

## COMPARISON OF THE REGENERATION PATTERNS OF WOODY SPECIES BETWEEN NORWAY SPRUCE PLANTATIONS AND DECIDUOUS FORESTS ON ALLUVIAL SOILS

Bruno HÉRAULT<sup>1,\*</sup>, Guy BOUXIN<sup>2</sup> and Daniel THOEN<sup>1</sup>

<sup>1</sup> Université de Liège, Département des Sciences et Gestion de l'Environnement,  
Avenue de Longwy 185, B-6700 Arlon, Belgium

<sup>2</sup> Haute Ecole de Namur Albert Jacquard, Rue des Sorbiers 33, B-5101 Erpent, Belgium  
(\* Author for correspondence ; e-mail : herault@ful.ac.be)

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ABSTRACT. — Restoration of floodplain forests has become a primary aim of sustainable forestry in Europe. Although several studies have investigated the conversion of coniferous stands outside of their biogeographical area and on unsuitable sites, none focused specifically on alluvial areas. We surveyed 208 riverine stands, distributed homogeneously throughout the Grand-duché de Luxembourg (western-central Europe) for the abundance of woody forest species (trees, saplings, seedlings and shrubs). The influence of both the canopy nature (Norway spruce or deciduous) and the biogeographical region (Oesling or Gutland) on the understory regeneration were tested. The mean species richness was 10.5 woody plants per stand. Correspondence analyses showed that canopy tree regeneration was not different between the two forest types. Following an analysis of variance, we found that functional species group distribution (regarding mode of dispersal, type of seed bank and establishment strategy) was more determined by the biogeographical variable than by the canopy variable. Most woody species were significantly more abundant in deciduous forests and in the Gutland area. Only *Rubus idaeus*, *Sambucus racemosa* and *Sorbus aucuparia* were strongly associated with Norway spruce stands or the Oesling region. The differences between deciduous forests and coniferous stands are mainly due to shrub abundance and not to the canopy tree regeneration. In conclusion, Norway spruce plantations act as nurseries for late-successional riverine species like *Fraxinus excelsior*, *Acer pseudoplatanus* and *Quercus robur*.

KEY WORDS. — Norway spruce, broad-leaved forests, floodplains, ecological restoration, Grand-duché de Luxembourg, regeneration.

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### INTRODUCTION

Around 7000 BP in Western Europe the boreal climate was followed by a more wet and warm oceanic one. First human settlements used alluvial deciduous forests non-intensively up to

the Middle Ages when the human population increased (DEVILLEZ & DELHAISE 1991). Floodplains along tranquil reaches were then cleared of forests and converted into meadows, which were mown annually. Very recently, this practice ceased in part as a direct consequence of the Common

Agricultural Policies of the European Union and large areas were abandoned to natural colonisation or were converted into Norway spruce (*Picea abies* (L.) Karst) or poplar (*Populus* spp.) plantations. Floodplain deciduous forests have effectively disappeared from all but a few fragmented sites (ADAMS & PERROW 1999, PETERKEN & HUGHES 1998). Today, restoration of floodplain forests has become a primary aim of sustainable forestry in Europe (RODWELL & PATTERSON 1994). The consciousness is growing that ecological restoration of forest areas will be necessary to ensure biodiversity conservation against natural losses in existing forests (HONNAY *et al.* 2002). The necessity for and the acceptance of a shift from Norway spruce monocultures towards mixed broadleaf forests was expressed by several authors in recent years (KAZDA & PICHLER 1998, ZERBE 2002). Biodiversity considerations, together with increasing damage (due to e.g., storms and insect invasions) to Norway spruce in Western and Central Europe, are the most cited reasons for this conversion (KAZDA & PICHLER 1998). The more natural rejuvenation processes can be incorporated in these conversion efforts, the more cost-effective the silvicultural management will be (HEKHUIS & WIEMANN 1999). Hence conversion of coniferous stands into either mixed or deciduous stands using natural regeneration methods is an important objective of ecologically sustainable silviculture.

As most forest plant species have a transient seed bank (BOSSUYT & HERMY 2001, BOSSUYT *et al.* 2002), plants have to colonise coniferous stands. The species colonisation process includes two key events: a dispersal event and a recruitment event. First, seeds have to reach habitat patches (dispersal). Second, the habitat has to provide suitable ecological conditions to ensure establishment (recruitment). In Norway spruce plantations, regeneration processes towards secondary broad-leaved forests can be characterised by prior vegetation analysis. Indeed, several authors have investigated patterns of the understorey woody regeneration in coniferous stands in Europe (e.g., MOSANDL & KLEINERT 1998, ZERBE 2002). However, none of these studies has focused specifically on the regeneration patterns

observed in alluvial areas. The aims of this study were (a) to assess the woody species regeneration under Norway spruce plantations and in deciduous forests, (b) to compare the occurrence of different functional ecological species groups (regarding dispersal mode, seed bank type and establishment strategy), and (c) to investigate the usefulness of natural regeneration to convert Norway spruce stands into broadleaf forests.

## MATERIAL AND METHODS

### STUDY AREA AND HABITATS

All stands are situated in the Grand-duché de Luxembourg (GDL) in central-western Europe (49°26'-50°10'N, 5°42'-6°32'E). The climate is continental with an oceanic influence; the mean annual temperature is 9°C. Annual rainfall ranges between 700 and 1000 mm. From a geographical and geological viewpoint, GDL has two natural regions which are extensions of Belgian biogeographical regions (DE SLOOVER & DUFRÈNE 1998, DUFRÈNE & LEGENDRE 1991). In the North, the 'Oesling', which is a continuation of the Belgian Ardenne, consists of Lower Devonian geological layers with shales and gritty shales with low calcium and phosphorous contents. The 'Oesling' covers one-third of the territory, is slightly mountainous (highest point: 555m) and is heavily forested. The South, called 'Gutland', has more recent layers consisting essentially of sandy and calcareous rocks, from the Triassic and Jurassic periods. Covering the remainder of the territory, it mainly consists of rolling farmlands and small forests as an extension of the French Lorraine plateau. The five main rivers of GDL are the Moselle, the Sûre, the Our, the Alzette and the Clerve. Only the Our and the Clerve flow completely through the Oesling.

Deciduous riverine hardwoods phytosociologically belong to the Alno-Padion alliance. *Fraxinus excelsior*, *Alnus glutinosa*, *Acer pseudoplatanus* are the main canopy trees of the forest. Stands near small streams are characterised by *Carex remota*, *Carex pendula* and *Lysimachia nemorum* (NOIRFALISE 1984). This community is very frequent throughout the Oesling. Stands near larger rivers are characterised by *Stellaria nemorum* and *Impatiens noli-tangere*. This group is common in the southern part of the study area, mainly throughout the Alzette watershed (PIER 1989).

The vegetation of Norway spruce plantations on alluvial soils has been superficially described by

NOIRFALISE & THILL (1975). According to NIHLGARD (1970), coniferous stands older than 40 years and with a low canopy closure represent the mature stage. Indeed, at this moment in the natural development of plantations, the understorey vegetation is representative for the planted tree species and of the environmental characteristics of the site.

## METHODS

Deciduous forests without any evidence of former plantation activity were selected randomly throughout the GDL. Norway spruce stands were systematically selected with regard to similar stand age (ca. 45 years old), canopy closure, and homogeneous stand distribution. We surveyed 208 riverine stands, ranging from 800 to 12000 m<sup>2</sup> for the abundance of woody forest species. Stand area averaged 3312 m<sup>2</sup> (Table 1). Stand area was estimated using digitised maps (A.C.T. 2002). The fieldwork was carried out during the growing period of 2002. All stands were completely and systematically surveyed twice : during spring, in order to determine easily the willow species, and during summer/autumn for the other species. All woody species were recorded. Forest margins were omitted. Canopy trees were described by the following developmental stages : seedlings (1- or 2-year-old), saplings (<10 cm diameter at breast height : dbh) and trees (>10 cm dbh). All shrubs (defined as low branching woody plants, usually smaller than trees) were also recorded in a distinct list. Each developmental stage and each shrub was characterised by an abundance coefficient. Low, medium and high cover percentage were coded as 1 (< 10%), 2 (10 to 50%), and 3 (> 50%), respectively.

The nomenclature of vascular plants follows LAMBINON *et al.* (1998).

## STATISTICAL ANALYSES

To investigate the main sources of variation within our data, two Correspondence Analyses (CA) were applied : (a) considering all the data (saplings, seedlings, and shrubs) without canopy trees and (b) considering canopy trees, saplings, and seedlings. CA was preferred above the more popular Detrended Correspondence Analysis which has been criticised (JACKSON & SOMERS 1991, WARTENBERG *et al.* 1987). Indeed, Detrended Correspondence Analysis was developed in order to reduce the arch effect and to perform gradient analyses. This study did not provide such gradients because both biogeographical area and forest type were binary variables. CA results in species and quadrat scores and in their relative contribution (RC) to

each CA-axis. To test the significance of RC, a permutation technique (MANLY 1998) was applied to the rows, which represent the species. Permutations provided a new data set, and a new CA was performed. The procedure was repeated 10000 times and the proportion of species for which  $RC_{\text{mini}} \geq RC$  gave the probability of the actual value of RC under the null hypothesis of randomness (BOUXIN 1992). Data analyses were carried out using original programs written in Access Basic (details in BOUXIN 1999 and MANLY 1998).

The indicator value method proposed by DUFRÈNE & LEGENDRE (1997) was then used to detect the association of each species with either the forest type or the biogeographical area. The method links the relative abundance (average abundance of a given species in a given group of stands divided by the average abundance of that species in all stands) and the relative frequency (% of stands in a given group where a given species is present) of a species (or a developmental stage) on the one hand and with a particular group (coniferous/deciduous or Oesling/Gutland) on the other hand. The combination, by multiplying relative abundance and relative frequency, provides an indicator value (IV) for each species in each group. The statistical significance of the IV is evaluated using a randomisation procedure performed with 99.999 permutations. The IV of a species is expressed as the percentage to which it fulfils the specificity and the fidelity within any particular group of sites (McGEOCH & CHOWN 1998). Analyses were performed using the computer program package Pc-ORD (McCUNE & MEFFORD 1999).

Functional ecological groups were determined by the type of dispersal [data derived from RAMEAU *et al.* (1989)], the type of soil seed bank [data from THOMPSON *et al.* (1997)] and the establishment strategy sensu GRIME *et al.* (1988) for each species. The relative contribution of each functional group to the total species richness was then compared between forest types and biogeographical regions applying an analysis of variance (GLM procedure) with interaction term using the software Statistica (StatSoft 2002).

## RESULTS

A total of 69 woody species were recorded (Table 1). The mean richness averaged 10.5 woody plants per stand. The total number of woody species was higher either in deciduous forests or in the Gutland area than in Norway spruce stands or in the Oesling area. Results for the mean species richness followed a same pattern (Table

TABLE 1  
*General characteristics of the surveyed forest stands*

	Number of stands	Area (m <sup>2</sup> )		Total woody species richness
		Mean	Standard Deviation	
All stands	208	3312.35	2245.77	69
Norway spruce plantations (NSP)	78	3156.80	2027.73	54
Deciduous woods (DW)	130	3404.48	2368.24	66
Oesling (O)	67	3079.02	1887.35	53
Gutland (G)	141	3481.57	2393.66	65
(NSP)*(O)	32	2965.84	1405.41	40
(NSP)*(G)	46	3285.50	2363.33	42
(DW)*(O)	35	3179.26	2246.12	43
(DW)*(G)	95	3447.46	2417.89	64

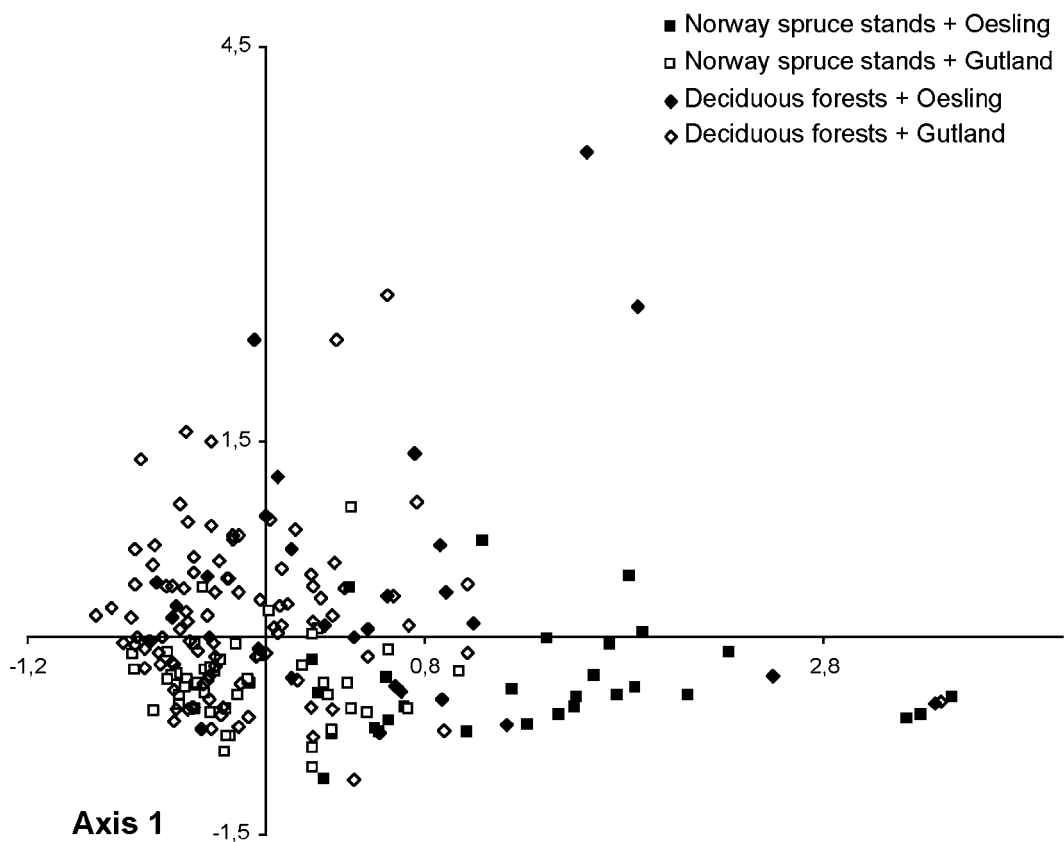


FIG. 1. – Relative position of the sampled stands on the first two axes of a correspondence analysis performed with saplings, seedlings and shrubs.

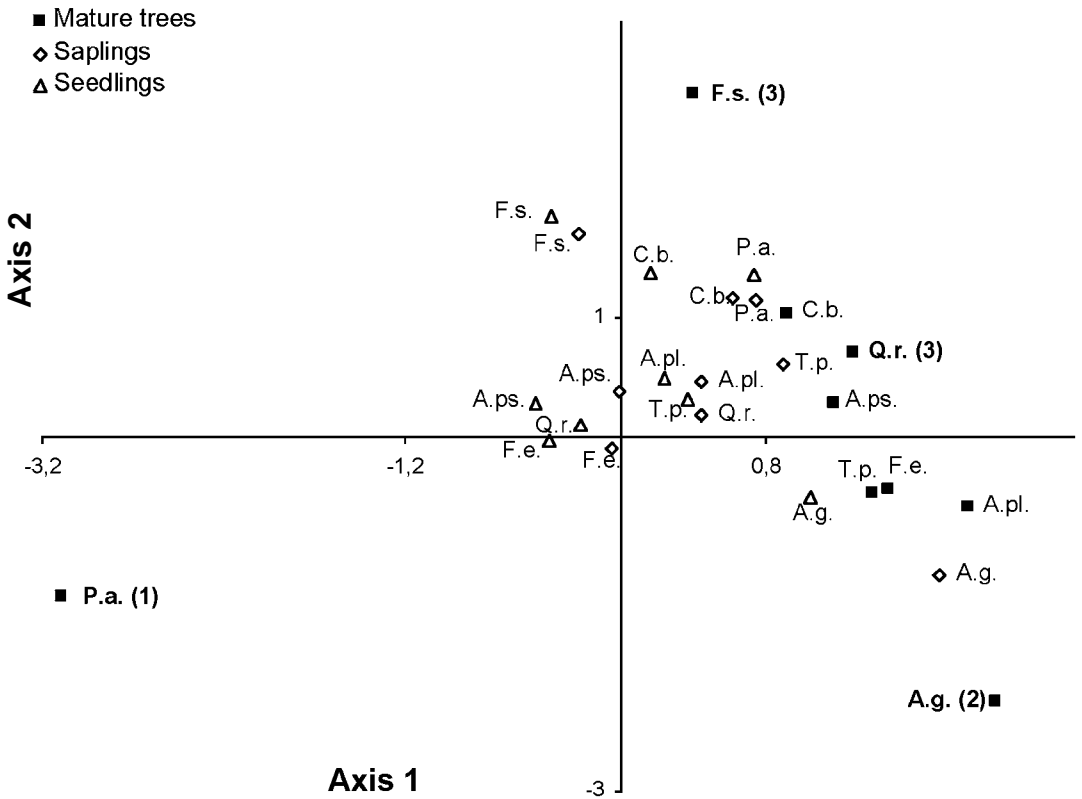


FIG. 2. — Relative position of mature trees, saplings and seedlings on the first two axes of a correspondence analysis. Labels in bold show statistically significant coordinates on the axis (1), (2) or (3). See text for details. A. g. : *Alnus glutinosa* ; A. pl. : *Acer platanoides* ; A. ps. : *Acer pseudoplatanus* ; C. b. : *Carpinus betulus* ; F. B. C. : *Fraxinus excelsior* ; F. s. : *Fagus sylvatica* ; P. a. : *Picea abies* ; Q. r. : *Quercus robur* ; T. p. : *Tilia platyphyllos*.

3); this richness was significantly higher in the Gutland than in the Oesling region.

On the first axis of the first CA, the stand distribution was less related to the stand type (coniferous or deciduous) than to the biogeographical area (Oesling or Gutland) (Fig. 1). Indeed, the CA scores on the first axis are on average higher for the Oesling stands (Mann-Whitney U test,  $p < 0.001$ ). On the first two axes of the second CA (Fig. 2), the mature Norway spruce was situated at the opposite of the other mature trees (filled dots) such as *Alnus glutinosa* or *Fagus sylvatica*. This axis revealed the shift between the Norway spruce stands and the deciduous stands (the *Picea abies* coordinate was negative whereas all the others were positive). This shift was logical because the canopy trees were not included in the first CA.

*Alnus glutinosa* and *Fagus sylvatica* had a highly significant contribution to the second and to the third axis, respectively. The second axis may reflect a hydrologic gradient. The hygrophilous alder and ash were on the opposite side from beech ; the latter cannot grow in swamp areas. Most seedling and sapling plots had a central position on the graph. These plots showed no preference for deciduous or for Norway spruce stands and were quasi-randomly distributed among stands (no significant relative contribution to any axis).

The indicator values of 30 out of 69 woody species changed significantly with at least one of the studied variables (Table 2). Most species had high indicator values for the deciduous forests and the Gutland area. Only the species *Rubus idaeus*,

TABLE 2

Indicator values of woody understorey species (shrubs, lianas, canopy tree saplings and canopy tree seedlings)

	Deciduous versus spruce stands				Oesling versus Gutland			
	Observed Indicator Value (IV)	IV <sup>a</sup> from randomized groups		<i>p</i> <sup>b</sup>	Observed Indicator Value (IV)	IV <sup>a</sup> from randomized groups		<i>p</i> <sup>b</sup>
		Mean	Stand. Dev.			Mean	Stand. Dev.	
<b>Shrubs</b>								
<i>Acer campestre</i>	18.9	12.2	2.14	d *	17.5	12.3	2.27	g *
<i>Cornus sanguinea</i>	24.1	14.4	2.32	d **	25.8	14.5	2.45	g **
<i>Corylus avellana</i>	43.2	38.1	2.34	d *	47.8	38.2	2.47	g **
<i>Crataegus laevigata</i>	24.5	11.7	2.11	d ***				
<i>Crataegus monogyna</i>	46.0	22.6	2.53	d ***	31.2	22.7	2.67	g **
<i>Daphne mezereum</i>					21.1	10.3	2.21	g **
<i>Euonymus europaeus</i>					38.7	16.3	2.59	g ***
<i>Lonicera xylosteum</i>					15.5	7.5	1.88	g **
<i>Prunus padus</i>	11.7	7.1	1.70	d *				
<i>Prunus spinosa</i>	28.9	15.8	2.33	d ***				
<i>Ribes rubrum</i>					35.7	18.8	2.63	g ***
<i>Ribes uva-crispa</i>	28.8	19.4	2.42	d **	44.3	19.5	2.58	g **
<i>Rosa canina</i>	10.7	5.8	1.62	d *	11.3	5.9	1.70	g *
<i>Rubus caesius</i>	21.9	13.9	2.13	d **	25.1	14.0	2.27	g **
<i>Rubus idaeus</i>	34.3	24.1	2.55	n **	37.6	24.2	2.69	o ***
<i>Salix caprea</i>	12.0	7.8	1.91	d *				
<i>Salix fragilis</i>	10.7	5.2	1.56	d **				
<i>Sambucus nigra</i>	51.6	32.5	2.53	n ***	40.2	32.6	2.65	g *
<i>Sambucus racemosa</i>	16.9	7.7	1.83	n ***	24.1	7.8	1.93	o **
<i>Sorbus aucuparia</i>	28.7	12.8	2.20	n ***	25.7	12.9	2.34	o ***
<i>Viburnum opulus</i>	35.1	22.7	2.57	d ***	42.7	22.8	2.73	g ***
<b>Lianas</b>								
<i>Clematis vitalba</i>					7.0	4.1	1.40	g *
<b>Canopy tree saplings</b>								
<i>Acer platanoides</i>					9.2	4.9	1.54	g *
<i>Acer pseudoplatanus</i>					46.8	29.9	2.63	g ***
<i>Alnus glutinosa</i>	19.7	10.9	2.03	d *				
<i>Carpinus betulus</i>	26.9	16.2	2.41	d *	26.7	16.3	2.53	g **
<i>Fagus sylvatica</i>					46.3	25.7	2.94	g ***
<i>Fraxinus excelsior</i>					52.4	31.9	2.66	g ***
<i>Picea abies</i>					8.5	4.7	1.54	g **
<b>Canopy tree seedlings</b>								
<i>Carpinus betulus</i>					10.7	7.5	1.9	g **
<i>Fagus sylvatica</i>					29.8	19.6	2.71	g *
<i>Fraxinus excelsior</i>					47.1	30.3	2.72	g ***
<i>Quercus robur</i>					24.9	17.3	2.74	g

<sup>a</sup> Indicator value (IV) calculated with method of DUFRÈNE & LEGENDRE (1997).

<sup>b</sup> Letters d or n, and g or o refer, respectively, to a greater abundance in deciduous or Norway spruce stands and Gutland or Oesling. Only species having at least one significant difference are shown.

\* : 0.01 < *p* < 0.05 ; \*\* : 0.001 < *p* < 0.01 ; \*\*\* : *p* < 0.001

*Sambucus nigra*, *Sambucus racemosa*, and *Sorbus aucuparia* were more associated with Norway spruce stands. The same species, except *Sambucus nigra*, were also more frequently associated with Oesling. Considering only species with the highest significance level ( $p < 0.001$ ), the shrubs *Crataegus laevigata*, *Crataegus monogyna*, *Prunus spinosa* and *Viburnum opulus* were more abundant in deciduous forests whereas other shrubs such as *Euonymus europaeus* and *Ribes rubrum*, saplings such as *Acer pseudoplatanus*, *Fagus sylvatica* and *Fraxinus excelsior* were associated with the Gutland area. Although a lot of shrubs were associated with deciduous forests, the forest type had only a slight effect on canopy tree saplings and had no effect at all on canopy tree seedlings.

The recorded woody plants consisted mainly of zoochorous species (70%, Table 3). Only few species, dispersed by wind, were observed in both Norway spruce and deciduous stands. Neither forest type nor biogeographical area had an effect on the distribution of species with different dispersal modes. Regarding establishment strategy, Norway spruce stands favoured stress tolerant species and competitors. Norway spruce stands were also more favourable to species with a short-lived seed bank. In agreement with the indicator species analysis, the biogeographical region was more influential on the functional ecological groups

than the type of forest was. Indeed, the Oesling strongly favoured stress-tolerators and competitors. Concerning the seed bank type, a transient one is associated with Gutland and a short-lived one with Oesling. *Rubus idaeus* and *Sambucus racemosa*, both having a short-lived seed bank, explained this result.

## DISCUSSION

### RIVERINE FOREST COMMUNITIES

Mixed deciduous forests that are rich in sycamore and ash are a widespread community type in Western Europe (RAMEAU *et al.* 1989). These forests are dominated by *Acer pseudoplatanus*, *Fraxinus excelsior*, *Quercus robur*, *Tilia platyphyllos* and *Ulmus glabra*. They are present in deep, damp soils at slope foots and are often associated with *Aegopodium podagraria*, *Urtica dioica*, *Silene dioica* or *Impatiens noli-tangere* on soils that are rich in bases and nutrients, especially nitrogen (ATKINSON 2002). It is well known that species richness is substantially higher in forests on alluvial soils compared to other forest types (e.g., DUMORTIER *et al.* 2002). These forests often contain a high number of canopy tree species. Seven of them were present in at least 10% of our studied deciduous forests. Among them, *Fraxinus excelsior* occurred frequently in fresh woods, on

TABLE 3

Comparison of woody species richness and of relative abundance of functional groups between regions and forest types, using a GLM ANOVA model  
(Response = Forest type + Biogeographical area + Forest type \* Biogeographical area)

	Forest type (Ft)		F	Biogeographical area (Ba)			Ft x Ba F
	coniferous	deciduous		Oesling	Gutland	F	
Woody species richness	9.35 (%)	11.28 (%)	2.26	7.41 (%)	12.04 (%)	45.52***	4.07*
Competitors	34.43	25.53	9.11**	37.75	24.77	19.64***	2.12
Stress tolerators	47.67	38.08	12.84***	46.46	39.44	5.27*	0.17
Anemochorous	26.27	28.98	1.29	29.64	27.21	1.65	0.25
Zoochorous	69.32	67.49	0.11	67.04	68.69	0.93	2.15
Transient seed bank	71.33	76.02	1.34	63.86	79.04	25.11***	0.34
Short-lived seed bank (<5 years)	23.05	15.55	4.05*	30.43	12.81	39.59***	0.14
Long-lived seed bank (>5 years)	0	0.38	0.979	0	0.35	0.979	0.979

\* :  $0.01 < p < 0.05$  ; \*\* :  $0.001 < p < 0.01$  ; \*\*\* :  $p < 0.001$

the river embankment. *Alnus glutinosa* is a hygrophilous species favoured by light-textured soils. *Acer campestre* and *Ulmus minor* are more thermophilous. *Ulmus minor* has become sparse because of Dutch elm disease, explaining its rarity in the area. *Acer pseudoplatanus* and *Ulmus glabra* are subatlantic, submontaneous species. *Acer platanoides* is more continental and occurs frequently in ravine forests. While the shrub *Crataegus monogyna* prefers basophilic, light textured deposits of the Gutland, *Crataegus laevigata* seems to appear more frequently in the Oesling area (although not significantly), where soils are coarser and acidic. Except *Hedera helix*, which is a typical forest species, lianas were rare in our data set because lianas are more frequent at forest margins and in forest gaps due to their heliophilous behaviour (SCHNITZLER 1995).

Few understorey species were associated with Norway spruce stands. Among them, *Sorbus aucuparia* is a short-lived species widely distributed throughout Europe and often acting as a pioneer tree. *S. aucuparia* is a shade tolerant species and is able to germinate in old-growth spruce forests under poor light and on a thick layer of raw humus (ZERBE 2001). In our data set, *Sambucus* spp. were strong indicators of Norway spruce stands. In agreement with ATKINSON (2002), *Sambucus nigra* was characteristic of disturbed, base-rich, nitrogen-rich, and phosphate-rich soils (Gutland) whereas *Sambucus racemosa* was more frequent on Ca-poor soils (Oesling). So, the Norway spruce canopy resulted in an overrepresentation of these three pioneer/ruderal species. Concerning canopy tree seedlings, no statistical differences were detectable between deciduous forests and Norway spruce stands. Thus, Norway spruce plantations are not real constraints on the first developmental stages of canopy tree species.

#### FUNCTIONAL GROUPS AND COLONISATION

As most temperate woody forest species do not form persistent seed banks (BOSSUYT & HERMY 2001, BOSSUYT *et al.* 2002), they have to colonise Norway spruce stands by seed rains from neighbouring forest sources. This is probably the reason why ornithochorous species were the main

functional group of species in the Norway spruce stands (69%). Riparian forests support large numbers of breeding bird as compared to more xeric forests and other upland habitats (INMAN *et al.* 2002). Because of the high mobility of their dispersers, the colonisation rate of ornithochorous species is considerably higher than that of plants having a short distance dispersal such as myrmecochorous and barochorous species (GRASHOF-BOKDAM & GEERTSEMA 1998). Moreover, seedling emergence and growth are often easier from defecated seeds (PAULSEN & HOGSTEDT 2002). Even if dispersal is a success, seeds have to remain viable until the time of their germination. At that moment predation can be intense. Species ripening in summer (*Prunus* spp., *Viburnum* spp.) are exposed to seed predation for a longer period than those fruiting in late winter and early spring such as *Hedera helix* (KOLLMANN *et al.* 1998). This gives a possible explanation of the ivy high abundance and of the rarity of *Prunus* spp. and *Viburnum* spp. in Norway spruce stands. Another explanation can be the light requirement (*Hedera helix* is skiophilous whereas *Prunus* spp. and *Viburnum* spp. are heliophilous species). Finally, seeds of pioneer, wind-dispersed woody species (*Alnus glutinosa* or *Salix alba*) need bare, mineral soil to germinate. As in Norway spruce stands litter is often thick, neither seedlings nor saplings of these pioneers are frequent (Table 2).

#### REGENERATION OF CANOPY TREES AND CONVERSION OF NORWAY SPRUCE STANDS

Correspondence and indicator value analyses suggest there was no difference in the abundance of canopy tree seedlings between deciduous and Norway spruce stands (Fig. 1 and Table 2). Indeed, *Fraxinus excelsior* and *Acer pseudoplatanus* were the main regenerating species in Norway spruce stands. Alluvial silty soils are the most suitable for the regeneration of *Fraxinus excelsior* and *Acer pseudoplatanus* in southern Belgium (CLAESSENS *et al.* 1999). Moreover, according to WEBER-BLASCHKE *et al.* (2002), growth and mineral nutrition of seedlings of these two species in pot experiments are excellent on soils with high Ca and Mg. The Gutland area, with

base-rich soils, is thus more favorable to the regeneration of *Fraxinus excelsior* and *Acer pseudoplatanus* (Table 3), even in Norway spruce stands. Other species with lower frequencies, such as *Quercus robur* and *Fagus sylvatica*, have their first-year seedlings rather well adapted to low light conditions (WELANDER & OTTOSSON 1998). Therefore, they regenerate also under a dense Norway spruce canopy.

In a perspective of conversion of Norway spruce stands, increasing the light intensity is a necessity to the future development not only of oaks (WELANDER & OTTOSSON 1998), but also of ashes and maples. Increase of light availability, however, leads to an increased growth of the surrounding herbaceous vegetation and thus to enhanced competition. For example, at low light intensity, the growth of tree saplings of *Acer pseudoplatanus* and *Fraxinus excelsior* seems less affected than the growth of various weeds (HELLIWELL & HARRISON 1979). An early removal of the Norway spruce canopy may then lead to increasing competition and finally to a loss of the regenerating valuable trees (ash, beech, maple and oak). We think, however, that the early growth of tree species, as shown in our results, and a slight canopy opening may improve the speed of conversion. Using these natural processes and applying few silvicultural measures permit some financial benefits (HEKHUIS & WIEMANN 1999). Such conversion strategies improve both economical and ecological results.

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