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# Impact of several common tree species of European temperate forests on soil fertility

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**Abstract** – The aim of the present work was to provide a synopsis of the scientific literature concerning the effects of different tree species on soil and to quantify the effect of common European temperate forest species on soil fertility. The scientific literature dealing with the tree species effect on soil has been reviewed. The composition of forest overstory has an impact on the chemical, physical and biological characteristics of soil. This impact was highest in the topsoil. Different tree species had significantly different effects on water balance and microclimate. The physical characteristics of soils also were modified depending on the overstory species, probably through modifications of the soil fauna. The rates of organic matter mineralization and nitrification seem to be dependent on tree species. A coniferous species, *Picea abies*, had negative input-output budgets for some nutrients, such as Ca and Mg. This species promoted a higher soil acidification and a decrease in pH. Thus, it should not be planted in very poor soils in areas affected by acidic atmospheric depositions. Nevertheless, the effect of the canopy species on soil fertility was rarely significant enough to promote forest decline. The impact of a tree species on soil fertility varied depending on the type of bedrock, climate and forest management.

**forest soils / tree species / fertility / sustainability / resiliency**

**Résumé** – **Effet des principales essences des forêts tempérées sur la fertilité des sols.** L'objectif de cet article est de fournir une synthèse bibliographique au sujet de l'effet des essences sur le sol, et, en particulier, de l'effet des principales essences utilisées en foresterie tempérée. La composition du couvert arboré a une influence importante sur les propriétés physiques, chimiques et biologiques du sol. Cet impact est le plus important dans les horizons superficiels. L'effet des essences se traduit au niveau du pédoclimat, modifiant fortement le bilan hydrique du sol. La modification des paramètres physiques est liée à l'activité biologique, elle-même dépendant de nombreux paramètres chimiques et biochimiques. La dégradation de la matière organique (minéralisation) et la nitrification semblent dépendre des essences. L'épicéa commun conduit à une acidification substantielle du sol qui se traduit parfois au niveau du pH ; les bilans d'éléments nutritifs calculés pour cette essence sont le plus souvent négatifs pour des éléments tels Ca et Mg. Cette essence ne doit pas être introduite sur des sols trop pauvres ou affectés par des apports atmosphériques acidifiants. Il faut cependant insister sur le fait que le seul effet des essences n'est jamais tel qu'il puisse conduire au dépérissement des forêts. L'impact des essences sur la fertilité du sol dépend du type de sol, du climat et des aménagements forestiers (essences et traitement).

**sols forestiers / essences forestières / fertilité des sols / durabilité / résilience**

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## 1. INTRODUCTION

### 1.1. Tree species in European forests

The development of human societies often has caused an overexploitation of forests and a decrease in their area. In Europe, the minimum of forest cover occurred during the 18th and 19th centuries [52]. Since the second half of the 19th century, policies of afforestation and increasing wood production have been imposed. One major characteristic of these policies has been the planting of large areas of productive coniferous tree species. In some cases, forests of native deciduous species have been replaced by plantations of coniferous species. The extensive use of coniferous species has modified the average composition of the western European temperate forest [52, 181]. These coniferous species were sometimes translocated within Europe (for example, Norway spruce, *Picea abies* and Scots pine, *Pinus sylvestris*). Others were imported from North America (for example, Sitka spruce, *Picea sitchensis* and Douglas fir, *Pseudotsuga menziesii*). Substitutions of tree species has given rise to considerable discussions in some western European countries. These discussions led to numerous studies on the effects of overstorey species composition on forest ecosystems. The existence of an overstorey species effect on soils has been known for a long time (Dokuchaev, in [95]) and has been observed by many authors (e.g. [2, 33, 56]). Nevertheless, the intensity of the species effect is estimated in very different or even contradictory ways, depending on the researcher. According to Stone [196] and van Goor [209], the effect of canopy species on soil fertility is minimal compared to the effects of soil management and forest management. In contrast, in studies of peatbogs [216] and artificial soils [77, 165, 200, 203] the composition of the tree cover can be one of the major factors determining the characteristics and the long term evolution of forest soils, at least for topsoil. The discrepancies among the various results concerning the effect of the tree species are partly explained by variations between soils of some of the study sites (see comments in [31]).

The aim of the present work is to review the scientific literature concerning differences in the qualitative and quantitative impact on soil fertility by the common overstorey species (often called “effect of tree species” in our study) of European temperate forests (see [31] for a review of the American tree species).

### 1.2. Soil fertility concept

Soil fertility is a rather complicated concept. It is commonly defined as the “capacity of a soil to produce a large harvest”. So, it is clear that the concept of soil fertility is linked to the physical, chemical, biological, climatic and anthropic characteristics of the site. Considering the numerous studies that have been done on the effects of different tree species, it appears that the overstorey composition probably does impact soil fertility. The crucial point is to determine if the nature and the intensity of the modifications caused by a tree species are sufficient to significantly decrease or increase soil fertility [32]. From a theoretical point of view, the impact of the overstorey species on soil fertility is not significant as long as the processes of the ecosystem which are modified do not become limiting factors for the trees or other parts of the system. That is to say that the tree species impact on soil fertility is the result of interactions between the trees and all the components of the ecosystem, and not just the effect of the trees on mineral soil [32]. Indeed, the impact of a canopy species on soil fertility could differ substantially on different bedrocks. For instance, stands growing on acidic soils which developed from crystalline rocks poor in Ca and Mg (e.g. sandstone, sand or granite rich in Si) could decline because of nutrient deficiencies [124, 146]. In such soils, planting a tree species which has a negative nutrient balance could promote a decline [70]. On the contrary, planting an acidifying tree species in shallow soils that have developed on compact limestones could increase the volume of soil exploitable by roots and thus improve soil fertility. This phenomenon has been observed with the cultivation of *Pinus nigra* (Bonneau, unpublished data). As the relationship between soil fertility and tree species is not unequivocal, our aim is to provide advice rather than general rules for forest management.

## 2. METHOD OF REVIEW

There are many papers dealing with the effects of different canopy species on soils. However, comparisons among tree species are very difficult because many factors should be taken into account. Most importantly, the strength of the experimental design determines the level of confidence in the study. We grouped the studies from the literature according to experiment design:

(i) studies with strong experimental designs that were carried out in stands which were replicated, of the same age, managed in the same way, and growing on the same

soil type (and thus on the same bedrock) with the same land-use history. There are few studies with this level of confidence (e.g. [8, 179]).

(ii) studies with moderately acceptable experimental designs that were carried out in stands which were growing on the same soil and bedrock with similar management and former land use. However, the stands had different ages (but were at the same stage of maturity) and were not replicated. Although we had less confidence in the design of these studies (e.g. [14, 27]), we assumed that by compiling numerous works we could detect reliable trends.

(iii) studies with weak experimental designs that were carried out in stands which were not growing on the same kind of soil. Such was the case of a study [68] which compared a spruce stand on a thick acidic soil (soil pH = 4.6; soil thickness > 1.5 m; soil moisture = 87%) with a hardwood stand on a thin neutral soil (soil pH = 6.1; soil thickness = 0.4 m; soil moisture = 47%). We did not use publications with weak experiment designs.

### 3. NUTRIENT INPUT-OUTPUT BUDGETS

The establishment of nutrient budgets is not required for non-intensively managed forests with high nutrient

stocks. However, in the case of intensively managed forests or growing on soils poor in nutrients, the sustainability of the ecosystem may depend on nutrient budgets. As the composition of the overstorey could modify the intensity of the various nutrient fluxes [70], tree species could have an impact on the input-output budget.

#### 3.1. Input fluxes and output fluxes

##### 3.1.1. Atmospheric deposition and fixation of N<sub>2</sub>

The capacity of trees to intercept atmospheric deposition depends on their height, leaf area index (LAI), foliage longevity, canopy structure, form or shape of leaves or needles, topographic position and the distance to the forest edge [19]. On similar soils, coniferous species usually are taller than hardwood stands of the same age [211], have a higher LAI [41], and often have persistent foliage. Thus, it is not surprising that coniferous species intercept more elements from the atmosphere, like sulphur and nitrogen, compared to hardwood species (*table I*). Atmospheric deposition of sulphur is 2 to 3 times higher in stands of *Picea abies* or *Pinus sylvestris* than in open areas. In stands of *Fagus sylvestris* or *Quercus petraea* the atmospheric deposition is only

**Table I.** Influence of tree species on atmospheric deposition.

References	sulphur Bulk Deposition  (kg ha <sup>-1</sup> yr <sup>-1</sup> )	Tree species						
		<i>Acer platanoides</i>	<i>Betula spp.</i>	<i>Carpinus betulus</i>	<i>Fagus sylvatica</i>	<i>Picea abies</i>	<i>Quercus spp.</i>	<i>Tilia cordata</i>
		(deposition under canopy / bulk deposition; %)						
[19]	14.0	.	.	.	+ 21	+ 114	.	.
[27]	14.6	.	+ 18	.	+ 32	+ 110	.	.
[27]	14.3	.	+ 40	.	+ 22	+ 203	.	.
[70]	9.6	.	.	.	+ 7	+ 120	.	.
[136]	7.9	.	.	.	+ 89	+ 432	.	.
[140]	13.5	.	.	+ 44	+ 65	.	+ 83	.
[140]	13.9	+ 107	.	+ 78	+ 98	.	+ 163	+ 76
[140]	15.9	.	.	+ 57	+ 80	.	+ 103	.
[167]	10.7	.	.	.	.	+ 120	+ 46	.
[205]	7.9	.	.	.	+120	+ 208	.	.
Mean	.	.	.	+ 60	+ 59	+ 187	+ 99	.
Standard Error	.	.	.	10	13	44	24	.
<i>n</i>	10	1	2	3	9	7	4	1

twice as high, at most, than in open areas (see [179] for a detailed review of *Picea abies*-*Fagus sylvatica* comparisons).

Fixation of atmospheric nitrogen is often very low (less than 5 kg ha<sup>-1</sup> yr<sup>-1</sup>) in forests where there is no symbiosis between trees and nitrogen-fixing microorganisms [193]. Some authors estimated that this flux can be more intense and may represent up to a few tens of kg ha<sup>-1</sup> yr<sup>-1</sup> in the presence of certain tree species (e.g. *Alnus* or *Robinia*) which have symbiotic relationships with nitrogen-fixing microorganisms (in [31]). However, N-fixation is not a major issue in Europe where neither *Alnus* nor *Robinia* play economic roles in forestry.

### 3.1.2. Nutrient input by soil mineral weathering

Very few studies have compared the effect of overstorey on mineral weathering. Indeed, the weathering flux is very difficult to estimate in situ [107]. The methods used

are indirect and based on hypotheses which are difficult to verify. Although imperfect, these studies showed that some tree species, like *Picea abies*, promote weathering of soil minerals. The weathering rate under *Picea abies* was 2 to 3 times higher than under hardwood species like *Fagus sylvatica*, *Quercus petraea* or *Betula* spp. (table II). These results are consistent with studies carried out in the laboratory [113] and in situ [13] which showed that the mineral weathering rate was higher under *Picea abies* and *Pinus sylvestris* compared to *Fagus sylvatica* and *Quercus petraea*.

According to Drever [61] and Raulund-Rasmussen et al. [172], the major factors controlling the weathering rate of soil minerals are soil pH and DOC soil concentration. Some studies carried out in situ showed that soil solutions under *Picea abies* were more acidic and contained between 2 and 3 times more DOC or low molecular-weight complexing organic acids than soil solutions under *Fagus sylvatica*, *Quercus petraea* or *Quercus*

**Table II.** Impact of tree species on in situ weathering rates.

**Table II.a** – Input-output balance method.

Reference	Depth (cm)	Localization	Bedrock	Soil	Tree species	Age (yrs)	K Na Ca Mg			
							(kg ha <sup>-1</sup> yr <sup>-1</sup> )			
[111]	watershed	Mont Lozère (France)	granite	cambic	<i>Picea abies</i>	.	6.5	5.1	11.2	5.5
				podzol	<i>Fagus sylvatica</i>	.	3.6	3.8	2.7	2.4
[27]	(0–50)	Munkarp (Sweden)	sandy moraine	haplic	<i>Picea abies</i>	48	18.3	17.3	13.5	7.0
				podzol	<i>Fagus sylvatica</i>	100	7.5	13.2	2.4	2.2
					<i>Betula</i> spp.	30	5.1	3.9	9.9	2.1
[27]	(0–50)	Nythem (Sweden)	sandy moraine	haplic	<i>Picea abies</i>	55	22.9	64.1	10.6	9.1
				podzol	<i>Fagus sylvatica</i>	90	6.6	15.3	3.9	1.9
					<i>Betula</i> spp.	40	1.8	6.8	3.0	1.1
[70]	(0–120)	Vosges (France)	granite	distric	<i>Picea abies</i>	85	8.7	0.5	5.1	0.9
				cambisol	<i>Fagus sylvatica</i>	140	3.7	1.4	1.6	0.4

**Table II.b** – Isoquartz balance method.

Reference	Depth (cm)	Localization	Bedrock	Soil	Tree species	Age (yrs)	K <sub>2</sub> O Na <sub>2</sub> O CaO MgO			
							(losses compared to bedrock; %)			
[190]	(0–20)	Ardennes (Belgium)	sandstone & shales	distric	<i>Picea abies</i>	88	-27.5	-25.8	+6.8	-60.3
				cambisol	<i>Fagus sylvatica</i>	+100	-16.4	-5.1	+14.6	-35.6
[143]	(0–85)	Ardennes (France)	loess	distric	<i>Picea abies</i>	60	-39.0	-9.7	+26.3	-31.9
				cambisol	<i>Quercus petraea</i>	140	-39.5	-9.5	+108.7	-20.0

*robur* [14, 172, 197]. As the DOC concentration in soil solutions under *Pseudotsuga menziesii* is intermediate compared to *Picea abies* and *Fagus sylvatica* [14], this suggests the weathering rate under Douglas-fir is also intermediate.

Tree species modify the pH and the composition of the complexing organic acids of soil solutions, which then influence the soil mineral weathering rate. The effect of trees on soil mineral weathering is almost exclusively located in the topsoil [13] or near the roots [55].

### 3.1.3. Nutrient outputs via water seepage

Some studies compared, in situ and over several years, the impact of different overstorey species on nutrient losses via water seepage. These studies showed that *Picea abies* stands loose between 2 and 4 times more nutrients than *Fagus sylvatica* stands (table III; see [179] for a more detailed review on *Picea abies*-*Fagus sylvatica* comparisons). As for the other fluxes, the difference between these tree species varied according to the sites and the nutrients. The greater nutrient output from *Picea abies* stands could result from greater atmospheric deposition, particularly of mobile anions such as nitrate and sulfate. However, leaching of nutrients under *Picea abies* in unpolluted areas is still slightly higher than under *Fagus sylvatica* [179].

### 3.1.4. Nutrient outputs via biomass removal

By harvesting forest biomass, significant amounts of nutrients are exported from the ecosystem (e.g. [74, 93]). This flux is dependent on the species of trees harvested. The nutrient contents in aerial biomass are usually higher for hardwood species than for coniferous species [12, 51, 60, 74, 160, 218]. There are also differences within classes of tree species, for example differences exist among coniferous species [12, 66].

However, the composition of the tree layer is not the major factor influencing the nutrient loss by biomass removal. Management systems strongly influence nutrient removals through harvesting, especially: stand age at harvest is especially important: the older the stand, the lower the average nutrient content [108, 168]. Selectivity of harvest is another factor because branches and foliage are much more concentrated in nutrients than trunks, particularly if trunks are debarked [169]. This is why whole-tree harvesting causes a much higher nutrient loss (e.g. [74, 76]) and soil acidification [147] than bole harvesting.

Ultimately, it is not possible to rank tree species in the order of their impacts on nutrient losses via biomass removal. For the same biomass, hardwood species have higher nutrient contents than coniferous species. But coniferous species produce more biomass [211] and their

**Table III.** Impact of tree species on deep seepage element losses.

Reference (location)	Seepage depth	Tree species	Element losses (kg ha <sup>-1</sup> yr <sup>-1</sup> )					
			K	Na	Ca	Mg	N	S
[111] (Lozère, France)	watershed	<i>Picea abies</i>	3.8	15.5	17.0	6.6	0.7	15.5
	streamflow	<i>Fagus sylvatica</i>	2.7	13.4	9.3	3.6	0.2	10.9
[27] (South Sweden)	50 cm	<i>Picea abies</i>	5.4	48.4	11.0	6.6	12.0	41.1
		<i>Fagus sylvatica</i>	2.0	36.5	2.6	2.8	1.2	24.0
		<i>Betula</i> spp.	2.1	21.2	10.3	2.8	8.9	18.3
[27] (South Sweden)	50 cm	<i>Picea abies</i>	5.6	102.0	9.1	9.8	10.1	63.2
		<i>Fagus sylvatica</i>	4.4	33.4	3.7	3.4	2.7	19.1
		<i>Betula</i> spp.	2.1	30.6	5.7	2.9	3.4	16.7
[70] (Vosges, France)	120 cm	<i>Picea abies</i>	11.0	8.8	11.5	2.3	22.4	19.4
		<i>Fagus sylvatica</i>	3.1	7.1	2.4	0.8	2.4	13.5
[123] (Solling, Germany)	50 cm	<i>Picea abies</i>	3.7	19.5	14.1	5.8	15.0	96.6
		<i>Fagus sylvatica</i>	3.4	12.0	9.4	3.1	5.0	40.8
[144] (Ardenne, France)	60 cm	<i>Picea abies</i>	6.9	8.4	14.0	2.7	40.3	51.1
		<i>Quercus petraea</i>	3.6	14.3	11.8	3.6	13.6	64.0

rotation lengths are lower than hardwood species. Matzner and Ulrich [122] estimated that the amount of protons released in the soil, following the uptake of cations by the trees, was higher under *Picea abies* (4.3 kg ha<sup>-1</sup> yr<sup>-1</sup>) than under *Fagus sylvatica* (1.3 kg ha<sup>-1</sup> yr<sup>-1</sup>). Finally, only a study which takes into account the stand, the soil and the management can determine the effect of a biomass removal on soil fertility.

### 3.1.5. Nutrient balance

It is quite difficult to establish the input-output budget of nutrients for an ecosystem [170]. The main difficulty is in estimating precisely and independently each flux. Very few studies have compared the effect of canopy species in this scope. All the same, it seems that hardwood stands (*Fagus sylvatica*; *Quercus petraea*; *Betula pendula*) have a balance close to equilibrium, whereas *Picea abies* stands in the same location have a significantly negative balance [27, 70, 144].

The impact of tree species on soil nutrient stock is even more difficult to demonstrate. In most studies, the effect of tree species on soil nutrient stock was either not significant or of low intensity [35, 76, 218]. The stock of exchangeable cations may increase under coniferous species, such as *Picea abies* or *Pinus sylvestris*, compared to hardwood species, such as *Fagus sylvatica* or *Quercus petraea* [36]. But the maintenance or increase of the exchangeable cation stock under some tree species, such as *Picea abies*, was partially due to a higher rate of mineral weathering which obscured a decrease in the total stock of nutrients in the soil [36]. However, it can not be concluded that such tree species would, over the long term, reduce the stock of nutrients to zero. An hypothesis is that some of the *Picea abies* stands are growing on former hardwood forest soils, and that the negative balance is the result of a change in functioning towards a new equilibrium between the soil and the overstory.

Moreover, in polluted areas, the nutrient losses of some coniferous stands are partially the result of high rates of atmospheric deposition, and would decrease as pollution is reduced in Europe.

For some nutrients, like phosphorus, it is difficult to show a constant and significant influence of overstory species on soil nutrient content because of inconsistent results [15, 171]. The effect of tree species on total nitrogen stocks in the soil is also inconsistent. Matzner [123], Miehlisch [127], Klemmedson [102] and Rothe [178] found no significant differences between broadleaves and conifers, although there were clear differences concerning the vertical distribution of nitrogen. On the other hand Kreuzer [109], Nihlgard [137] and Emberger [64] reported nitrogen stocks that were 2 to 3 t ha<sup>-1</sup> higher in broadleaved stands than in *Picea abies* stands.

We concluded that some coniferous species, like *Picea abies* or *Pinus sylvestris*, can promote losses of nutrients, especially in regions where acidic atmospheric depositions are high. Thus, they should not be planted in the soils of these regions with low nutrients stocks. *Picea abies* and *Pinus sylvestris* growing on such soils should be managed to limit nutrient losses by wood removal (see 3.1.4.).

## 3.2. Internal fluxes of the forest ecosystem

### 3.2.1. Litter and soil organic matter

In temperate forests, the annual amount of litterfall of a mature stand is only slightly influenced by the species of the overstory because the major influences are latitude, that is climate [177, 213], and stand management. The average annual litterfall is between 3.5 and 4.0 t ha<sup>-1</sup> yr<sup>-1</sup> (table IV). On the contrary, the chemical composition of foliage is dependent on tree species and site: foliage of hardwood species usually has higher concentrations of

**Table IV.** Mean annual litterfall under various tree species (mature stands).

Litterfall (t ha <sup>-1</sup> yr <sup>-1</sup> )	Tree species							
	<i>Betula</i> spp.	<i>Carpinus</i> <i>betulus</i>	<i>Fagus</i> <i>sylvatica</i>	<i>Picea</i> <i>abies</i>	<i>Pinus</i> <i>sylvestris</i>	<i>Pseudotsuga</i> <i>menziesii</i>	<i>Quercus</i> <i>petraea</i>	<i>Quercus</i> <i>robur</i>
Mean	2.2	2.9	3.5	3.8	3.9	3.4	3.7	3.8
Std Error	0.3	0.1	0.1	0.2	0.4	0.2	0.5	0.2
<i>n</i>	3	11	43	44	20	23	6	15

Data from: [6; 1 stand]; [16; 3 stands]; [30; 1 stand]; [31; 2 stands]; [In 47; 57 stands]; [Dambrine, com. pers.; 2 stands]; [76; 1 stand]; [In 99; 61 stands]; [121; 1 stand]; [132; 2 stands]; [138; 2 stands]; [In 139; 12 stands], [141; 9 stands]; [144; 2 stands]; [Nys, com. pers.; 1 stand]; [155; 2 stands]; [177; 6 stands].

N, K, Ca and Mg than coniferous species [28, 37, 219]. Thus, litterfall of hardwoods can be richer in nutrients than coniferous species. This effect was described by Ebermayer as early as the 19th century [63]. Nutrient input via litterfall was 12% higher for N, 200% higher for Ca and 400% for K in *Fagus sylvatica* stands compared to *Pinus sylvestris* stands. These findings are confirmed by more recent investigations [44, 167, 178]. Nutrient input via litterfall was 10 to 50% higher for N and P and 100 to 400% higher for Ca, Mg and K in broadleaves than in conifers.

The mass of the forest floor is influenced by the overstory species. For instance, the litter weight under *Picea abies* could be up to twice that of hardwood species like *Fagus sylvatica* (table V). Indeed, the decomposition rate of litter depends on characteristics which are tree species dependent, such as hardness, morphology, lignin/N ratio, foliage longevity or the content of hydrosoluble components, [1, 20, 21, 25, 76, 82, 186].

By accepting the hypothesis that the lignin/N and C/N ratios are correlated, it appeared that litters with a low decomposition rate (table VI) have a higher C/N ratio than litters with a high rate of decomposition (table VI). So, the composition of the tree layer is a significant factor in the litter decomposition rate [133], but decomposition is strongly controlled by environmental factors [20, 21, 126].

The soil carbon content and the soil organic weight are dependent on the canopy species. Raulund-Rasmussen and Vejre [171], Belkacem et al. [22] and Gärdenäs [72] showed that *Picea* and *Pinus* stands have higher stocks of

carbon than hardwoods. *Abies* and *Pseudotsuga* seemed to be intermediate.

### 3.2.2. Mineralization and nitrification

Numerous studies have provided evidence that canopy composition has an impact on nitrogen mineralization [30, 53, 54, 76, 192, 194]. Jussy [96] measured a net flux of nitrogen that was 50% greater under a *Fagus sylvatica* stand than under a *Picea abies* stand. The differences among tree species are partially because of the litter characteristics, particularly the lignin/N ratio as shown by Gower and Son [76] and Scott and Binkley [186]. According to others [137, 214], there was no difference among tree species.

It should be noted that mineralization of organic matter is a source of acidity. Matzner and Ulrich [122] estimated that the acidity resulting from incomplete mineralization was 1.0 kg ha<sup>-1</sup> yr<sup>-1</sup> of protons under *Picea abies* but 0.1 kg ha<sup>-1</sup> yr<sup>-1</sup> under *Fagus sylvatica*.

Nitrification is also a flux which is influenced by tree species [53, 54, 96, 192, 194, 214]. Jussy [96] measured a net nitrification flux that was 68% greater under a *Fagus sylvatica* stand than under a *Picea abies* stand. It seems that the effect of particular tree species on nitrification is partially due to the production of components that are inhibitory to microflora. According to Howard and Howard [92] and Wedraogo et al. [215], the inhibitory capacity of litter is highest for *Picea abies* and lowest for hardwoods and some coniferous species like *Abies alba* or *Pseudotsuga menziesii*. However, if the overstory

**Table V.** Litter weight under various tree species (t ha<sup>-1</sup>).

Reference	Tree species							
	<i>Abies alba</i>	<i>Betula</i> spp.	<i>Fagus sylvatica</i>	<i>Picea abies</i>	<i>Pinus sylvestris</i>	<i>Pseudotsuga menziesii</i>	<i>Quercus petraea</i>	<i>Quercus robur</i>
[8]	.	11.0	.	17.0	19.0	.	.	.
[66]	44.6	.	.	47.2	.	.	.	.
[in: 31]	.	.	.	25.7	45.1	.	36.7	.
[137]	.	.	5.2	18.5	.	.	.	.
[144]	.	.	.	37.3	.	.	17.3	.
[145]	.	.	26.8	54.2	.	57.0	.	14.0
[149]	.	.	.	17.4	.	10.9	6.0	.
[149]	.	.	10.7	25.5	12.7	8.3	5.0	3.7
[204]	.	.	29.7	49.0	.	.	.	.

**Table VI.** C/N ratio of litter under various tree species.

Reference	Tree species							
	<i>Abies alba</i>	<i>Betula</i> spp.	<i>Fagus sylvatica</i>	<i>Picea abies</i>	<i>Pinus sylvestris</i>	<i>Pseudotsuga menziesii</i>	<i>Quercus petraea</i>	<i>Quercus robur</i>
[8]	.	31	.	27	29	.	.	.
[20]	24	.	21	.	.	.	.	.
[20]	.	.	21	.	27	.	.	.
[20]	.	.	18	21	.	.	.	.
[20]	.	.	.	18	.	.	15	.
[75]	.	.	28	36	33	25	.	.
[137]	.	.	14	20	.	.	.	.
[144]	.	.	.	22	.	.	19	.
[145]	.	.	14	22	.	15	.	13
[149]	.	.	.	46	.	48	19	.
[149]	.	.	22	41	.	.	22	19
[204]	.	.	18	24	.	.	.	.

species have an impact on the nitrification rate, the main factors influencing this rate are the climate (temperature and moisture) or the former land-use [96]. Nitrification can cause soil acidification when nitrates are leached and not taken up [175]. So, tree species which could promote nutrient losses through deep seepage, for example *Picea abies*, may acidify.

We conclude that some coniferous tree species have foliage which is not easily decomposed. In soils with low nutrient stocks, stands should be thinned to increase the transmittance of light, and subsequently the decomposing activity of the microflora and ultimately the turnover of nutrients.

It should be noted that all the studies mentioned deal with net mineralization (and net nitrification), in other words, fluxes calculated without taking into account the microbial immobilization of nitrogen. As the flux of microbial immobilization is quite high in forest soils, net mineralization (and nitrification) are not significantly correlated to gross mineralization [83]. This important point implies that all the hypotheses made regarding the effects of different tree species on nitrogen dynamics should be verified by taking into account the microbial immobilization of  $\text{NO}_3^-$  and  $\text{NH}_4^+$ .

#### 4. SOIL ACIDIFICATION

The addition of acidic components to soils can decrease their buffering capacity (acid neutralising capacity, ANC) and/or their pH. The effect of overstorey species on soil ANC has not been widely studied, but it is established that the impact on soil pH is significant [148]. A canopy species can decrease soil pH through four basic processes [31]:

(i) species may increase the quantity of anions in soil solutions;

(ii) species may increase the quantity of acids reaching the soil. These acids originate from atmospheric deposition or biomass [122];

(iii) species may increase the degree of protonation of the stabilised soil acids. This increase could be at the origin of a lower earth-alkaline cations saturation index. For example, it has been observed that the soil saturation index under *Picea abies* was significantly lower than under *Fagus sylvatica* and *Quercus petraea* [15].

(iv) species may increase the strength of soil acids (lower pK; [197]).

#### 4.1. Modification of soil pH

The effect of different tree species on soil pH is most significant in the first ten centimetres of the topsoil [15, 30, 141]. The pH difference between two tree species could be as much as 1 pH unit in the topsoil. Nevertheless, the mean pH difference in soil was between 0.2 and 0.4 pH unit (table VII). The topsoil pH under *Picea abies* and *Pinus sylvestris* was significantly lower than under *Fagus sylvatica*, *Quercus petraea* or *Quercus robur*. *Abies alba* and *Pseudotsuga menziesii* appeared to be intermediate. Norden [141] showed that *Acer platanoides*, *Carpinus betulus* and *Tilia cordata* had a lower acidifying impact than *Fagus sylvatica* or *Quercus robur*.

The strong acidifying impact of *Picea abies* probably has several origins: (i) the higher capacity of *Picea abies* to intercept atmospheric deposition which is potentially acidic (table I); (ii) the acidity of *Picea abies* and *Pinus sylvestris* litters [8, 21, 142, 148]; (iii) the amounts of proton which are released after the uptake of cations by trees [122]; (iv) the higher amounts of acids, and their lower pK, released under *Picea abies* [197]; (v) the modification of the soil microclimate (to be discussed later); and (vi) the removal of biomass (in harvested forests).

Long-term soil monitoring has shown that the species of the overstorey could promote the acidification of soil by atmospheric deposition [5, 81]. Furthermore, there seem to be cyclic trends following the life cycles of stands [130]. Surface accumulation and acidity increase as stands grow. With canopy closure, microclimate becomes less favourable for organic matter decomposition.

#### 4.2. Modification of soil solution pH

The acidification of the ecosystem by some tree species could be significant with respect to the pH of soil solutions. Soil solution pH was lower under *Picea abies* compared to *Fagus sylvatica* and *Quercus* spp. (−0.33 pH unit;  $n = 10$ ; data from: [14, 42, 58, 96, 105, 144, 197]). This acidity may, in some cases, cause the acidification of surface waters (e.g. [7, 90]).

As modifications of the pH of soil and soil solutions could have an impact on the biogeochemical processes of forest ecosystems (e.g. mineral weathering of soil and faunal composition) or surface waters (discussed later), we conclude that watersheds with low acid neutralising capacity should not be planted entirely with coniferous species, like *Picea abies* or *Pinus sylvestris*, to prevent the soils and the surface waters from being acidified.

**Table VII.** Mean tree species impact on topsoil pH (water).

Tree species comparisons			pH Difference	
first tree species		second tree species		Mean Difference ( $n$ )
<i>Picea abies</i>	-	<i>Fagus sylvatica</i>	−0.35 ( $n = 27$ )	***
<i>Picea abies</i>	-	<i>Quercus</i> spp.*	−0.34 ( $n = 18$ )	**
<i>Pinus sylvestris</i>	-	<i>Fagus sylvatica</i>	−0.27 ( $n = 5$ )	*
<i>Pinus sylvestris</i>	-	<i>Quercus</i> spp.*	−0.27 ( $n = 11$ )	***
<i>Abies alba</i>	-	<i>Fagus sylvatica</i>	−0.24 ( $n = 5$ )	*
<i>Picea abies</i>	-	<i>Betula</i> spp.	−0.43 ( $n = 3$ )	n.s. ( $P = 0.07$ )
<i>Picea abies</i>	-	<i>Abies alba</i>	−0.19 ( $n = 6$ )	n.s. ( $P = 0.15$ )
<i>Pseudotsuga menziesii</i>	-	<i>Fagus sylvatica</i>	−0.22 ( $n = 8$ )	n.s. ( $P = 0.16$ )
<i>Pseudotsuga menziesii</i>	-	<i>Quercus</i> spp.*	−0.21 ( $n = 9$ )	n.s. ( $P = 0.15$ )
<i>Fagus sylvatica</i>	-	<i>Quercus</i> spp.*	−0.11 ( $n = 6$ )	n.s. ( $P = 0.34$ )
<i>Picea abies</i>	-	<i>Pinus sylvestris</i>	−0.03 ( $n = 10$ )	n.s. ( $P = 0.69$ )

\* = significant difference ( $P < 0.05$ ); n.s. = non significant difference ( $P \geq 0.05$ ).

Data from: [8; 3 stands]; [15; 80 stands]; [26; 4 stands]; [27; 6 stands]; [58; 4 stands]; [86; 2 stands]; [96; 2 stands]; [105; 2 stands]; [137; 2 stands]; [148; 12 stands]; [151; 16 stands]; [166; 2 stands]; [167; 2 stands]; [171; 8 stands]; [189; 3 stands].

\* *Quercus* spp. refers here to *Quercus petraea* or *Quercus robur*.

## 5. WATER FLUXES AND MICROCLIMATE

### 5.1. Water fluxes

#### 5.1.1. Interception of bulk precipitation

Interception rates of different tree species have been studied intensively, however most data are applicable to *Picea abies* and *Fagus sylvatica*. (see reviews: [131, 154, 158, 221]). Interception rates of conifers are usually higher than to hardwoods. The differences are most pronounced during the dormant season, when interception rates are low in hardwood stands. During the vegetative period, interception rates are also often higher in conifer stands because of higher leaf area indices [41]. Another important factor is stemflow, which is usually < 3% of throughfall precipitation for tree species with a rough bark (that is nearly all conifers, but also some hardwood species like oak), but can be 10 to 15% of throughfall precipitation for hardwood species with a smooth bark like *Fagus sylvatica*. Average yearly interception rates are around 25% for hardwood species and around 35% for coniferous species (table VIII). The differences between individual hardwood and softwood species are less pronounced and other factors may dominate the effect of the overstory species. Repeatedly it has been documented that interception rates are positively correlated with stand density [41, 131]. Another important factor is the vertical structure of the stand. Multilayered canopies tend to intercept more water than single-layered canopies [85]. Species effects are also strongly influenced by climatic factors. In some mountain or coastal areas with a lot of mist, negative interception rates occur in conifer stands (i.e. throughfall precipitation is higher than bulk precipitation) and throughfall precipitation is higher in conifer stands than in hardwood stands [84].

#### 5.1.2. Transpiration

While interception rates can be measured easily, the determination of transpiration rates on a stand level is highly complex and linked with significant uncertainties. Relatively few studies have compared the transpiration rates of different species growing next to each other (e.g. [17, 18, 24, 40, 50, 136]). Differences among species concerning average transpiration rates tend to be small [131]. The wide range of transpiration rates for individual species (see [158]) indicates, that effects of climate and stand structure are more pronounced than effects of different tree species. The effects of conifers and hardwoods seem to be more important with respect to temporal patterns than for total water consumption. Evergreen conifer species may start transpiration as early as late winter and, depending on the climatic situation, significant transpiration rates may occur before deciduous trees begin to flush [131, 178]. During the vegetation period, species effects depend on climatic and site factors. In situations with low water supply, stomatal conductance limits transpiration and the differences among species tend to be small [119, 176], or transpiration rates of hardwoods may be slightly lower than those of some conifer species [79]. In a situation with unlimited soil water supply and high transpirational demand of the atmosphere, maximum transpiration rates were significantly higher for *Fagus sylvatica* than for *Picea abies* [114, 178]. In this case transpiration is limited by the conductance of the roots and the matrix potential in the soil. This limitation is less severe in *Fagus sylvatica* stands because of higher fine root surface [138, 220]. These patterns may explain why transpiration rates of *Picea abies* stands were higher [24], identical [136] or lower [178, 201] than those of *Fagus sylvatica* stands. The ratio between *Picea abies* and *Fagus sylvatica* may vary even within individual years [65, 178]. In years with hot summers and

**Table VIII.** Bulk precipitation interception by tree species (%).

Reference	Tree species								
	<i>Abies alba</i>	<i>Betula</i> spp.	<i>Carpinus betulus</i>	<i>Fagus sylvatica</i>	<i>Picea abies</i>	<i>Pinus sylvestris</i>	<i>Pseudotsuga menziesii</i>	<i>Quercus petraea</i>	<i>Quercus robur</i>
Mean	36	17	27	22	35	40	41	23	24
Standard Error	2	4	2	1	2	5	5	3	2
<i>n</i>	2	4	3	30	25	7	4	4	5

Data from: [3; 2 stands]; [4; 2 stands]; [17; 4 stands]; [18; 2 stands]; [27; 6 stands]; [29; 6 stands]; [in: 31; 3 stands]; [Dambrine, pers. com.; 2 stands]; [71; 4 stands]; [in: 71; 2 stands]; [115; 2 stands]; [123; 2 stands]; [136; 2 stands]; [in: 139; 19 stands]; [140; 9 stands]; [178; 2 stands]; [179; 2 stands]; [188; 2 stands]; [189; 3 stands]; [206; 6 stands]; [217; 2 stands].

sufficient precipitation, yearly transpiration rates were higher for *Fagus sylvatica* than for *Picea abies*; in years with high temperatures in March and April and a cool summer, rates were lower for *Fagus sylvatica*. However, over a longer time span, transpiration rates of both species usually are of the same magnitude and differences among tree species concerning total evapotranspiration are clearly dominated by the interception of bulk precipitation.

### 5.1.3. Deep-seepage water yield and soil moisture

Deep seepage is usually higher for hardwoods (e.g. *Fagus sylvatica*) than for conifers because of the higher interception loss in conifer stands (e.g. *Picea abies*: mean, +25%; *n*, 11 pairs of stands; [179]). The proportion of bulk precipitation which leaves the rooting zone is 10% to 15% higher in *Fagus sylvatica* stands than in *Picea abies* stands. However, the quantitative effects depend strongly on climatic and site factors. In areas with low precipitation rates and less permeable soils, water yield was similar for both species [185 in: 131]. In special climatic situations, *Picea abies* may yield even more seepage than *Fagus sylvatica* [84].

Higher throughfall rates in hardwood stands influence soil moisture. Several authors reported higher topsoil moisture contents under hardwoods compared to conifers [14, 23, in: 31, 96, 137]. Similarly, Lévy [112] reported shorter periods of soil waterlogging under *Picea abies* and *Pinus sylvestris* compared to *Quercus* spp. and *Fagus sylvatica*. However, this scenario may be modified by site and climatic factors. Throughfall differences among species are most pronounced in the dormant season. In areas with sufficient precipitation, soil moisture in conifer stands is high (above field capacity) during winter time, and additional input of rain effects seepage rates rather than soil moisture. In such a situation, soil moisture during winter time is similar in conifer and hardwood stands [178, 185]. Soil moisture is generally lower in conifer stands in early spring, since transpiration in conifers starts before the leaves of deciduous trees flush. During summertime, soil moisture may be even lower in hardwood stands because of higher transpiration rates during periods with high transpirational demands [114, 131]. Another important consideration is the morphology of the fine root system. The deeper rooted species *Fagus sylvatica* takes up more water from the subsoil, leading to a lower soil moisture compared to the shallow rooted species *Picea abies*.

## 5.2. Microclimate

### 5.2.1. Light transmittance

The influence of different tree species on light transmittance has been widely observed (e.g. [56, 162]) or measured [46]. Indeed, light transmittance is negatively correlated with canopy cover and to LAI [34, 46] which are also tree species dependent [34, 41, 46, 103]. Considering North American tree species, light transmittance is lower under coniferous species than under hardwood species [34, 46]. Among European tree species, *Abies alba*, *Picea abies*, and sometimes *Fagus sylvatica*, transmit low levels of light [94, 100, 137]. However, silvicultural management, particularly the initial stand density and the thinning intensity, can greatly modify light transmittance [57].

### 5.2.2. Air temperature and moisture

Lower light transmittance appears to lower temperature slightly under *Picea abies* compared to other tree species such as *Fagus sylvatica* [135] and *Pinus sylvestris* [17]. Pasak [157] reported a decrease in the thermic amplitude under *Picea abies* compared to a mixed stand of *Quercus* spp. and *Pinus sylvestris*. On the contrary, Vanseren [212] did not observe any temperature difference between *Picea abies* and *Fagus sylvatica*.

Nihlgard [135] measured air moisture in a *Picea abies* stand and a *Fagus sylvatica* stand, and found more humidity in the *Picea abies* stand.

We conclude that species of the trees in the overstory has significant effects on water fluxes and microclimate. However, these effects are highly dependant on other factors, like forest management, climate and soil characteristics.

## 6. FOREST COMMUNITIES AND PHYSICAL FEATURES OF SOIL

### 6.1. Modification of forest communities

#### 6.1.1. Understory

According to several studies [62, 101, 103, 104, 150], the composition and the amount of cover in the understory are dependent on the species of trees present in the overstory. The different tree species may influence the understory differently by modifying the transmittance

of the light [150], the microclimate, the characteristics of the forest floor [162, 198, 199] and the soil, or by releasing toxic compounds [159]. However, there is no consensus about the effects of different tree species on understory species richness and floral diversity [9, 15, 45, 67, 89, 101, 116, 161]. Even so, it seems that some coniferous species with dense canopies (e.g. *Picea abies*, *Abies alba* or *Pseudotsuga menziesii*) probably reduce the cover of ground vegetation, especially for spring flora [150, 162]. Moreover, moss cover is higher and herb cover is lower under *Picea abies* compared to hardwood species [15, 87, 129, 182, 187].

Factors such as silvicultural management [43], human and former land-use [106, 161], and atmospheric deposition [69] could impact the understory which more seriously than the overstory species. According to Hill [88], the ground vegetation under coniferous species such as *Picea abies* is not significantly different from that of the understory of a hardwood stand if the coniferous stand has been heavily thinned.

### 6.1.2. Soil microflora

Soil bacteria play an important role in soil processes. For instance, bacteria can decrease mineral alteration by decomposing weathering organic components [117], or they can increase it by producing organic acids [38, 113].

Soil microflora seems to be strongly influenced by the species of the overstory [20]. Mardulyn et al. [120] observed that the biomass and the activity of the soil microflora under *Fagus sylvatica* were higher than under *Picea abies*. However, the complexity of the interaction between different tree species and microflora *sensu lato* is too high for generalisations [159]. Even if most tree species produce compounds inhibitory to the soil bacteria [20, 139], there is no strong evidence that this process is the only one involved in the relationship between tree species and soil microflora.

Mycorrhizas also play an important role in soil processes, like mineral weathering by producing complexing organic acids [113, 153, 208]. Tyler [202] showed that numerous fungi which are symbiotic with trees are present only in soils under particular tree species.

### 6.1.3. Soil fauna

Different tree species influence the composition and the abundance of soil fauna differently, particularly the litter fauna [59, 139, 163]. Under *Pinus sylvestris*, *Pseudotsuga menziesii* or *Picea abies*, earthworm

density is lower than under hardwood species or *Abies alba* [31, 139]. Saetre [183] also observed this same effect in a comparison of *Picea abies* and *Betula pendula*.

When litter from one tree species is placed under a stand composed of another species but growing on the same soil, the litter may decompose more slowly [125]. This observation suggests that the decomposition rate of litter from a particular tree species depends on the presence of particular soil fauna and microflora.

## 6.2. Modification of physical features

The composition of the overstory has an impact on soil structure [173]. In an artificial soil, Graham et al. [77, 78] have shown that the soil structure and its stability were tree species dependent, probably because of differential effects on worm activity.

In Europe, Grieve [80] and Nys et al. [145] estimated that the structural stability of soil was lower under *Picea abies* compared to *Quercus* spp. and *Fagus sylvatica*. Challinor [48] and Nihlgard [137] have measured lower water infiltration rates in soils under *Picea abies* compared to other tree species. This finding could be linked to the lower porosity under *Picea abies* observed by Nys et al. [145]. However, the long term effects of *Picea abies* on soil structure and porosity are still unclear and site factors seem to play an important role. Much work on this topic has been done in Germany because of concerns that long-term cultivation of *Picea abies* may have negative impacts on the physical properties of soil (see overview [174]). On loamy glacial soils there was no evidence that long-term mono-cultivation of *Picea abies* decreased the porosity of the soil. In some cases, pore volume in the uppermost mineral soil was actually higher in *Picea abies* stands than in broadleaf stands (this was attributed to root movement of shallow-rooting *Picea abies* during windy periods).

We conclude that the effect on forest communities having different tree species in the canopy is significant. Although there is no strong evidence of a decrease in floral diversity under coniferous species, it appears that other communities like soil microflora or microfauna changed under some coniferous species such as *Picea abies*. However, no clear effect of this tree species via effects on worm activity has been demonstrated.

## 7. CONSEQUENCES ON SOIL FERTILITY

### 7.1. Localisation and intensity of soil modifications

On the time scale of a few decades, the impact of the species of the overstorey on soil characteristics is often significant only in the forest floor and the ten first centimetres of topsoil [15, 30, 49], or near the roots [10, 113, 191]. The intensity of this impact is positively correlated with the stand density [180].

The effect of the overstorey species could also extend to ecosystems larger than the forest stand, notably in surface waters. It has been established that the cultivation of some coniferous tree species on soils with low ANC could acidify and increase the toxic  $Al^{3+}$  content of surface waters [7, 91, 156]. This phenomenon could extirpate trout populations [164].

### 7.2. Groups of tree species according to their impact

Our understanding of the effects of tree species on soils remains very incomplete, but the available information allows us to suggest some rankings of species with respect to their potential effects on soil fertility. Foresters and scientists may not uniformly agree these rankings, but we hope that in coming decades, the ranks can be tested more thoroughly and revised as necessary.

#### 7.2.1. Acidity

Based on current knowledge, we would rank these tree species in the order of decreasing acidifying ability, as follows: (*Picea abies*; *Picea sitchensis*; *Pinus sylvestris*)  $\geq$  (*Abies alba*; *Pseudotsuga menziesii*)  $\geq$  (*Betula pendula*; *Fagus sylvatica*; *Quercus petraea*; *Quercus robur*)  $\geq$  (*Acer platanoides*; *Carpinus betulus*; *Fraxinus excelsior*; *Tilia cordata*).

According to Vanmechelen et al. [210], 65% of European forest topsoils are acidic ( $pH_{CaCl_2} \leq 4.5$ ) and more than 30% of soils are desaturated ( $BS \leq 15\%$ ). As highly acidic conditions could be an important problem for forest growth, we recommend that tree species with high acidifying impact, like *Picea abies*, not be planted on soils with a very low buffering capacity, especially if the area receives a high amount of acidic atmospheric deposition. We would also discourage the planting of

acidifying species on the entire surface area of watersheds with low buffering capacity. The acidifying impact of a tree species can be reduced by managing it in mixed stands at low densities and by exporting low amounts of nutrients during wood harvests.

Alternatively, the ability of some coniferous species to acidify and weather soil minerals could be useful, for instance in thin calcareous soils, for increasing the stock of exchangeable cations.

#### 7.2.2. Tree nutrition

The limitation of tree growth by lack of nutrients is usually the result of N, Ca, Mg or K deficiencies [110]. In central Europe, N nutrition is naturally deficient but it seems to be compensated for by atmospheric deposition; this is not the case in the rest of Europe [110]. Potassium deficiencies often occur in dense stands on calcareous soils associated with droughts [110]. Thus, the K deficiency on calcareous soils seems to be the consequence of climate and silviculture more than overstorey species. Calcium and magnesium deficiencies are also associated with droughts and dense stands but they are encountered in acidic soils developed on bedrocks very poor in these elements [110]. As Ca and Mg deficiencies can be promoted strongly by soil acidification and nutrient turnover, some coniferous species have the capacity to reduce the nutrient turnover at a site because of the quality of their litterfall and dead roots (e.g. lignin/N ratio, hardness, etc.), and because of their capacity to produce particular organic components (e.g. complexing acids, toxic inhibitory components, etc.), we would discourage cultivation of acidifying tree species or tree species which limit the nutrient turnover in very poor soils. However, the effect of overstorey species is strongly influenced by forest management (e.g. low density stands or mixed stands can promote litter decomposition).

#### 7.2.3. Water fluxes

It is quite clear that overstorey species modify water fluxes: some coniferous species have higher interception and lower deep seepage fluxes compared to hardwoods. This characteristic, and the characteristics of the area, should be taken into account by the forest manager in selecting tree species for planting.

#### 7.2.4. Forest communities and physical features of soil

Even if the effect of overstory species was significant on the composition of many communities and on some physical features of soil, it was not possible to establish a general rule. Indeed, as previously said, the effect of tree species is closely linked to forest management.

#### 7.3. Mixed stands

Mixed stands are often, but not always, intermediate compared to monospecific stands in terms of several processes. These processes are acidification [36], atmospheric deposition [180], soil fauna and microflora composition [97, 128, 163, 184], and species composition of communities in general [48, 73]. Moreover, mixed stands have better nitrogen and phosphorus nutrition [180]. However, it seems that there are no general rules about the effects of mixed stands on litter decomposition, nitrification, mineralization, soil nutrient availability or biomass increment [180]. For these variables, the effect of the species mix depends on its composition and also strongly on the site characteristics.

#### 7.4. Interactions between natural and human factors

The impact of an overstory species on soil varies significantly with factors like climate, geology and silvicultural management. Thus, the soil carbon stock, the C/N ratio and degradability of litter, mineral weathering and microflora composition depend on the species of the overstory (see previous discussion) but they also depend strongly on soil type and climate [20, 22, 36, 126]. For instance, if some tree species such as *Picea abies*, *Picea sitchensis* or *Pinus sylvestris* can promote soil podzolisation [86, 130, 134, 190], then this soil process does not occur if climate and geology are not predisposed to it [118]. In the same way, the so-called “improving” tree species can not prevent a soil from being podzolized if the environmental factors are very predisposed to it.

The form of silvicultural management is also a very important factor. Indeed, the effects of different overstory species on nutrient losses by biomass removal, or understory composition, depend strongly on the silvicultural management [88, 43, 168]. Moreover, the influence of the tree species on the ecosystem varies during the rotation of the stand [152, 195].

#### 7.5. Biological value of a site, the resiliency of the soil and the choice of tree species

Before considering the choice of a tree species for a plantation, the manager should take into account the ecological and landscape values of the site. Based on these values, it may be better to not modify an ecosystem, or group of ecosystems, which has a high biological value (e.g. rare species) or an important landscape function (e.g. protection from soil erosion). When the site does not have a high ecological or landscape value, it is important to estimate the amount of wood production that is sustainable by the ecosystem without jeopardizing its numerous other functions [98]. It is possible to broadly quantify the soil resiliency to acidification by estimating its buffering capacity [207], its total reserve of basic cations [39], or by taking into account the general characteristics of the site [11]. On sites where the soil resiliency is low and where there is no restitution of fertility (e.g. liming), tree species with a high impact on soil should not be planted in dense stands and over large areas. In soil with a high resiliency all kinds of tree species can be planted.

### 8. CONCLUSION

Overstory composition significantly influences the physical, chemical and biological characteristics of topsoil. By modifying the fluxes of matter or energy, the trees have the potential to impact the current soil fertility. To ensure the sustainable management of forests, the resiliency of the ecosystems should be estimated to determine the most appropriate tree species and silvicultural management. However, the tree species factor is strongly influenced by other factors like climate, pollution or geology. Therefore, the tree species should not be the only consideration during the planning of the forest management.

Many complementary studies are needed to better understand the effect of tree species selection on long-term fertility. One of the soil parameters which may be very interesting to investigate is the N dynamic because it is not clearly understood. These studies might be designed to limit possible biases by considering replicate stands under the same conditions and by using careful quality assurance procedures.

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