

Spontaneous ingrowth of tree species in poplar plantations in Flanders

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Abstract – Today a tendency exists to transform a number of traditionally managed poplar plantations, which are considered to have a poor nature conservation value, towards closer to nature stands. Herewith the question arises to what extent such conversion can occur naturally by spontaneous ingrowth of native tree species. Therefore this study formulates the following objectives: To what extent does spontaneous ingrowth occur in poplar plantations? Which parameters determine this process? Can this ingrowth be used as a base for an indirect conversion of poplar plantations?

To answer these questions, surveys were carried out in 175 poplar plantations. It is found that spontaneous ingrowth of many tree species in poplar plantations is often so important that it can be used as a base for stand conversion. This ingrowth is related to the parameter “forest age”, meaning the number of years that the site has been planted with poplars.

The ingrowth can often be used for the development of mixed, well structured and multifunctional forest stands, with higher ecological, recreational and landscape value.

poplars / spontaneous ingrowth / conversion / diversity / Flanders

Résumé – Développement spontané d'espèces d'arbres dans les plantations de peupliers en Flandre. La tendance actuelle est à la transformation de certaines peupleraies « traditionnelles » de peu de valeur écologique, en peuplements plus « naturels ». Ainsi la question suivante se pose-t-elle : dans quelle mesure une telle transformation peut-elle se réaliser par le biais du développement spontané d'espèces autochtones ? Cette étude a pour objectifs de répondre aux questions suivantes : dans quelle mesure y a-t-il un développement spontané dans des plantations de peupliers ? Quels paramètres déterminent ce processus ? Ce développement spontané peut-il être employé comme base de transformation indirecte de plantations de peupliers ?

Pour répondre à ces questions, des mesures ont été réalisées dans 175 plantations de peupliers. On a constaté qu'un développement spontané de plusieurs espèces d'arbres est souvent si important qu'il peut être employé comme base de transformation des peuplements. Pour quelques espèces ce développement est déterminé par le paramètre « âge de la forêt », c'est-à-dire la période durant laquelle la station a été conduite en peupleraie. L'établissement d'autres espèces peut être employé pour le développement de peuplements mixtes, bien structurés et multifonctionnels, d'une plus grande valeur écologique, récréative et esthétique.

peupliers / développement spontané / transformation / diversité / Flandre

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1. INTRODUCTION

In spite of the indisputable advantages linked to monoclonal and homogeneous poplar plantations, it is recently often recommended, e.g. by the Flemish government, to transform them. Indeed, poplar plantations do not sufficiently correspond to the general requirements of multifunctional forestry. They score especially low with regard to the criteria of sustainable forestry, Pro Silva and FSC (Forest Stewardship Council) [2, 27, 36]. Moreover they are regularly established at the expense of worthwhile nature areas. The dominant presence of *Urtica dioica* is considered as the proof of the ecological poverty of such plantations [4]. Protagonists of poplars, however, claim that the ecological value of poplar plantations should not be underestimated. In this regard, Hermant [12] points out that biodiversity is greater than it is generally accepted. Muys [27] refers to the high number of earthworms in poplar soils, Jacobs [18] and Pinto [31] to the collembola populations and Opdam et al. [29] to the interesting bird populations. Also Laquerbe [22] stresses that the understory plant communities of cultivated poplar groves constitute a rich and diversified zone. Species richness of plant communities of the understory increased accordingly to the upkeep level. This trend was mainly due to annual species and secondarily to biennials ones.

Anyway, several foresters are becoming more critical towards poplar plantations, in line with the development of the ideas of sustainable forest management and the introduction of the European Natura guidelines [2, 6]. Consequently, there is a tendency to transform a number of poplar plantations towards closer to nature stands. The question then arises to what extent such conversion can occur naturally by spontaneous ingrowth and development of native tree species. Therefore this study addresses the following objectives:

1. To what extent does spontaneous ingrowth occur in poplar plantations?
2. Which parameters determine spontaneous ingrowth in poplar plantations?
3. Can this ingrowth be used as a base for an indirect conversion of poplar plantations towards mixed hardwood stands?

A visual evaluation of the present situation allows to conclude that spontaneous ingrowth is not negligible. Quantitative data are however necessary. Furthermore, based on the study of De Keersmaecker and Muys [4], the hypothesis is assumed that “forest age” (the period

during which forest is present) is a determining factor for the presence of some species.

2. MATERIALS AND METHODS

The survey was carried out over an area of 160 km² in the region Gavere-Oosterzele (51° N and 4° E), a region of the province East-Flanders in Belgium representative for the normal poplar situation in Belgium. It is a flat region, with an altitude varying around 50 m a.s.l., with mean annual rainfall 780 mm and mean annual temperature 9.6 °C. The poplar plantations are very fragmented and the average area is some 2 hectares. The rotation period in the past varied around 30 years. Most of the present poplars belong to the clone “robusta” and were planted at a distance of 6 to 8 m. Generally, no soil preparation, such as ploughing, and vegetation control happened. Treatment is normally restricted to pruning.

The overall forest cover of the region appropriates 7%. A preceding study showed that only 30% of the current forests existed in 1870 [36].

To test the hypothesis concerning “forest age” it was aimed to select some 25 poplar plots in different classes of “forest age”, meaning poplar plantations on sites which were planted in different time periods.

By processing seven existing land use maps by GIS, we know that poplar plantations in this region are existing since 1870. Therefore for the periods after 1870 only these parcels, of which one can be certain that no other tree species than poplar were present before 1870, were retained. On the contrary, for forests pre-existing 1870, it is known that they were afforested in former times with other tree species, but we don’t know exactly the period of the first poplar plantation.

In accordance with the existing land use maps seven time periods were distinguished. Finally 175 poplar stands were selected, divided as follows (*table I*).

The above means that a difference exists between “forest age” and “age of present poplar plantation”. Forest age refers to the period of the first afforestation of the sites: the present poplar plantation was planted on a site which was for the first time planted with poplars in the mentioned period, at least for the period after 1870, or that was already forest before 1870. So, since the normal rotation period of poplars in this region was around 30 years, we can assume that in the class 1893–1937 already the third or fourth rotation of poplar plantation is nowadays occurring.

Table I. Distribution of plots in the different “forest age” classes.

Period of first poplar planting	Number of years that plantations (or forests) are already present (forest age)	Number of selected poplar plots
1978–1990	10–22	23
1965–1978	22–35	27
1937–1965	35–63	30
1893–1937	63–107	34
1870–1893	107–130	22
1775–1870	130–225	12
before 1775	more than 225	27

In each of these poplar stands the following measurements were carried out:

1. Survey of the ingrowth. In stands smaller than 0.5 ha and in larger stands with a limited ingrowth all individuals were measured. In larger stands counts happened in five randomly distributed plots of 10 are. Only established ingrowth of tree species, with a minimal height of 1 m, was noted. Nomenclature happened according Lambinon et al. [21].

2. Environmental variables: forest age, texture, drainage class, presence of ditches, vegetation type, age of plantation, stem number/ha, area and distance of the nearest adjacent ancient forest (by definition a forest present before 1870) [14, 15, 36]. Moreover, as we know that dispersion of plants is strongly dependent on the neighbourhood of forests [1, 9, 15, 19, 34] for each period a border variable was created: “border a” indicates a poplar stand with part of its perimeter forming a border with a forest originating between 1978 and 1990, “border b” indicates the same situation for the period 1965–1978, etc. for “border c” and so on.

Soil types and drainage classes were for each plot derived from the Belgian soil map [13]. Sandy-loam soils cover 52.5% of the forest soils, whereas loam soils cover 14.4% and light sand-loam soils 10.0%. Drainage class e (wet) dominates with 32.2%, followed by class d (moderately wet) with 20.0% and class f (very wet) with 11.1%. The foregoing means that the poplar plantations are mostly occurring on appropriated sites.

The vegetation type was surveyed in a simple way: herbs, shrubs, ruderal plants, stinging-nettle, blackberry, etc. were noted, together with the degree of dominance [32].

In order to identify the determining environment variables, at first a classification with Twinspan (Two Way Indicator Analysis) [37] was carried out. It groups similar species, parameters, or surveys. In a second step an ordination with CCA (Canonical Correspondence Analysis) was carried out in order to find out to what extent the variables are significant. Since CCA accounts for only 8% of the variance (for the first three axes), an alternative method had to be applied. The environmental variables were compared with each other by non-parametric tests (Mann-Whitney; Kruskal-Wallis). The exact influence of significant variables ($P < 0.05$) was further tested by cross tabulation. The calculated Spearman correlations were used as indications for the importance of the variable.

3. RESULTS

The frequency of the ingrowth is shown in different ways in *table II*:

- the percentage of presence of a species over all stands;
- the average number of individuals of a species, calculated over all stands;
- the average number of individuals of a species, calculated for the stands in which the species is present.

As most interesting results are to mention:

1. In total, 29 tree species and shrubs were present. 9 species occur in at least 30% of the stands and 15 in at least 15% of the stands. The most frequent species can be grouped as follows:

- group 1 (> 50%): *Sambucus nigra*, *Quercus robur*, *Fraxinus excelsior*, *Alnus glutinosa*, *Corylus avellana* and *Crataegus monogyna*;
- group 2 (\pm 30%): *Salix alba*, *Acer pseudoplatanus*, *Prunus avium*, *Betula pendula* and *Viburnum opulus*;
- group 3 (\pm 20%): *Ribes rubrum*, *Salix caprea*, *Ulmus spp.* and *Sorbus aucuparia*.

2. The ingrowth averages 1600 individuals per ha, with 34% of them being *Sambucus nigra*. Four species (*Sambucus nigra*, *Fraxinus excelsior*, *Alnus glutinosa*, and *Corylus avellana*) account for 69% of the total ingrowth.

3. *Sambucus nigra* does not only appear in the largest number of stands, it also scores highest with respect to average of individuals per presence, 652 ha⁻¹. Other species with good ingrowth are *Ulmus spp.*, *Fraxinus excelsior*, *Corylus avellana*, *Alnus glutinosa* and *Acer*

Table II. Frequency of tree species in ingrowth of 175 poplar stands.

Species	Presence of species (% of plots)	Average number of species over all plots ($N\ ha^{-1}$)	Average number of species in plots where present ($N\ ha^{-1}$)
<i>Sambucus nigra</i>	86	543	652
<i>Quercus robur</i>	69	43	64
<i>Fraxinus excelsior</i>	64	220	354
<i>Alnus glutinosa</i>	57	174	313
<i>Corylus avellana</i>	51	160	320
<i>Crataegus monogyna</i>	49	48	100
<i>Salix alba</i>	38	42	113
<i>Acer pseudoplatanus</i>	33	72	223
<i>Prunus avium</i>	31	36	120
<i>Betula pendula</i>	29	25	90
<i>Viburnum opulus</i>	28	17	64
<i>Ribes rubrum</i>	23	21	93
<i>Salix caprea</i>	20	14	702
<i>Ulmus spp.</i>	20	69	357
<i>Sorbus aucuparia</i>	18	29	166
<i>Populus cv.</i>	16	38	247
<i>Cornus sanguinea</i>	9	83	93
<i>Prunus serotina</i>	8	8	93
<i>Prunus spinosa</i>	6	4	67
<i>Frangula alnus</i>	6	2	36
<i>Quercus rubra</i>	6	8	152
<i>Carpinus betulus</i>	5	8	186
<i>Euonymus europaeus</i>	4	1	13
<i>Ilex aquifolium</i>	4	2	43
<i>Fagus sylvatica</i>	2	1	26
<i>Sambucus laciniata</i>	2	1	31
<i>Prunus padus</i>	1	2	170
<i>Ribes uva-crispa</i>	1	0	4
<i>Acer campestre</i>	1	1	167

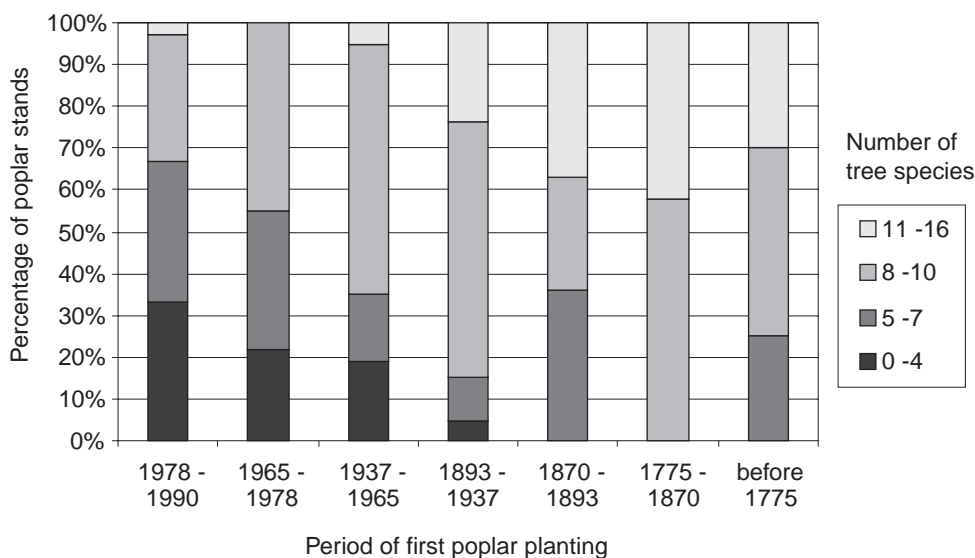
**Figure 1.** Distribution of the number of tree species in the spontaneous ingrowth in relation to the period of first poplar planting.

Table III. Correlations between significant environmental variables and the main colonisation species (bold numbers indicate significant correlations).

Variable	<i>Ace pse</i>	<i>Aln glu</i>	<i>Cor avel</i>	<i>Cra mon</i>	<i>Fra exc</i>	<i>Pru avi</i>	<i>Pru ser</i>	<i>Qu rob</i>	<i>Rib rub</i>	<i>Sal alb</i>	<i>Sam nig</i>	<i>Ulm spe</i>	<i>Vib opu</i>
Forest age	0.38	0.46	0.57	0.15	0.57	0.26			0.21		0.45	0.36	0.22
Ditch		0.33	0.28	0.22	0.33							0.29	0.23
Distance	0.00		-0.4										

pseudoplatanus. The stem number of *Quercus robur*, which is present in many stands, is restricted to an average number of 64 ha⁻¹.

4. Only 5 stands (of 175) lack ingrowth. All uncolonised stands belong to the more recent periods. *Figure 1* shows that in the youngest stands less than four species occur in more than 30% of the plots, nevertheless at least 7 species colonise more than 30% of these stands. In all stands originating from before 1893 at least five species appear and at least eight species are present in all stands planted before 1870. The species diversity, however, decreases for stands planted in the oldest period.

The Kruskal-Wallis test indicates that the average species richness differs significantly according to the period of afforestation. Generally speaking, species richness increases with forest age. The Spearman correlation coefficient (0.43) shows a relatively strong relationship.

5. Pearson correlations between significant environmental variables and the main colonisation species are presented in *table III*.

The Spearman correlation with significant environment variables is in general very low. Only forest age, the presence of ditches and the distance to an adjacent forest have a significant relationship with colonisation. No correlation is found between the ingrowth and the variables texture, drainage class, density of plantation and vegetation type.

– For six species (*Fraxinus excelsior*, *Corylus avellana*, *Alnus glutinosa*, *Sambucus nigra*, *Acer pseudoplatanus*, *Ulmus spp.*) the forest age plot is apparently the most significant variable. This variable accounts for more than 35% of the variability in colonisation of these species. Forest age is, however, not significant for *Quercus robur*, *Salix alba* and *Prunus serotina*.

– The presence of a ditch ranks the second most determining factor for *Fraxinus excelsior* and *Salix alba*.

– Distance to the adjacent forest is only significant for *Corylus avellana*.

4. DISCUSSION

An important spontaneous ingrowth often occur in poplar plantations. Only 5 out of 175 investigated poplar stands have no ingrowth. In all, 29 different species are found in the spontaneous ingrowth. (Additionally, a little but almost negligible artificial underplanting is found in a small number of recent plantations.) Spontaneous ingrowth averages a number of 1,600 individuals ha⁻¹.

A large number of species per stand can occur: 15 species appear in 15% of the stands and at least 9 species are found in 30% of the stands. This ingrowth completely changes the structure and the nature value of monoclonal poplar plantations [6, 14, 17].

Independent of the criteria *Sambucus nigra*, *Fraxinus excelsior*, *Alnus glutinosa* and *Corylus avellana* are the most frequent colonisers. *Sambucus nigra* is by far the most dominant coloniser, with an appearance of 86% and an average number of 650 ha⁻¹. *Fraxinus excelsior* is undoubtedly the second most frequent coloniser, with an appearance of 64% and an average number of 350 ha⁻¹. Its presence is not surprising, because many poplar plantations were planted on typical ash stands. Moreover it is a species with easy seed dispersal. Taking into account its limited migration capacity, the presence of *Corylus avellana* shows that many poplar plantations were carried out before 1870 in former broad-leaved stands, in which the species was already present.

A special position is taken by *Quercus robur*, which appears in 69% of the stands. Its presence is limited, on average 64 individuals ha⁻¹, meaning that this valuable species can hardly be used with the indirect transformation of the poplar stands.

The investigation shows, that only a few number of variables significantly contribute to natural ingrowth in poplar stands. Besides, two points are striking.

1. The Spearman correlation coefficient is low. In some cases it reaches little more than 0.3. This means,

that the impact of the individual environmental variables is not so strong and that “coincidence” is likely to have great importance. This is in line with the point of view of many authors, which claim that the reasons for the non-appearance of natural regeneration are often unknown [10, 13, 30, 33].

2. It is obvious that the parameter “forest age”, the time during which the parcel was continuously afforested, influences ingrowth into poplar plantations.

In average, poplar plantations must exist for at least 50 years at the same site, before a reasonable spontaneous development occurs. Ingrowth in recently planted poplar plantations is low. “Forest age” is considered as important both for the development of the specific herbaceous forest vegetation [14, 36], and for the spontaneous development of trees and shrubs [4].

Regeneration is only absent in very recent plantations. Forest age determines the appearance of species such as *Corylus avellana*, *Alnus glutinosa*, *Sambucus nigra*, *Acer pseudoplatanus*, *Ulmus spp.*, *Prunus avium*, *Crataegus monogyna* and *Ribes rubrum*. The period of origin, however, is not important for colonisation by *Quercus robur*, *Salix alba* and *Prunus serotina*. *Corylus avellana* is, moreover, also linked to the presence of other ancient forests in the vicinity [36].

The importance of forest age, the presence of old forest and, in general, the history or past land use is confirmed by the results of De Keersmaecker and Muys [4], Dzwonko and Gawronski [7], Dzwonko and Loster [8], Koerner et al. [19], Peterken [30] and Tack et al. [36]. From his side Laquerbe [23] found already an important settlement and biomass of *Cornus sanguinea* after a period of 30–35 years.

The presence of ditches is a significant variable too. This refers, of course, to the appearance of wet soils. The presence of ditches is, however, strongly linked with forest age. They are only found in older forests and not in younger ones. This shows, that the recent poplar plantations were planted on drier sites. The presence of ditches is mainly determining for two species, viz. *Fraxinus excelsior* and *Salix alba*. This is not surprising for these species, though Schreiber [33] claims that natural regeneration does not appear on wet sites.

The vertical structure of the poplar plantations is, of course, depending on the density, the age and the development of the ingrowth. The current vertical structure of these poplar stands is very heterogeneous. On one hand, recent plantations with almost no ingrowth have a typical monoclonal structure. On the other hand, some well developed stands have a structure comparable with young

irregular forest stands, with canopies in the lower and middle storey. Individuals of *Fraxinus excelsior* and other tree species even reach the upper storey of the poplars, and are looking very promising from the economic point of view. Other stands are dominated by an almost homogeneous lower storey of *Sambucus nigra*.

The answer to the question whether the spontaneous ingrowth is useful as a base for forest conversion mainly depends on the objectives of the conversion. When it is aimed at an (almost) homogeneous, uniform, and densely closed stand of one (or two) species with a high economic value, this ingrowth is only useful in a limited number of cases. Indeed, the stand density of the valuable species and individuals is insufficient. However, in many cases the number of elements, useful for timber production, should not be underestimated. *Fraxinus excelsior*, *Alnus glutinosa* and *Acer pseudoplatanus* reach an average over all parcels of 466 individuals ha⁻¹. Next to that *Quercus robur*, *Salix alba*, *Prunus avium*, *Castanea sativa*, *Alnus incana*, *Betula alba*, *Quercus rubra*, *Carpinus betulus*, *Populus alba* and *Fagus sylvatica* have together on average a number of 225 individuals ha⁻¹. (A few of them were artificially planted.) So, the total number of so called useful species averages almost 700 individuals ha⁻¹. In a restricted number of stands the number of valuable individuals is much higher, with a maximum of 6,400 ha⁻¹, which is more than the double of the usual number planted in broad-leaved stands. Provided the necessary treatment, these stands are certainly valuable.

Moreover, one should also consider the numerous shrubs which appear in the understorey and which fulfil an important role. When the conversion is aimed at more multifunctional forests and mixed stands with a heterogeneous structure, a greater naturalness, a higher landscape and recreational value, or when the forest owner is more interested in game, it is evident that such ingrowth is useful in many cases. These stands are anyway strongly appreciated in the frame of Natura 2000 [6].

Plantations with a rich and well structured natural ingrowth are even of interest from an economic point of view. There are no (high to very high) reforestation costs and (in Flanders) subsidies for such forest types are higher. In such a case, however, the ingrowth must be treated in an appropriate manner, which has not occurred in the past. The quality of such stands can strongly be improved by a number of measures, such as vegetation control, pruning of a restricted number of selected elements, mixture regulation and control of *Sambucus nigra*.

The fast and abundant appearance of *Sambucus nigra* is frequently the main problem of such stands. It is a

typical pioneer tree species, occupying rapidly a great area and consequently hindering the establishment of other more valuable individuals. Moreover, its control is not easy, since it shows a very high coppicing capacity and its dispersal is very simple. Chemical control, by means of a stump treatment, might be the most efficient manner and is also little harmful to other organisms.

Exploitation is, of course, a specific problem of each conversion. Different investigations, however, proved already that exploitation damage could be restricted [11, 20, 24, 25].

5. CONCLUSIONS

Spontaneous ingrowth of many tree species in plantations, where poplars occur for at least 50 years, is frequently so high, that it could be well used as a base for indirect stand conversion. If wanted, this ingrowth can be used for the development of mixed, well structured and multifunctional forest stands, with a higher nature conservation, recreational and landscape value. Such conversion is to be recommended in areas where nature value is more stressed than the economic value of the forests, e.g. when the objectives of Natura 2000 are aimed at.

“Forest age” significantly contributes to the appearance of the spontaneous ingrowth. The impact of other environmental variables, such as texture, drainage class and vegetation type, is not so obvious and “coincidence” is likely to have a greatest importance.

The main conclusion of the research is in accordance with the results of Knol [20], who claims that the possibilities of (artificial) underplanting in poplar forests are almost unlimited.

REFERENCES

- [1] Brunet J., von Gheimb G., Colonization of secondary woodlands by *Anemone nemerosa*, *Nordic J. Bot.* 18 (1998) 369–377.
- [2] Buysse W., Van der Aa B., Sustainability the Pro Silva way. Tweede internationaal Pro Silva congres, Apeldoorn 29–31 mei 1997, *De Boskrant* 27 (1997) 131–133.
- [3] Debussche M., Isenmann P., Bird-dispersed seed rain and seedling establishment in patchy Mediterranean vegetation, *Oikos* 69 (1994) 414–426.
- [4] De Keersmaeker L., Muys B., De kruidvegetatie van populierenbossen, *Groene Band* 95 (1995) 1–25.
- [5] De Keersmaeker L., De Schrijver A., Nachtergale L., Mussche S., Lust N., Evaluatie van bosvorming als effectgerichte maatregel tegen verzuring en vermessing van bossen, *Groene Band* 105 (1998) 1–31.
- [6] Dumortier M., Butaye J., Jacquemyn H., Van Camp N., Lust N., Hermy M., Predicting vascular plant species richness of fragmented forests in agricultural landscapes in Central Belgium, *For. Ecol. Manag.*, in press.
- [7] Dzwonko Z., Gawronski S., The role of woodland fragments, soil types and dominant species in secondary succession on the western Carpathian foothills, *Vegetatio* 111 (1994) 149–160.
- [8] Dzwonko Z., Loster S., Effects of dominant trees and anthropogenic disturbances on species richness and floristic composition of secondary communities in southern Poland, *J. Appl. Ecol.* 34 (1997) 861–870.
- [9] Grashof-Bokdam C.J., Forest plants in an agricultural landscape in the Netherlands: effects of habitat fragmentation, *J. Veg. Sci.* 8 (1997) 21–28.
- [10] Harmer R., Natural regeneration of broadleaved trees in Britain: seed production and predation, *Forestry* 67 (1994) 275–286.
- [11] Harvey B.D., Bergeron Y., Site patterns of natural regeneration following clearcutting in northwestern Quebec, *Can. J. For. Res.* 19 (1989) 1458–1469.
- [12] Hermant F., Le peuplier dans son environnement : éléments de réflexion sur la populiculture et ses impacts écologiques. Projet, Université des sciences et technologies de Lille, 1996, 137 p.
- [13] Hofman G., Bodemvruchtbaarheid. *Cursusnota's*, Faculteit landbouwkundige en biologische wetenschappen, Gent, 1996, 325 p.
- [14] Honnay O., Degroote B., Hermy M., Ancient-forest plant species in western Belgium: a species list and possible ecological parameters, *Belg. J. Bot.* 130 (1998) 139–154.
- [15] Honnay O., Hermy M., Coppin, P., Impact of habitat quality on forest plant species colonisation, *For. Ecol. Manag.* 115 (1999b) 157–170.
- [16] Howell J.B., Some thoughts on natural regeneration of oak, *Quart. J. For.* 90 (1996) 150–152.
- [17] Fuller R.F., *Birdlife of Woodland and Forest*, Cambridge University Press, Cambridge, 1995, 244 p.
- [18] Jacobs W., Een vergelijkende studie van collembolengemeenschappen in bodems van verschillende bostypes. *Afstudeerwerk*, Universiteit Gent, Faculteit van landbouwkundige en toegepaste biologische wetenschappen, 1997, 105 p.
- [19] Koerner W., Dupouey J. L., Dambrine E., Benoit M., Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France, *J. Ecol.* 85 (1997) 351–358.
- [20] Knol R.F., Op weg naar duurzaam bos in Flevoland, *Bosbouwvoorlichting* 36 (1997) 79–81.
- [21] Lambinon J., De Langhe, J.E., Delvosalle, L., Duviigneaud J., *Flora van België, het Groothertogdom-Luxemburg*,

Noord-Frankrijk en de aangrenzende gebieden (Pteridofyten en spermatofyten), Nationale Plantentuin van België, Meise, 1998, 1091 p.

[22] Laquerbe M., Richesse spécifique et phytomasse des sous-bois de peupleraies cultivées en bordure de Garonne (Sud-Ouest de la France), *Ann. For. Sci.* 57 (2000) 767–776.

[23] Laquerbe M., Communautés de sous-bois des peupleraies artificielles relation entre phytomasse, richesse spécifique et perturbations, *Ann. For. Sci.* 56 (1999) 607–614.

[24] Lust N., Die Beziehung von Waldwirtschaft zu Umwelt- und Naturschutzproblemen, *Silva Gand.* (1997) 117–135.

[25] Meiresonne L., Excursie Pro Silva Nederland: de rol van de populier. Intern Rapport, Instituut voor Bosbouw en Wildbeheer, 1994, 12 p.

[26] Mosandl R., Kleinert A., Development of oaks (*Quercus petraea* (Matt. Liebl.) emerged from bird-dispersed seeds under old-growth pine (*Pinus silvestris*) stands, *For. Ecol. Manag.* 106 (1998) 35–44.

[27] Muys B., Kritische beoordeling van de natuurwaarde van populierenbossen en de gevolgen voor hun aanleg, *De Boskrant* 22 (1992) 7–10.

[28] Oosterbaan A., Van Den Berg C.A., Natuurlijke verjonging van Zomereik op beekerdgrond, *Nederlands Bosbouw-tijdschrift* 68, 1996, 150–153.

[29] Opdam P.F.M., Kalkhoven J.T.R., Phillippona J., Verband tussen broedvogelgemeenschappen en begroeiing in een

landschap bij Amerongen. Reeks Landschapsstudies No. 5, 1984, 117 p.

[30] Peterken G.F., Woodland conservation and management, Chapman and Hall, London, 1981, 374 p.

[31] Pinto C., Sousa J.P., Graca M.A.S., Da Gama M.M., Forest soil collembola, do tree introductions make a difference?, *Pedobiologia* 41 (1997) 131–138.

[32] Rogister J., De belangrijkste bosgemeenschappen in Vlaanderen. Werkenreeks A No. 29, Ministerie van Landbouw, Rijksstation voor Bos en Hydrologie, Groenendaal, 1985.

[33] Schreiber K.F., Grundzüge der Sukzession in 20-jährigen Grünland-Bracheversuchen in Baden-Württemberg, *Forstwissenschaftliches Zentralblatt* 116 (1997) 243–258.

[34] Skov F., Stand and neighbourhood parameters as determinants of plant species richness in a managed forest, *J. Veg. Sci.* 8 (1997) 573–578.

[35] Stimm B., Böswald K., Die Häher im Visier. Zur Ökologie und waldbaulichen Bedeutung der Samenausbreitung durch Vögel, *Forstwissenschaftliches Zentralblatt* 113 (1994) 204–223.

[36] Tack G., Van Den Bremt P., Hermy M., Bossen van Vlaanderen: een historische ecologie, uitgeverij Davidsfonds, Leuven, 1993, 320 p.

[37] Turnspan S.A., A Fortran program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes, Cornell University, New York, 1979, 58 p.