Growth and development of ash (*Fraxinus excelsior* L.) seedlings on different humus types under a closed forest canopy

TABARI, M., LUST, N. & ZAHEDI, G.

Laboratory of Forestry, Ghent University, Geraardsbergsesteenweg 267, B-9090 Melle-Gontrode, Tel +32-9-2522113, Fax +32-9-2525466, E-mail Noël.Lust@rug.ac.be

Abstract

In Sep. 1995, in stands with ash and oak - beech, 116 two to four-year-old ash (*Fraxinus excelsior* L.) seedlings were selected in 12 plots in order to assess collar diameter growth, number of leaves, branches and growth flushes (episodes) per seedling, produced during the next two years. At the same time, 30 seedlings were selected to measure the root length and the root : shoot ratio. Seedlings were growing on different levels of soil fertility (humus types of typical mull, acid mull and mull moder), under a dense canopy (2.5% light intensity).

The investigation reveals that, under the high shade of the stands, the length of roots as well as root : shoot ratio is greater on more fertile sites (typical mull and acid mull), than on less fertile site (mull moder). However, the mean root length of the seedlings in this deciduous forest never reaches 9 cm, presenting a limited growth on the various humus types and a rather low stability in the thick litter layer on the mull moder humus type. There are no significant differences ($P < 0.05$) in growth and foliage development of the seedlings produced on the different humus types. After 2 growing seasons, the mean diameter increment does not exceed 0.6 mm. The mean number of branches and leaves increases respectively with 1 and 4-5 units per seedling and that of the growth flushes varies from 2 to 3 units per seedling. As a whole under the full canopy, ash seedlings prove a very poor response to the humus types.

The study suggests a proper felling in the closed canopy of the stand in order to encourage the growth and foliage development of the ash seedlings growing on the different humus types.

1. Introduction

Growth and development of ash (*Fraxinus excelsior*) seedlings, as well as of indigenous oak (*Quercus robur*) and beech (*Fagus sylvatica*) seedlings, are generally a complicated problem in the Aelmoeseneie experimental forest, located in the north of Belgium. In the research site ashes bear seed annually or biannually and regenerate profusely. In spring 1998 on average 220 seedlings/m^2 occurred, indicating a substantial and very dense natural regeneration. Ash seedlings, however, under the dominant cover of ash on a humus type of typical mull, with a pH ranging from 5.3 to 6.5, grow too slowly. The same growth rate is observed under the full canopy of ashes and hazels on acid mull, and also under an oak - beech stand with mull moder.

The most limiting factors of regeneration seem to be light, nutrient deficiency, increased acidification of the topsoil, soil vegetation, infestations by insects and soil fungi. Humus conditions, as well as chemical soil characteristics, directly or indirectly influence regeneration results (Lust, 1994). A thick raw humus layer, characteristic for many oak and beech stands, also strongly hampers natural regeneration. Nutrient deficiency complicates the process and especially the increasing acidification of the upper 5 cm soil layer, often with an acidic pH, strongly hinders not only the germination but also the development of primary roots and besides that it favours the development of fungi (Gehrmann and Ulrich, 1983). Generally, low pH values seem to increase the aggressiveness and pathogenicity of the soil fungi too (Bressem, 1988).

Pearsall (1938) and Heimburger (1934, 1941) produce evidence to show that nitrification does not take place below pH 3.8. Puri (1948, 1949) reports that the distribution of ash, as distinct from its growth, shows to be related to pH and generally it is not found below pH 4.4-5. According to Wardle (1957), ash does not occur on soils with a pH lower than 4.2, because its roots does not tolerate such acidity, which corresponds reasonably well with Puri's values. Evans (1986) suggests that, of all broadleaves, ash is the species which shows most potential for response, notably to nitrogen. In this regard, Brown (1950) also describes ash seedlings growing up to 20 cm in their first year on coral rag limestone rendzinas in the south of England, where nitrogen is considered not limiting. No first-year ash seedlings are ever observed to grow this amount on the other natural forest soil. These suggestions, indeed, demonstrate the importance of the soil nitrogen and its absorption in the nitrate form by plants.

Tabari *et al.* (1998), working on ash potted seedlings, report that on different humus types, the lowest height growth is produced under high shade and the greatest one under moderate and the highest light levels. Helliwell (1965) on maple and Clark (1992) on spruce state that growth does not occur on any soil at light intensities less than about 3%. Helliwell (1965), concerning to *Acer pseudoplatanus* and *A. platanoides,* similarly reports the poor growth at most of the forest sites with a light intensity between 3% and 20%. In this respect, Wardle (1959) expresses that *Fraxinus* seedlings on the shaded woodland floors demonstrate marked persistence but little growth. When gaps are formed, however, seedlings respond rapidly to the increased light. The investigation made by Schmidt (1996) reveals that the growth of broadleaved seedlings is closely correlated with the available light, whereas seedling density and proportions of beech and valuable hardwoods, such as ash, Norway maple and sycamore, depend on conditions prevailing before the gaps are made. Similar results are also reported by Stern (1989), who claims that a two-storied high forest with an ash over-storey is less satisfactory, due to the lack of light. It is also seen that copious natural seedlings occur under full canopy of sycamore, ash and beech but mostly do not grow above 15 cm.

From the above mentioned, it can be concluded that growth and development of ash seedlings closely depend on radiation supply and nutrient availability of top soil. This way, this study aims to evaluate the growth and the foliage development of ash seedlings, subject to different levels of humus quality under a closed forest canopy (in an in-situ experiment).

2. Materials & methods

2.1. Site study

The experimental forest, Aelmoeseneie, is a semi-natural forest, situated 12 Km southeast of Gent (Northern Belgium), and on the territory of the community Melle-Gontrode with centered coordinates: 50° 58' 35" N and 3° 49' 30" E. This covers an area of 1.8 ha, which has been fenced for protection to possible disturbances. The elevation ranges from 18.5 m up to 21 m above sea level, whereas every 10 m a shallow ditch occurs, which is accumulated by litter. The climate has a temperate Atlantic character. Based on the climatoligical data in 1984-1993, the mean annual precipitation is 791 mm, and the mean annual temperature is 10.1 °C. The number of frost days averages to 53 days/year. The geology formations coming up to day are sub-horizontal sediments of the Tertiary (clay and sand). The niveo-eolic upper layer of Quaternary is sandy-loam. The water-economy is variable, depending on the elevation and on the texture and depth of Tertiary layer, but is never dry, even in summer (Muys, 1987).

2.2. Vegetation types

The vegetation conditions of the higher and lower part of the study area differ considerably. At a glance, two main forest types can be observed as oak-beech and ash stands, both being some 75 years old.

On the lower part of the study area an ash stand, with 0.8 ha in area, is dominated. Ashes in the overstorey are also mixed with a number of *Quercus robur* and *Acer pseudoplatanus* and a few *Populus*. The understorey is very densely covered by mostly *Corylus* and saplings and thickets of *Acer pseudoplatanus*. Herbal vegetation is well developed by mesotrophic species, especially the vernal vegetation. *Anemone nemorosa*, *Oxalis acetosella*, *Lamium galeobdolon* and *Ranunculus ficaria* are the main herbaceous species in this stand. Moss layer is dominated by rather mesotrophic species like *Fissidens taxifolium* and *Eurynchium praelongum*.

On the higher part of the research site an oak - beech stand, with 1 ha in area, consists of dominant oak and beech mature trees. *Sorbus aucuparia* and *Corylus avellana* are the understorey of this stand. Herbal vegetation is dominated by *Pteridium aquilinum* and *Rubus fruticosus*. Moss layer mainly consists of acidophile species like *Dicranella heteromella* and *Polytrichum formosum*.

2.3. Soil characteristics

In the ash stand, situated on the lower part of the study area, soil is an alluvial deposit with thick Quaternary of the loamy texture, where the impermeable layer ceases and the Tertiary origin can not be found at least at 4 m depth. In the oak - beech stand, located on the slope side of the study area, soil is a typical thin Quaternary deposit of the sandy loam texture on a shallow impermeable clay and sand complex of the Tertiary formation.

In the investigated area, humus classification, based on the morphological description and chemical properties of the ectorganic horizons, can be specified with 3 vegetation groups (Zahedi, 1998). In fact, from the edaphical point of view, these vegetation groups have different characteristics. Vegetation groups (1) and (2), occurring in the ash stand, consist of species which are good indicators respectively from more rich sites with a higher pH value to the relative rich sites with moderate pH value. Group (3), appearing in the oak - beech stand, includes more distinct vegetative elements, whereas indicator species tend to a lower pH value in comparison with previous group.

Likewise, based on the phytosociological classification of Noirfalise (1984) and the humus quality indication (Rogister, 1985), three main humus types are arranged on the basis of the vegetation groups (Zahedi, 1998): group (1) and (2), in the order with typical mull and acid mull conditions, indicate a higher nutrient availability and pH value. Group (3), with mull moder humus characteristic, exhibits a lower nutrient availability and pH value. The two first groups are located in the ash stand and the last one in the oak - beech stand. In the ash stand, along with the rich-nutrient vegetation elements, suitable conditions are created for microbial activity and increased decomposition rate, presenting the conditions connected with typical and acid mull humus. Whilst, in the oak - beech stand, on the raw humus layer with a lower pH value, acidophile species are established, showing conditions related with moder humus.

As a whole, 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. Indeed, in the research site, seedlings were growing on humus types of typical mull, acid mull and mull moder, with a pH ranging between 5.3-6.5, 4.4-5.2 and 3.8-4.3, respectively. Table 1 represents some characteristics of the humus types and the stands.

Table 1. *Soil acidity (pH) and Carbon : Nitrogen value of humus layers, litter thickness and herbal vegetation at three humus types, located in the ash and oak - beech stands*

Humus type	Stand	pH	C/N ratio	Litter thickness (cm)	Herbal vegetation
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

2.4. Light measurement

Light recording in different points of these stands was conducted by a Lux-meter unit (Weston Illumination Meter), giving average values of 2.5% light intensity (Table 2). The readings were recorded during overcast and sunny weather, daily during 4 weeks, between 08.00 and 20.00 h in July and August 1995.

2.5. Sampling and field records

At the end of the growing season 1995, 116 two to four years old ash seedlings were investigated in 12 plots within this 1.8 ha-mixed dense hardwood stand. Frequency of seedlings in these plots ranged from 6 to 16 (Table 3). At the beginning of September 1995, the first measurements with the ash seedlings were executed for the following parameters:

- collar diameter;
- number of leaves per seedling;
- number of branches per seedling;
- number of growth flushes per seedling.

These characteristics were again recorded in Sep. 1997, together with the following additional parameters:

- root length;
- root : shoot ratio.

In this investigation the statistical analyses were performed by one-way analysis of variance (ANOVA). Differences between the various terms of the ash seedlings were evaluated at the 5% level of significance, using Tukey's studentized range.

Table 2. *Average values (%) (during 4 weeks) of the light intensities on locations with ash seedlings, (July and August 1995)*

Reading times (h)				
8.00-9.00	12.00-13.00	16.00-17.00	19.00-20.00	Mean light intensity (%)
2.4	2.9	2.6	2.0	2.5

Table 3. *Frequency of 2-4 years old ash seedlings in 12 plots, in the two stands and on the three humus types, recorded in Sep. 1995*

	Light intensity (2.5%)											
Stands	Ash								Oak - Beech			
Humus types	Typical mull				Acid mull				Mull			
Frequency of seedlings in plots	6	7	7	11	10	12	14	16	6	8	9	10
Sum of seedlings at the humus type	31				52				33			

3. Results

3.1. Collar diameter growth

Collar diameter of 2 to 4-year-old ash seedlings increased during 2 years but never reached 3 mm on either of three humus types at the end of Sep. 1997 (Fig. 1).

Generally, collar diameter, with a total increment of 0.6 mm, was very poor during this time (ranging between 0.5 and 0.7 mm). Statistical analysis revealed that there were no substantial differences between the seedlings growing on the three humus types under the closed canopy (P = 0.102) (Table 4).

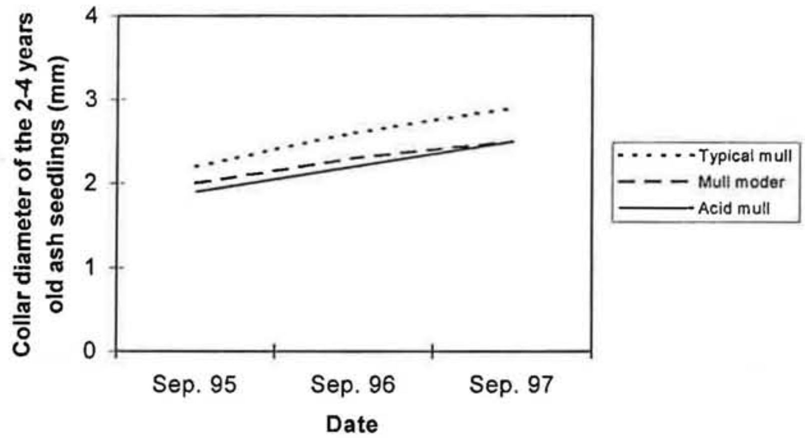

Figure 1. *Collar diameter of 2 to 4-year-old ash seedlings in 3 successive years, grown on the three humus types under a closed canopy.*

Table 4. *Collar diameter growth (mean ± s e) of 2 to 4-year-old ash seedlings, grown on different humus types*

Humus type	No. of seedlings	Collar diameter in Sep. 1995 (mean ± s e) (mm)	Collar diameter growth (mm)	
			1 year (mean ± s e)	2 years (mean ± s e)
Typical mull	31	2.2 ± 0.20	0.4 ± 0.06	0.7 ± 0.10
Acid mull	52	1.9 ± 0.06	0.3 ± 0.03	0.6 ± 0.05
Mull moder	33	2.0 ± 0.10	0.2 ± 0.06	0.5 + 0.09
Mean ± s e		2.0 ± 0.05	0.3 ± 0.03	0.6 ± 0.04

3.2. Number of leaves per seedling

Generally, the number of leaves per seedling, produced by 4 to 6 years old ash seedlings in 1997, ranged from 14 to 17 (Fig. 2). The mean number was, in comparison with 1995, increased with 4 to 5 units per seedling (Table 5). According to the ANOVA, no marked differences could be found in the increase of the number of leaves per seedling, grown on the different humus types (P = 0.550).

3.3. Number of branches per seedling

The number of branches per seedling on the different humus types ranged from 2.6 to 3.0 in 1995 and from 3.4 to 4.0 in 1997 (Table 6). The increase of number of branches during the period 1996 and 1997 was very poor, namely 0.7 on mull moder and 1.0 on typical mull.
Analysis of variance (ANOVA) revealed that no clear differences of this characteristic appeared among the seedlings growing on the three humus types (P = 0.125).

Table 5. *Increase of number of leaves per seedling (mean ± se), grown on the three different humus types, under 2.5% light intensity*

Humus type	No. of seedlings	increase of no. of leaves during 2 years (mean ± s e)
Typical mull	31	4.3 ± 0.5
Acid mull	52	4.6 ± 0.3
Mull moder	33	4.5 ± 0.6
Mean ± s e		4.5 ± 0.4

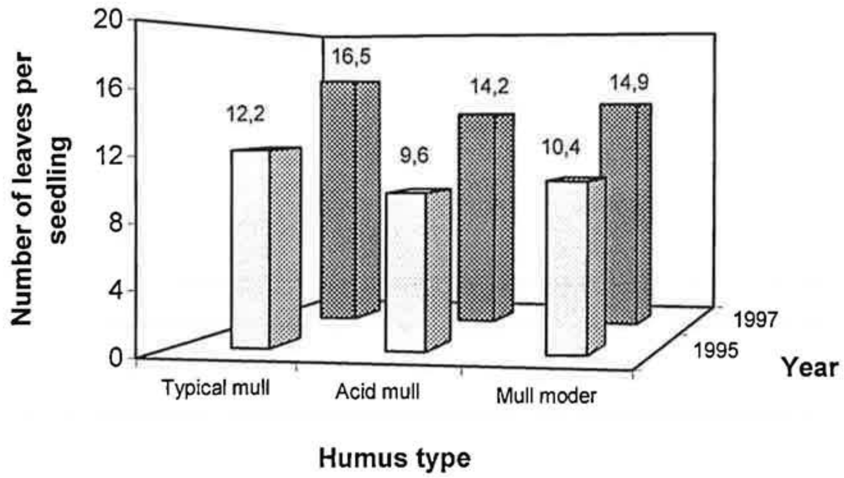

Figure 2. *Number of leaves per seedling in 1995 and 1997, grown on the three humus types under a closed canopy.*

Table 6. *Number of branches per seedling (mean ± s e), grown on different humus types*

Humus type	Number of seedlings	Number of branches per seedling (mean ±		Increase of number of branches (mean ± s e)
		Sep. 1995	Sep.1997	
Typical mull	31	3.0 ± 3.0	4.0 ± 1.0	1.0 ± 0.2
Acid mull	52	2.6 ± 0.1	3.5 ± 0.2	0.9 ± 0.1
Mull moder	33	2.7 ± 0.2	3.4 ± 0.3	0.7 ± 0.3
Mean ± s e		2.8 ± 0.2	3.6 ± 0.2	0.7 ± 0.2

3.4. Number of growth flushes

Generally, a growth flush (episode) is the portion of a shoot produced during a single growth flush (Barthelemy and Caraglio, 1991). The results showed that the number of growth flushes per seedling on the different humus types ranged from 3.5 to 4.4 in 1995 and from 5.8 to 7 in 1997 (Fig. 3). As a whole, the mean number of growth flushes per seedling increased with 2 and 3 (Table 7). According to ANOVA, no remarkable differences could be detected in the increase of the number of growth flushes per seedling on the different humus types (P = 0.150).

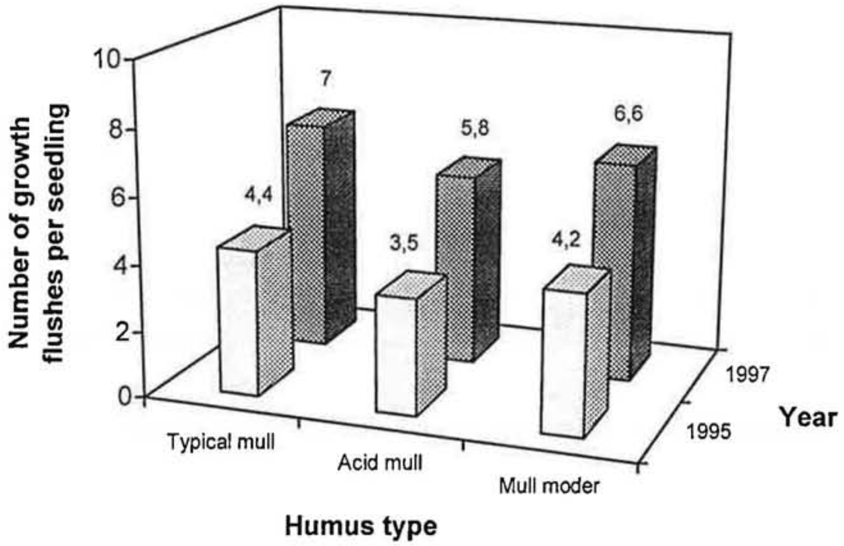

Figure 3. *Number of growth flushes per seedling in 1995 and 1997, grown on the three humus types under a closed canopy.*

Table 7. *Number of growth flushes per seedling (mean ± s e), grown on three different humus types*

Humus type	Number of seedling	Increase of number of growth flushes per seedling (mean ± se)
Typical mull	31	2.6 ± 0.3
Acid mull	52	2.3 ± 0.2
Mull moder	33	2.4 ± 0.3
Mean ± s e		2.4 ± 0.3

3.5. Root length

The mean root length amounted to 85 mm (with a range between 65 and 93 mm). Comparison of means, using Tukey's test, showed that root length, produced on typical and acid mull humus, was significantly greater than that on mull moder humus ($P = 0.000$) (Table 8). In fact, humus remained a highly significant ($P < 0.01$) effect on root length.

Table 8. *Root length (mean ± se) of ash seedlings, grown on different humus types, under 2.5% light intensity, at the end of the growing season 1997*

Humus type	Number of seedlings	Root length (mean ± s e) (mm)
Typical mull	7	93 ± 3.9 $_a$
Acid mull	15	92 ± 2.4 $_a$
Mull moder	8	65 ± 3.5 $_b$
Mean ± s d	30	85 ± 2.8

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

3.6. Root : Shoot ratio

According to the analysis of variance, the root : shoot ratio of ash seedlings, occurred at 2.5% light intensity, varied according to the humus types (P = 0.025). Comparison of means, using Tukey's test, revealed that this attribute was higher on the typical mull and acid mull than on the mull moder (Fig. 4). In other words, this ratio was affected by humus type. Root : Shoot ratio was about 0.6 for ash seedlings growing on typical and acid mull (in the ash stand), whilst this attribute reached only 0.47 on mull moder (in the oak - beech stand). The mean root : shoot ratio of all seedlings in this hardwood stand did not exceed 0.57.

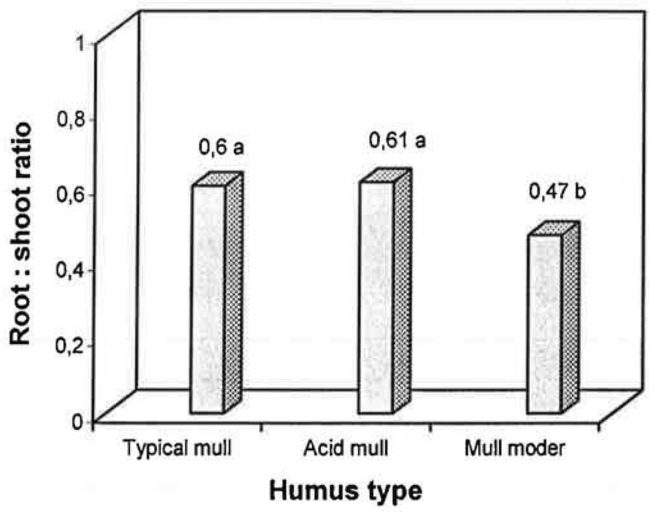

Figure 4. *Root : Shoot ratio for ash seedlings, growing on three humus types, with 2.5% light intensity.*

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

4. Discussion

The present study exhibited that, under 2.5% radiation level, root length and root/shoot ratio of 2 to 4 years old ash seedlings, located on more fertile sites (typical and acid mull), appeared clearly higher than those on a less fertile site (mull moder). In the experimental area, in fact, both shoot length and root length occurred very weak. The mean root length never reached 9 cm, describing a low solidity for the ash seedlings growing in the thick litter layer, placed on the mull moder humus type. The number of growth flushes increased with about 1 unit per seedling/yr. Generally, it seems that the frequency of growth flushes (episodes) depends on the development of the root system, limited by the radiation energy supply. Similar results with oak are reported by Dostál (1967), who points out that under equal light intensities, fertilized potted plants of *Quercus petraea* with well developed root systems flush two or three times during summer, whereas those with poorly developed roots produce one flush at most.
The investigation also showed that under a closed canopy no significant differences could be found in terms of collar diameter, number of leaves, branches and growth flushes per seedling, produced on typical, acid or mull moder. The diameter increment was very poor, as its average during 2 years did not exceed 0.6 mm. The increase of the number of branches and leaves during this period was about 1 and 4 units per seedling, respectively. The number of the growth flushes varied from 2 to 3 units per seedling at most. As a whole, the results of this study make clear that under the closed canopy most of the above characteristics respond very poor to the humus types.
Generally, the effect of nutrient availability on the growth and the development of tree seedlings is well known. Madsen & Larsen (1997) state that soil carbon content seems to give an indication of the nutrient supply, since height growth of beech seedlings reduces as soil carbon content increases. Soil carbon content is on a long term scale related to the conditions for the litter decomposition and the litter quality. Gordon (1962) underlines that, when C/N ratio is above 18, growth will be minimal and no variation in growth will occur with a pH ranging from 4.3 to 5.2.

Tabari (in prep.), studying on ash potted seedlings, shows that in high nutrient availability, number of leaves, branches and growth flushes as well as increment of collar diameter are remarkably more frequent, compared with those in low nutrient availability. It is also declared by Harmer (1989 a) that the *Quercus petraea* potted seedlings produce bigger plants with more leaves than those receiving smaller amounts of fertilizers. Likewise, the plants growing under conditions with higher nutrient availability are more vigorous, producing longer shoots with more buds and branches than those on less fertile sites. The researches made on *Q. petraea* (Harmer, 1989 a, b) also reveal that multiple flushing, originating from the high nutrient availability, shows to be associated with the increase of the number of branches. Nevertheless, high resource availability may increase branching defects by inducing multiple flushing.
Correspondingly, Collet *et al.* (1997) also state that the lack of strong apical control in young oaks induces branching defects, which may persist and reduce the future value of the stem.

Besides the nutrient availability, generally, growth and development of seedlings depend on a number of other environmental variables which may be either abiotic, such as light, water and temperature, or biotic such as competition and browsing (Crow, 1992; Harmer, 1995). From these, light intensity may be the most effective in growth and development of seedlings. This is stressed by numerous authors. According to Cochet (1977), under a dense canopy of beech decomposition of litter is very slow, resulting in production of raw humus layer with an acidic pH.

In such a condition, the creation of a proper canopy is unavoidable in order to decay more quickly the litter and to enable the seedlings to a satisfactory survival and a good growth. This proves that, provided a suitable light in the stand and, consequently, the gradually decomposition of thick litter layer and the improvement of raw humus, seeds will germinate more rapidly and the seedlings will establish more vigorously. As a whole, this is confirmed that, under low light intensities, seedlings are not able to grow well and develop. In this regard, it is also underlined that growth of maple (Helliwell, 1965) or spruce (Clark, 1992) would not take place at light intensities below 3%. The paper, made by Van Miegroet and Lust (1972) reveals that for fast growth and foliage development, ash seedlings require a high light condition. Similar results show that the number of leaves, branches and growth flushes of ash seedlings in the rich humus type progressively increases with increasing radiation supply (Tabari, in prep.). In this regard, Tapper (1992) points out that ash juveniles in the shade, occurring below a closed canopy, are unable to produce more than one pair of leaves and a prosperous growth. However, when light increases by a gap formed in the canopy, seedlings respond with a substantial increase of growth, irrespective of their age.

In an investigation made on ash seedlings, Helliwell (1979) deduces that root/shoot ratio is significantly ($P < 0.01$) affected by light intensity. Likewise, there is a tendency for less root biomass to be produced in the more acid soils, and for the seedlings to produce proportionately more roots at the higher light intensities. Concerning to the influence of light on collar diameter, Fairbairn and Neustein (1970) report that this characteristic in conifer seedlings reaches its interpolated maxima slightly below full light. The effect of light intensity on the incidence of recurrent flushing in oak is cited by (Farmer, 1975). Moreover, it is claimed by Lavarenne-Allary (1965), Longman and Coutts (1974), that, provided the appropriate conditions, *Q. petraea* may produce up to four or five growth flushes in a growing season. However, the unfavourable growing conditions often confine production to only one or two flushes, thus restricting the full growth potential. On the other hand, in an in-situ experiment, Lyr and Garbe (1995), studying on beech seedlings, reveal that a high soil temperature, originating from the high radiation energy supply, significantly enhances the root/shoot ratio.

From the above results, it appears that diameter growth and increased number of leaves, branches and growth flushes of ash seedlings as well as their development of root and shoot length, in the ash stand and on sites with a higher nutrient availability (typical and acid mull humus types) will depend on the creation of suitable light conditions. In the oak - beech stand and at the mull moder, with a thick raw humus layer, a light thinning in the overstorey, associated with the removal of a few shrubs in the understorey, will stimulate the growth and the development of ash seedlings.

5. References

Barthelemy, D., and Caraglio, Y. (1991). Modélisation et simulation de l' architecture des arbres. *Forêt-Entreprise 73*, 28-39.

Brown, J. M. B. (1950). Some factors governing the occurrence and growth of ash natural regeneration in the forests. *For. Dip. Thesis*. Imperial Forestry Institute, Oxford.

Clark, G. C. (1992). The natural regeneration of spruce. *Scottish Forestry. Vol. 46. No. 2*, 107-129. Derbyshire Limestone. *Ph.D. thesis*. University of Sheffield.

Cochet, P. P. (1977). Etude et culture de la forêt. Manuel pratique de gestion forestière. 397 pp. École Nationale du Génie Rural des Eaux et des Forêts, Nancy.

Collet, C., Colin, F. & Bernier, F. (1997). Height growth, shoot elongation and branch development of young *Quercus petraea* grown under different levels of resource availability. *Ann Sci For. 54*, 65-81.

Crow, T. R. (1992). Population dynamics and growth pattern for a cohort of northern red oak (*Quercus rubra*) seedlings. *Oecologia 91*, 192-200.

Dostál, R. (1967). On integration in plants. In: Thimann, K. V., Harvard University Press, Cambridge, Massachusetts, 218 pp.

Evans, J. (1986). Nutrition experiments in broad-leaved stands: I. Pole-stage ash and oak. *Q. J. For. 80 (2)*, 85-94.

Fairbairn, W. A. & Neustein, S. A. (1970). Study of response of certain coniferous species to light intensity. *Forestry. 43*, 57-71.

Farmer, R. E. (1975). Growth and assimilation rate of juvenile northern Red oak: Effects of light and temperature. *Forest Sci. 21*, 373-381.

Gehrmann, J. & Ulrich, B. (1983). Der Einfluss des sauren Niederschlages auf die Naturverjüngung der Buche. Sonderheft der Mitteill. Der Lolf: Immissionsbeelastungen von Waldökosystemen, 32-36.

Gordon, A. G. (1962). The nutrition and growth of ash (*Fraxinus excelsior*) in natural stands in English lake district as related to edaphic site factors. *J. Ecol. 52*, 169-187.

Harmer, R. (1989 a). The effect of mineral nutrients on growth, flushing, apical dominance and branching in *Quercus petraea* (Matt.) Liebl. *Forestry. Vol. 62, No. 4*, 383-395.

Harmer, R. (1989 b). Some aspects of bud activity and branch formation in young oak. *Ann Sci For. 46* (Suppl), 217 -219.

Harmer, R. (1995). Natural regeneration of broad-leaved trees in Britain: III Germination and establishment. *Forestry. 68*, 1-9.

Heimburger, C. C. (1934). Forest-type studies in the Adirondack region. Mem. *Cornell Agric. Exp. Sta*. 165.

Heimburger, C. C. (1941). Forest-site classification and soil investigation on Lake Edward Forest Experiment Area. *Silvic. Res. Note Can. 66*, 1-60.

Helliwell, D. R. (1965). Factors influencing the growth of seedlings of sycamore and Norway maple. *Quart. J. For. 59*, 327-337.

Helliwell, D. R. & Harrison, A. F. (1979). Effects of light and weed competition on the growth of seedlings of four tree species on a range of soils. *Q J. For. No.3*, 160-171.

Lavarenne-Allary, S. (1965). Recherche sur la croissance des bourgeons de chênes et de quelques autres espèces ligneuses. *Ann. Sci. For. 22*, 1-203.

Longman, KA & Coutts MP. (1974). Physiology of the oak tree. In: The British Oak: its history and natural history (MG Morris, FH Perring, eds), the botanical Society of the British Isles, Classey Ew, Faringdon, UK,194-221.

Lust, N. (1994). Regeneration and problems in mixed forests. *Silva Gandavensis, No. 55*, 1-14.

Lyr, H., & Garbe, V. (1995). Influence of root temperature on growth of *Pinus sylvestris, Fagus sylvatica, Tilia cordata* and *Quercus robur. Trees, 9*: 220-223.

Madsen, P. & Larsen, J. B. (1997). Natural regeneration of beech (*Fagus sylvatica* L.) with respect to canopy density, soil moisture and soil carbon content. *Forest Ecology and Management. 97*, 95-105.

Muys, B. (1987). Earthworm populations of a hardwood stand in northern Belgium. *Silva Gandavesis*, No. 52, 29-55.

Noirfalise, A. (1984). Forests et stations forestières en Belgique. Les Presses Agronomiques de Gembloux, Gembloux.

Pearsall, W. H. (1938). The soil complex in relation to plant communities. II. Characteristics woodland soils. *J. Ecol. 26*, 194-203.

Pryor, S. N. (1985). The silviculture of wild cherry or gean. *Quart. J. For. 79*, 95-109.

Puri, G.S. (1948). The ash-oak woods of the English lake district. *J. Indian Bot. Soc. 27*, 211-227.

Puri, G.S. (1949). The vegetation of some disused quarries at Ingleton, Yorkshire, England. *J. Indian Bot. Soc. 28*, 212-220.

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.

Schmidt, W. (1996). Development of regeneration in two selection gaps in a beech forest on limestone. *Forst-und-Holz. 51: 7*, 201-205.

Stern, R. C. (1989). Sycamore in Wessex. *Forestry 62*, 365-382.

Tabari, K. M., Lust, N. & Neirynck, J. (1998). Effect of light and humus on survival and height growth of ash (*Fraxinus excelsior* L.) seedlings. *Silva Gandevensis, No. 63, 36-50.*

Tapper, P. -G. (1992). Demography of persistent juveniles in *Fraxinus excelsior. Ecography, 15:* 385-392.

Van Miegroet, M. & Lust, N. (1972). Aufbau, Wachstum und Reaktionsvermögen von unterdrückten Eschenverjüngungen. *Silva Gandavensis. 34*, 38 pp.

Wardle, P. (1957). The autecology of *Fraxinus excelsior. Ph.D. thesis*, University of Cambridge.

Wardle, P. (1959). The regeneration of *Fraxinus excelsior* in woods with a field layer of *Mercurialis perennis. J. Ecol.* 47, 483-497.

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.