup>	
	Acid mull	56 $\pm$ 22		
	Mull moder	25 $\pm$ 13		
	Total	38 $\pm$ 9		
Oak - Beech	Acid mull	100 $\pm$ 58		1.884 <sup>ns</sup>
	Mull moder	42 $\pm$ 5		
	Total	63 $\pm$ 22		
Ash	3 humus types combined	38 $\pm$ 9		1.129 <sup>ns</sup>
Oak - Beech	2 humus types combined	63 $\pm$ 22		
Total	50 $\pm$ 12			
Ash and oak - beech pooled	Typical mull	33 $\pm$ 12	0.083 <sup>ns</sup>	
	Acid mull	80 $\pm$ 33		
	Mull moder	37 $\pm$ 5.0		
	Total	50 $\pm$ 12		

ns = non significant

### 3.3. Survival rate of the regenerated species

In the ash stand, the mean survival rate of seedlings amounted to 37%. This rate was 55%, 28% and 15%, respectively on typical mull, acid mull and mull moder. Analysis of variance revealed that, generally, survival rate of the seedlings grown on typical mull was greater than those on acid mull and mull moder (d. f. = 2,  $P = 0.044$ ) (Fig. 2).

According to Table 4, in the oak - beech stand, survival rate on acid mull (54%) and mull moder (35%) did not differ statistically ( $t = 1.284$ , d. f. = 18,  $P = 0.215$ ).

By combining the humus types, mean survival rate averaged 37% in the ash stand and 42% in the oak - beech stand. No substantial differences could be detected between the survival rate of seedlings grown in the two stands ( $t = 0.517$ , d. f. = 38,  $P = 0.608$ ).



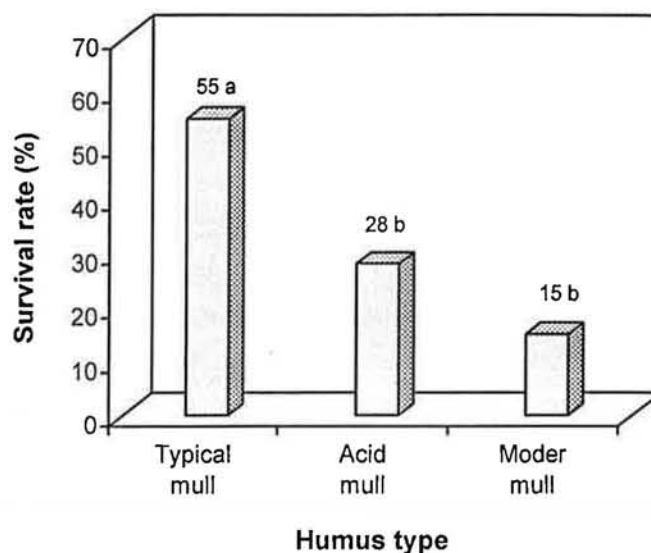


Figure 2. Survival rate of the seedlings over 3 years, grown on 3 humus types under a dominant cover of the ash stand.

(Means, followed by different letters are significantly different at 5% probability level according to Tukey's test).

Table 4. Survival rate (mean  $\pm$  se) of seedlings over a 3-year period, grown on different humus types in the ash and oak - beech stands

Stand	Humus type	(Mean $\pm$ se)/are	P value (ANOVA)	T-test
Oak - Beech	Acid mull	54 $\pm$ 7.2	0.135 <sup>ns</sup>	1.284 <sup>ns</sup>
	Mull moder	35 $\pm$ 9.9		
	Total	42 $\pm$ 7.1		
Ash	3 humus types combined	37 $\pm$ 7.0		0.517 <sup>ns</sup>
Oak - Beech	2 humus types combined	42 $\pm$ 7.1		
	Total	39 $\pm$ 4.9		
2 stands pooled	Typical mull	55 $\pm$ 11.8	0.135 <sup>ns</sup>	
	Acid mull	42 $\pm$ 5.9		
	Mull moder	30 $\pm$ 7.8		
	Total	39 $\pm$ 4.9		

(Means  $\pm$  se, followed by different letters in subscript, are significantly different at 5% probability level according to Tukey's test).

\* = significant

n s = non significant

By pooling the data from the two stands, survival rate of seedlings on the 3 humus types was not noticeably different (d. f. = 2, P = 0.135).

### 3.4. Ingrowth characteristics (regeneration in 1996 and 1997)

In the ash stand, the mean ingrowth, recorded in 1996 and 1997, was about 9 units/are on typical mull, 37 units/are on acid mull and 5 units/are on mull moder (Fig. 3). Analysis of variance revealed that ingrowth was higher on acid mull, compared with those on typical mull and mull moder (d. f. = 2,  $P = 0.000$ ).

The mean regeneration density occurring in this period in the oak - beech stand was 11 and 7 units/are, respectively on acid mull and mull moder. The statistical analysis demonstrated no clear differences between the ingrowth on the 2 humus types ( $t = 1.489$ , d. f. = 18,  $P = 0.154$ ) (Table 5).

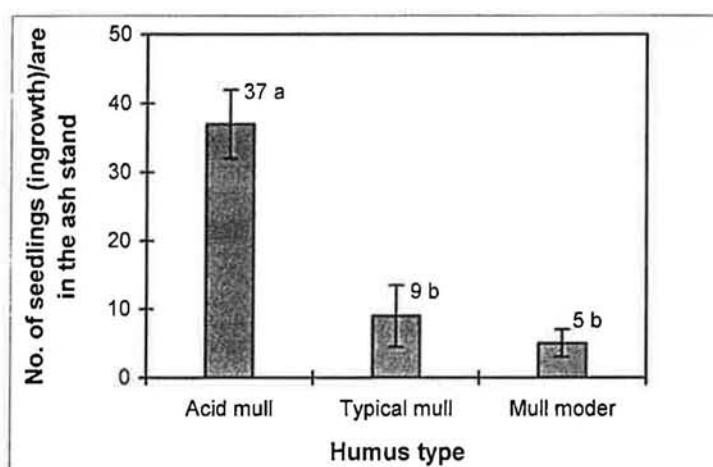


Figure 3. Number of seedlings which appeared and survived in 1996 and 1997, on 3 humus types in the ash stand.

(Means, followed by different letters, are significantly different at 5% probability level according to Tukey's test. Bars indicate standard error).

Table 5. Number of seedlings (mean  $\pm$  se) (per are) in 1996 and 1997, on different humus types in the ash and oak - beech stand

Stand	Humus type	Mean $\pm$ se (are)	T-test
Oak - Beech	Acid mull	11 $\pm$ 1.1	1.489 <sup>ns</sup>
	Mull moder	7 $\pm$ 1.0	
	Total	8 $\pm$ 1.0	
Ash	3 humus types combined	16 $\pm$ 4	0.078 <sup>ns</sup>
Oak - Beech	2 humus types combined	8 $\pm$ 1.0	
	Total	12 $\pm$ 2.5	

ns = non significant

Average regeneration number over both stands was 12 seedlings/are. This ingrowth averaged 16 and 8 seedlings per are, respectively in the ash stand and in the oak - beech stand. In fact, when combining the humus types, there was no appreciable difference between the regeneration number in the two stands, appeared during this period ( $t = 0.369$ , d. f. = 38,  $P = 0.714$ ).

By pooling the data from the two stands, the mean regeneration number/are on typical mull was 9, on acid mull 23 and on mull moder 6 (Fig. 4). According to Tukey's test, regeneration density on acid mull was more frequent than those on the other humus types.

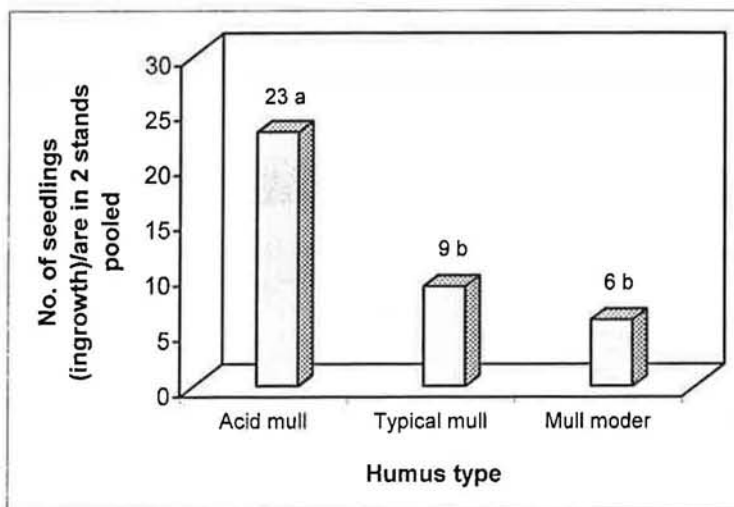


Figure 4. Number of seedlings which appeared and survived in 1996 and 1997, on 3 humus types in 2 stands pooled.

(Means, followed by different letters, differ significantly at 5% probability level according to Tukey's test).

### 3.5. Dynamical process of regeneration in the stands

In the ash stand, total seedlings number amounted to 38 and to 12 individuals/are, respectively at the first record (1995) and at the last record (1998) (Table 6). In addition, in total 16 seedlings/are emerged in 1996 and 1997 (ingrowth). In the oak - beech stand, total seedlings number was 63 units/are in 1995. Out of these, 27 individuals/are remained at the end of the period (1998) but 8 individuals/are (ingrowth) appeared during the period (1996 and 1997) (see Table 6).

According to Fig. 5, at the first record, *Fraxinus* seedlings benefited from the most abundant number with on average 23 units/are. Their ingrowth was 11 units/are but their total remaining seedlings did not proceed 5 units/are in 1998. *Acer* seedlings came on the second place but in each measurement their number did not exceed 5 units/are. Abundance of other species was strongly poor, whereas none of them presented more than 2 seedlings/are.

Fig. 6 demonstrates that in the oak - beech stand *Fraxinus* seedlings at the first and last records were more abundant than the other tree species. In fact it amounted to 33 individuals/are in



1995 and 7 individuals /are in 1998. Likewise, their ingrowth appearing during 1996 and 1997 was 15 individuals /are. In this stand *Acer* seedlings were relatively more plentiful than those in the ash stand. In the oak - beech stand, just like in the ash stand, broadleaved tree seedlings were either very poor or mostly absent.

According to Fig. 7, in the entire forest (2 stands), number of *Fraxinus* seedlings at the first record was 28 units/are. Total *Fraxinus* ingrowth amounted to 9 units/are during the two growing seasons (1996 and 1997) and to 10 units/are at the last record (1998). Number of *Acer* seedlings at the first measurement was 13 units/are, their ingrowth amounted to 2 units/are and their total remaining seedlings to 5 units/are. Other tree and shrub regeneration species occurred virtually poor.

Generally, in the entire stands, both total ingrowth and also survival rate were entirely poor (see Table 6), whereas in total at the end of the period only 31 seedlings/are (19 units in 1998, 12 units in 1996 and 1997) could be found.

Table 6. *Distribution of number of seedlings over the years*

Year	Mean number of seedlings (per are)		
	Ash stand	Oak - beech stand	Total (2 stands)
Recorded in 1995	38	63	50
Survived in 1998	12	27	19
Emerged in 1996 and 1997 (total ingrowth)	16	8	12

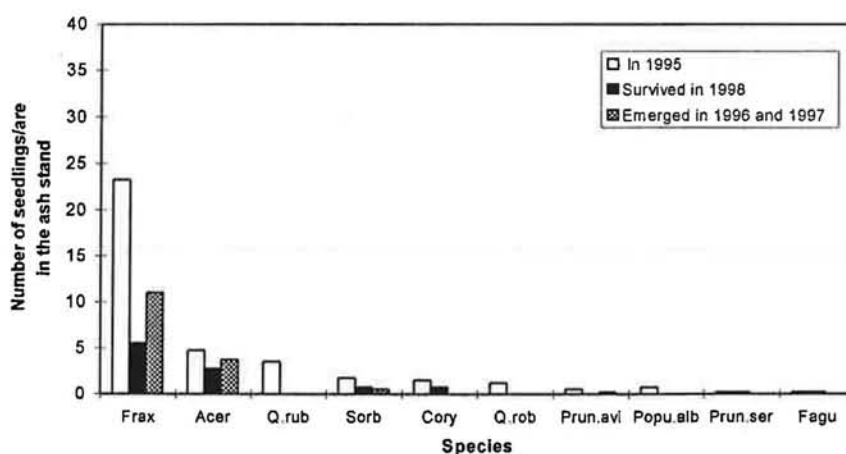


Figure 5. *Regeneration abundance (per are) of species in the ash stand.*

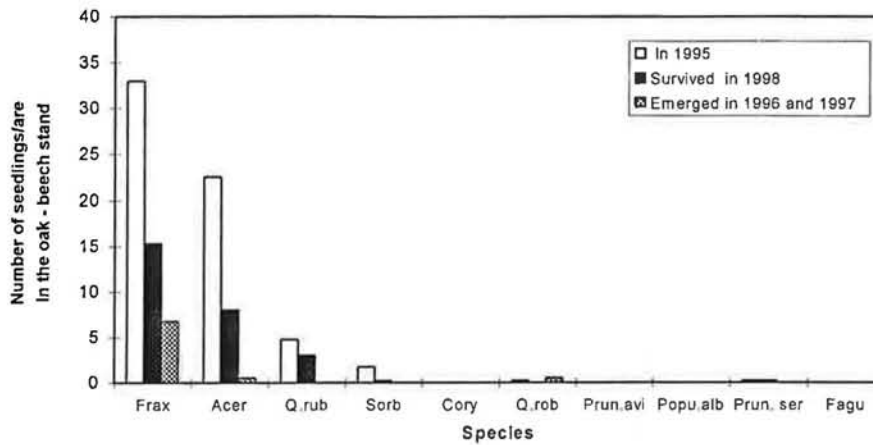


Figure 6. *Regeneration abundance (per are) of species in the oak - beech stand.*

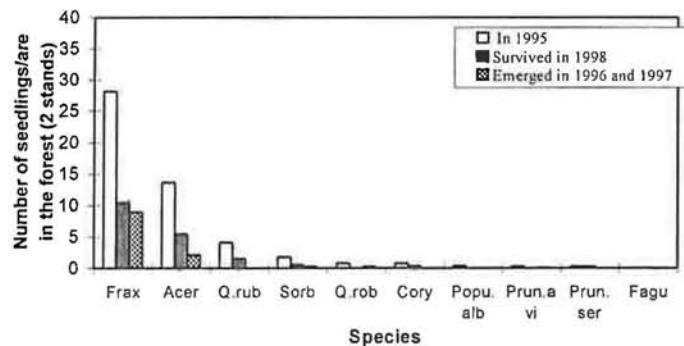


Figure 7. *Regeneration abundance (per are) of species over the whole experimental site.*

#### 4. Discussion

The present study indicates that the total regeneration number in 1995 amounts to 50 seedlings/are (see Table 6). This number is 38 and 63 units/are, respectively in the ash and oak - beech stands. There is no significant difference in number of the present seedlings in either of the stands. Likewise, no substantial differences can be found in number of seedlings recorded on the various humus types of the two stands as well as in the 2 stands pooled.

Survival rate of seedlings over a 3-year period averages to 39%. This rate is 37% in the ash stand and 42% in the oak - beech stand. However, there is no remarkable difference in survival rate of seedlings between the two stands. Only on the humus types in the ash stand a marked difference in this term can be detected.

Total number of new seedlings in 1996 and 1997 (ingrowth) averages to 12 seedlings/are. This number is 16 units/are in the ash stand and 8 units/are in the oak - beech stand. In no case, appreciable difference is shown regarding to the number of seedlings appearing in the two stands. Whilst in each stand as well as in the two stands pooled, ingrowth on acid mull is more frequent than that on other humus types.

Among the all naturally regenerated species, *Acer* following *Fraxinus* demonstrates the most abundant species in either of the measurements. Other broadleaved tree seedlings appear

drastically poor. Apparently number of seedlings occurring in the ash stand is not more abundant than that in the oak - beech stand. On the other hand, the results of this analysis obviously demonstrate that the abundance and variety of regenerated species, either at the first record or at the last record, is rather weak. In other words, the low value of the mean number of seedlings appearing in this forest (12 seedlings/are/2 yr) (see Table 6) reveals that the process of regeneration development in the experimental site encounters with serious difficulties.

Besides, the total height of seedlings is principally less than 40 cm and, in reality, no higher growth stage of development is found in the investigated area. As a matter of fact, this forest with a low survival rate and a poor ingrowth and a lack of the older growth stages of species, such as ash, oak and beech, shows that the dynamical process of these stands will likely result in a decline in stability and evolution, or probably lead to an alteration in climax. The data, obtained by Tabari and Lust (1999), exhibit that sycamore, in spite of inadequate number of parents trees in the ash stand, seems to succeed to reach the higher growth stages rather than ash. If this process continues, sycamore will become dominant over the forest. In reality, it may also be stated that in the ash stand consequently the successional process will develop gradually in favour of sycamore. However it will be relatively difficult that ash and or even the neighbour main trees, such as oak and beech, are easily able to compete with sycamore and or overcome it. Invasion of sycamore in the ash stand and its alteration in formation of stand is confirmed by Van Miegroet (1956), Scurfield (1959), Okali (1966), Van Miegroet *et al.* (1981), Taylor (1982, 1985), Waters and Savill (1992). However, the direct interventions in order to regulate the primary patterns of mixture are a necessity.

Data, determined in respect with regeneration condition in different growth stages in some canopy openings of the oak - beech stand of the experimental site, demonstrate that germination and regeneration establishment in this stand is too restricted (Tabari, 1999). Several adult oaks in this stand demonstrate symptoms of drought or disease and even death. Also, a number of dominant beeches seem to cease diameter growth and to reach gradually to senescence and, as a consequence, to encounter with the failure of the natural regeneration.

Besides that, the existence of a dense understorey (hazel and rowan) and a rank herbal layer, such as *Rubus* and *Pteridium*, as well as a deep litter layer and raw humus formation do not allow to establish a good regeneration for beech, oak and other tree broadleaved species as ash. With respect to the above mentioned, therefore, if such a dynamical process continues, the future of this stand will result in senescence and gradual death of the chief species and, consequently, replacement by less valuable species. This way, a decline or a degradation in the ecosystem of this forest will not be unlikely.

Matic (1996) reports that forests of pedunculate oak in Croatia, with regard to their natural and structural properties, are mixed with species such as narrow-leaved ash (*Fraxinus angustifolia*), black alder (*Alnus glutinosa*), lowland elm (*Ulmus minor*), field maple (*Acer campestre*), and others. These species are more aggressive in terms of their biological properties and ecological requirements compared to the less aggressive pedunculate oak. This is why any failure in regeneration and tending of pedunculate oak stands results in the degradation of these, and the establishment of the stands dominated by the above mentioned pioneering or transitional species. Iversen (1969) holds, nevertheless, the opinion that, even on extreme and poor sites, progressive acidification of base-poor soils can, over thousands of years, produce profound

changes in the nutrient-status of the exposed soil. Such a development can lead to reduced resistance of the dominant species, with enhanced vulnerability of the system as an ultimate consequence. It can also be sufficient to provoke gradual replacement of light demanding species such as ash and lime (*Tilia cordata*) in Northern Europe by less light demanding species such as birch (*Betula pendula*).

Generally, in beech and oak stands, beech and to a lesser extent oak, with the litter which takes a long time to decompose, provide litter accumulation, storing the organic matter on the soil surface, soil acidification and possibly gradual soil degradation. Soil degradation will likely be irreversible, where topsoil pH decreases below pH4. In this condition and below this threshold earthworms disappear and the soil enters the aluminium-buffer range (Muys and Lust, 1993). In our research, most of the area of the oak - beech stand has a critical problem for soil acidification (Zahedi, 1998). This may show the difficulties of the natural regeneration in this stand. Even though, Moller (1889), Wittich (1952), Toutain (1981) and Kreuzer (1986) emphasize that the acidified soils have a tendency toward a weak soil biological activity and Röhrig *et al.* (1978) underline that they are accordingly identified by the raw humus layer, superficial rooting and particularly inadequate natural regeneration. Likewise, in parts of this stand, where acidity is the highest (pH = 3.8-4.3) and the litter layer is the thickest (10 cm), natural regeneration is drastically poor and diversity is mainly weak. The failure of regeneration is also critical where acidity (pH) of the thick raw humus layer (moder mull) varies from 3.3 to 3.7 and litter thickness exceeds 10-12 cm (Tabari and Lust, *subm.*). In this way, only the dominant beech and oak trees and some planted shrubs, such as hazel, as well as herbal vegetation can be found. This can show the effect of acidification on the vegetation diversity as Ulrich (1981) points out that increased acidification results in disappearance of the secondary tree species such as ash, elm, cherry, hornbeam, lime and many mesophilous forest herbs.

Concerning to the above mentioned, in particular the grave problem for acidification of this stand, it may also be predicted that the possibility of a decline in growth and development of this stand and a gradual replacement towards the less valuable species is conceivable. This can be confirmed by Ulrich *et al.*, (1980), who claim that the main effect of soil acidification would be an increased mobilization of  $Al^+$ , injury to plant roots, reduced growth and finally forest damage. In other words, under such a condition in the long term, the forest soil would gradually become deficient in the nutrient availability and most likely effect would be a gradual decline in forest.

Likewise, cations leaching, particularly a nitrogen leaching, is perceived in the oak - beech stand of this forest (Zahedi, 1998). This may show a tendency toward degradation if such a defect develops throughout the stand. It can also be in line with Ulrich (1978), who maintains that the critical phases towards soil degradation and afterwards forest degradation is loss of phosphorus and rapid leaching of nitrogen.

## 5. References

- Bray, J. R. (1956). Gap phase replacement in a maple-basswood forest. - *Ecology* 37, 598-600.  
Connell, J. H., and Slatyer, R. O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. - *Am. Nat.* 111, 1119-1144.



- Fenner, M. (1987). Seed characteristics in relation to succession. - In: Gray, A. J., Crawley, M. J. and Edwards, P. J. (eds), Colonization, succession and stability. Blackwell Scientific, London, 103-114.
- Grubb, P. J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. - Biol. rev. 52, 107-145.
- Grubb, P. J. (1985). Plant populations and vegetation in relation to habitat, disturbance and competition: problems of generalization. - In: White, J. (ed.), The population structure of vegetation. Dr W. Junk Publishers, Dordrecht, The Netherlands, 595-621.
- Iversen, J. (1941). Landam i Danmarks Stenalder. Danm. Geol. Unders. RII. No. 66.
- Knight, D. H. (1975). A phytosociological analysis of species rich tropical forest on Barro Colorado Island, Panama. Ecol. Mon. 45, 259-284.
- Kreutzer, K. (1986). Zusammenfassende Ergebnisse aus experimentellen Freilanduntersuchungen über den Einfluss von sauren Niederschlägen und Kalkung in Fichtenbeständen [*Picea abies* (L.) Karst.]. Forstw. Cbl. 105, 371-379.
- Martínez-Ramos, M., Alvarez-Buylla, E., and Sarukhán, L. (1989). Tree demography and gap dynamics in a tropical rain forest. - Ecology 70, 555-558.
- Matic, S. (1996). Silvicultural treatments in regeneration of pedunculate oak stands. 426-439 In: Pedunculate oak (*Quercus robur* L.) in Croatia. Vinkovec - Zagreb, 559 pp.
- Moller, P. E. (1889). Recherches sur les formes naturelles de l'humus et leur influence sur la végétation et le sol. (Translation from Danisch). Ann. de la science Agr. Tome, 85-423.
- Muys, B., and Lust, N. (1993). Ecological changes following afforestation with different tree species on a sandy loam soil in Flanders, Belgium. In: Ecological effects of afforestation. Studies in the history and ecology of afforestation in western Europe. CAB International, on behalf of European Science Foundation, 179-189.
- Noble, I. R. & Slatyer, R. O. (1980). The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. - Vegetatio 43, 5-21.
- Noirfalise, A. (1984). Forests et stations forestières en Belgique. Les Presses Agronomiques de Gembloux, Gembloux.
- Peet, R. K. & Christensen, N. L. (1980). Succession: a population process. - Vegetatio 43, 131-140.
- Pickett, S. T. A., Collins, S. L. & Armesto, J. J. (1987). Models, mechanisms and pathways of succession. - Bot. Rev. 53, 335-371.
- Pinero, D., Martinez- Ramos, M. & Sarukhán, J. (1984). A population model of *Astrocaryum mexicanum* and a sensitivity analysis of finite rate of increase. - J. Ecol. 72, 977-991.
- Platt, W. J. & Strong, D. R. (eds) (1989). Treefall gaps and forest dynamics. - Ecology 70, 535-576.
- Rogister, J. E. (1985). The main forest plant association of Flanders (in Dutch with English summary). Rijksstation Voor Bos- en Hydrobiologisch Onderzoek, Groenendaal - Hoeilaart, België. Werken, Reeks A 29, 106 pp.
- Röhrig, E., Bartels, H., Gussone, H. A. & Ulrich, B. (1978). Untersuchungen zur natürlichen Verjüngung der Buche (*Fagus sylvatica*) Forstw. Cbl. 97, 121-131.
- Schupp, E. W. (1990). Annual variation in seedfall, postdispersal predation, and recruitment of a neotropical tree. - Ecology 71, 504-515.



- Silvertown, J. W. (1982). Introduction to plant population ecology. - Longman, London.
- Tabari, K. M. (1999). Factors determining regeneration of ash (*Fraxinus excelsior* L.) in a mixed hardwood stand. Ph. D. thesis. University of Gent, Belgium.
- Tabari, K. M. & Lust, N. (1999) (subm.). Regeneration restrictions of broadleaved tree species in canopy gaps of a mixed oak - beech stand.
- Tabari, K. M. & Lust, N. (1999). Regeneration and succession in a mixed ash (*Fraxinus excelsior* L.) stand. Abstracts of the 6<sup>th</sup> Agricultural Seminar of Iranian Students in Europe. Manchester, UK. May 9, 1999.
- Taylor, N. W. (1982). The ecology and status of sycamore, and its value to wildlife, M. Sc. Dissertation in conservation. University College, London.
- Taylor, N. W. (1985). The sycamore (*Acer pseudoplatanus*) in Britain - its natural history and value to wildlife. Discussion Papers in Conservation No. 42. University College, London.
- Toutain, F. (1981). Les humus forestiers : biodynamique et modes de fonctionnement. Revue forestière française 33 (6), 893-896.
- Ulrich, B. (1978). A systems approach to the role of nutrients in controlling rehabilitation of terrestrial ecosystems. - In: Holdgate, M. W., & Woodman, M.J., (Eds). The breakdown and restoration of ecosystem. Plenum Press. New York & London, 105-122.
- Ulrich, B. (1981). Destabilisierung von Waldökosystemen durch Biomassenutzung. Forstarchiv. 52 (6), 199-203.
- Ulrich, B., Mayer., R. & Khanna P. K. (1980). Chemical changes due to acid precipitation in a loess-derived soil in Central Europe. Soil Sci. 130, 193-199.
- Van der Valk, A. G. (1981). Succession in wetlands: a Gleasonian approach. - Ecology 62, 688-696.
- Van Miegroet, M. (1991). The nature of forest degradation. Silva Gandavensis 56, 1-55.
- Van Miegroet, M., Verhegge, J. F. & Lust, N. (1981). Trends in the development of the early stages of mixed natural regeneration of ash and sycamore. Silva Gandavensis 48, 22 pp.
- Waters, T. L. & Savill, P. S. (1992). Ash and Sycamore Regeneration and the Phenomenon of their Alternation. Forestry, Vol. 65, No. 4, 417-433.
- Watt, A. S. (1947). Pattern and process in the plant community. - J. Ecol. 35, 1-22.
- Whitmore, T. C. (1975). Tropical rain forest of the Far East. Oxford Univ. Press. London & New York.
- Whitmore, T. C. (1978). Gaps in the forest canopy. - In: Tomlinson, P. B., and Zimmermann, M. H. (eds), Tropical trees as living systems. Cambridge, 639-655.
- Wittich, W. (1952). Der heutigen Stand unseren Wissens vom Humus und neue Wege zur Lösung des Rohhumusproblems im Walde. Schriftenreihe der Forstl. Fak. Univ. Gottingen, Band 4, 106 pp.
- Zahedi, A. G. (1998). Relation between ground vegetation and soil characteristics in a mixed hardwood stand. Ph. D. thesis. University of Gent, Belgium, 319 pp.