ANNEX 1: COPY OF THE PUBLICATIONS

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REVIEW

Simulating ectomycorrhizal fungi and their role in carbon and nitrogen cycling in forest ecosystems

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Abstract: Although ectomycorrhizal fungi play an important role in forest ecosystem functioning, they are usually not included in forest growth or ecosystem models. Simulation is hampered by two main issues: a lack of understanding of the ecological functioning of the ectomycorrhizal fungi and a lack of adequate basic data for parameterization and validation. Concerning these issues, much progress has been made during the past few years, but this information has not found its way into the forest and soil models. In this paper, state-of-the-art insight into ectomycorrhizal functioning and basic values are described in a manner transparent to nonspecialists and modelers, together with the existing models and model strategies. As such, this paper can be the starting point and the motivator to include ectomycorrhizal fungi into existing soil and forest ecosystem models.

Key words: ectomycorrhizae, forest ecosystem, soil, model, review, simulation.

Résumé : Même si les champignons ectomycorhiziens jouent un rôle important dans le fonctionnement des écosystèmes forestiers, ils ne sont habituellement pas inclus dans les modèles d'écosystème ou de croissance forestière. Deux problèmes principaux compliquent l'utilisation des modèles de simulation : un manque de compréhension du fonctionnement écologique des champignons ectomycorhiziens et l'absence de données de base adéquates pour le paramétrage et la validation. Beaucoup de progrès a été accompli au cours des quelques années passées au sujet de ces questions mais cette information n'a pas été intégrée dans les modèles édaphiques et forestiers. Dans cet article, les connaissances les plus récentes concernant les données de base et le fonctionnement des ectomycorhizes sont présentées de façon transparente pour les profanes et les modélisateurs. En soi, cet article pourrait servir de point de départ et de motivation pour inclure les champignons ectomycorhiziens dans les modèles édaphiques et d'écosystème forestier existants. [Traduit par la Rédaction]

Mots-clés : ectomycorhizes, écosystème forestier, sol, modèle, examen, simulation.

Introduction

Most (80%–90%) trees in temperate and boreal forest ecosystems live in symbiosis with ectomycorrhizal (EM) fungi (Read 1992). These fungi receive energy from their host plant and, in return, deliver key tree nutrients such as nitrogen (N) and phosphorus (P). As most root tips of EM host trees are covered by EM fungal tissue, these fungi form the main interface between the tree and the soil (Read et al. 2004). Therefore, EM fungal functioning has to be acknowledged in studying soil–plant interactions (for a review, see Smith and Read 2008). There is growing attention concerning the role of EM fungi in ecosystem and soil-forming processes, as illustrated in several reviews in the field of soil organic matter (SOM) dynamics (Read and Perez-Moreno 2003; Talbot et al. 2008) and soil mineral weathering (Landeweert et al. 2001; Finlay et al. 2009), but up to now, EM fungi have been widely ignored in forest soil models.

Concerning the role of arbuscular mycorrhizal (AM) fungi, intracellular fungi mainly found in grasslands and tropical rainforest, besides research articles, some excellent modeling studies have been performed (Collins Johnson et al. 2006; Schnepf and Roose 2006; Deressa and Schenk 2008). For EM fungi, extracellular symbiotic fungi found mostly in temperate and boreal forests, emphasis has been on experimental studies, but inclusion into forest and soil models has so far been rather limited. Nonetheless, some models for EM fungi growth exist (Meyer et al. 2010; Deckmyn et al. 2011; Orwin et al. 2011). In this manuscript, a review of the main data and processes that are potentially important for simulation of EM fungi in forests is given. Furthermore, a review of the existing models is supplied. Because of the very limited number of EM models, some relevant AM models are also included. The purpose of this review is to stimulate the development and improvement of existing soil models through inclusion of the most important EM mechanisms and effects. Furthermore, by listing the main data requirements for development and validation of forest soil models, we hope to stimulate experimental scientists to produce relevant and necessary data.

In the first section, the necessary information for a very basic EM model is described. In the following sections, the most useful possible extensions to a simple model are described.

1. Simple EM models

EM fungi constitute a major sink of plant-fixed carbon in EM forests. Up to now, most EM models focus on the fate of this belowground carbon (C) flow, and the linked N flow to the host plant, and do not include possible interactions with other soil processes. In this section, we describe the fundamental basics

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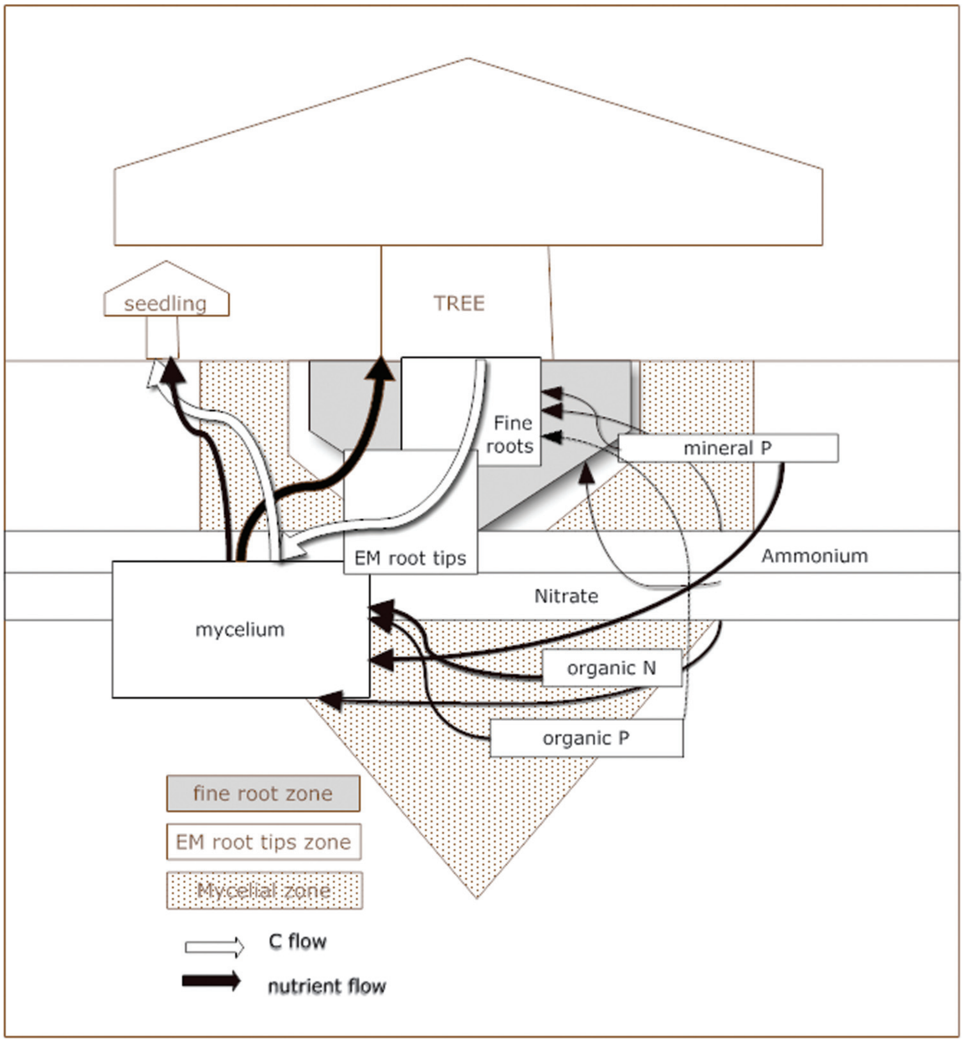
Fig. 1. Simple flow chart of C and nutrients (P and N) between soil, plant, and ectomycorrhizal (EM) fungi.



and appropriate parameter values of the role of EM biomass in the belowground C and N dynamics (see Fig. 1). An overview of existing simple models is included. Estimated parameter values can be found in Table 1.

1.1. Basic values: pool size, growth, turnover, and respiration

The first question concerns the size of the fungal biomass belonging to the mycorrhizal pool. This pool comprises fungal tissues in EM root tips and extramatrical mycelium (EMM), formed predominantly by differently organized and structured single hyphae, rhizomorphs, and sclerotia; in hypogeus fungi, fruit bodies can also be considered. Most published values concern only the EMM (see also section 1.3). Högberg and Högberg (2002) estimate (girdling experiment) that 32% of the soil microbial biomass in a Scots pine (*Pinus sylvestris* L.) forest was contributed by EMM. This contribution was calculated to be equivalent to 145 kg·ha^{-1}, corresponding to 58 kg C·ha^{-1}. It is not possible to fully differentiate between saprotrophic and EM mycelia in the field. Estimations are that around 50% of mycelia in boreal forests are from EM fungi, but this fraction is highly variable (Bååth et al. 2004). Furthermore, it is difficult to differentiate between live and dead mycelium. Wallander et al. (2004) used a specific phospholipid fatty acid (18:2ω6,9) as proxy for living fungal biomass, and its degradation in incubated soil samples was used as a measure of EM fungal biomass. Total EM biomass estimates by this method ranged from 4.8×10^3 kg·ha^{-1} (spruce) to 5.8×10^3 kg·ha^{-1} (mixed oak–spruce). Nilsson and Wallander (2003) found 120–800 kg EMM·ha^{-1} (depending on nutrient availability and season), while Hagerberg et al. (2003) reported 110 kg·ha^{-1} for EMM in the upper 5 cm. EMM has often been expressed in length units. For example, Jones et al. (1990) reported values from 20 to 50 m·g^{-1}, with reported conversion factors ranging from 1 to 3×10^5 m·g^{-1} (Wallander et al. 2004) to 8.3×10^5 m·g^{-1} (Hunt and Fogel 1983) to convert length to biomass or from 2.75 (Stahl et al. 1995) to 4.12 mg·m^{-1} to convert length to C content values (Miller et al. 1995). Interestingly, the EM fungal biomass followed a similar trend as the fine root distribution in these sites, which could be an incentive for modeling purposes (Wallander et al. 2004; Thelin et al. 2002). In fungal mats, sometimes found at the boundary between the organic soil and the mineral soil, up to 600 km·g soil^{-1} has been measured (Ingham et al. 1991).

The standing pool of EMM biomass is the product of hyphal growth and mortality. Under laboratory conditions, growth rates of the mycelial front of up to 8 mm·day^{-1} (Donnelly et al. 2004), but typically 2–4 mm·day^{-1} (Read 1992), have been reported. The growth rate of the mycelial front in forest soils is unknown, but estimates from the radial spread of fungal genets of *Suillus bovinus* (L.) Roussel (1806) averaged about 0.7 mm·day^{-1}, as estimated by Ekblad et al. (2013) from data in Dahlberg and Stenlid (1994). For soil-scale modeling purposes, it is more useful to express EM fungal growth as kilograms per hectare of soil (kg·ha^{-2}). Over the last

Table 1. Basic parameter values for ectomycorrhizal (EM) models.

Parameter	Tissue	Value	Species	Reference
C:N	Rhizomorph	20–40	FACE *Pinus taeda*	Wallander et al. 2003
	EM root tip	26.4	*Pinus sylvestris*	Trocha et al. 2010
		23.0	*Quercus robur*, seedlings	
	Fruit body	9.1–14.2	Boreal forests	Taylor et al. 1997
		11.5–11.6	*Pinus sylvestris*	Taylor et al. 2003
		10.1	*Picea abies*	Zeller et al. 2007
	EMM	4.6–60	Boreal forests	Taylor et al. 1997
		22.2	Mixed species	Fogel and Hunt 1983
		14–20	*Picea abies*	Nilsson and Wallander 2003
Turnover rate	Rhizomorph	Up to 11 months	*Pinus–Juniperus*, minirhizotrons	Treseder et al. 2005
			FACE *Picea sitchensis*	
		Several months	FACE *Pinus taeda*	Coutts and Nicoll 1990
		304 days	Mixed temperate	Pritchard et al. 2008
		400 days		Vargas and Allen 2008
	EM root tip	1–6 years	*Pinus edulis*	Treseder 2004
		1.3 years	*Picea abies*	Majdi et al. 2001
		73–137 days	FACE *Pinus taeda*	Pritchard et al. 2008
		139 days	*Pinus ponderosa* seedlings	Rygiewicz et al. 1997*b*
	Fruit body	1–2 weeks	*Pinus edulis*	Treseder et al. 2005
	EMM	A few days	Poplar forest	Staddon et al. 2003
			Conifer–oak	Smith and Read 2008
		9 days	FACE *Populus*	Godbold et al. 2006
		<1 week average	Mixed temperate	Vargas and Allen 2008
Respiration	Rhizomorph	No value found		
	EM root tip	25.4	*Pinus sylvestris*	Trocha et al. 2010
		13.5 nmol O_2·g^{-1}·s^{-1}	*Quercus robur*, seedlings	
	Fruit body, hypogeous	0.005–0.030 μmol CO_2·m^{-2}·s^{-1}	*Tuber aestivum* in mixed *Carpinus–Quercus* forest	Grebenc and Ferlan (unpublished data)
	Fruit body, epigeous	0.010–0.027 μmol CO_2·m^{-2}·s^{-1}	*Paxillus involutus* in mixed *Carpinus–Quercus* forest	
	EMM	20–150 μmol CO_2·mg^{-1}·s^{-1}	12 species, including rhizomorph *Pinus sylvestris*	Malcolm et al. 2008
		97.9–160 mg CO_2·m^{-2}·h^{-1}		Högberg and Högberg 2002
Pool size	Rhizomorph	Up to 50%	FACE *Pinus taeda*	Pritchard et al. 2008
	EM root tip	20%–40%	*Pinus sylvestris*	Wallander et al. 2001
		64 kg·ha^{-1}	*Picea abies*	Ostonen et al. 2005
		250–400 kg·ha^{-1}	*Picea abies*	Dahlberg et al. 1997
	Fruit body	<1%	*Pinus sylvestris*	Wallander et al. 2001
		6 kg·ha^{-1}·year^{-1}	*Picea abies*	Wiklund et al. 1994
		1.1–167 kg·ha^{-1}·year^{-1}	*Pinus sylvestris*	Dahlberg and Stenlid 1994
		8.8 kg·ha^{-1}·year^{-1}	*Picea abies*	Dahlberg et al. 1997
	EMM	44%	*Picea abies*	Robert B. Björk (personal communication)
		60%–80%	*Pinus sylvestris*	Wallander et al. 2001
		32% = 145 kg·ha^{-1}	*Pinus sylvestris*	Högberg and Högberg 2002
		120–800 kg·ha^{-1}	*Picea abies*	Nilsson and Wallander 2003
	Sclerotia	440 kg·ha^{-1}	*Picea abies*	Dahlberg et al. 1997
	Total	4.8 × 10^3 kg·ha^{-1}	*Picea abies*	Wallander et al. 2004
		5.8 × 10^3 kg·ha^{-1}	*Picea abies–Quercus robur*	Wallander et al. 2004
Percent infection		10%–74% (shade–sun)	*Fagus sylvatica*	Druebert et al. 2009
		26%–82%	*Populus* sp.	Baum and Makeschin 2000
		>90%	FACE *Populus* sp.	Godbold et al. 2006
		>95%	*Picea abies*	Dahlberg et al. 1997
		100%	*Picea abies*	Kraigher 1999

Note: C:N, ratio of carbon to nitrogen; FACE, free-air CO_2 enrichment; EMM, extramatrical mycelium.

decade, it has become popular to use mycelial in-growth bags to estimate the production of EMM (Wallander et al. 2001; for a recent compilation of studies using this technique, see Ekblad et al. 2013; for a review of this and other methods to estimate the production and turnover of EMM, see Wallander et al. 2013). One advantage with in-growth bags is that they are colonized mainly by mycorrhizal fungi and the contribution of saprotrophs seems to be small (Wallander et al. 2001; Kjøller 2006; Parrent and Vilgalys 2007; Hedh et al. 2008), which is an advantage compared with the traditionally used mycelium length estimates (e.g., Söderström 1979; Vogt et al. 1982; Fogel and Hunt 1983). Wallander et al. (2004) measured 590 kg·ha^{-1}·year^{-1} in spruce stands and 420 kg·ha^{-1}·year^{-1} in mixed spruce–oak stands. In a recent survey of EMM production estimates from ~140 temperate forest sites, an yearly average production of 160 kg dry mass·ha^{-1}·year^{-1} in the upper 10 cm soil (range of 20 to 980 kg·ha^{-1}·year^{-1}) was estimated (Ekblad et al. 2013). These values should probably be at least doubled for a whole soil profile, based on the very few studies that report production estimates from more than one soil depth (Rosling et al. 2003; Egerton-Warburton et al. 2003).

Turnover of mycelia has mostly been measured on arbuscular mycorrhizae (e.g., Fitter 2006; Rillig et al. 2007; Staddon et al. 2003). Only few measurements are available from EM. The turnover rate of the EMM depends on the ratio between fine mycelium and rhizomorphs (see section 1.2). The C and nutrient content of EM tissues should be known to link the dynamics of fungal tissues with belowground cycles of carbon and nutrients. The C-to-N ratio (C:N) of EM mycelium in forest soils is typically lower than of the host plant, values around 15–22 (Nilsson and Wallander 2003; Boström et al. 2007) are generally reported. Besides C and N, P is an important component: C:N of 10 (or 89.2 $mg \cdot g^{-1}$) and C-to-P ratio (C:P) of 50 (or 17.8 $mg \cdot g^{-1}$) are found in literature for AM fungi (Landis and Fraser 2007). For EM mycelia, P from 1.7 $mg \cdot g^{-1}$ under P-limited conditions up to 13 $mg \cdot g^{-1}$ was measured (Cairney and Smith 1992), equivalent to a C:P of 558 to 71. For rhizomorphs, a P content of 0.5–0.6 $mg \cdot g^{-1}$ was determined by Wallander et al. (2003).

An EM carbon balance should also include a respiration rate. Both isotopic analysis (Trumbore 1997, 2006) and field manipulation studies (Högberg et al. 2001) demonstrate that over a growing season, less than half of the total forest soil respiration is accounted for by the breakdown of soil organic matter (SOM). Belowground allocation of photosynthate products and rapid (<1 week; Ekblad and Högberg 2001; Ekblad et al. 2005) transition into CO_2 is responsible for the other half of total soil respiration (see also Högberg and Read 2006). EM fungi probably play an important role in regulating this part of the respiration, because of (*i*) higher respiration rates of fungal tissues compared with plant roots (Malcolm et al. 2008), (*ii*) high turnover rate of fine mycelium (Staddon et al. 2003; Smith and Read 2008; Godbold et al. 2006), and (*iii*) exudation of easily degraded organic molecules (Högberg and Högberg 2002; Johansson et al. 2009). In situ estimations of the contribution of EM fungi to total soil respiration range from 18% in an oak forest to 25% in a young pine forest (Heinemeyer et al. 2007, 2011). Yi et al. (2007) reported that 20%–37% of soil respiration in a subtropical forest is mycorrhizal. Phillips et al. (2012) found a 16% increase in soil respiration at dense mats of EM fungal mycelium, compared with neighbouring soil, and calculated that EM respiration represented 40% of rhizosphere respiration. Thus, also from a modeling perspective, the understanding of the regulation of fungal respiration is of major importance (Hughes et al. 2008). For fungi in general, maintenance respiration rates of 0.06–0.12 $g \cdot g^{-1} \cdot h^{-1}$ have been reported (Lynch and Harper 1974). Malcolm et al. (2008) reported between 20 and 150 $\mu mol\ CO_2 \cdot mg^{-1} \cdot s^{-1}$ for EM fungi.

A relatively large number of studies include the colonization by EM as percent infected or colonized fine roots, as this is relatively easy to measure (values ranging from 10%–100%; for a review, see Read et al. 2004). Infection rates are species- and site-dependent and sometimes influenced by management, nutrients, and (or) CO_2. However, the infection percentage is not clearly related to the associated EM biomass or to functional or taxonomic diversity (Rosling et al. 2003).

1.2. Basic C and nutrient exchange

Besides the obvious flow of C from the host plant to the EM, the nutrients studied most frequently with regard to their impact on ectomycorrhiza are N and P; therefore, we will focus on these three in the following paragraphs.

1.2.1. C exchange

Although it is assumed that ectomycorrhizal fungi have some capacity to degrade complex organic compounds (Smith and Read 2008; Durall et al. 1994; Hobbie and Hobbie 2006; Rineau et al. 2012; see also section 2.1), the majority of species seem to rely on the host plants' C supplies to a very high degree (Nehls 2008; Courty et al. 2010).

From field and laboratory studies, it is estimated that between 5% and 50% of the plant's recent photoassimilates can be transferred to the EM fungi (Leake et al. 2004; Jones et al. 2009; Leake 2007, 10%–30%; Simard et al. 2002, 10%–50%). C transfer is complex, and both regulated and unregulated transfer of recent photoassimilates and stored C to the EM have been described (Druebert et al. 2009; Pena et al. 2010, see chapter 4). At an ecosystem level, the published estimates of C allocation into belowground EM (EM root tips, EMM, and fruit bodies) varied from 0%–20% (Hobbie and Hobbie 2006) to 12.5%–15% (Smith and Read 2008) of the net primary production (NPP) of a forest stand. In a recent review, Ekblad et al. (2013) estimated an overall average of 7.2% of NPP allocated to EM as a realistic value, based on the current knowledge of EMM growth and turnover rates.

1.2.2. N uptake

In general, plant N uptake is improved by association with EM fungi through four possible mechanisms: (*i*) efficiency of the uptake mechanisms, (*ii*) exploration of bigger soil volume, (*iii*) uptake of organic forms (e.g., amino acids), and (*iv*) release of nutrients from nonplant available sources (e.g., complex organic matter). Potential uptake rates for EM have been determined under controlled conditions and were reviewed by Plassard et al. (1991). Their findings show high diversity in potential uptake rates as ammonium uptake ranged as much as 19–600 $\mu mol \cdot g$ root $tip^{-1} \cdot h^{-1}$ between species. Nitrate uptake was estimated to be much lower (39–45 $\mu mol \cdot g$ root $tip^{-1} \cdot h^{-1}$) but could only be given for two species. In general, EM fungi are not necessarily more efficient in taking up mineral N compared with plant per unit surface area, but because of the high surface area (EM fungi are much thinner than fine roots), total uptake is higher. The increase in exploration area has been often shown, although it is highly species-variable (see section 2). Uptake of organic forms (amino acids) appears to be more common in EM fungi than in plant roots, but no estimates of rate have been published to our knowledge. Concerning the breakdown of complex organic compounds and the related release nutrients, especially P but also N (Finlay 2008; also see section 3 of this review), although important, this matter is too complex for inclusion in simple models. A more general approach, without focusing on the uptake mechanisms, was used by Bending and Read (1995), giving nutrient uptake rates from the fermentation horizon SOM as 0.7% $N \cdot day^{-1}$ (or 45–78 $\mu g \cdot g\ SOM^{-1} \cdot day^{-1}$) above the mineralisation rate of the substrate (although these data are from an artificial microcosm).

1.2.3. P uptake

Even more for P than for N, because of the lower mobility of P, the extended foraging range and high surface area are very important in explaining increased P uptake by mycorrhizal trees (Hayman 1983; Harley and Smith 1983). P uptake has been studied extensively in AM, whereas only a few values for P uptake rates exist in literature for EM. Van Tichelen and Colpaert (2000) found 0.13–0.62 $nmol \cdot g$ EM root $tip^{-1} \cdot s^{-1}$ in growth medium compared with 0.08 $nmol \cdot g$ root $tip^{-1} \cdot s^{-1}$ for nonmycorrhizal root tips. Cairney and Smith (1993) reported 11.5–24.7 $\mu mol \cdot g\ EM^{-1} \cdot 16\ h^{-1}$ in growth medium. For modeling purposes, it can be assumed that EM take up all available mineral P. Because of the high uptake efficiency of mineral P and the low mobility in the soil, in a forest, P is generally derived from organic compounds that are less available as a source of P to plants. Bending and Read (1995) gave P uptake rates from the fermented horizon SOM pool as 4.1 $\mu g\ P \cdot g\ SOM^{-1} \cdot day^{-1}$, or 0.7% $P \cdot day^{-1}$. However, much uncertainty still exists about the P sources available to EM (for a review, see Plassard and Dell 2010), so these rates will depend very much on the available SOM pools but can be quite high (60%–70% of organic P within 90 days; Plassard and Dell 2010).

1.2.4. Nutrient transfer to the host plant

Uptake by the EM fungi is generally not the goal of the modeling exercise. More important is the transfer to the host plant. Global estimations of fungal contribution to plant N uptake range around 90% (Hobbie and Hobbie 2008; van der Heijden et al. 2008); in a controlled experiment, Brandes et al. (1998) reported 70%, but these rates differ probably between fungal species (Lang and Polle 2011). For P, even fewer studies exist, but estimates are similar to those of N contribution (e.g., Brandes et al. 1998: 73%). Next to N and P, fungi are known to also improve plant Mg, Ca, K, Zn, and Fe nutrition (Marschner and Dell 1994). The high transfer rates are a combination of increased exploitation area and enhanced uptake rate but are also explained by the envelopment of the fine roots with the fungal mantle so that direct fine root uptake is reduced by the EM. The impact of this root envelopment on root nutrient uptake is still not completely clarified. Direct root uptake without passage over the fungal plasma membrane is inhibited, as reviewed by Taylor and Alexander (2005), but selective passage of certain nutrients from the soil to the root is possible.

1.3. EM structures

From a modeling perspective, it can be useful to limit the EM fungal biomass to one carbon pool, but even simple models tend to include some differentiation between the different EM tissues as they are very different in terms of turnover time, respiration, and C:N (see values provided below and in Table 1). EM fungi show high morphological diversity (Agerer 1991, Agerer 1987–1993), but in general, the following tissues are recognized.

1.3.1. EM root tip

The EM root tip is the interface between the plant and the fungus. Fungal tissues envelop short lateral roots, and a net of hyphae (Hartig net) penetrate between epidermal and cortical root cells down to the endodermis. Because of the intergrowth of fungal and plant tissues, it is challenging to obtain parameter values for modeling this fraction of the EM biomass. However, values for complete EM root tips are often found in literature and can be used to estimate the fungal pool. For conversion of EM root tip dry mass to grams of fungal C, a correction factor of 0.5 g C·g dry mass^{-1} has been used (Smith and Read 2008). Grebenc and Kraigher (2009) calculated 0.0083–0.0692 mg C·root tip^{-1}, with an average value across the 20 EM for European beech of 0.0169 mg C·root tip^{-1}. Dahlberg and Stenlid (1994) proposed 11%–30%, and Dahlberg et al. (1997) used a conversion factor from total fine root dry mass of 3% (spruce) and 4.5% (Scots pine), whereas Ostonen and Löhmus (2003) suggested that 18% is an appropriate value for conversion of EM root tip to fungal tissue, from which Ostonen et al. (2005) calculated fungal EM root tip biomass of 64 kg·ha^{-1} in a Norway spruce forest, while Dahlberg et al. (1997) reported 250–400 kg·ha^{-1}. EM root tips have higher respiration rates (Marshall and Perry 1987; Rygewiecz and Andersen 1994; Martin and Stutz 2004) but decreased turnover rates and C:N (Langley and Bruce 2003) compared with nonmycorrhizal root tips.

1.3.2. Fine mycelium and rhizomorphs

The EMM comprises the EM fungal tissues extending from the root tip into the surrounding soil. This network is built up by a complex network of branching and joining of fungal cords (hyphae); these hyphae are sometimes bundled into thick strands (rhizomorphs). The structure and size of the extraradical mycelium varies widely between EM species and is well described for a great number of species (Agerer 2001). For modeling purposes, it is useful to divide the extraradical mycelium into fine mycelium and rhizomorphs. Rhizomorphs have a much higher longevity than the fine mycelium, a higher C:N (Vargas and Allen 2008; Pritchard et al. 2008), and probably lower respiration rates, although no published data were found. Unfortunately, most published data on EM biomass in the soil do not distinguish between fine mycelium and rhizomorphs (Ekblad et al. 2013). Also, measurements in the field are difficult and the results are variable. The few studies on rhizomorphs suggested that up to 50% of EM C is located in rhizomorphs (Pritchard et al. 2008), but the amount is highly dependent on EM species (see section 2) and soil and host plant nutrient status (Pritchard et al. 2008). EMM respiration was determined by Malcolm et al. (2008) for 12 species and ranged between 20 and 150 μmol CO_2·mg dry mass^{-1}·s^{-1}. Sclerotia, another extramatrical structure of several EM fungi (dense aggregation of hyphae), remain mostly unstudied in terms of their C budget contribution and longevity but may also be regarded as not an important parameter for separate soil C modeling. Dahlberg et al. (1997) measured 440 kg sclerotia·ha^{-1} in a spruce forest, so pool size is quite large.

1.3.3. Fruit bodies of EM fungi

Fruit bodies form a small part of the total EM biomass (0.6% of fungal C as found by Wallander et al. (2001); Smith and Read 2008) or 6 kg·ha^{-1}·year^{-1} (mean value during 1989–1993) (Wiklund et al. 1994). Together with their short longevity (weeks), fruit bodies are not an important pool for soil C modeling. Concerning the dynamics of fruit body formation, a review by Egli (2011) indicates a shortage of knowledge concerning environmental and management effects on fruit body productivity.

1.4. Abiotic effects on EM growth

Temperature and moisture content generally have direct effects on soil microbial growth and respiration. However, in the case of EM fungi, the effects are highly dependent on the interactions with the plant partner as temperature, drought, nutrients, and CO_2 also mediate EM respiration through effects on the host plants (Staddon et al. 2002; Ekblad et al. 2013).

Temperature was frequently studied as a potential modifier of EM respiration rates. Whereas some studies reported an increase in respiration rate with increasing temperature (Bååth and Wallander 2003; Hawkes et al. 2008), other studies showed an acclimation effect (Malcolm et al. 2008) or no response (Moyano et al. 2007). Basic values of fungal respiration and growth responses to temperature were described by Pietikäinen et al. (2005) as square-root functions, and Malcolm et al. (2008) reported between 20 and 150 mmol CO_2·mg^{-1}·s^{-1} for most species with a Q_{10} of 1.67 to 2.56. On the other hand, according to Heinemeyer et al. (2007), EM hyphal respiration does not respond directly to changes in soil temperature but is rather regulated by the availability of carbohydrates. It was mainly the soil heterotrophic flux component that caused the commonly observed exponential relationship with temperature (Heinemeyer et al. 2007), which is in line with measurements on variations in total soil respiration (Ekblad et al. 2005) and an elevated CO_2 experiment by Comstedt et al. (2006). An increase in plant C tends to increase C to the EM. Conditions in which root growth is promoted (N or P deficiency, drought) increase relative allocation to the EM, but if the absolute values of C are significantly reduced, EM growth will also be significantly reduced. The plant photosynthesis and C allocation to the EM fungus have a strong seasonal variation (Rygiewicz et al. 1997*a*; Nilsson and Wallander 2003). From the modeling point, a temperature-related higher fungal biomass for AM and EM fungi (Gavito et al. 2005; Hawkes et al. 2008; Heinemeyer et al. 2006), as well as a higher fungal colonization (Heinemeyer and Fitter 2004), should be noted.

Concerning the effects of moisture, EM hyphal respiration responded strongly to reductions in soil moisture (Heinemeyer et al. 2007). Because of hydraulic lift and the extended exploration area of the EMM, EM root tips may survive drought, though large changes in EM roots and rhizomorph biomass in response to

Table 2. Existing mycorrhizal models and their main characteristics.

Model	Type	Differentiation	Ecosystem model	Elements	Effect on aggregate	Decomposition of SOM	CMN	Turnover rate
ANAFORE, Deckmyn et al. 2011	EM	None	Yes	C, N	Yes	Yes	No	
Deressa and Schenk 2008	AM	AMc	No	P	No	No	No	No
Dorneles 2001, 2004	Not specified	None	No	C, P			Yes	
Jolicoeur et al. 2002	AM	AMc	No	P	No	No	No	No
Landis and Fraser 2007	AM	Arbuscules, AMc	Yes	C, N, P	No	No	No	Yes
MoBilE + Mycofon, Meyer et al. 2010, 2012	EM	EMc-HN	No or yes	C, N	No	No	No	Yes
MySCaN, Orwin et al. 2011	Not specified	None	Yes	C, N, P	No	Yes	No	Yes
Neuhauser and Fargione 2004	Not specified	None	No	—	No	No	No	
Ruotsalainen et al. 2002	All	None	No	P	No	No	No	
Schnepf and Roose 2006, Schnepf et al. 2008	AM patterns	AMc	No	P	No	No	No	Yes
Staddon 1998	AM	Intra–extra radical	Yes	C	No	No	No	No

Note: SOM, soil organic matter; CMN, common mycorrhizal networks; EM, ectomycorrhizal; EMc, EM colonization; AM, arbuscular mycorrhizal; AMc, AM colonization; HN, hartig net.

drought have been measured (Pritchard et al. 2008). However, the sensitivity of the EMM to drought possibly varies considerably between different exploration types of fungi, and rhizomorps may also grow rapidly at very low soil water content (Vargas and Allen 2008).

The changing (increasing) atmospheric CO_2 concentrations have mainly indirect effect and, from field experiments on EM colonization and EMM production, seem to be insignificant in most cases, except for rhizomorphs (Pritchard et al. 2008; Rygiewicz et al. 1997*b*). Besides this, Finzi et al. (2007) noted that effects were mostly plant-mediated and led to an increase in fungal biomass due to higher photosynthesis and higher belowground C allocation (e.g., Gavito et al. 2000; Treseder 2004; Wiemken et al. 2001). Indications for any different response are too uncertain and scarce to assume differences for a modeling approach.

1.5. Modeling approaches and implications

1.5.1. Existing models

Several models that involve mycorrhizal symbioses have been developed so far and can be distinguished between purely AM and EM models and models that have no clear distinction in mycorrhizal type (Table 2). The majority of existing models focus on AM, as they are considered important in P nutrition of agricultural plants (Collins-Johnson et al. 2006; Schnepf and Roose 2006; Deressa and Schenk 2008). These models are mostly stand-alone models that only consider a mycorrhized root and the fungi and concentrate on the fungal P uptake dynamics and its contribution to the plant P nutrition (Deressa and Schenk 2008; Jolicoeur et al. 2002; Schnepf et al. 2008; Schnepf and Roose 2006). In contrast, the mycorrhizal P uptake route has been widely neglected in EM models. Incorporating P uptake concepts of the AM models into EM models could elucidate the possible role of EM in the plant uptake of this important nutrient. The increase in N levels (through pollution), together with increasing acidity, have been shown to shift forests from N-limited to P-limited (Gress et al. 2007). Inclusion of P effects on forest growth is therefore becoming more relevant. It is possible that by simulating mineral uptake of P only, an overestimation of P limitation of tree growth is made, as mineral P content is very low in many soils. Even a model simply including organic P uptake (without explicit simulation of the EM fungi responsible) could improve the simulations.

AM models are generally a good starting point for simple EM models, but attention needs to be paid to some important differences: EM fungi are a more diverse group than AM fungi. All known species of AM-forming fungi are placed in the same phylum (Glomeromycota), are obligate mycorrhizal, and are thought to have one common symbiotic ancestor (Smith and Read 2008). EM fungi, on the other hand, are placed in several phyla (Basidiomycota, Ascomycota, and Zygomycota), and there is strong evidence that EM lifestyle has arisen at least 15 times independently from saprotrophic ancestors (Plett and Martin 2011). As a consequence, EM fungi show a huge variation in growth morphology, physiology, and EM–plant interactions, but all of the diversity remains neglected in models involving EM.

EM fungi are found more in N-poor environments, so N uptake is important to the host trees. EM fungi appear to be more efficient in uptake of organic forms of N than AM fungi and, in most conditions, increase tree N uptake. In AM systems, generally, only mycorrhizal P uptake is beneficial to the host plants, while for N uptake, there is competition between fungi and host plant for mineral N. A detailed model emphasizing the increase in surface area by AM fungi as the most important factor in P uptake (which is highly efficient, i.e., uptake rate is not the limiting factor) has been developed by Schnepf and Roose (2006) and Schnepf et al. (2008)). If modified to include N uptake from organic pools, this model could be useful for EM systems.

Deckmyn et al. (2011) were the first to develop a full ecosystem model with explicit mycorrhiza consideration, though the EM are considered as a single pool (no differentiation in mycorrhizal roots and EMM). In their ANAFORE model, EM fungi also possess some degrading capacity of organic matter. Meyer et al. (2010) developed a simple plant–fungi feedback model that captures the main C and N exchange between a fungal C and N pool and a root C and N pool (Meyer et al. 2010, 2012). This is the only model that considers the effect of the hyphal mantle on plant nutrient uptake directly. Staddon (1998) simulated the C dynamics between a mycorrhized plant and the fungal community depending on ambient CO_2 concentration and photosynthetic activity. His aim was to investigate the effect of elevated CO_2 on fungal colonization. Also, Orwin et al. (2011) described mycorrhiza explicitly in the MySCaN model and linked them to the ecosystem C and N cycles. They found that explicit mycorrhiza implementation has considerable effects on simulated organic matter pools and degradation. They do not explicitly distinguish between AM and EM fungi.

1.5.2. C and nutrient flow between host plant and mycorrhiza

In existing mycorrhizal models, different simple approaches have been used to simulate mycorrhizal growth, but all assume that the main C source is from the host plant. Orwin et al. (2011) defined a constant fraction of plant C assimilates that is potentially available to the fungus and that is modified further by the intrinsic nutrient availability in the fungal and plant tissues (Orwin et al. 2011). In ANAFORE, a fraction of the C allocated to the roots (modified by the water and nutrient availability) by the host plant yields similar results (Deckmyn et al. 2011). Both models increase allocation towards roots and EM when nutrients and (or) water is limiting. N uptake is simulated in a function of available pools (mineral and organic), and transfer to the host plant is unregulated and complete (EM fungi are simply simulated as "tubes" for N uptake, although some N is used for EM growth at a constant C:N).

In the model by Meyer et al. (2010, 2012), the maximum C available for fungal growth is defined by a fraction of plant C assimilates, but the actual C demand of the fungus is determined by assuming that a certain ratio between root and fungal biomass exists to produce sufficient fungal biomass to reach the optimum (defined) degree of mycorrhization. The growth of the fungi is directly related to the N availability of the soil, as well as to the N supplies to the root delivered by the fungi.

P might very well be the more important nutrient but is not included in many ecosystem models. P uptake by EM is very efficient and includes uptake from organic pools not available to plants (Bolan 1991). Therefore, inclusion of this aspect, even in a simplified way, should influence ecosystem functioning significantly as P might be limiting in an increasing number of forest ecosystems as N pollution increases (Plassard and Dell 2010; Cumming 1996; Naples and Fisk 2010), although other authors suggest that N (Vitousek and Howarth 1991; Linder 1995) is generally still more limiting. Orwin et al. (2011) included P uptake from organic pools, which had previously been considered only in purely arbuscular models (e.g., Schnepf and Roose 2006; Schnepf et al. 2008), and the results clearly showed a significant impact on plant growth and soil C dynamics.

In conclusion, N transfer in existing models is implemented usually as a constant supply rate from the N and P taken up by the EM fungi. For an even more basic model, EM can be seen as simply enhancing plant N and P uptake from the soil by a constant factor and (or) by allowing a larger soil area or a constant fraction of organic N and P pools to be exploited. This does not necessarily imply explicit simulation of the EM but can be included into the fine root characteristics. Alternatively, another very simple way to model both C and nutrient transfer would be to explicitly set an exchange rate, thus only allocating C to the EM if N and (or) P (or other nutrients) are provided. Although this is easy to implement and can yield good results locally and averaged over longer time, experimental data show that there is no constant exchange ratio (Jones and Smith 2004) and that C is possibly allocated to EM even when N and P are not immediately provided (see section 4.3.1, parasitical behavior of EM).

1.5.3. Turnover and respiration

Mycorrhizae turnover and respiration in models are generally described very simplistically. Fungal C losses due to turnover can be defined as a certain fraction of C that is lost per time unit. The easiest option to model mycorrhizal respiration is to set a certain fraction of fungal C that is respired. Another possibility is to follow the concepts developed for plant root respiration, e.g., Thornley and Cannell (2000) as in Meyer et al. (2012), or to follow Arrhenius (Q_{10}) temperature dependencies (Deckmyn et al. 2011), but a direct link to carbohydrate supply might be more realistic. One aspect that could easily be included in models is the recirculation (autolysis and reuse in production of new materials in the mycelium). However, it is unknown how high a proportion of the N and P (and C) is reused. Either experimental data or a model analysis could elucidate whether this aspect is important for the soil nutrient balance.

From a modeling perspective, distinction is often made between live and dead fungal tissue (Deckmyn et al. 2011; Meyer et al. 2012), but field measurements cannot always make this distinction. Turnover rate from a modeling perspective is the death rate of a tissue that subsequently enters the litter pool and is decayed depending on recalcitrant proportion and C:N.

1.5.4. EM structures

In a very simple model, there is no separation into different fungal tissues. However, because their different functions and properties have a major impact on soil nutrient content and fungal nutrient uptake and turnover capacity, it is important to distinguish them in more advanced model approaches. Meyer et al. (2010) offered a parameter to divide EM biomass between the hyphal mantle and the extraradical mycelia, which are both characterized by different turnover rates. Rhizomorphs have not been implemented in any model yet but are clearly important due to their function as fast nutrient transport ways and extension structures, besides having a longer residence time and higher C:N. They can constitute a high fraction of the total fungal biomass and probably have a high impact on the total fungal C and N demand (Agerer 2001). Moreover, uptake of nutrients does not take place in the rhizomorphs, but at the tips of individual hyphae in the fine mycelium and EM root tips.

1.5.5. Fine root infection

In AM models, percent infection has played a central role (assumed to be a good measure of the C allocated to the AM), but this approach has been questioned (Allen 2001). In EM models, some models assume that all fine roots are infected and no size of the infected root system is simulated or do not explicitly simulate rate of infection (ANAFORE, Deckmyn et al. 2011; MySCaN, Orwin et al. 2011).

Another option would be to use a species-specific maximum infection rate or to calculate infection from plant and EM growth rates (Meyer et al. 2010). To our knowledge, the Meyer model (Meyer et al. 2010) is the only one to include feedback between the percent infection and root uptake and turnover characteristics. Thus, although infection is rather well documented based on the experimental data, in models, it is not evident how to use this information because of the lack of knowledge on the implications. In models that do not differentiate between EM tissues, inclusion of percent infection is of little value. It is also important to note that in many ecosystems, 100% infection rate is found (Kraigher 1999).

Assuming that EM fungi are simulated as a single pool in the simplest model, they can be associated with trees of different species and ages at the same time. It could be effective and more realistic to simulate one EM pool with different associations to different tree species (allocating more nutrients to the species that has the highest infection) instead of simulating an EM pool for every tree species. One way to distribute the nutrient and C fluxes over the EM pools is to add all C available from the plants into a single pool. For the P and N taken up by the EM in surplus of the growth of the EM itself (depending on a maximum growth rate + available C, N, and P), a simple rule linked to the mycorrhization degree of each tree or tree category (this can be the weight of mycorrhized fine roots per tree) seems the most obvious. This implies simulating the degree of mycorrhization, which is included so far only in the plant-scale models (Meyer et al. 2012), not in the forest-scale models (Deckmyn et al. 2011), as a function of allocated C and fine root surface area. For the simplest model, a species-dependent constant percent mycorrhization could be a reasonable assumption. Of course, if EM fungi are not explicitly simulated but only as part of the fine roots of each species, these issues do not need to be considered.

1.5.6. Sensitivity to changes in environmental factors

Most environmental indirect effects (through the host plants) are more important and better understood than direct effects. Even the simplest EM models should simulate the link between C available from the host plant and EM growth. The relationship between the decrease in fungal abundance and biomass and the increase in soil N availability has been confirmed in a high number of published reports (see above), though infection rate is often 100%, even under high N availability. Most models (Deckmyn et al. 2011; Meyer et al. 2010, 2012; Orwin et al. 2011) include either a direct or indirect mechanism leading to a reduction in plant C allocation into fungal biomass when N and (or) P are not limiting.

Effects of climatic factors such as temperature and soil moisture on fungal growth have so far been treated mainly as plant-mediated (effects through the changes in available C), but direct effects of such factors on respiration (using response curves similar to those of the plant) have also been implemented. However, this assumption is subject to high uncertainty and simulated C and N fluxes might be changed considerably if response curves differ.

From a modeling perspective, the indirect effect of mycelia formation on water uptake is relatively simple to consider in ecosystem models and would be expressed by, e.g., a higher water uptake efficiency of mycelia compared with roots or a higher potential uptake area.

1.5.7. *Missing concepts*

From the data above, it is clear that relatively simple EM models can be implemented into forest ecosystem models using average values. Such models are able to deal with the uptake of nutrients from pools not accessible to plants (i.e., P from the organic layer) and simulate the interaction between host plants and EM dynamically depending on the most limiting factor (P, N, energy). The following are some important limitations to such models:

- very large differences between different EM fungi, the use of one average set of parameters may not cover cases in which the community of EMs changes over time;
- simple models are focused mostly on the plant–EM interaction, ignoring the significant direct and indirect effects of the EM on the soil organic pools;
- the interaction between host plant and EM appears more complex (Högberg et al. 1999; Kohzu et al. 2000) and has been shown to vary seasonally, during forest development, etc.; many studies have been performed to elucidate this relationship.

In the following sections, each of these aspects is further described.

2. How to overcome large species and functional diversity in EM

Although it can be tempting to simulate a single, unchanging, pool of EM fungi from a modeling perspective, there are several publications that suggest that this might not be adequate to catch the full diversity of EM effects in ecosystems. In contrast to AM, where about 200 fungi species infect about 200 000 different plant species, in EM, roughly 25 000 EM species connect to ca. 8000 plant species (Rinaldi et al. 2008). Cairney (1999) reviewed a number of physiological characteristics of different EM species, but the number and taxonomic, structural, and functional diversity of EM species are far too high to attempt simulating them separately. Besides this, for the majority of EM fungi, very little is known about their biology, physiology, growing demands, and environmental limits, with commercial truffles such as the Périgord black truffle (*Tuber melanosporum* Vittad.) as a rare exception. Agerer (2001) introduced the concept of exploration types based on the large differences in morphology of the EMM, which may represent a promising grouping of the high EM diversity into a manageable number of classes applicable in EM and forest ecosystem modeling.

The categorization into types is based on the amount of EMM formed, the occurrence of more or less differentiated rhizomorphs, and also how far the extramatrical hyphae are reaching from the mycorrhizal root tip. The ectomycorrhizal mantle itself does not have a large contact area with the soil, so the emanating hyphae and rhizomorphs determine the volume of exploited soil (Read 1992; Smith and Read 2008). There appears to be a relationship between distance and the internal differentiation of rhizomorphs, the farthest reaching types being the most differentiated. Smith and Read (2008) and Kammerbauer et al. (1989) showed a clear relationship between the extent of rhizomorph organization and transport rates of phosphate therein. Besides this, rhizomorphs and rhizomorphs bearing EM have been shown to have a slower turnover compared with single hyphae (Pritchard et al. 2008; Vargas and Allen 2008). Five main exploration types have been distinguished with different putative ecological roles, each of which represents a distinct foraging strategy (Agerer 2001):

1. contact exploration type — EM tips and emanating hyphae, when present, are in close contact with the surrounding substrates (Brand 1991) enabling EM to successfully explore the substrate in their close vicinity;
2. short-distance exploration type — characterized by a voluminous envelope of emanating hyphae from the mantle, but rhizomorphs are not formed;
3. medium-distance exploration type — forms rhizomorphs and can be divided into three subtypes with respect to rhizomorphal features: (*a*) fringe, (*b*) mat, and (*c*) smooth medium distance type:
    (*a*) fringe medium-distance exploration type — forms fans of emanating hyphae and rhizomorphs, which ramify and interconnect; rhizomorph surfaces are hairy and form emanating hyphae with extended contact;
    (b) mat medium-distance exploration type — forms undifferentiated or, at most, slightly differentiated rhizomorphs, thus individual mycorrhizae have only a rather limited range of exploration;
    (c) smooth medium-distance exploration type — EM mantles appear rather smooth with almost no, or only a few, emanating hyphae; rhizomorphs belong to the type B (Agerer 1987–1993) and are internally undifferentiated or slightly differentiated or, very infrequently, with a central core of thick hyphae;
4. long-distance exploration type — characterized by rather smooth ectomycorrhizae with few but highly differentiated rhizomorphs that can be well over >20 cm long;
5. pickaback ET — a combination of two EM fungi that, from the outer morphology, would be sorted into contact or smooth medium-distance exploration types (Agerer 2001), one of which can grow within rhizomorphs and (or) mantles of another EM.

Relevant parameters for each type can be found in Table 3.

So far, several environmental changes have caused shifts in the EM community through differences in rhizomorph characters and consequently in exploration type presence and abundance. N and P availability influences EM morphotype, as has been shown by Baum and Makeschin (2000) where fertilization reduced the number of rhizomorph-forming EM. Changes in temperature are also known to lead to shifts in EM composition, as do increased ambient ozone (Matyssek et al. 2010) and antiozonant chemicals (Katanić et al. 2013). Deslippe et al. (2011) found increases in hydrophobic hyphae and longer range, rhizomorph-forming EM types under warming. Simulated grazing experiments show that reduction in the carbon supply is affecting the EM community such that contact and short-distance exploration types increase, whereas the rhizomorph formers decrease in abundance (Barto and Rillig 2010). These shifts can be significant and might lead to considerable changes in the ecosystem C and N cycling pattern.

Table 3. Some general characteristics of the EM types.

Type	Contact	Short-distance exploration	Medium-distance exploration, fringe	Medium-distance exploration, mat-forming	Medium-distance exploration, smooth	Long-distance exploration
Exploration distance	<0.5 mm	0.5–3 mm	3 mm–20 cm	3 mm–20 cm	3 mm–20 cm	>20 cm
Specific EMM length (m·cm^{-1}·EM^{-1}) (Weigt et al. 2012)	0	3.72±1.19	6.91±0.54 (data not specified for a particular medium-distance subtype)			55.92±0.54
Biomass distribution, root tip : fine EMM			50.35:0.65 (EMM)			
Rhizomorphs	No	No	Yes	Yes, undifferentiated to slightly differentiated	Yes, undifferentiated, slightly or infrequently highly differentiated	Yes, highly differentiated
Water repellency	Hydrophilic	Mostly hydrophilic	Hydrophilic, hydrophobic	Hydrophobic	Hydrophilic	Mostly hydrophobic except distant parts
Degradation of complex organic matter	Yes	Yes	Yes or no	Yes	Yes or no	Yes or no, long-distance P transport
Environmental conditions	Upper soil layers					
Typical forest ecosystem	Late stage	Early stage?	Multistage or late stage	Early and late stage	Early and late stage	Early or late stage?

Note: EM, ectomycorrhizae; EMM, extrametrical mycelium. Data from Agerer (2001), Castellano et al. (1999), Raidl (1997), Unestam and Sun (1995), Weigt et al. (2012).

It might be questioned if the role of fungal diversity is of major importance in old established forest ecosystems where negative effects of certain species might be compensated by others. Fungal diversity could play a major role though when ecosystems are disturbed, e.g., after logging or due to acid rain. Kowalski et al. (1990) found that after being exposed to acid rain, the initial EM community of a mixed stand vanished and was replaced by acid-tolerant EM species, which were smaller in diversity and formed only a thin sheath around root tips. These observed changes are likely to have decisive consequences for plant physiological and phytopathological functions.

2.1. Model implications

From a forest-modeling perspective, simulating the different EM taxa is clearly too complex. Modeling the exploration types is a useful intermediate step, as it allows simulation of different behaviors and groups all of the EM diversity into only five (seven) different groups (modeling pools). Simulation of one EM pool with parameters for the exploration type and rhizomorph formation is possible, but a more complex model with competing ecotypes might yield new insights. This requires a clear link between the ecotypes and their characteristics.

At the moment, several parameters of different exploration types were proposed with possible implications in modeling EM (Weigt et al. 2012). Specific EMM length and exploration distance may serve as relevant measures for the potential distance occupied by a particular exploration type, whereas parameter-specific potential (actual) mycelial space occupation gives a potential (actual) space occupation (e.g., the complete hyphal depletion zone; Weigt et al. 2012).

For modeling purposes, it would be an advantage to define fungal communities with certain properties that associate with certain tree species or that are present under particular defined soil properties. The main difficulties are as follows:

- lack of understanding of the ecological significance of the exploration types;
- fungal species do not always form the same exploration type (although most species do), and in a given site, different types can co-exist;
- EM exploration type might change in response to environmental changes, i.e., the most competitive type under the given circumstances survives;

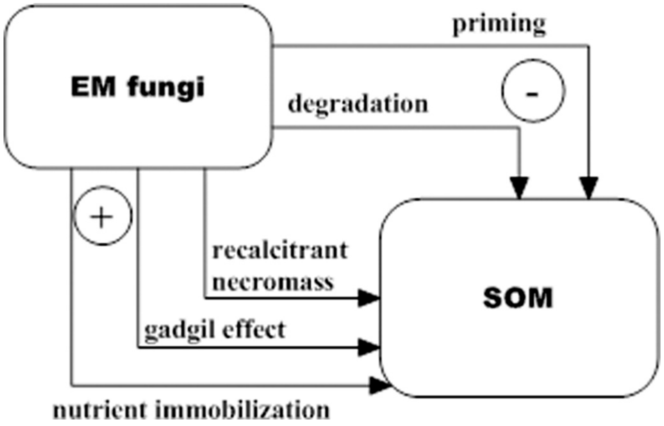
For AM fungi, a recent model study calculates the theoretical optimum number of symbiotic AM fungi in a grassland using asymptotic diminishing returns as a function of the number of symbionts (Veresoglou and Halley 2012); a similar approach could yield interesting results for EM fungi.

In conclusion, it might be possible to construct a model simulating a full range of EM, and the economics (cost benefits) can be calculated to predict which type of symbiosis emerges. It is clear, however, that at the moment, data are lacking and only a very theoretical approach (such as in the AM study of Veresoglou and Halley 2012) would be possible at short notice.

3. Effects of mycorrhiza on nutrient pools and other microorganisms

The net effect of EM on total soil C is a sum of interacting effects (Fig. 2). (1) EM fungi degrade SOM. (2) EM fungi compete with saprotrophic microorganisms for nutrients. As a consequence, the saprotrophic microorganisms can be suppressed, and this can reduce SOM degradation because the EM fungi degrade some compounds more slowly (the "Gadgil effect"). (3) On the other hand, the belowground allocation of plant energy fuels the activity of EM fungi and associated microorganisms, increasing SOM degradation of energy-poor SOM (priming effect). (4) Nutrients are immobilized into the EM tissue. (5) EM fungi form relatively

Fig. 2. Effects of ectomycorrhizal (EM) fungi on soil organic matter (SOM).



recalcitrant hyphae (cell walls can have a chitin content of up to 60%; Langley and Hungate 2003) that enter the SOM pool after their death and could increase aggregate formation in the soil. However, Fernandez et al. (2012) questioned whether chitin is recalcitrant, so this obviously needs to be elucidated before it can be incorporated into models.

3.1. Exploitation of organic versus mineral pools

Only small fractions of soil N and P are available in mineral form. Most nutrients are stored in organic (N and P) form or as part of the crystal lattice of soil minerals (P and base cations). EM fungi are highly efficient in uptake of mineral N and P, but they are also involved in the mobilization of nutrients from less available pools. A number of studies have demonstrated the ability of EM fungi to break down all major classes of organic matter (e.g., Norkrans 1950; Trojanowski et al. 1984; Haselwandter et al. 1990; Read et al. 2004). A complication is that EM fungi show much variation in their abilities to utilize certain nutrient sources, e.g., some species do not show a significant growth on organic N forms, whereas other species can use amino acids as an energy source (Sangtiean and Smith 2002; Smith and Read 2008; Abuzinadah and Read 1986; Finlay et al. 1988, 1989; Koide et al. 2008). In vitro experiments show different results on the lignin- and cellulose-degrading abilities of EM fungi (e.g., Bending and Read 1995; Colpaert and van Laere 1996; Colpaert et al. 1997; Martin et al. 2008; Nagendran et al. 2009). The role of EM fungi in the actual breakdown of complex organic matter as an energy source in the field has been questioned. It can be assumed that EM only degrade SOM as a C source when the supply from the host is limited (Högberg et al. 2001; Read and Perez-Moreno 2003). Courty et al. (2007) showed that before and during budbreak, EM fungi (*Lactarius quietus* (Fr.) Fr. (1838)) might be able to use SOM as a C source.

On the other hand, the availability of plant energy could enhance the degradation of SOM ("priming effect") in search for nutrients (Talbot et al. 2008), as has been demonstrated in non-EM plants (Dijkstra et al. 2006). Nutrients in degraded plant litter are protected by lignocellulose structures. A recent study showed a strong reduction of dissolved complex organic matter in the presence of an EM fungus, driven by a process involving the formation of radicals ("Fenton" reaction) (Rineau et al. 2012), which is suppressed by the absence of readily available energy (glucose) or the presence of ample inorganic N (Rineau et al. 2013). These results support the view that degradation of complex organic matter is an energy-limited process (Kuzyakov et al. 2009) and driven by nutrient (N and (or) P) demand.

3.2. Competition with other microorganisms

The Gadgil effect (Gadgil and Gadgil 1971), in which inclusion of EM fungi reduced the degradation of SOM due to competition with saprotrophs, has been described by several authors (Zeller et al. 2007). This does not need to contradict the enhanced SOM degradation by EM found in other studies. Several studies demonstrated a vertical differentiation of the microbial community in the soil profile (Dickie et al. 2002; Landeweert et al. 2003; Rosling et al. 2003; Lindahl et al. 2007). More than half of the EM root tips in a Swedish mixed coniferous forest were found in the mineral soil horizons (Rosling et al. 2003). Also, the majority of EM fungal biomass was found in the mineral soil horizons (Wallander et al. 2004). A detailed study of changes in C:N and ^{15}N abundance with depth of the organic horizon revealed a distinctive shift from saprotrophic fungi in the coarse plant litter to EM fungi in the more decomposed litter and humus (Lindahl et al. 2007). From this spatial separation, the authors conclude that the process of organic nutrient mineralization is not dominated by saprotrophic fungi but by EM fungi and is ultimately fueled by the energy flux from the host trees into the EM hyphal network. Gadgil and Gadgil (1971) proposed that both EM and saprotrophic fungi compete for nutrients: saprotrophs win in energy-rich fresh litter but lose in deeper soil where C is limiting. To date, there is no consensus as to what limits the growth of EM fungi (C, N, or P). Meta-analyses suggest that EM respond to CO_2 with increased biomass and decreased N and P content, which suggests that EM fungi are still C-limited (Treseder 2004), but this has not been confirmed in field studies so far.

To further complicate matters, EM fungi support an associated community of helper bacteria (Garbaye 1994; Frey-Klett et al. 2007). These helper bacteria are thought to be involved in (*i*) nutrient mobilization from minerals and organic matter, (*ii*) fixation of atmospheric nitrogen, and (*iii*) protection of plants against root pathogens (Frey-Klett et al. 2007).

3.3. SOM and micro- and macro-aggregate formation

The flux of carbon into the belowground mycorrhizal network adds directly to the belowground organic matter pool when fungal hyphae die. Mycorrhizal fungi influence the formation or stabilization of soil at macroaggregate (53–250 μm) and microaggregate (<53 μm) scales with different mechanisms, which Rillig and Mummey (2006) differentiated into physical, biochemical, and biological processes. Biochemical effects include the release of mycelial products, including glomalin in AM fungi and polysaccharide polymers ("biofilms") in EM fungi. Biological effects include the influence of mycorrhizal mycelia on other microbial (e.g., bacterial) communities and fungal interactions with the soil food web. Physical effects include hyphal enmeshment of particles and microaggregates, altered water regimes (dry–wet cycles), alignment of particles, and exertion of pressure. Different aspects of the fungal mycelium may have different roles in these processes. Additionally, the fungal diversity is of highest importance, as EM fungal species differ in their effects on root hydraulic conductivity, influence differently root biomass, and possess diverse mycelium architecture (Rillig and Mummey 2006).

3.4. Model implications

Existing forest models generally do not include any effects of EM on SOM. N and P (if simulated) are often only taken up by the plants in the mineral form, which might induce an important overestimation of P and N limitation on tree growth. Inclusion of decay rates for the dead hyphal matter, possibly depending on C:N but generally lower than for dead plant matter, is relatively simple and should be feasible in most ecosystem models, though chitin decay should be better understood and parameterized first. Effects on aggregate formation are less evident to simulate, but if aggregate formation is included in a model, EM can be added as a linear modifier for this process (as in ANAFORE; Deckmyn et al. 2011).

Inclusion of interaction between soil microorganisms is possible if a fundamental change is taken from the popular view of decay rates being driven by the soil organic pools (modified by environmental factors) to a dynamic simulation of the soil microorganisms. One nice example is a modeling study by Banitz et al. (2011) on the effects of fungal networks on degradation by bacteria. With three or more pools of microorganisms with different requirements in C, N, and P and different efficiencies in decaying the soil C pools, a more realistic representation of the complex web of interactions between the decay rates and the organisms can be created. However, an intermediate solution in which the pool size of the microorganisms is a modifier for the decay rates of the soil organic pools could be an easier way to implement at least some of the effects described above.

Regarding organic matter degradation abilities of fungi, only in the ANAFORE (Deckmyn et al. 2011) and MySCaN (Orwin et al. 2011) models does EM have a capacity for litter degradation, which is about one-tenth of the capacity of simulated saprophytic fungi. The AM model of Schnepf and Roose (2006) also includes uptake of P and N from the organic litter layer, depending on the surface area of the AM and limited by a maximal uptake rate. Although these models simulate a direct link between EM biomass and SOM degradation rate in competition with saprotrophic fungi, it would be possible in a more simple model to attribute a constant fraction (10%) of the SOM degradation to EM.

4. Variability in host–fungi interaction

4.1. Factors influencing the symbiotic benefit: from mutualism to parasitism?

EM are often considered symbiotic, with C being exchanged only if nutrients are limiting. From a modeling perspective, a simple solution is to allocate a fixed percentage of NPP to the EM. However, these approaches do not cover the diversity of responses found in experiments.

Many studies have shown reduced C transfer to EM fungi under nutrient-rich conditions (Nilsson and Wallander 2003; Jones et al. 1990). However, many cases have been reported in which the exchange between fungi and plant was not balanced and (temporary) negative effects on plant growth occurred (see e.g., Johnson et al. 1997). Whether the relation between fungi and plant turns parasitic seems to depend on a variety of factors such as plant age (Colpaert et al. 1996; Jones and Smith 2004), plant nutritional status (Correa et al. 2006, 2011), soil nutrient availability (Correa et al. 2011; Hammer et al. 2011), and environmental conditions such as drought (Davies et al. 1996) and C availability (light) (Bücking and Heyser 2003). These studies are mainly under laboratory conditions, and it appears that EM fungi in the field are almost always beneficial to the host. Johnson et al. (1997) recommended considering mycorrhiza as a principally mutualistic relationship that is interrupted by exceptional periods when the net plant costs exceed the benefits. Collins Johnson et al. (2010) found that locally adapted AM fungi are generally mutualistic, whereas artificial combinations used in laboratory experiments are not always.

Concerning the C source, EM mainly use the new photosynthates, but some access to starch has also been shown (Druebert et al. 2009; Pena et al. 2010). The envelopment of the fine root with the fungal mantle, which constrains root nutrient uptake, implies that the plant is mainly accepting fungal supplies instead of controlling the symbiosis. However, there are indications that the plant indeed has some ability to regulate the C transfer to the fungal partner from photosynthates. Nehls (2008) and Nehls et al. (2010) analysed the distribution of carbohydrate transporters in the root–fungal interface and concluded that there are several ways for the plant to down-regulate the C supply:

- the activity of photosynthesis can be regulated according to the fungal C sink strength;
- the sucrose transport into the apoplast can be controlled;
- the plant seems to have control over the magnitude of hydrolysis of sucroses to fungal-available hexoses; and
- root and fungi compete for hexoses in the apoplast, i.e., the root can redirect hexoses into root cells if fungal nutrient exporters are not active.

In a recent meta-analysis, Correa et al. (2012) concluded that C allocation to the mycorrhizae is not the reason for the reported negative effects of EM on plant growth. They concluded that EM become parasitic when they reduce the plant nutrient uptake instead of increasing it. However, because of the complexity of the matter, we will explore the different environmental effects on the plant–fungi interaction by giving a short overview about the current state of research, by analysing the observed patterns with regard to their importance from a modeling perspective, and by considering the potential to include the observed patterns in ecosystem models.

4.1.1. Effects of meteorological factors on plant–fungi interaction

4.1.1.1. Drought

Increased allocation to mycorrhizae under drought conditions has been found in a study on EM fungi (Vargas and Allen 2008). This is a useful adaptation as several published studies indicated that ectomycorrhizal fungi can significantly contribute to drought resistance of plants and use several direct and indirect ways for that, e.g., the increased production of mycelia and lateral hyphae enhancing water uptake and the protection of root tips due to the hyphal coverage (see, e.g., Davies et al. 1996; Runion et al. 1997; Jany et al. 2003; di Pietro et al. 2007). Hydraulic redistribution and lift through mycelia and mycorrhizal plant roots should also be considered in this respect (Prieto et al. 2011; Smith and Read 2008). However, the magnitude of protection seems to vary considerably between species, and some particular drought-resistant fungal types such as, e.g., *Cenococcum geophilum* have been identified (di Pietro et al. 2007; Jany et al. 2003). However, some studies indicate that the plant limits its C investments when a certain threshold is reached, e.g., as soon as the prospect of a benefit fades or the fungal C requirements exceed the plant capacity (Volkmer 1999; Shi et al. 2002). Swaty et al. (2004), who studied plant drought stress symptoms and mycorrhizal colonization in a pine forests in USA, indicated that trees with intermediate drought stress showed a much higher fungal colonization (58%) compared with trees under very high drought stress (29%). Systems with seasonal droughts seem to be dominated by rhizomorph formers that are more drought-resistant.

4.1.1.2. Light and temperature

The effects of temperature and light changes cannot be fully separated as they both go along with a change in the available C resources. Light reductions, as well as reduction in temperature, lead to lower C supply and can lead to proportional decreases in fungal C supply. However, relative C investment from the plant can temporarily increase if the nutrient supply and colonization remain constant. A reduction in EM fungi abundance has sometimes been observed (Son and Smith 1988; Johnson et al. 1997) so that the impact of light or temperature deficit probably depends on the plant vitality and its remaining C sources (Johnson et al. 1997). In this respect, it is important that EM appear to have some access to stored C (starch) from the host plant during periods with insufficient supply of new photosynthates (Druebert et al. 2009; Pena et al. 2010).

The effect of higher temperatures has been observed to lead to both proportional increases in available C and different respiration response curves of roots and fungi so that increased fungal C demand might lead to higher C losses for the plant (Bååth and Wallander 2003; Malcolm et al. 2008). These findings, however, were usually investigated in lab experiments, and the effects are not necessarily the same in established forests.

4.1.2. *Influence of nitrogen and phosphorus soil availability and plant nutrient status*

The nutrient status of the plant is the key determinant in carbon allocation between above- and below-ground parts of the plant (Ericsson 1995; Poorter and Nagel 2000). More specifically, plant limitations in the nutrients N, P, or S lead to increased investment belowground, whereas limitations of K, Mg, or Mn lead to reduced allocation belowground (Ericsson 1995). Addition of P or N often leads to a severe reduction in EM infection rate or growth (Nilsson and Wallander 2003; Jones et al. 1990). The same trends are also visible in the C investment in the EM and arbuscular fungal biomass, the number of EM fungal fruiting bodies, and the degree of mycorrhization (for reviews, see Koide 1991; Wallenda and Kottke 1998; Wallander et al. 2011; Lilleskov et al. 2002; Nilsson et al. 2007; Frey et al. 2004; Parrent et al. 2006).

It is often observed under N shortage that C flow to the fungi is not reduced even when the plant shows some evidence of growth depressions (Johnson et al. 1997). This seems to be a result of high N retention in the fungal tissue rather than a C deficit in the plant (Correa et al. 2008, 2012). In an in vitro experiment by Colpaert et al. (1996), the fungal mycelia stored about 6%–16% of the total plant and fungal biomass but retained between 12% and 32% of the total N. Consequently, it can be assumed that the plant accepts not only high C investments from the fungi but also parasitic appearances of the fungi if it suffers from nutrient shortage, i.e., that classic view of the mycorrhizal symbiosis might not apply at every point in time. In such cases, it can be seen as an investment in the future: in the long run, the mycorrhiza will have a mostly positive effect and investing in mycorrhizae to increase soil exploration is a strategy that increases the chance of survival on average. High soil N decreases the C allocated to EM in almost all studies, but the P availability may change that picture.

In an excellent review by Treseder (2004), it was shown that under high P levels, allocation to EM is more reduced than under high N levels. Deslippe et al. (2011) found no reduction in percent root mycorrhization with N fertilization. On the other hand, low P levels increase C allocation to EM even when plant growth is reduced. Laboratory experiments show that the effect of high N on EMM production was dependent on the P availability such that low P stimulated EMM production irrespective of the N availability (Wallander and Nylund 1992; Ekblad et al. 1995). This suggests that P availability is the dominant effect, which can be explained by the nonmobility of soil P. Increasing the foraging range of the plant by EM is more important for P uptake than for N uptake.

4.1.3. *Influence of forest and tree age and seasonality on C allocation to EM*

Plant age seems to be of major importance when assessing the benefit that the plant takes from the EM infection. Young saplings often show a growth depression or lower vitality than noninfected trees (Correa et al. 2006) in vitro or on forest establishment. However, in a mature forest, seedlings have been found to receive C from the mycelial network (originating from mature trees) (see section 4.2.2). In accordance, it was found in field studies that trees make high C investments into the EM network until canopy closure (at a forest age of about 20–30 years, depending on the forest). After that, C investments seem to be lower because the mycelial network is fully established and soil exploration by mycelia production is complete, so the existing mycelia only has to be maintained (Wallander et al. 2010). Therefore, young trees very likely "accept" C investments, although no immediate benefit can be taken to establish a network that will benefit the whole ecosystem in the long term. Very little data concerning seasonality are available. Because EM use mainly fresh photosynthates (see above), highest growth rates are expected in summer. In autumn, C allocation to the roots is relatively higher but might be less accessible (storage C). Also, relatively more ectomycorrhizal C is invested in fruiting bodies.

4.2. Additional benefits in the mycorrhizal symbiosis

Besides the direct reciprocal exchange of C and nutrient between plants and the fungal symbionts, other plant benefits have also been reported. Increased protection of tree sapling against pathogens has been reported for both AM and EM. The infection of saplings with different mycorrhizal species has been shown to drastically reduce pathogen damage on saplings infected with *Fusarium* and *Cylindrocladium* (Chakravarty and Unestam 1987; Morin et al. 1999). Luo et al. (2009) report increased abiotic stress tolerance in EM-colonized trees explained by priming effects on stress-related signaling pathways. In addition, it has been shown that the fungal hyphal mantle that covers the root tips can significantly reduce root decomposition rates (Langley et al. 2006).

There is clear evidence that there is not only a direct nutrient and C exchange between one ectomycorrhizal plant and the EM community, but in forest ecosystems, nutrients (C, N, P) and water are exchanged between trees over extended "common mycorrhizal networks" (CMNs) (Arnebrandt et al. 1993; Simard et al. 1997, Brearley et al. 2007, Warren et al. 2008) according to source–sink relationships (Simard et al. 1997). These transfer processes imply that nutrients, C, and water shortages for single species can be overcome by these transfer strategies and that parasitic appearances between single fungi–tree connections may lose importance. The stability of a forest ecosystem is thus probably highly related to the tree–fungi–soil transfer of nutrients and water within CMNs.

Infection with EM does not lead to a stimulation of plant diversity (Lang and Polle 2011). On the contrary, poorly diverse patches within tropical forest areas have been reported and were deduced to be due to the infection of trees with EM (Connell and Lowman 1989).

4.3. Modelling implications

4.3.1. *C and nutrient exchange*

Although a lot of research and models have focused on this aspect of EM fungi, uncertainty remains quite high. Because the mechanisms of the control are unclear and too complex for forest-scale models, three main model strategies can be followed: (1) simplify to a constant C supply, (2) modify C supply as a function of nutrient availability or uptake, or (3) modify C supply following economic principles (optimal allocation).

4.3.1.1. *Models simulating C supply as a function of soil or plant nutrient status*

From all of the evidence above, although there is evidence of changes in the relationship between the fungi and the plant, in most stable ecosystems and at a larger time scale, it seems reasonable to have C supply to the EM as a constant fraction of photosynthesis (10%–30%; Staddon 1998). Although this is the simplest way to model the interaction, it does allow negative effects on growth if N and P are limiting plant growth. However, the often-reported reduction in EM under high nutrient conditions is obviously not represented. Assuming forest nutrient conditions to be stable, this does not need to be a problem, and a simple model as described in (1) can be used.

In the more advanced models, modification of the C fraction allocated to the EM as a function of nutrient availability and drought can be implemented, by either direct link to the C allocated to fine roots or linked to N or P shortage of the plant. In the latter, this implies plant control of the C supply in a simple way.

For example, Orwin et al. (2011), Deckmyn et al. (2011), and Meyer et al. (2012) included mechanisms that lead to a reduction in EM fungal abundance with higher soil fertility. Orwin et al. (2011) used an indirect approach and reduced C allocation to the fungus with increasing N concentration in the plant, and Deckmyn et al. (2011) reduced C allocation to the root under high nutrient availability.

4.3.1.2. Models simulating C supply following economic principles

Several models include more explicit economic principles and trading concepts (for a review, see Johnson et al. 2007) and calculate an optimal ratio between shoot, plant root, and mycelial biomass (Fitter 2006; Ruotsalainen et al. 2002). Plant C is allocated to mycelia only in return for N and (or) P. Such models cannot simulate parasitical behavior but yield quite good results for longer term simulations (over several years), especially under stable conditions where an optimal host–fungi relationship can be expected. Neuhauser and Fargione (2004) used a predator–prey model to investigate the mutualistic–parasitic behavior of EM in a conceptual way. Economic models are extremely relevant to simulate the reduced C allocation to EM under high nutrient availability, especially for AM systems, where N and P fertilization is an important issue. For natural forest ecosystems and EM fungi, nutrient limitation is probably more frequent.

Along the same economic principles, but with the allocation blind to the actual pools (i.e., C is allocated to the mycelia under P shortage even though the fungi do not supply P), a better agreement with experimental data under P limitation is found (AM model of Landis and Fraser 2007). Other AM models, e.g., Collins Johnson et al. (2010), are based on the C, N, and P in the soil nonstructural pools to determine which is limiting. Economic principles allocate C to the plant shoot when C is limiting, to the root when N is limiting, and to the root and mycelia when P is limiting.

An intermediate approach was applied by Meyer et al. (2012) in which C is allocated to the fungi aiming towards an optimal fungi-to-root ratio but is further regulated by the N transfer from the fungal symbiont. C delivery to the fungi would only be reduced considerably when less than 30% of the total plant uptake is covered by the fungal N supplies.

A compromise between the different modeling concepts might be to have a fixed minimal amount of C (possibly starch) always available (parasitic under high nutrients) with no plant control, but to allow plant control on the percent photosynthates allocated to the EM depending on the nutritional status.

Furthermore, for N and P supply, other regulating mechanisms could apply. Published studies reported that with limiting P supplies, plants did not reduce their C allocation to EM (Wallander and Nylund 1992; Ekblad et al. 1995). Therefore, it might be more appropriate to use different response functions for N and P when insufficient N supply by the EM leads to reduced C delivery, whereas insufficient P does not or less so.

4.3.1.3. Simulating drought and light effects

The above-described effects of drought and light restriction on the plant–fungi interactions are hardly quantifiable and strongly linked to the local species composition and nutrient supply, i.e., resistance against drought or light deficit strongly depends on the respective intrinsic resilience of the plant and fungal species, on their C and N uptake efficiency, and on the overall combination of stressors. The modeling strategies described above can be used for light, temperature, and drought effects as well. Allocation is either a constant fraction of photosynthesis (and therefore lower under stress) or is influenced by root–shoot allocation (increase under drought) or follows economic trading concepts (optimized for every condition).

4.3.1.4. Simulating the influence of community composition and plant–fungal species

Consideration of fungal communities and their effect on plant vitality is related to the discussion on fungal ecotypes already mentioned above. For a simple mycorrhiza model, the consideration of different fungal species and their impact on nutrient exchange and plant vitality is too advanced and probably unnecessary when considering old established forest ecosystems that show a high degree of stability. However, when including either processes that alter ecosystem stability (e.g., acid rain, forest fires) or forest management activities (logging, fertilization), it might be necessary to simulate fungal communities as these might change which would have considerable impact on tree productivity. Including these in a more complex mycorrhiza model would require the existence of a community composition model that considers the respective characteristics of the described fungal species and their respective interaction with the plant. One step towards this is a study by Verbruggen et al. (2012), who tested how plant C allocation differs between high-quality and low-quality fungal partners and how this depends on the spatial structure. To our knowledge, no fungal community model exists so far, and model development is hampered by the difficulties in describing functional groups. As mentioned above, the definition of functional groups or exploration types of fungi associated with trees under specific environmental conditions could be a further step in this direction.

4.3.2. Additional benefits

Modelling the additional benefits such as pathogen protection has, to our knowledge, not yet been attempted. The main reason is that these observations are hardly quantifiable and especially not transferable into mathematic equations. The magnitude of the effect depends highly on composition and vitality of species so that high uncertainties would be produced. At the current state of research, it is this probably not advisable to implement these aspects.

Only one simple model has attempted to consider the formation of CMNs by focusing on the nutrient transfer between two plants (Dorneles et al. 2001, 2004). This model could be implemented into a more complex model by including the other EM functions. The model of Banitz et al. (2011) focused on the simulation of bacterial degradation but included the effect of dispersal along CMNs. So far, no inclusion into forest ecosystem models has been tested, which is probably explained by the high complexity of the system and the hampered transferability into ecosystem models. Also, it is unclear how important the relatively small fluxes of C between trees are at an ecosystem level. Next to the challenge of modeling different fungal ecotypes, the pattern of mycorrhization between different tree species is hardly representable. However, the formation of CMNs has important implications for the implementation of a mutualistic or parasitic mycorrhiza concept as the parasitic appearance of certain single species might not be of significance anymore, at least in the long-term perspective.

5. Conclusion and summary: missing data and concepts

Most current forest ecosystem models do not include the role of EM fungi, although some of the EM effects are implicitly built into the fine root parameters after optimization (increased uptake efficiencies and longevity of fine roots). If tree growth is the main emphasis, attributing some EM characteristics to the fine roots can improve model results, as almost all fine roots are associated with EM. The most important characteristics that can be included in this way are increased surface area and explored soil volume and the accessibility of nonmineral nutrient pools. Such models can simulate tree growth quite well, but this simplified approach will induce important errors in respect to soil C dynamics. If the goal of the forest ecosystem model is to accurately simulate soil C dynamics, then the role of EM fungi should be included in a more detailed way.

Obviously, the focus of models to be included in ecosystem models will be on plant–EM interaction and effects on soil processes. Nonetheless, for specific applications, formation of sporocarps can be an important model output.

Although many EM parameters still lack accurate estimates, we believe that enough data and insight are available to allow inclusion of EM in soil models. More data are necessary concerning the following mechanisms:

- drought effects on EM through C allocation and hydraulic lift;
- plant control over symbiosis;
- EM species or ecotype changes in response to climate or management;
- balance between increasing soil stabilization and potential to degrade SOM using C from plants;
- recirculation (autolysis and reuse in production of new materials in the mycelium); and
- the fate of chitin in the soil: is it recalcitrant? What is the turnover rate?

A drawback of many reported studies is that they are conducted under artificial laboratory conditions that often do not reflect natural conditions and might in consequence lead to wrong assumptions when using the observations to construct model concepts. This is a general problem as these experiments are often much more progressing when aimed at developing model mechanisms because cause and consequence of observed relationships are much easier to identify compared with in field studies. The findings from lab experiments thus need to be considered with caution, and more field experiments are needed to either support or dismiss findings from lab observations.

However, of more concern is the lack of field data to evaluate EM models. Ideally, field measurements of forest soil C dynamics should include the following data:

- total EM biomass for different ecotypes, differentiated in rhizomorphs, hyphae, and EM root tips;
- turnover rates and respiration rates of hyphae and rhizomorphs in the field;
- standing EMM necromass and its turnover rate;
- C:N:P stochiometry of the different tissues; and
- average characteristics (extension, rhizomorph formation, capability of SOM degradation) of the ecotypes and the link between forest type and EM ecotype.

Besides difficulties in determining transfer rates, further information on environmental dependencies would be necessary to narrow model uncertainties. To fill some of these gaps, microcosm studies with ^{15}N labeling and sequential harvesting under different environmental conditions could be an appropriate tool.

Concerning the existing EM models, the most useful improvements could be

- implementation of fungal diversity (either as diversity parameters of some kind of grouping (functional, taxonomic)) and subsequent parameterization and validation;
- implementation of effects on SOM including priming, competition with saprotrophs, and hyphal turnover; and
- improvement and validation of the different concepts of host–EM interaction.

In summary, experimental and modeling efforts need to be better tuned towards each other in the future. We sincerely hope that this paper will contribute to a better cooperation between modelers and experimentalists to the benefit of both communities. Nonetheless, inclusion of EM in forest and soil models, even with the current data limitations, can be an important improvement to model functioning and validity.

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Concentrations and distributions of Al, Ca, Cl, K, Mg and Mn in a Scots pine forest in Belgium

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ABSTRACT

A *Pinus sylvestris* stand located in Mol, Belgium was studied for its content of six elements: Ca, K, Mg, Al, Cl and Mn. A fractionation of tree components was carried out into 8 classes (heart and sapwood, inner and outer bark, living branches, twigs and young/old needles) and their element contents were measured.

Comparisons were made between the different compartments in terms of absolute and relative element contents. Quantitatively, Ca and K are the main elements: in young needles, Ca + K reach 83% of the elements' whole stock. The wood compartments (heartwood + sapwood) have generally low element content, as does the outer bark except for Ca (which is bound to suberin) and Al, possibly from atmospheric clay deposition. The inner bark, twigs and needles have high element contents possibly linked to high symplasmic content. The Inner bark shows high Ca and K contents as these elements are involved in phloem transport. Positive correlations were found between Ca and Al, Mn and Cl, K and Cl and K and Mn, attributed to similarity in chemical and biological function.

A simple empirical compartment model was developed to derive numerically the transfer rates that reproduce the element distribution within tree compartments. The calculated mass flows appear to be within range of the limited data available from other pine tree studies.

This study highlights the potential for coupling of specific elements (including radionuclides) to Ca, K, Mg, Al, Cl and Mn in context of vegetation modelling, by assuming that these elements follow the same pathways. We found indication that ^{36}Cl, ^{90}Sr and ^{137}Cs (environmentally important from the perspective of nuclear power and waste management) can be coupled to Cl, Ca and K fluxes within the tree, increasing the understanding of the cycling of radionuclides in a forest ecosystem.

1. Introduction

The Scots pine (*Pinus sylvestris*) is one of the main constituents of European forests, exceeding 20% of the productive area of forests in Europe (Mason and Alía, 2000). This conifer is widespread in continental, alpine, coastal and Mediterranean climates (Médial, 2001).

Due to its long life and high biomass turnover, Scots pine forests can absorb and recycle a considerable amount of macronutrients, micronutrients and pollutants when compared to the soil bioavailable reserve (Ranger and Turpault, 1999). The uptake and distribution of elements depend on stand characteristics and vegetation type (e.g. tree species) (Stroble et al., 2001), as well as on their availability in the soil (Misra and Tyler, 1999; Mengel and Kirkby, 2001). Soil input combined with plant selectivity for some elements (micro, macro and contaminants) are likely to be the main factors regulating transfer of elements from the soil to the plant root (Pessarakli, 1999; Mengel and Kirkby, 2001).

Understanding the role of pine forests in element cycling is therefore important, and studies have been performed from the point of view of forest ecosystem functioning (Wright and Will, 1958; Lim and Cousens, 1986a, 1986b; Helmisaari and Mälkönen, 1989; Johansson, 1993; Rautio et al., 1998). These studies illuminate our understanding of the long-term cycling of contaminants at the biosphere-geosphere interface. It is important to capture the essential processes regulating the entry, circulation, storage and exit of substances to the tree – in other words, the biogeochemical cycling (Raven et al., 2001). The key processes involved are root uptake (Li et al., 2001) and sap (xylem and phloem) flow (Hölttä et al., 2006), driven by the biological pumping function of trees, or transpiration (Monteith and Unsworth, 2007), translocation between perennial (trunk, branches) and non-perennial (foliage) parts of

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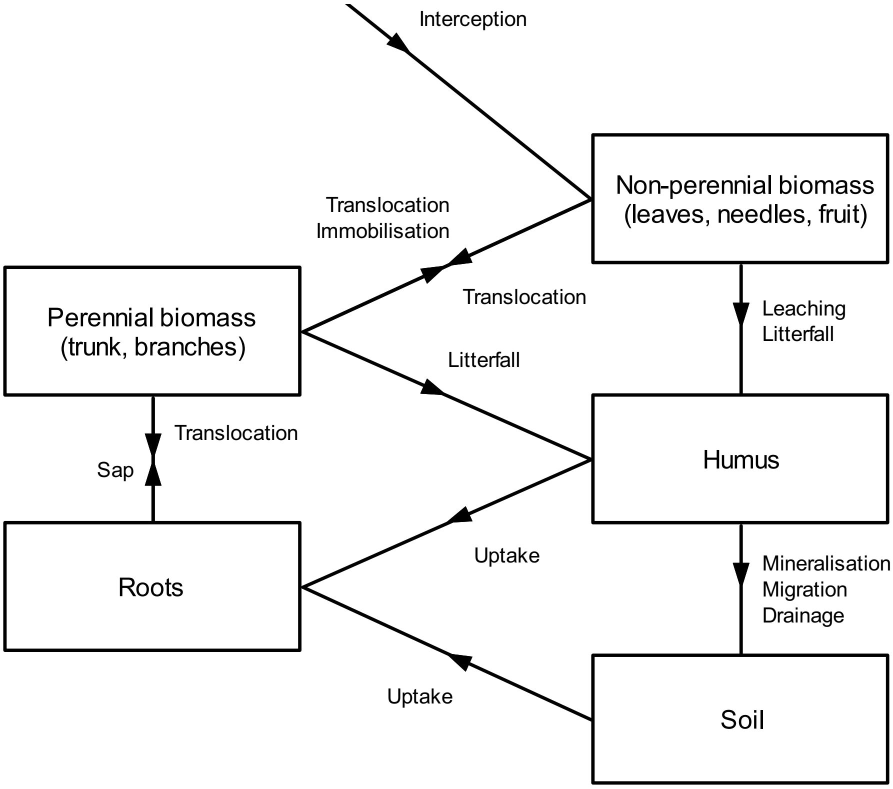


Fig. 1. Generally accepted forest biogeochemical cycle in terms of the major compartments (boxes) and fluxes (indicated by arrows) based on the BIOMASS approach (IAEA, 2002).

the tree, immobilisation and storage (from foliage to trunk and branches), washout (throughfall and weathering), litterfall (Berg, 2000; Copplestone et al., 2000) and element redistribution in the soil, as illustrated in Fig. 1.

Trees are often deep-rooted and may therefore access deeper soil profiles than annual grasses (Boutton et al., 1999). Together with their longevity, forest stands can over time store large amounts of elements in the tree biomass, and thereby act as an effective biological sink (Thiry et al., 2005). Once the elements have been taken-up, they will be expected to distribute to the different parts of the plant through conducting systems, namely xylem and phloem (Raven et al., 2001). Unwanted elements (such as aluminium or excess chlorine) are expected to be displaced towards the non-living parts of the plant. Other elements (e.g. Mg, Mn) may be transported to metabolically active parts and partake in several processes (e.g. photosynthesis) or functions (e.g. regulating turgor pressure) (Raven et al., 2001). Elements return to the soil either through leaching and/or through litterfall, thus completing the biogeochemical cycle.

The objective of this study was to investigate Al, Cl, Ca, K, Mg and Mn concentrations and pools in a Scots pine forest in the Campine region in Belgium, focussing on element distributions in different tree compartments, similarities and differences between these elements and associated interrelations. As a secondary objective, element fluxes between the different compartments of the ecosystem were investigated (soil, forest floor, roots, wood and foliage) using a simple linear pool and flux empirical model, taking advantage of a forest stand well characterised and well monitored for water flows in vegetation in previous studies (Vincke, 2006; Vincke and Thiry, 2008a; Van den Hoof and Thiry, 2012). The observed distributions of these elements are related to wider issues of chemical and physiological functional properties, and to the water and nutrient circulation in the forest vegetation.

2. Materials and methods

2.1. Forest stand, biomass and soil sampling

The pine forest in Mol is a monocultural Scots pine forest approximately 60 years old. The stand is a pine stand with an unclosed canopy having a surface area of 4489 m^2 (Vincke, 2006). The location and dimensions of the forest stand are shown in Fig. 2. In 2006, when samples used in this study were collected, the stand presented a typical even-aged distribution (55 years old) with a mean height of 22.4 ± 3.7 m (dominant height is 26 m) and a mean circumference of 91.1 ± 15.4 cm for 161 trees (i.e. 358.7 trees ha^{-1}). The understorey vegetation is mainly constituted by *Sorbus aucuparia*, *Prunus serotina*, *Rubus* sp. and *Athyrium filix-femina*. A shallow water table appears at 0.50–1.20 m depth at the end of the winter (Vincke, 2006).

The soil is a podzol, classified as a dystric Cambisol (FAO, 1998). Six distinct horizons are observed down to 110 cm deep; the main constituent was invariably sand (>91%) with a small fraction of silt. The soil was found to have a pH H_2O of about 4.5 (varying between 4 and 5 depending on the horizon) (Vincke and Thiry, 2008a).

Previous research (Vincke and Thiry, 2008a) quantified the water table cycle in Scots pines in the plot studied here. Continuous monitoring in 2005 revealed a shallow water table. Pine transpiration was estimated to be <1.85 mm d^{-1}, 25% of the potential evapotranspiration (PET). Understorey transpiration was estimated as 18–20% of the stand water use. The maximum soil water reserve measured over the soil rooted zone was 250 mm, in which 145 mm was extractable water. The contribution of the water table to forest transpiration reached 61% (98.5% in dry periods).

Six pine trees were felled in March 2006 for use in this study. These trees were randomly chosen as part of a forest management plan from a sample consistent with the average diameter of trees in the plot, reflecting its typical even-aged distribution (the trees

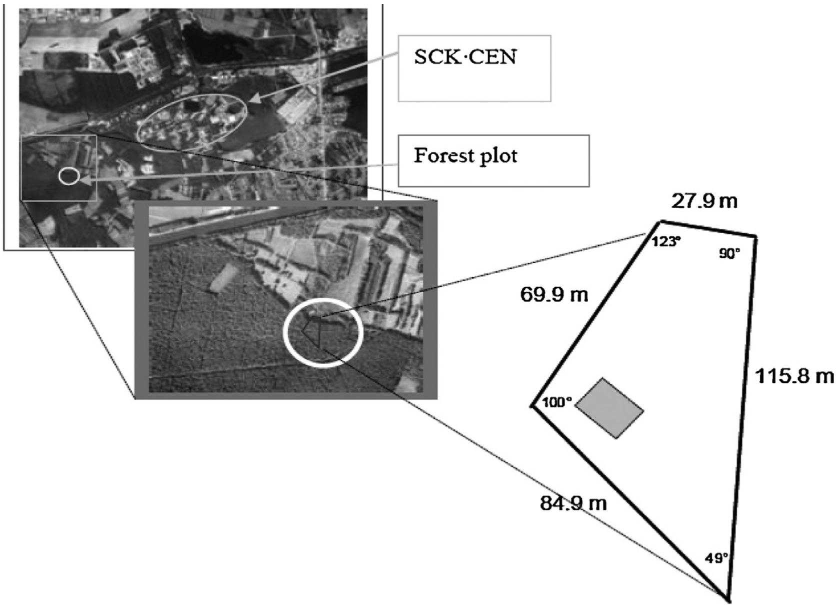


Fig. 2. Localisation of the studied pine forest in Mol (Vincke, 2006).

chosen have a circumference of 93 ± 16 cm and a mean height of 22.3 ± 0.6 m). The tree ages are therefore below 55 years old, an important consideration given that, in older trees (e.g. 65 years) the total content of N, P, and K in Scots pine would fall, whilst the Ca content would to rise due to progressive heartwood development (Wright and Will, 1958). According to these authors, P and K contents in the heartwood of pine trees are very low, but Ca accumulates, contrary to the sapwood zone immediately surrounding the heartwood, where higher levels of all nutrients are found.

Trunks, branches, twigs and needles (younger and older than 1 year) were separated. Discs of 5 cm thickness were cut from the trunk at several heights above the ground (0, 6, 12 and 18 m). A tree disc at zero level was chosen to assess the ground influence in the outer bark, consistent with previous studies in the Mol pine forest (Vincke and Thiry, 2008b; Van den Hoof and Thiry, 2012). The discs were separated into sapwood, heartwood, inner bark (phloem) and outer bark and the total biomass per compartment per tree was calculated. The method of separation, which was also used in Thiry et al. (2009), begins with the separation of the outer bark (a hard and dry material) by carefully peeling-off by hand. The layer below (inner bark), which is softer and moist, is separated by careful slicing with a scalpel until the sapwood, which is a harder material, is reached. The sapwood can be separated from the hardwood on the basis of the distinctive change of colour that exists between the two layers.

Litterfall was collected during one year at monthly intervals into five trays located on different sites throughout the stand. The content of the trays was sorted in needles, bark, twigs and fruit samples on a monthly basis. The fresh biomass was weighed and normalised to surface area. The needles and bark were not washed to remove external contamination (e.g. from the atmosphere) because this distorts the samples. We wanted to evaluate the amount of radionuclide contained in them without risking to dissolve elements loosely absorbed in the sample matrix.

Ten soil cores were taken to a depth of 110 cm (exclusive humus layer). The organic top soil layer was divided conforming to the three observed horizons (Of, Oh and Oa). The soil was further separated per soil layer (0–23 cm, 23–53 cm, 53–66 cm, 66–89 cm and 89–110 cm), reflecting the soil vertical profile underneath the humus layer. Three composite samples were prepared for analysis. Fifteen boreholes were drilled within the soil to obtain root samples and biomass within each soil layer (3 composite samples, representing 5 boreholes each). The average root biomass per soil layer was expressed relative to surface area (tonne/Ha). The roots of Scots pine and of understory plants could not be readily separated.

After removing extraneous materials, the soil samples were oven dried at 105 °C and ground until a homogeneous powder suitable for analysis was obtained. Plant tissue samples underwent the same treatment.

3. Analysis

Instrument neutron activation analysis (INAA) is a costly technique but was chosen for this study due to availability of a facility on-site. This method has the advantage of requiring minimal sample preparation (no need to prepare the chemical matrix) as well as that many elements can be analysed at once. We performed INAA on the biomass samples (roots, heartwood, sapwood, inner and outer bark, needles, twigs and litter) and on the soil samples (including humus) (classified by depth). The elements measured were Mg, Mn, Ca, Al and Cl. Al in soil cannot be measured by this method due interferences with Si. Additional atomic absorption spectrometry (AAS) analyses were carried out to determine the K and Mg concentrations in the samples. K could not be detected by INAA using the selected irradiation protocol. Mg could not be measured in the soil samples due to primary interferences with the other elements (e.g. Si).

The INAA samples were neutron-activated in the Belgian Nuclear Research Centre (SCK•CEN) Belgian Research Reactor BR1, which has a power capacity of 700 kW and a neutron fluence rate of 10^{12} n cm^{-2} s^{-1} (Wagemans et al., 2010), using a protocol for short-term (600-s) irradiation (Vermaercke et al., 2009, 2010). After irradiation, the samples were measured for ten minutes by germanium lithium (GeLi) detector. The PC spectrum analysis software Genie 2000 was used for the recording of the spectra and the Hyperlab software was used for the peak fitting.

For the AAS analysis, samples were ashed in an oven of 550 °C during 1 day to destroy any organic matter present. Then, they were dissolved into 2 ml of 1 M HCl solution and 18 ml H_2O. After dilution the samples were measured using a SANGJI GBC 932AA atomic absorption spectrophotometer equipped with a flame atomiser.

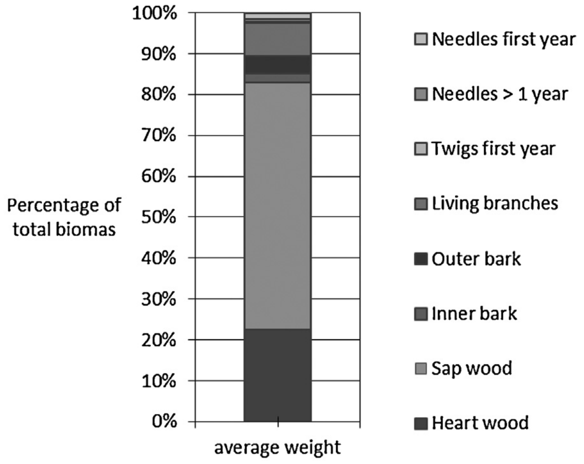


Fig. 3. Relative distribution of the aboveground tree biomass in dry mass (average of 6 trees).

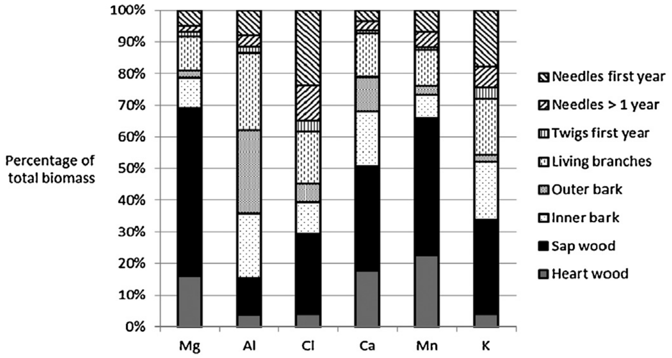


Fig. 4. Relative distribution of the mass of Mg, Al, Cl, Ca, Mn and K in Scots pines from the forest stand in Mol, Belgium (average of 6 trees).

The full analytical procedure is described elsewhere (Wannijn, 2002).

The INAA procedure followed established procedures, namely the Guide to the Expression of Uncertainty in Measurement approach (ISO, 1993). Measurement times and sample quantities were selected such that the combined uncertainties of the weighting of the samples, irradiation and measurement were lower than 5%. For the AAS analysis, the instrument repeats the measurement of each individual sample 3 times and the relative standard deviations of the replicate measurements were found to be lower than 2%, as calculated by the AAS instrument itself. One series of samples was divided in three identical sub-samples to assess deviations caused by the sample preparations following the grinding of the initial sample, and the relative standard deviations of these sample triplicates were found to be less than 7% in most cases, except for heartwood (16%) and young needles (11%).

Table 2
Correlation coefficients (black) and p-values (grey) for the comparison of the relative mass distributions between Mg, Al, Cl, Ca, Mn, K. Significant correlations (>0.85) are marked in bold.

Element	K	Mn	Ca	Cl	Al	Mg
Mg	0.76	**0.98**	**0.90**	0.57	0.07	1.00
	0.03	**0.00003**	**0.002**	0.14	0.87	
Al	0.38	0.02	0.38	0.26	1.00	
	0.35	0.95	0.35	0.53		
Cl	**0.88**	0.54	0.40	1.00		
	0.004	0.16	0.32			
Ca	0.67	**0.89**	1.00			
	0.07	**0.003**				
Mn	0.70	1.00				
	0.05					
K	1.00					

4. Results and discussion

4.1. Tree biomass distribution

For the Scots pine stand that was investigated in this study, the relative distribution of the aboveground tree biomass between different parts of the tree (Fig. 3) shows that, heartwood and sapwood represent respectively 23 ± 5% and 60 ± 17% of the tree biomass. Yet, according to Whitehead (1978) the sapwood depth of Scots pine at breast should be within 5.81 cm and 10.56 cm (based on the allometric formula sapwood area = 0.7188 × basal area – 0.77). Larcher (2003) presents a graph indicating that the outer 2/3 of a *P. sylvestris* is actually involved in water transport, suggesting that our results are in the correct ballpark.

The inner bark accounts for 2 ± 1% of the total mass, somewhat lower than outer bark (4 ± 2% mass). Branches represent 8 ± 6% mass. Twigs and needles together contain 3 ± 1% mass of the total tree biomass.

4.2. Relative element mass distribution and mass related correlations

The purpose of presenting first mass distribution (rather than just expressing the data in the form of concentrations) is to bring to evidence the role of elements that have low concentrations but, due to high mass of the compartment, are more significant when expressed in absolute terms.

The elemental masses in different aboveground tree compartments (representing compartment mass relative to total mass) for Mg, Al, Cl, Ca, Mn and K are shown in Fig. 4. The complementary Table 1 shows the element actual masses and associated standard deviations (n = 6 – although 7 trees were sampled, results are presented for 6 trees due to an experimental artefact found in one of the samples). These are calculated as average concentration in the different tree compartments multiplied by average biomass.

Correlation coefficients, along with the p-value of the ANOVA test at the 96% confidence level (Table 2), were calculated using the regression tool included in the Excel *Analysis ToolPak*. These

Table 1
Percentage element mass and their standard deviations (n = 6) in the different tree compartments for Mg, Al, Cl, Ca, Mn and K.

Compartment	Mg	Al	Cl	Ca	Mn	K
Heartwood	16 ± 3	4 ± 1	4 ± 1	18 ± 3	23 ± 4	4 ± 2
Sapwood	53 ± 9	12 ± 4	25 ± 3	33 ± 4	43 ± 5	30 ± 6
Inner bark	10 ± 3	20 ± 7	10 ± 3	17 ± 4	7 ± 1	18 ± 4
Outer bark	2.3 ± 0.5	21 ± 4	6 ± 1	11 ± 6	2.6 ± 0.3	2.2 ± 0.6
Living branches	11 ± 4	28 ± 11	17 ± 6	14 ± 5	12 ± 5	18 ± 5
Twigs first year	1.5 ± 0.3	2.4 ± 0.9	3.4 ± 0.8	0.9 ± 0.2	0.9 ± 0.2	3.5 ± 0.6
Needles first year	5 ± 2	9 ± 3	24 ± 3	4 ± 1	7 ± 2	18 ± 3
Needles > 1 year	1.8 ± 0.8	4 ± 1	11 ± 4	3 ± 1	5 ± 2	7 ± 2

Table 3
Concentrations of the elements (Mg, Al, Cl, Ca, Mn and K) per tree compartment expressed as ppm$_w$ (mg kg^{-1} on dry mass basis).

Compartment	Mg	Al	Cl	Ca	Mn	K
Heart wood	128 ± 41	6 ± 1	6 ± 3	805 ± 67	41 ± 7	74 ± 42
Sap wood	160 ± 48	7 ± 2	14 ± 1	572 ± 66	30 ± 6	195 ± 58
Inner bark	816 ± 163	374 ± 125	159 ± 35	8548 ± 993	148 ± 36	3423 ± 279
Outer bark	94 ± 18	247 ± 54	44 ± 7	3430 ± 1073	26 ± 5	205 ± 60
Living branches	274 ± 34	130 ± 17	79 ± 12	2055 ± 210	67 ± 13	1040 ± 207
Twigs first year	656 ± 18	200 ± 59	278 ± 54	2342 ± 364	90 ± 20	3444 ± 388
Needles first year	614 ± 74	208 ± 59	550 ± 59	2570 ± 565	199 ± 35	4894 ± 868
Needles > 1 year	449 ± 53	205 ± 32	548 ± 86	4263 ± 771	298 ± 57	3910 ± 344

correlation coefficients encapsulate information about similar distribution of different elements within the tree.

The high Mn mass content of 66% in the heartwood + sapwood fraction could potentially be due to its involvement in the synthesis of lignin (Barker and Pilbeam, 2007). Calcium, more than half of which is distributed towards sapwood and heartwood, is important in woody tissues (Lautner and Fromm, 2010). These physiological explanations are necessarily hypothetical at this stage. For Mg we cannot find a ready hypothesis for the fact that it distributes similarly to Ca but it is not unreasonable to assume that this is related to chemical similarity as these elements belong to the same group in the periodic table (Greger, 2004).

Cl and K are less present in the heartwood + sapwood fraction. These elements are, instead, established in the foliage (young + old needles) to a high degree, a factor of around 3 higher compared with Mg, Al, Ca and Mn). Cl and K are well represented in foliage, possibly reflecting the fact that they are needed by the plant due to their role in the opening of the stomata (Raven et al., 2001). Cl is more present in the foliage and a hypothetical link can be made with its role in water splitting during the photosynthesis process (Séquin, 2012).

The elements that accumulate most in the outer bark are Al and Ca. Al is a beneficial element when present in small amounts, but toxic in larger quantities (Barker and Pilbeam, 2007). Displacement towards the outer bark is the possible mechanism by which the tree eliminates this element, although no literature could be found to confirm this. Aluminium can also be transported through calcium channels, but very little is known about this process (Barker and Pilbeam, 2007). For Ca, several studies suggest that it accumulates in bark (Colin-Belgrand et al., 1996).

It is possible that the elevated Al content in outer bark could originate from atmospheric clay contamination. However, we cannot test this hypothesis with the data at hand; moreover, resuspension of soil particles is unlikely in the relatively humid Belgian Scots pine site studied.

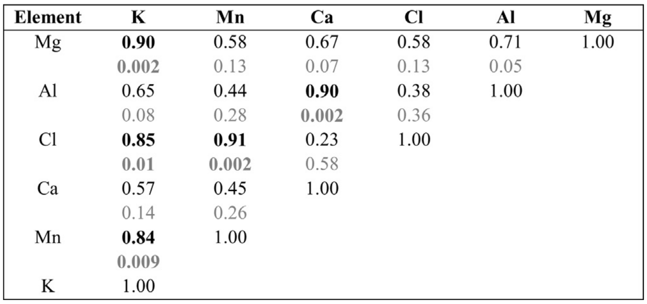
4.3. *Concentration per tree compartment and concentration-related correlations*

The element concentrations in different tree compartments are shown in Table 3. Table 4 shows correlations between different pairs of elements.

Identification of the soil upon which the stand is based as a sandy podzol/distric cambisol is significant in that most podzols are poor soils due to the sandy portion, resulting in low nutrient levels. Perhaps reflecting this, the foliar concentrations of macronutrients observed in Table 3 tend to oscillate between the lower end of the normal range and upper end (latent) deficiency (Mellert and Götlein, 2012).

However, in general, our element concentrations are still broadly comparable with other chemical analyses of bark, sapwood and heartwood in pine trees (Lambert, 1981). Indirect evidence shows that the trees studied in this project do not suffer from low concentrations of any of the studied elements: the production tables of *P. sylvestris* in France, which are the closest reference, indicate that the dominant height of the trees is 26-m (Trees 56 years old) in 2005, the year of the present study. This allows classification of our plot under the productivity class I, which means that the trees were on a site where they grew well, not particularly suffering from deficits of essential elements or toxicity (Decourt, 1984).

Table 4
Correlation coefficients (black) and *p*-values (grey) for the comparison of concentration distributions between Mg, Al, Cl, Ca Mn and K. Significant correlations are marked in bold.



Element	K	Mn	Ca	Cl	Al	Mg
Mg	**0.90**	0.58	0.67	0.58	0.71	1.00
	0.002	0.13	0.07	0.13	0.05	
Al	0.65	0.44	**0.90**	0.38	1.00	
	0.08	0.28	**0.002**	0.36		
Cl	**0.85**	**0.91**	0.23	1.00		
	0.01	**0.002**	0.58			
Ca	0.57	0.45	1.00			
	0.14	0.26				
Mn	**0.84**	1.00				
	0.009					
K	1.00					

Cl and K are the only elements for which statistically significant lower concentrations can be said to have been obtained in the heartwood than the sapwood (Table 3). This may represent a method whereby the tree redistributes nutrients and can be compared with nutrients being removed from foliage prior to litterfall (Jessy, 2011; Staelens et al., 2011). The reverse is only true for Ca. The fact that Ca increases from the outer sapwood into the heartwood is not spurious as it has been observed previously for this species as for *Pinus radiata* and *Pinus taeda* (Lambert, 1981).

Also noteworthy are the relatively high concentrations of Cl, Mn and K in needles (both young and old); compared to other compartments. Mn takes part in the photosynthesis during the water splitting process (Yocum, 2008) and is therefore mainly located in the needles, the compartment where this process takes place. Mn can follow Mg as the centre of the chlorophyll molecule (Cowan, 2002). When sucrose and glutamine are formed during photosynthesis, it is K$^+$ that loads these molecules into the phloem (Philippar et al., 2003).

Chlorine is a contributing factor in the water splitting process, a part of the photosynthesis process (Séquin, 2012). Together, Cl$^-$ and K$^+$ are responsible for the opening of the stomata (Raven et al., 2001). The high concentration of Cl is partially caused by foliar deposition (Van den Hoof and Thiry, 2012). As a mobile element in the environment, chlorine can enter the tree through the stomata in the foliage (Greger, 2004; Vincke, 2006).

The relatively high concentration of Cl in the inner bark phloem is due to the redistribution of chlorine taken-up by the foliage. For Mn, it is well known that complexes are formed during the photosynthesis. These heavy molecules can be translocated via the inner bark phloem (Greger, 2004). The functions and thus presence of Cl, Mn and K in the metabolically active compartments result in high

Table 5
Concentrations of the elements (Mg, Al, Cl, Ca, Mn and K) per tree compartment expressed as a percentage of the highest value found among them.

Compartment	Mg	Al	Cl	Ca	Mn	K
Heart wood	15.7	1.6	1.1	9.4	13.8	1.5
Sap wood	19.6	1.9	2.5	6.7	10	4
Inner bark	100	100	28.9	100	49.7	70
Outer bark	11.5	66	8	40	8.7	4.2
Living branches	33.6	34.8	14.4	24	22.5	21.3
Twigs first year	80	53.5	50.5	27.4	30.2	70.4
Needles first year	75.2	55.6	100	30	66.8	100
Needles > 1 year	55	54.8	99.6	49.9	100	80

concentration related correlations, i.e. 0.91 for Mn and Cl, 0.85 for K and 0.84 K and Mn. The correlation between K and Mg (0.90), can be attributed to their similar roles in enzyme activation (Barker and Pilbeam, 2007).

Ca (3430 ± 1073 ppm_w) and Al (247 ± 54 ppm_w) have high concentrations in the outer bark. It is also suggested that Al^{3+} can be transported through calcium channels, but very little is known about this kind of aluminium transport across membranes (Liu and Luan, 2001).

The physiological considerations referred to above may give some indication of the roles played by the different elements, but they remain as hypotheses to be tested in a future model incorporating the physiology of the pine trees. What can be concluded is that there are two spaces to be considered within the tree: an apoplastic space, constituted of dead material (which represents the main part of tissues such as heartwood or the outer bark) and a symplastic space, constituted of living cells with cytoplasm, much water and biological membranes. This is well-represented in the inner bark, with living parenchyma cells and phloem cells and vessels. It is also a main part of the young needles, although the cell walls are thick in pine trees. Each of these spaces has its own characteristic element distribution depending on element functionality.

4.4. Distribution of elements as percentage of the highest value

The distributions of elements in the tree can be further understood by expressing it as percentage of the highest value found among them (Table 5). In this format, the wood (heartwood + sapwood) shows a relatively low element content. The outer bark also has poor element content except for Ca (known to be bound to suberin) and Al.

It is possible that the elevated aluminium content in outer bark could originate from atmospheric clay contamination. However, we cannot test this hypothesis with the data at hand; moreover, resuspension of soil particles is unlikely in the relatively humid Belgian Scots pine site studied. Conversely, the inner bark, twigs and needles exhibit high element contents, potentially linked to high symplasmic content. In the inner bark, high contents of Ca and K are registered, which is not surprising because these elements are involved in phloem transport.

4.5. Inter-compartment concentration ratios

Inter-compartment concentration ratios were calculated to obtain information concerning the partitioning of the different elements in different compartments (Table 6).

For the partitioning between inner and outer bark, Al is the element with the highest inter-compartment ratio which (provided that this element does not enter the bark from atmospheric clay contamination) would indicate displacement towards the outward compartments of the tree, i.e. the outer bark. In contrast, almost no K (<0.1) is transported to the outer bark. The outer bark/inner bark ratio for Ca, like for Al, is relatively high. This can be explained by the accumulation of Ca in the outer bark. Previous studies have shown that calcium in the stem flow can infiltrate the outer millimetres of the bark (Schulz et al., 2000). The ratios for Mn and Mg are low because both elements are present in high concentrations in the inner bark. Mg is a very mobile element and therefore can be displaced via the inner bark phloem (Barker and Pilbeam, 2007). Mn is necessary for the synthesis of lignin, a hydrophobic molecule that improves the watertightness of the xylem (sapwood) and phloem (inner bark) (Barker and Pilbeam, 2007).

The partitioning of elements between old and young needles shows a different behaviour. For Ca and Mn, the concentration ratio exceeds unity because, with the ageing of the needles, the plant will accumulate Ca and Mn in them (Barker and Pilbeam, 2007). Al and Cl are equally distributed between both compartments with ratios of close to unity, indicating that they do not undergo a displacement process. Mg and K are mobile elements (Barker and Pilbeam, 2007) and are displaced to the most vital parts of the tree, in this case the younger needles. Therefore, the old needles/young needles ratio is <1.

A comparison between the old needles and needles fallen from the tree (needle litter) confirms that Ca keeps accumulating until the needles fall (Lin and Wang, 2001). The possibility of contamination of the needles by bacteria bringing calcium into them once the needles have already fallen was considered. However, needles were collected weekly, and on such timescale they could not have become significantly contaminated as the process of decomposition occurs over a larger timescale of hundreds of days (Larcher, 2003). In fact, Blair (1988) shows an initial decrease of Ca during the first 50 days followed by a much slower increase in the subsequent 2-year period.

Al is accumulated in the senescing needles that are ready to fall off the tree. As a result, both elements (Al and Ca) have a litter needle/old needle ratio above 1.3. For Al, this is a complementary way in which the tree eliminates excess aluminium, which at higher concentration would be toxic for the plant (Barker and Pilbeam, 2007).

Since the litter samples were not washed, it could potentially be argued that the enhanced litter (needles, bark and twig) relative to the rest of the tree from Table 6 originate from soil contamination. However, since the litter was collected in appropriate litter trays and thus was not in contact with the soil, we think that this is highly unlikely.

Like Ca, Mn is also an immobile element. Therefore, a ratio similar to that of Ca is expected. However, the ratio for Mn is close to 1, which does not suggest further accumulation nor return to the plant. This indicates two possibilities: (a) Mn stops accumulating in the needles when the needles reach a certain age, or (b) a fraction of the Mn is already re-mobilised through decomposition.

K and Mg have a litter needles/old needles ratio of approximate 1. This means that both elements are not displaced towards the tree before the needles fall of the tree, indicating perhaps that the tree has enough of these elements available to make reuse unnecessary. In contrast, Cl has a low ratio of 0.27. This low ratio indicates that Cl is translocated back in large amounts. Since chlorine is a very mobile element (Barker and Pilbeam, 2007; Marschner, 2012), this was not unexpected.

Concerning the ratio between twigs and litter twigs, a similar pattern as for the litter/old (>1 y) needles ratio can be observed for Al and Ca. The litter twigs/young twigs ratios for both elements exceed unity. Mg, Cl and K have a ratio <1, which is expected for mobile elements (Barker and Pilbeam, 2007). For Mn, an immobile element (Barker and Pilbeam, 2007), the ratio is also below 1. This can be explained in several ways in addition to measurement uncertainties: (a) Mn having a high re-mobilisation rate, resulting in a loss of Mn towards the forest floor (humus layer) or (b),

Table 6
Inter-compartment concentration ratios for Mg, Al, Cl, Ca, Mn and K.

Compartments	Mg	Al	Cl	Ca	Mn	K
Dead/living branches	0.5 ± 0.2	0.5 ± 0.2	1.6 ± 0.8	0.4 ± 0.2	0.4 ± 0.2	0.1 ± 0.1
Outer/inner bark	0.11 ± 0.03	0.7 ± 0.3	0.27 ± 0.07	0.4 ± 0.1	0.17 ± 0.06	0.06 ± 0.02
Old (>1 y)/young needles	0.7 ± 0.1	1.0 ± 0.3	1.0 ± 0.2	1.7 ± 0.5	1.5 ± 0.4	0.8 ± 0.2
Litter bark/outer bark	3.7 ± 0.8	2.4 ± 0.6	2.0 ± 0.5	1.6 ± 0.5	2.9 ± 0.7	2.0 ± 0.6
Litter needles/old (>1 y) needles	0.9 ± 0.1	1.5 ± 0.3	0.27 ± 0.06	1.3 ± 0.3	1.0 ± 0.2	1.0 ± 0.1
Litter twigs/young (<1 y) twigs	0.7 ± 0.1	2 ± 1	0.5 ± 0.2	1.5 ± 0.3	0.9 ± 0.3	0.2 ± 0.1

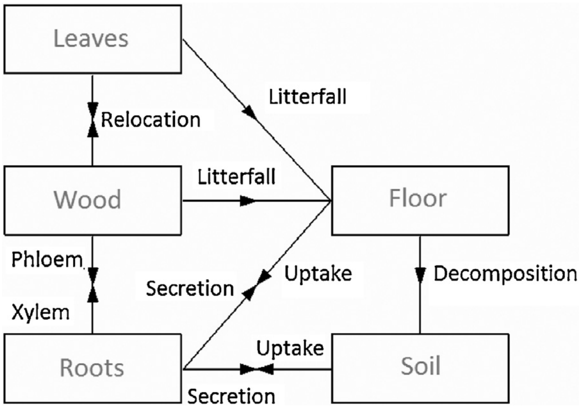


Fig. 5. A simple box model for the calculation of inter-compartment transfer rates in trees, developed with the software ModelMaker (Citra, 1997; Rigas, 2000).

Table 7
Mass (kg ha^{-1}) of Mg, Al, Cl, Ca, Mn and K in the soil, at different depths.

Depth (cm)	Mg	Cl	Ca	Mn	K
0–23	172 ± 12	130 ± 31	1181 ± 104	185 ± 66	549 ± 66
23–53	203 ± 11	121 ± 13	1145 ± 62	128 ± 52	701 ± 154
53–66	107 ± 25	81 ± 19	816 ± 211	64 ± 6	366 ± 85
66–89	255 ± 89	123 ± 18	1701 ± 194	135 ± 38	886 ± 410
89–110	229 ± 30	96 ± 4	1238 ± 465	111 ± 22	824 ± 138

Table 8
Mass (kg ha^{-1}) of Mg, Al, Cl, Ca, Mn and K in the forest floor, categorised according to the OH, OA and OF horizons.

Horizon	Mg	Cl	Ca	Mn	K
OF	8.4 ± 0.9	10 ± 3	78 ± 21	4 ± 1	13.1 ± 0.4
OH	12 ± 2	12 ± 3	76 ± 21	2.6 ± 0.7	15.7 ± 0.7
OA	37 ± 3	14 ± 3	114 ± 35	13 ± 2	47 ± 7

translocation of Mn from foliage towards the phloem, possible to a limited extent, as previously suggested by Greger (2004).

5. Simple compartment model

Although this study presents element comparisons between the different tree compartments, the turnover rates of the elements from one compartment into another cannot be directly measured (beyond conjecturing that they are probably slow in heartwood and very fast in phloem tubes). In other words, the only data that can be directly measured are the element concentrations themselves at a point in time and, in relative terms, the mass and concentration ratios between adjacent compartments.

A linear, first-order compartment model of the tree was developed in order to obtain some indication of the likely transfer rates (flow per unit mass, in d^{-1}) between vegetation compartments (Fig. 5). The model, which is a simplified version of Fig. 1 in that it does not include atmospheric input, has 5 compartments (foliage, wood, floor, roots and soil, linked to the observed element distributions) and 11 parameters (the inter-compartmental transfer rates). Since the model is designed to calculate numerically the inter-compartment kinetic transfer rates that would give rise to the observed element distributions, it is not a process-based but a rather simple empirical model.

To obtain a basic indication of the transfer rates, an iterative procedure was used. Initial values were chosen based on the model from Van den Hoof and Thiry (2012), originally designed for studying natural chlorine cycling in the same forest stand. Although some of the parameters are Cl-specific, many are based on general considerations (interception, translocation and leaching rates, rate of canopy weathering, litterfall, the ratio of xylem/phloem nutrient fluxes in the plant and the balancing of root absorption to the tree water demand). These considerations, which combine plant physiology and the water cycling/hydrology of the site, generally allow initial 'best-guess' transfer rate values to be deduced for other elements.

The data which were not known were typically the input from litter to soil, which is a measured flux. Here, we assumed that the uptake rate equals the litterfall rate, requiring an assumption that uptake through foliage is less important. Then, the model was run with an initial condition of zero element content in the different compartments except soil until every pool reached equilibrium (defined as when the net uptake – the uptake minus what passes to the next pool – reaches zero). The uptake rates were modified iteratively until the deviation between the simulated content in the model compartments and the experimentally measured content in forest floor, soil, roots, wood and foliage reached a minimum level. Given the possibility of different mathematical solutions, this calculation is only illustrative, to give an insight on the different transfer processes involved.

The model structure of Fig. 5 is a simplified version of a previous model for ^{36}Cl in pine trees (Van den Hoof and Thiry, 2012), made sufficiently simple and general to cover the other elements. Aluminium modelling was not attempted due to lack of concentration data for this element in soil, caused by primary interferences in measurements. The simple model from Fig. 5 is based on the assumption that there is no external input of the elements into the forest (closed ecosystem). It is further assumed that the transfer rates from a donor to an acceptor compartment are constant in respect of time and depend on the element mass (kg ha^{-1}) in the donor compartment, assuming a tree density of 359 trees per hectare typical of *P. sylvestris* in the Mol forest stand (Van den Hoof and Thiry, 2012).

For model development, soil, representative forest floor and root data with which to estimate the input flux are needed, and these are shown in Table 7 (soil) and Table 8 (forest floor).

Obvious limitations of this simple model are that it does not account for biomass growth and excludes atmospheric input, owing to data availability issues, known to result in underestimation of content for the needle and floor compartments in airborne elements. A reason for not including atmospheric deposition is the preference for a uniform model for simple calculation of transfer rates which in any case is only intended to give an indicative estimate. A further limitation of this approach, which should always

Table 9
Model-fitted inter-compartment transfer rates and mass flows for different elements.

From	To	Transfer rate (d^{-1})					Mass flow (kg ha^{-1} y^{-1})				
		Mg	Cl	Ca	Mn	K	Mg	Cl	Ca	Mn	K
Floor	Roots	5.00E−06	1.20E−05	5.00E−05	6.00E−05	9.00E−05	0.10	0.15	4.82	0.45	2.51
Floor	Soil	3.60E−05	2.00E−05	6.10E−05	3.50E−05	2.10E−04	0.74	0.25	5.88	0.26	5.85
Foliage	Floor	1.20E−03	5.00E−04	3.00E−03	2.10E−03	1.60E−03	0.67	0.26	8.95	0.50	6.54
Foliage	Wood	4.00E−04	3.00E−04	1.00E−04	2.00E−03	7.00E−04	0.22	0.16	0.30	0.47	2.86
Roots	Floor	5.00E−05	1.00E−04	6.00E−05	9.00E−04	5.50E−04	0.07	0.11	0.30	0.19	1.68
Roots	Soil	5.00E−05	1.00E−04	6.00E−05	9.00E−04	5.50E−04	0.07	0.11	0.30	0.19	1.68
Roots	Wood	7.50E−04	5.00E−04	2.20E−03	5.20E−03	3.20E−03	1.00	0.55	10.92	1.10	9.76
Soil	Roots	2.30E−06	1.80E−06	2.80E−06	2.00E−06	6.20E−06	0.81	0.36	6.21	0.45	7.53
Wood	Floor	1.40E−05	3.00E−05	3.20E−05	1.40E−05	1.00E−05	0.11	0.03	1.48	0.02	0.13
Wood	Foliage	1.10E−04	4.00E−04	2.00E−04	5.50E−04	7.00E−04	0.89	0.42	9.27	0.98	9.40
Wood	Roots	2.70E−05	2.50E−04	1.00E−05	3.20E−03	2.30E−04	0.22	0.26	0.46	5.70	3.09

Table 10
Litterfall, uptake and leaching data (kg ha^{-1} dry mass^{-1}) simulated for our investigated plot with a forest density of 432 trees ha^{-1}, an average tree age of 55 years and a basal area of 24.4 m^2 ha^{-1}.

Translocation	Mg	Cl	Ca	Mn	K
Litterfall	0.78	0.29	10.43	0.52	6.67
Uptake	0.91	0.51	11.03	0.9	10.04

be taken into account in reverse modelling, is that there is not one unique combination of transfer rates that will generate the model output. This can only be improved upon by proper mechanistic modelling, which is the object of a follow-up study currently underway.

6. Transfer rates

The transfer rates (d^{-1}) between different compartments (soil, roots, wood, foliage and floor) are given in Table 9. These transfer rates were multiplied by the mass of a specific element present in the donor compartment, giving the mass flow (kg ha^{-1} d^{-1}) to the acceptor compartment for the system. The annual mass flow (kg ha^{-1} y^{-1}) is also shown in the Table 9. The mass flows inputting and exiting each compartment should cancel in the equilibrium state (mass balance). This was checked satisfactorily.

7. Mass flow

The calculated annual mass flows (kg ha^{-1} y^{-1}) were compared to other studies (Tables 11 and 12). This comparison is for illustration purposes only, because there are physiological differences between the species considered and they do not always grow on the same soil types. Compared to the mass flows for litterfall measured by other authors, given in Table 11, our values (Table 10) tend to be within published ranges.

For Mg, the mass flow for litterfall is rather low, but close to the values found elsewhere (Helmisaari, 1995; Paavilainen and Päivänen, 1995), both studying *P. sylvestris*. The amount of Ca that is returned to the floor through litterfall is somewhat high compared to these studies, but other studies (Gholz et al., 1985; Kavvadias et al., 2001) show that this is not a particularly abnormal deviation. The mass flow for litterfall of Mn is very similar to the observations of Helmisaari (1995). The values for K are high compared to Helmisaari (1995) and Paavilainen and Päivänen (1995), but compared to the other pines, not remarkably high. For the mass flow of Cl via litterfall, no observations were available for comparison.

8. Conclusions

In our study, we have encountered large differences between how Ca, Cl, K, Mn and Mg are taken-up by and redistributed within Scots pine trees. We have suggested biological mechanisms that may explain these processes. The relative mass distribution results show that Ca, Mn and Mg are mainly present in the woody compartments. This is partly explainable because Ca has a structural role in woody tissues and Mn participates in the synthesis of lignin. The presence of Mg in the woody compartments is more difficult to explain. Conversely, Cl and K are more present in the needles as these elements are both involved in opening the stomata. Cl also participates in the water splitting during the photosynthesis process. Ca and K are the principal elements. The wood compartments have generally low element content, as does the outer bark except for Ca. The inner bark, twigs and needles have high element contents (especially Ca and K) possibly linked to the high symplasmic content. The Inner bark in particular shows high Ca and K

Table 11
Litterfall data (kg ha^{-1} dry mass^{-1}) for *Pinus sylvestris* with varying forest density, tree age and basal area.

Density (trees ha^{-1})	Age (y)	Basal area (m^2 ha^{-1})	Study	Litterfall (kg ha^{-1} dry mass)				
				Mg	Cl	Ca	Mn	K
432	100	25.7	Helmisaari, 1995	1.05	–	6.11	0.55	1.52
Ombrotrophic site			Paavilainen and Päivänen (1995)	1.12	–	8.64	1.23	1.37
Minerotrophic site			Paavilainen and Päivänen (1995)	1.44	–	6.93	0.91	1.08

Table 12
Tree uptake data (kg ha^{-1} dry mass^{-1}) for *Pinus Sylvestris* with varying forest density, tree age and basal area.

Density (trees ha^{-1})	Age (y)	Basal area (m^2 ha^{-1})	Study	Tree uptake from soil (kg ha^{-1})				
				Mg	Cl	Ca	Mn	K
432	100	25.7	Helmisaari, 1995	4.23	–	7.47	0.84	11.91
Ombrotrophic site			Paavilainen and Päivänen (1995)	4.20	–	18.10	1.59	10.50
Minerotrophic site			Paavilainen and Päivänen (1995)	2.24	–	11.93	0.72	4.56

contents as these elements are involved in phloem transport. Positive correlations between different elements almost certainly indicate similarity in chemical and biological function.

The mobility of an element within the vegetation compartments is deduced from inter-compartment ratios. This enables us to distinguish between two groups: Cl, Mg and K, which have rather low inter-compartment ratios, and Ca and Mn, for which the ratios are higher. A high ratio is also obtained for Al, which is toxic in high amounts and will be translocated to compartments where it will be blocked to avoid toxicity, resulting in high inter-compartment ratios for this element.

A simple compartment model has been used to calculate element transfer rates and mass fluxes within plant compartments. These transfer rates are undoubtedly affected by xylem loading processes, nutritional requirements of the various plant organs, photosynthesis and depuration of contaminants. The model developed, although simple and not mechanistically based, gives results broadly consistent with several studies on pine trees.

An output of this study (with work currently underway) is the coupling of specific elements (including radionuclides) to the elements covered considered herein (Ca, K, Mg, Al, Cl and Mn), for the purposes of modelling. It is possible to assume, on the basis of analogue chemical behaviour, that these elements follow the same pathways. For example, the nuclear industry-sourced radionuclides ^{90}Sr and ^{137}Cs (which are important from the perspective of environmental impact) can be coupled to Ca and K, and on that basis one can deduce that they would accumulate in young needles and inner bark with some presence of ^{90}Sr in the outer bark. This is actually observed in *P. sylvestris* from the Chernobyl Red Forest (Thiry et al., 2009).

Likewise, the radionuclide ^{36}Cl, which is of potential concern for long-term management of radioactive wastes, can be directly linked to the flux of stable Cl and in this way we could conclude that it is less present in heartwood and sapwood and more established in the foliage (needles). A previous ^{36}Cl modelling study (Van den Hoof and Thiry, 2012) indeed shows that the foliage has the largest chlorine concentration (some 35% of the total chlorine present in the tree).

Similar analogies could be made between radionuclides and the stable elements Mg, Al and Mn, making it possible to develop a model describe a forest stand in a way that helps us understand the cycling of radionuclides in a forest ecosystem. Other links are also possible with chemical pollutants, such as heavy metals, signalling the direction for future investigations.

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Validation of the ALARO-0 model within the EURO-CORDEX framework

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Abstract. Using the regional climate model ALARO-0, the Royal Meteorological Institute of Belgium and Ghent University have performed two simulations of the past observed climate within the framework of the Coordinated Regional Climate Downscaling Experiment (CORDEX). The ERA-Interim reanalysis was used to drive the model for the period 1979–2010 on the EURO-CORDEX domain with two horizontal resolutions, 0.11 and 0.44°. ALARO-0 is characterised by the new microphysics scheme 3MT, which allows for a better representation of convective precipitation. In Kotlarski et al. (2014) several metrics assessing the performance in representing seasonal mean near-surface air temperature and precipitation are defined and the corresponding scores are calculated for an ensemble of models for different regions and seasons for the period 1989–2008. Of special interest within this ensemble is the ARPEGE model by the Centre National de Recherches Météorologiques (CNRM), which shares a large amount of core code with ALARO-0.

Results show that ALARO-0 is capable of representing the European climate in an acceptable way as most of the ALARO-0 scores lie within the existing ensemble. However, for near-surface air temperature, some large biases, which are often also found in the ARPEGE results, persist. For precipitation, on the other hand, the ALARO-0 model produces some of the best scores within the ensemble and no clear resemblance to ARPEGE is found, which is attributed to the inclusion of 3MT.

Additionally, a jackknife procedure is applied to the ALARO-0 results in order to test whether the scores are robust, meaning independent of the period used to calculate them. Periods of 20 years are sampled from the 32-year simulation and used to construct the 95 % confidence interval for each score. For most scores, these intervals are very small compared to the total ensemble spread, implying that model differences in the scores are significant.

1 Introduction

The climate projections used in the Fifth Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (IPCC, 2013) are based on the set of global climate model (GCM) simulations performed within the fifth Coupled Model Intercomparison Project (CMIP5; Taylor et al., 2011). The horizontal resolution of the contributing GCMs is limited to typically 1–2° by computational constraints. For many local climate impact studies, regional climate models (RCMs; Giorgi and Mearns, 1999) are needed to reveal the fine-scale details of potential climate change (Teutschbein and Seibert, 2010). In addition, specific downstream models which simulate processes such as vegetation interactions, urban effects (e.g. Hamdi et al., 2015) or extreme hydrological events in river catchments often require high-resolution (both in time and space) forcing data from atmospheric models.

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The Coordinated Regional Climate Downscaling Experiment (CORDEX; Giorgi et al., 2009) aims to perform both empirical–statistical downscaling and regional climate simulations on different areas across the globe using an ensemble of RCMs. By prescribing several integration domains and resolutions, a direct quantitative comparison between the participating models' performances and projections is feasible. The domain of interest in this study, is the EURO-CORDEX domain shown in Fig. 1 (inner orange box). Several RCM groups have performed simulations on this domain with horizontal resolutions of both 0.11 and 0.44°.

All RCMs have a history in Numerical Weather Prediction (NWP) and often consist of a modified NWP code which is further developed separately from or parallel to the NWP code, borrowing for example its dynamical core but using different physics parameterisations or surface schemes (Dudhia, 2014). In the present day, NWP limited area models (LAMs) are designed for resolutions down to a few kilometres, with adapted physics parameterisation schemes. At even higher resolutions, these models can (partly) resolve clouds and convective systems. Since a correct treatment of the cloud feedback is of critical importance for climate modelling (e.g. Sun et al., 2009; Lin et al., 2014), some of these NWP models have been used in climate mode: studies by De Meutter et al. (2015), Hohenegger et al. (2008), Kendon et al. (2012) and Chan et al. (2014), where models with resolution at the kilometre scale are used without convection parameterisation, show a better representation of the intensity of extreme precipitation, the diurnal cycle, afternoon convection onset and less drizzle. For instance, ALADIN-CLIMATE of the Centre National de Recherches Météorologiques (CNRM; Spiridonov et al., 2005) is a climate version of the ALADIN limited area model that has been developed in the context of the international ALADIN consortium (ALADIN international team, 1997).

Over the past decade, within the context of the ALADIN consortium, a physics parameterisation scheme called 3MT (Modular Multiscale Microphysics and Transport) has been developed and used as the central feature of a new NWP model, ALARO-0 (Gerard and Geleyn, 2005; Gerard, 2007; Gerard et al., 2009). It is based on a parameterisation of deep convection and optimally adapted to be used at resolutions in the so-called grey zone. Several countries have used and tested the model for operational weather forecasting and regional climate studies. The main feature of 3MT is scale awareness, i.e. the parameterisation itself works out which processes are unresolved at the current resolution, in contrast to traditional parameterisations which are switched on or off or have different tuned parameter values at different resolutions. This allows 3MT to generate consistent results across scales, as shown by De Troch et al. (2013) in an extended downscaling experiment covering the period from 1961 to 1990. In their study, for every day, short-term simulations were performed at different horizontal resolutions between 40 and 4 km. Both the initial and lateral boundary conditions were provided by either the ERA-40 reanalysis (Uppala et al., 2005) or model simulations at a lower resolution in a double nesting procedure. Given the large amount of required computing resources for such a simulation, this type of validation is rather unusual for NWP models. The results showed that extreme precipitation values are correctly and consistently reproduced for all horizontal resolutions by a model version including 3MT, whereas extreme precipitation was progressively overestimated when increasing the resolution by a model version without 3MT.

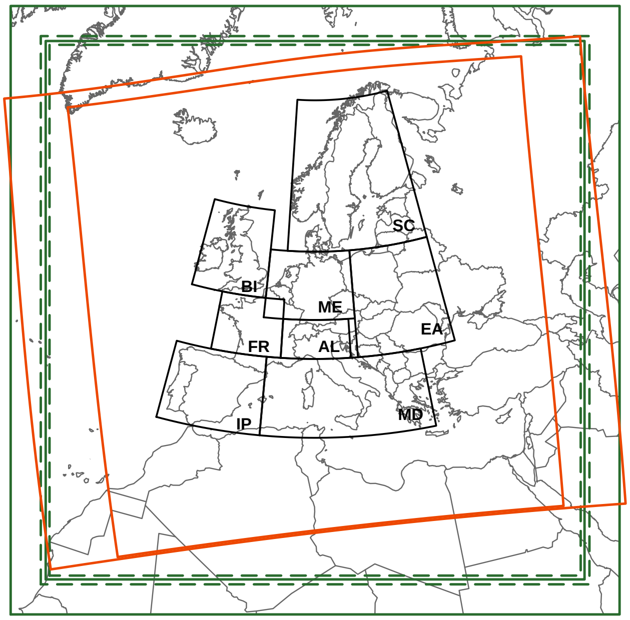

Figure 1. Domain boundaries of the used integration grids. The CORDEX community prescribes the rotated lat–long EURO-CORDEX domain (inner orange box) which is completely encompassed by the E-OBS domain (outer orange box). The outer green boxes show the RMIB-UGent-11 (dashed lines) and RMIB-UGent-44 (full lines) conformal Lambert domain boundaries. The inner green boxes exclude the eight grid point Davies coupling zone. In black the different European climatic regions as defined in Christensen and Christensen (2007) are shown (BI: the British Isles, IP: the Iberian Peninsula, FR: France, SC: Scandinavia, ME: mid-Europe, AL: the Alps, MD: the Mediterranean, EA: eastern Europe).

In the present study the ALARO-0 model has been used to perform the EURO-CORDEX validation simulations, i.e. the conditions of ERA-Interim reanalysis (Dee et al., 2011) is used as lateral boundary conditions allowing for a direct comparison to observations. The model setup differs from the setup used in De Troch et al. (2013), since in the current study simulations are initialised on the 1 January 1979, after which they are only forced at the boundaries by ERA-Interim. This allows the model and its surface fields in particular to become independent of the initial state. Results are then compared to an ensemble of 17 other EURO-CORDEX experiments which have been evaluated in Kotlarski et al. (2014), which we will refer to as K14 from now on. In K14, seasonal means of near-surface air temperature and precipitation amounts are compared to observations using several metrics which quantify the spatiotemporal performance of the ensemble. In their article, they evaluate the 20-year period 1989–2008, while for this study the 32-year period 1979–2010 was simulated.

The objective of the present work is (1) to quantify the performance of the ALARO-0 model within the existing K14 ensemble and (2) to assess the robustness of the calculated scores given the rather short 20-year period used in K14.

This paper is organised as follows. In Sect. 2, the existing K14 ensemble, details on the setup of ALARO-0 and the methods used to attain the goals of this paper are discussed. In Sect. 3, results are presented for ALARO-0 and compared to the K14 ensemble, followed by a discussion in Sect. 4. Finally, in Sect. 5, we come back to the goals that were set, formulate conclusions and present an outlook.

2 Data and methods

K14 ensemble

The CORDEX community prescribes two European integration grids which differ only in resolution. The low-resolution EUR-44 domain's grid points are 0.44° apart on a rotated lat–long grid limited to Europe (see inner orange box in Fig. 1, 106 × 103 grid boxes). For the high-resolution EUR-11 experiment, each EUR-44 grid box is divided into 16 0.11°-wide grid boxes. In K14, a total of 17 experiments were analysed by 9 different research groups. Eight groups performed both the EUR-11 and EUR-44 simulations, one group only EUR-11, and three groups used the same model (WRF) but with different physics parameterisations. All models are forced directly by ERA-Interim except for the experiment performed by CNRM. This group set up the global model ARPEGE (version 5.1) to be strongly nudged towards ERA-Interim outside of the CORDEX domain, but allowed the model to evolve freely inside of it. Further details on all models can be found in Table 1 of K14.

The main conclusions of K14 were that the higher resolution simulations did not perform significantly better and the models in the ensemble generally had a cold and wet bias, except for summers in southern Europe which are commonly warm and dry biased.

Setup of the ALARO-0 model

The ALARO-0 model used for this study is the identical configuration of the ALADIN system (ALADIN international team, 1997) described in detail and validated by De Troch et al. (2013). Essentially, ALARO-0 uses the dynamical core of ALADIN, but with different physics routines (e.g. for radiation, microphysics and convection, cloudiness, turbulence), which are designed to tackle the issues that arise when using resolutions of 1–15 km, which is known as the grey zone for convection. Here, we only describe the EURO-CORDEX specific setup of the model, which is the coupling to the boundary conditions and the definition of the integration grids.

Similar to all other models in K14 (except for the global CNRM model), ALARO-0 is coupled to ERA-Interim by the classical Davies procedure (Davies, 1976). The relaxation zone consists of eight grid points irrespective of resolution, and new boundary conditions are provided every 6 hours. No further nudging or relaxation towards the boundary conditions was done inside of the domain. Some fields in ALARO-0 are constant during runtime, most notably sea surface temperatures (SSTs). Simulations are, however, interrupted and restarted monthly to allow for SSTs to be updated. Other fields that have monthly updates, but are constant during any given month are surface roughness length, surface emissivity, surface albedo and vegetation parameters. All other variables were computed continuously from 1 January 1979 to 31 December 2010 and thus, in contrast to De Troch et al. (2013), no daily restarts were done.

It would be preferable to use the exact rotated lat–long grids defined by the CORDEX community for the simulations. However, ALARO-0 does not support this projection but instead uses a conformal Lambert projection. Following the CORDEX guidelines, two new grids with a 12.5 and 50 km resolution were defined for the ALARO-0 simulations. Figure 1 shows the bounding boxes of the low-resolution (full green lines) and high-resolution (dashed green lines) ALARO-0 Lambert domains. The outer boxes show the complete domain, while the inner boxes exclude the relaxation zone. The grids were chosen such that the common EURO-CORDEX analysis domain (inner orange box in Fig. 1) is completely included in the non-coupling zone. The low-resolution Lambert domain consists of 139-by-139 grid points, while the high-resolution domain consists of 501-by-501 grid points (both including eight coupling grid points at every boundary). In both simulations, the number of vertical levels was 46. Following K14, we will refer to the results with the acronym of the institute performing the simulations, yielding RMIB-UGent-11 and RMIB-UGent-44, for the high- and low-resolution simulations, respectively. These model data will be uploaded to the Earth System Grid Federation (ESGF, website: http://esgf.llnl.gov/) data nodes.

Data

As an observational reference set, the E-OBS data set version 7 was used (Haylock et al., 2008). The E-OBS data set has a 0.22° rotated lat–long version (outer orange box in Fig. 1) which encompasses the complete EURO-CORDEX domain. In the overlapping area, each E-OBS grid box contains four grid boxes of the EUR-11 domain and by consequence each EUR-44 box contains four E-OBS boxes.

In order to effectively compare model and observations, both need to share a common grid. The same approach as in K14 was taken to interpolate all data to a common grid. For the high-resolution simulations, first the values of the closest grid point were taken to go from the native Lambert ALARO-0 grid to the EUR-11 grid for both precipitation and temperature. For the latter, an additional height difference correction between the ALARO-0 and closest EUR-11 grid point was performed using the standard climatological lapse rate of $0.0064\,\mathrm{K\,m^{-1}}$. Second, on this grid, for both precipitation and temperature, two-by-two grid box averages were calculated to obtain an identical grid to the E-OBS data set.

For the low-resolution simulations, again a closest grid point mapping from the native grid to the EUR-44 grid and temperature-height correction was performed. Then, the E-OBS data set was averaged over two-by-two grid boxes that are in every EUR-44 grid box and used as reference.

Analysis methods

In K14, model performance is quantified for several metrics in different regions and seasons based on seasonal mean values of near-surface air temperature (or simply temperature from now on) and precipitation. All considered regions and their acronyms are shown in Fig. 1 and details regarding the definition of the different metrics can be found in K14, more specifically in Appendix A. Here, we only consider mean bias (BIAS), 95th percentile of the absolute grid point differences (95 %-P), ratio of spatial variability (RSV), pattern correlation (PACO), ratio of interannual variability (RIAV) and temporal correlation of interannual variability (TCOIAV). The climatological rank correlation (CRCO) and ratio of yearly amplitudes (ROYA) were not considered here, since these metrics showed very similar performance for all other models. Reanalysis forced simulations are by construction correlated with the observed weather at the seasonal timescale. For this reason, low correlation in time, even for short time periods, can be interpreted as an RCM deficiency for these simulations. This is not true for GCM-driven simulations, where only the correct number of occurrences in a certain time period (typically 30 years) are supposed to be represented and correlations at the shorter-than-decadal scale are meaningless due to strong interannual variability. Therefore, we expect TCOIAV to be positive for the simulations in this study, i.e. relatively cold/warm seasons in the simulations should coincide with relatively cold/warm observed seasons, while for GCM-driven simulations TCOIAV is expected to be zero. By contrast, all other scores should be similar for reanalysis-driven and GCM-driven RCM simulations if the GCM boundary conditions sufficiently represent the observed climatology. Due to realistic boundary conditions from reanalyses, the typical 30-year verification period for GCM-driven simulations can be shortened to 20 years, as in K14 where all scores are calculated based on the period 1989–2008. However, as the authors of K14 state, this implies that the "short evaluation period, leading to a sample size of only 20 seasonal/annual means, also hampers a sound analysis of statistical robustness". The 32-year long integration period of ALARO-0 allows us to quantify how the scores change for different 20-year analysis periods and as such to test their robustness.

A jackknife procedure was applied for this purpose; let $\mathcal{I} = \{1979, \ldots, 2010\}$ be the set of 32 years for which the ALARO-0 simulations were performed and I a random subset of length 20 of $\mathcal{I}$. We write the score for the metric s for a certain subregion j and season k based on the set of years I as $s_{jk}(I)$ with $j \in \{$BI, IP, FR, ME, SC, AL, MD, EA$\}$, $k \in \{$DJF: winter, MAM: spring, JJA: summer, SON: autumn, YEAR: year$\}$. For example, in K14, values for s_{jk} are calculated based on $I_{\mathrm{K14}} = \{1989, \ldots, 2008\}$. To study the robustness of s_{jk} we study the distribution of $s_{jk}(I)$ for all possible I. The number of possible 20-year subsets from 32 years without repetition and ordering is given by the binomial coefficient: $32!/(20!(32-20)!) = 225\,792\,840$. It is, however, not feasible to perform the calculations for all possible combinations and therefore only 1000 random sequences were chosen. The width of the 95 % confidence interval, limited by the 25th and 975th value of the ordered series of s_{jk}, then quantifies the robustness of the score.

3 Results

3.1 Temperature

Figure 2 shows the spatial distribution of the daily mean temperature RMIB-UGent-11 BIAS in winter (DJF, left) and summer (JJA, right) for the years in I_{K14}. Compared to Fig. 2 from K14, the spatial bias of RMIB-UGent-11 in winter looks very similar to CNRM-11. Both models show a general cold bias in southern Europe, a warm bias in north-eastern Europe and a large east–west bias gradient linked to orography in Scandinavia. Compared to CNRM-11, the cold biases in mountainous regions are smaller for RMIB-UGent-11. In summer, again CNRM-11 and RMIB-UGent-11 share some biases although the difference is larger than in winter, and again the orographic forcing of the bias of CNRM-11 is more pronounced. Generally we find a cold bias, except in southern Europe where a warm bias is present.

Figure 3 shows all metrics in separate columns for all different domains and seasons for seasonal and yearly mean temperature. The scale is shown at the bottom of each column, the full grey line shows the "optimal" score of the metric (0 K for BIAS and 95 %-P, 1 for all others). The grey circles show the scores for the high-resolution K14 ensemble (nine models). For each season and region, two transparent red bands are superimposed, which show the jackknife 95 % confidence interval for the high-resolution (top band) and low-resolution (bottom band) simulations with ALARO-0. The vertical red dashes show the value of $s_{jk}(I_{\mathrm{K14}})$,

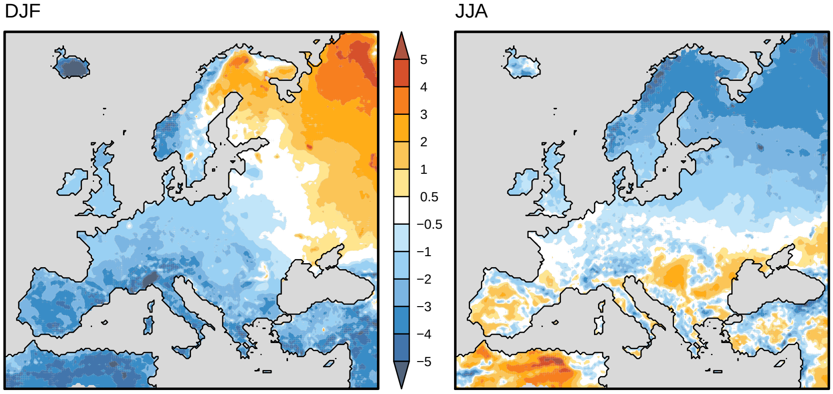

Figure 2. Spatial BIAS of near-surface air temperature (K) over the sample I_{K14} for DJF (left) and JJA (right) for RMIB-UGent-11. Compare to Fig. 2 of Kotlarski et al. (2014).

again for the high-resolution (top) and low-resolution (bottom) simulation. When the background colour is white, the RMIB-UGent-11 value of $s_{jk}(I_{\mathrm{K14}})$ lies within the K14 high-resolution ensemble spread. If the background colour is yellow, this value lies outside and is "worse" than the other members of the K14 ensemble. "Worse" means that the absolute distance from the RMIB-UGent-11 value based on I_{K14} (top red dash) to the optimal value (grey line) is larger than that of any other K14 ensemble member. For example, the bias for the Iberian Peninsula in winter (in short written as BIAS-IP-DJF) is more negative than any other model, and it is in absolute value the furthest from the optimal 0 K. If instead the background colour is green, this indicates again the value is outside of the K14 ensemble but not the furthest from the optimal value. This implies that either RMIB-UGent-11 outperforms all other models (e.g. RSV-AL-DJF) or is not the worst model as defined above (e.g. RSV-EA-DJF is outside of the K14 ensemble, but not as bad as models at the other end of the ensemble).

Overall, Fig. 3 shows that (i) RMIB-UGent-11 mostly falls within the K14 ensemble (white background colour), (ii) the jackknife confidence intervals are always much smaller than the total spread of the K14 ensemble, except for RIAV and TCOIAV where the intervals often cover half of the ensemble spread, (iii) the difference between the RMIB-UGent-11 (top red dash) and RMIB-UGent-44 (bottom red dash) scores is very small considering the total range covered by the ensemble and the calculated jackknife confidence intervals.

A more detailed analysis shows that for BIAS, RMIB-UGent is almost always on the "cold side" of the K14 ensemble and even outside of its range on a fairly large amount of occasions. Especially for IP-DJF and SC-MAM, the cold bias is considerable. Also, RMIB-UGent-44 is slightly (~ 0.2 K) colder than RMIB-UGent-11, which may be due to regridding and the resolution difference. For 95 %-P, RMIB-UGent-11 is the worst model on four occasions among which most notably again are IP-DJF and SC-MAM.

For spatial correlation (PACO) and variability (RSV) RMIB-UGent-11 performs better. Although in K14 these two metrics are plotted on a Taylor diagram, we choose to show them here separately in one figure for clarity and conciseness. RSV for RMIB-UGent is almost always larger than 1, even where other models show less variability (e.g. ME). In the Alpine region (AL), RMIB-UGent seems to be able to grasp RSV well, but not at the right locations, as shown by the low PACO, especially in DJF. The jackknife confidence intervals are very small here, which indicates that both RSV and PACO produce very robust scores.

For RIAV and TCOIAV, RMIB-UGent again shows acceptable scores, some being outside of the K14 ensemble in a limited amount of cases. More notably, the jackknife confidence intervals are relatively large for these scores and this questions the robustness of these metrics. For example, for FR-MAM the TCOIAV based on I_{K14} is 0.6, but the jackknife confidence interval extends from 0.6 to 0.8, covering all but two other models. For RIAV a similar situation for AL-JJA can be seen.

3.2 Precipitation

Figure 4 shows the spatial distribution of the relative seasonal precipitation BIAS (in %, (model − observed)/observed) for the winter and summer season for the years in I_{K14}. Comparison to Fig. 3 of K14 shows that in winter, like all other models, RMIB-UGent-11 generally overestimates precipitation amounts, except in northern Africa. In contrast to temperature, RMIB-UGent-11 clearly differs from CNRM-11, with the latter showing large dry biases. In summer, RMIB-UGent-11 overestimates precipitation amounts, especially in the Mediterranean. Again, no clear resemblance to CNRM-11 is found.

Figure 5 is constructed in the same way as Fig. 3 and shows all precipitation scores for all different metrics, regions and seasons. Similar to the temperature scores, the results for precipitation reveal that the majority of scores

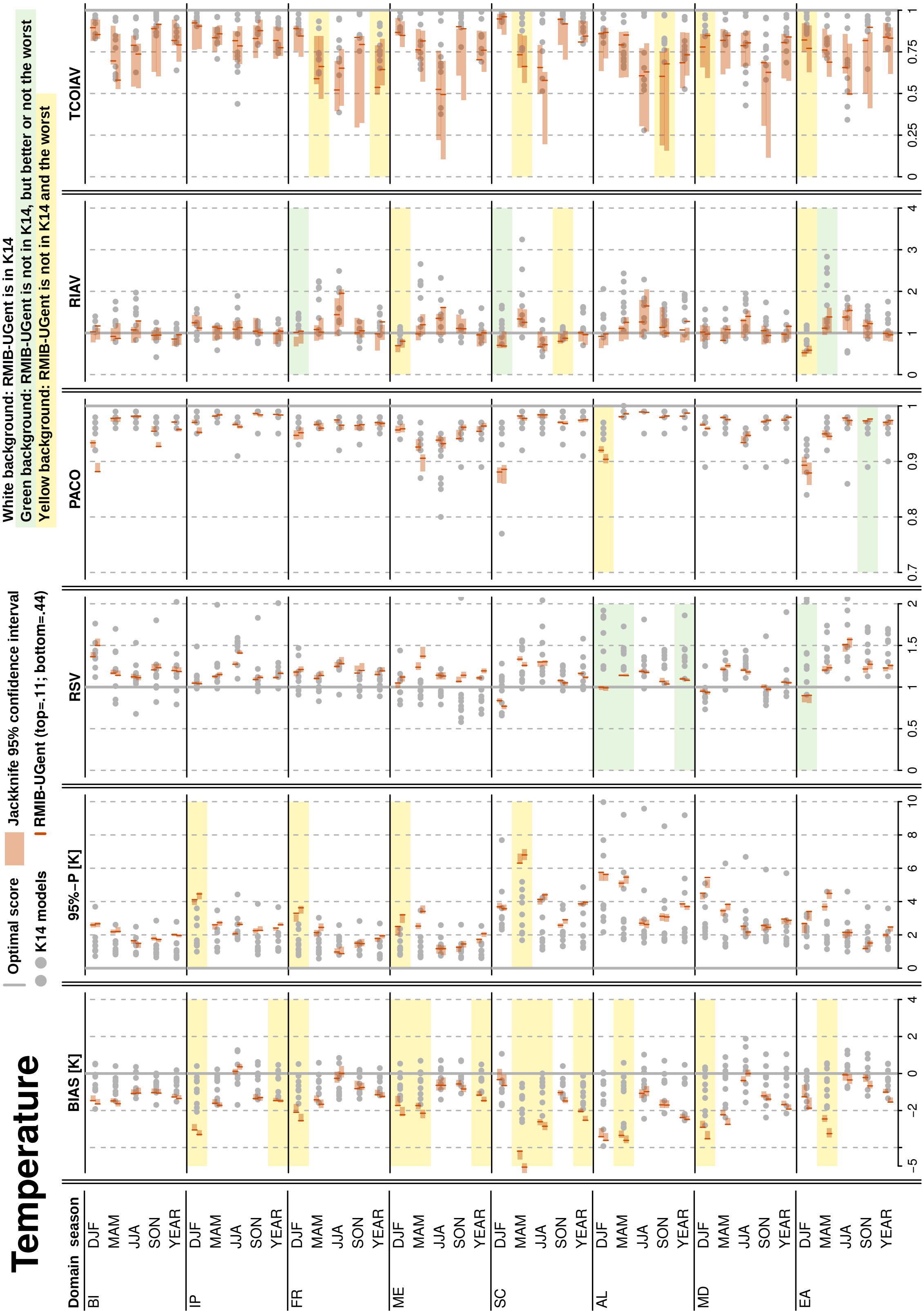

Figure 3. Scores for near-surface air temperature for all domains (first column), seasons (second column) and metrics.

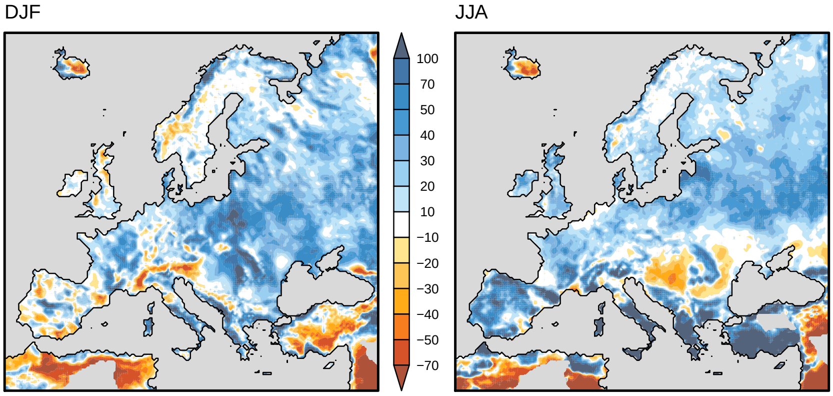

Figure 4. Spatial BIAS of precipitation (%) over the sample I_{K14} for DJF (left) and JJA (right) for RMIB-UGent-11. Compare to Fig. 3 of Kotlarski et al. (2014).

lie within the K14 ensemble, no difference between RMIB-UGent-11 and RMIB-UGent-44 is found and the jackknife confidence intervals are much smaller than the total ensemble range except for RIAV and TCOIAV. However, there is a clear absence of yellow scores and an increased presence of green scores, indicating that RMIB-UGent precipitation scores are generally better than the temperature scores.

RMIB-UGent has a wet BIAS for almost all regions and seasons. Remarkably, the best BIAS scores are obtained for SC-MAM and AL-DJF, where large temperature biases were found. Additionally, the corresponding 95 %-P scores are also on the low side which shows that the good performance is not due to compensating biases.

For RSV, RMIB-UGent performs relatively well and for PACO it excels, with 10 out of 80 region–season combinations performing better than the complete K14 ensemble. Only for AL-MAM is its performance not satisfactory, but remark that the actual score is an extreme outlier considering the jackknife confidence interval.

For RIAV, RMIB-UGent again performs consistently well, especially compared to the K14 ensemble which sometimes shows a large overestimation of interannual variability, i.e. very large values of RIAV. On the other hand, TCOIAV is mostly on the low side of the K14 ensemble, which shows that although RMIB-UGent gets the variability right, the actual temporal correlation is not well grasped. As for temperature, the large jackknife confidence intervals question the robustness of the scores.

4 Discussion

This is the first time ALARO-0 was used for a climate experiment. Nevertheless, the performance of ALARO-0 on seasonal and yearly scales for both near-surface air temperature and precipitation is satisfactory. Generally ALARO-0 performs well, which is quantified by the large number of white boxes in Figs. 3 and 5 indicating that the ALARO-0 score lies within the existing K14 ensemble. For precipitation, ALARO-0 even outperforms all other models on numerous occasions. These results are encouraging, given that ALARO-0 does not yet have the experience in climate modelling that some of the other models of the K14 ensemble had, but was directly ported from its NWP setup. Although the 12.5 km resolution was also a novelty for the K14 models, their performance undoubtedly benefited from previous optimisations for climate experiments, albeit at a lower resolution of 50 km.

Some issues still remain. Most notably, this study has revealed some large temperature biases in Scandinavia and eastern Europe. The spatial pattern of the BIAS resembles CNRM's ARPEGE model (shown in Fig. 2 of K14). In winter, the common east–west bias gradient can possibly be attributed to the shared dynamical core and the strong synoptic scale forcing in winter. In NWP applications of the ALADIN system similar symptoms have been diagnosed and have been shown to be related to stable boundary layer issues. The dampened bias patterns for RMIB-UGent-11 compared to CNRM-11 in the Alps and other mountainous regions is probably due to the different surface and snow cover scheme that is used by both. In summer, RMIB-UGent-11 is generally cold biased, except in southern Europe where it suffers from the common summer warm bias, probably due to soil moisture feedbacks. Also, the RMIB-UGent-11 and CNRM-11 bias patterns are less alike than in winter, possibly due to the increased number of local processes that influence and feed back into the mean fields. Both spatial and temporal variability are very well reproduced by ALARO-0, while correlations are on the low side compared to other models. The latter could partly be explained by the comparatively larger domain of ALARO-0 which could imply a weaker control of the boundary forcing.

For precipitation, ALARO-0 performs very well. Aside from some large wet biases in summer for the Iberian Peninsula (IP) and the Mediterranean (MD), biases are almost al-

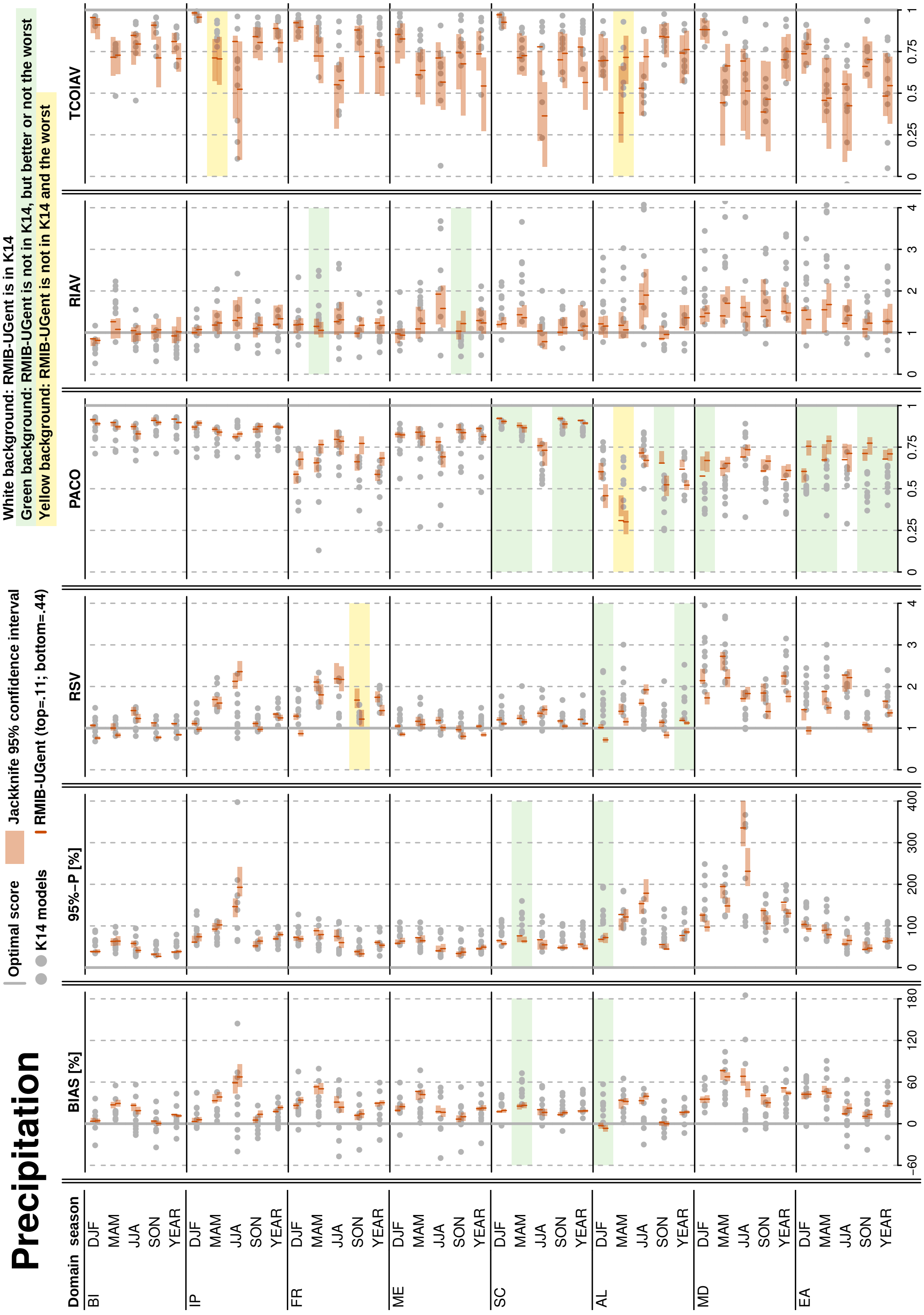

Figure 5. Scores for precipitation for all domains (first column), seasons (second column) and metrics.

ways below 50 %. Contrary to temperature, the precipitation bias pattern shows no resemblance to ARPEGE (shown in Fig. 3 of K14). This can be attributed to the different microphysics and convection parameterisation schemes that are used by both models. A similar result was found for the three WRF experiments that were analysed in K14. These only differed in the parameterisation schemes used, but often covered the complete ensemble spread. Remarkably, in Scandinavia all precipitation scores are very good, although temperature scores are sometimes very bad. It is very possible that the two are linked and some compensating effects or feedbacks exist, which is an additional incentive for a more thorough study. The good scores for spatial variability (RSV) and correlation (PACO) show that ALARO-0 is capable of producing not only the right amount of precipitation but also at the right locations. The common model overestimation of spatial variability is also present in the RMIB-UGent simulations, but as stated in K14, this could be due to a smoothing of the reference E-OBS data set. Temporal variability is very well reproduced, but correlations are again rather low.

Similarly to the conclusions in K14, no consistent difference between the low- and high-resolution simulations in the scores is shown. However, based on preliminary results, we expect that at the sub-daily scale the timing of precipitation is better represented by the high-resolution simulation.

Finally, it is clear that the period I_{K14} (1989–2010) used in K14 is sufficient to produce robust scores for BIAS, 95 %-P, RSV, PACO and partly RIAV. This is quantified by the fact that the jackknife intervals for these metrics are very small compared to the total ensemble spread and they therefore do not depend strongly on the period used to compute them. For example, temperature biases calculated for I_{K14} are mostly within 0.1 K of the jackknife mean. This does not hold for some RIAV and most of the TCOIAV scores due to the fact that these exactly assess interannual variability. For model intercomparison a larger period should be considered for these scores.

5 Conclusions

The ALARO-0 model has its origins in the general circulation model ARPEGE and mainly its limited area model ALADIN. The new microphysics and convection scheme 3MT was implemented in ALADIN to form ALARO-0, which is used operationally for daily weather forecasts at the Royal Meteorological Institute of Belgium (RMIB). In this study, for the first time ever, the ALARO-0 model was used to perform continuous climate simulations on a European scale for a 32-year period. Within the framework of the CORDEX project, one low- and one high-resolution simulation were done on the EURO-CORDEX domain for the period 1979–2010, using the ERA-Interim reanalysis as boundary conditions. The results are compared to an existing ensemble of 19 similar simulations using different models that were analysed in Kotlarski et al. (2014), referred to as K14 in this text. One of the models used in K14 is the ARPEGE model by the Centre National de Recherches Météorologiques (CNRM), which, due to its relation to ALARO-0, serves as a first reference for the performed simulations.

The main conclusions are that (1) ALARO-0 is able to represent both seasonal mean near-surface air temperature and accumulated precipitation amounts well and (2) all scores computed in K14 are robust, except for RIAV and TCOIAV.

The first conclusion is founded by the fact that most of the ALARO-0 scores lie within the K14 ensemble, thus not performing worse or better than other models. This is qualified in Figs. 3 and 5 by a white background. For temperature, some clear cold biases remain, which will be the subject of a follow-up study. Also, for temperature ALARO-0 seems to share some large biases with ARPEGE, while for precipitation this is not the case due to the inclusion of the 3MT scheme in ALARO-0. For precipitation, ALARO-0 performs very consistently for all scores, regions and seasons and better on several instances than all other models in the K14 ensemble.

In the second conclusion, robust means “independent of the time period used to compute the scores”. The RMIB-UGent simulations span the 32-year period 1979–2010, which is longer than the 20-year period 1989–2008 used in K14. By taking 1000 random 20-year samples from the 32-year pool, we computed 95 % confidence intervals for all scores. Figures 3 and 5 show that the confidence intervals (red transparent bands) are generally much smaller than the total ensemble spread. Assuming this also holds for other models, this shows that model differences are significant. For RIAV this does not always hold and a longer period should be taken into account to compute the scores. For TCOIAV the situation is even more problematic and scores or model ranking should not be interpreted too strictly.

The outcomes of this study confirm the potential of ALARO-0 as a climate model on European scales. Future work will focus on pinpointing the causes of some of the remaining biases and performing simulations in which ALARO-0 is driven by a GCM, rather than ERA-Interim.

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Variance decomposition of predictions of stem biomass increment for European beech: Contribution of selected sources of uncertainty

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ABSTRACT

The contribution of selected sources of uncertainty to the total variance of model simulation results of stem biomass increment – calculated from annual stem biomass predictions – of European beech (*Fagus sylvatica* L.) was quantified. Sources of uncertainty were defined as the selected variables that influence the total variance of the model results. Simulations were made: (i) for ten regional climate models (RCMs) based on the IPCC scenario A1B and providing an ensemble of climate projections up to 2100; (ii) with two forest model types (FMTYPEs); (iii) for four forest management intensities (MANFORs); and (iv) for three time windows (TIMEWINDs), each spanning 15 years, starting in 2019, in 2049 and in 2079. Both models, the empirical SIBYLA model and the process-based ANAFORE model, were calibrated using experimental tree growth data from four plots in central Slovakia between 1989 and 2003. Three of these plots, representing the four MANFORs, were subject to different prior intensities of thinning while one was left untouched as a control. The FMTYPE explained most of the total variance in the simulation results (39.9%), followed by MANFOR (i.e. thinning intensity; 22.2%) and TIMEWIND (12.0%), while the effect of RCMs on model uncertainty was limited (<1%). Stem biomass increment results obtained from the two FMTYPES were different in absolute terms, but the models agreed well in their relative response to RCM, to MANFOR and to TIMEWIND. The total variance of the predictions was 10 times higher for the process-based model (ANAFORE) than for the empirical model (SIBYLA). These observations are the reason for the large contribution of FMTYPE to the total variance of the simulated stem biomass increment results.

1. Introduction

As trees grow old, forests unavoidably face the impact of imminent climate change. Forest management measures can contribute significantly to mitigation of and adaptation to these environmental changes. Conventional statistical models implicitly based on the assumption of stationary conditions may not be applicable for forest management decisions, but novel and improved process-based models predict forest growth under changing conditions. Management plans developed using either type of model require appropriate risk assessments (Walker et al., 2003). Uncertainty analysis of forest model results is thus crucial to support management decisions. The model uncertainties partly originate from input variables, including data required for the model set-up and the calibration, as well as from climate and forest management predictions. Uncertainty is also associated with the model boundaries (i.e., the extent of the ecosystem complex covered by the model), with the model structure itself and with the model parameters (Jones, 2000; Reyer et al., 2013). Only a part of this model uncertainty, however, is reflected in the variance of the model results. Other sources of error may also contribute to model uncertainty, but may not be quantifiable: either because they are unknown or because they are not included in the model.

Forest models incorporate aspects of system complexity as well as the non-linear relations and the feedback mechanisms among

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the system drivers (Tian et al., 2012). Over the last three decades forest models have become more process-driven and they now incorporate a multitude of parameters (Landsberg, 2003; Matala et al., 2003). Process-based models (PBMs) integrate the mechanistic functioning of the ecosystem by reproducing the ecological and physiological processes that drive the system, as well as their responses to external factors (Landsberg, 2003; Kurbatova et al., 2008). PBMs are useful tools for understanding the dynamics of an ecosystem and they can provide answers to questions on how ecosystems should be managed under changing environmental conditions (Korzukhin et al., 1996; Matala et al., 2003; van Oijen et al., 2005). However, having a multitude of parameters does not necessarily guarantee that the model predictions will be reliable (Larocque et al., 2014). The complexity of PBMs can be a strength, but also a weakness, because they rarely provide a unique answer to a practical management question (Mohren and Burkhart, 1994; Sands et al., 2000; Matala et al., 2003; van Oijen et al., 2005). Model improvements can result from a better understanding of the internal processes of the system, e.g., carbon allocation processes, nutrient availability in soils, nutrient uptake by trees, and competitive interactions (Seidl et al., 2011b). A better knowledge of the external impacts and disturbances – often human-induced – as well as their dependence on site location is also required (Landsberg, 2003; Kearney and Porter, 2009; Seidl et al., 2011a). The feedbacks and compensating mechanisms between ecological drivers create challenges in model development (Ceulemans et al., 1999; Matala et al., 2005; Penuelas et al., 2008).

In contrast, empirically-based models (EBMs) are built on statistical relationships between forest growth and environmental variables obtained from field measurements (Fabrika, 2007; Hlásny et al., 2014; Pan et al., 2014). The choice of the forest model best suited for a particular research or management question is of crucial importance. Efforts have been made to combine the advantages of PBMs (theoretical understanding, flexibility, predictive power under changing conditions) and EBMs (robustness, limited input demand, ease of interpretation) by using multi-model inference (Hlásny et al., 2014) or by developing hybrid models (Makela et al., 2000; Baldwin et al., 2001; Peng et al., 2002; Girardin et al., 2008; Taylor et al., 2009).

When climate predictions provide an input for forest models, uncertainty is transferred from the climate model to the forest growth simulation (Lindner et al., 2014; Keenan, 2015). The uncertainties in regional climate predictions are caused by three sources: (i) the climate model uncertainty, which is resulting from the model structure and the parameterization and causes different responses to the same radiative forcing, (ii) the scenario uncertainty, which arises from the uncertainty in future environmental changes, as e.g. greenhouse gas emissions, and (iii) the internal variability, which is the inherent temporal randomness of climate in the absence of any radiative forcing (Hawkins and Sutton, 2009, 2010). The relative importance of these three sources of uncertainty changes with the spatial and temporal scale. The internal variability becomes more important with decreasing spatial scale and with an increased occurrence of extreme events (Lindner et al., 2014). Model uncertainty increases with longer prediction periods. Scenario uncertainty increases even more with lead time (Hawkins and Sutton, 2009). Uncertainties from regional climate models (RCMs) can be quantified by using an ensemble approach, combining the results of multiple models to give the statistical probability of possible future climates (Lindner et al., 2014). Beside the physiological aspects, the state of a forest – i.e., its extent, species composition and canopy structure – and its biogeographical location also affect its response to disturbance and vice versa (Allen et al., 2010; Seidl et al., 2011b; Jactel et al., 2012). The effects of forest state and forest history should be correctly understood and taken into account in forest simulation studies, especially for European forests that are generally intensively managed (Spiecker, 2003; Boisvenue and Running, 2006; De Vries et al., 2006; Solberg et al., 2009). It is important to correctly estimate the costs and the benefits of different forest management measures and to account for a wide range of forest situations and potential future climate conditions.

In this contribution we (i) quantified the variance coming from different sources of uncertainty on predictions of tree growth; (ii) tested the significance of these sources of uncertainty; and (iii) assessed the contribution of different RCMs to the total uncertainty in the climate predictions. So, this study only investigated the uncertainty of the model results and it did not consider the effects of the different sources of variance on the actual predictions.

In this study we have modelled the annual stem biomass increment (ASBI) of European beech (*Fagus sylvatica* L.), a dominant tree species in European forests and the most common deciduous species in central Europe (Dittmar et al., 2003). Drought-induced growth reduction and/or a decline of the species have been reported in southern Europe (Ciais et al., 2005; Jump et al., 2006; Piovesan et al., 2008; Bontemps et al., 2010; Charru et al., 2010; Kint et al., 2012; Zang et al., 2014), but for central Europe an accelerated growth has been reported (Pretzsch et al., 2014).

2. Materials and methods

2.1. Site description and sampling design

The forest site was located in the Kremnické Vrchy Mountains of the Western Carpathians, Slovakia (48° 38′ N, 19° 04′ E). The altitude ranged from 470 m to 510 m, with a total area of 4.5 ha having a slope with a western aspect and an inclination of 13–20%. The soil substrate consisted of andesite-tuff agglomerates and the soil type was Andic Cambisol with a high skeleton content (10–60%). During the measurement period (i.e., the calibration period) of 1989–2003 the annual average temperature was 8.6 °C and the average annual precipitation was 677 mm.

At the start of the 1989–2003 calibration period, the forest was 100 years old. Before 1989, it was managed according to usual forestry practice of less intensive thinning interventions from below (mostly the removal of damaged and low-quality trees). In the 30 years preceding the calibration period, the stand was thinned three times. In the period 1963–1972, 54 $m^3\ ha^{-1}$ were harvested from the stand. In the following two periods (1973–1982 and 1983–1988) the harvested thinning was 54 and 40 $m^3\ ha^{-1}$, respectively. European beech (*F. sylvatica* L.) was the dominant species (65–90%) in the forest stand, but hornbeam (*Carpinus betulus* L.), oak (*Quercus robur* L.) and fir (*Abies alba* Mill.) were also present. In February 1989 three plots of 0.35 ha each were established. These plots were subjected to strip shelterwood cutting of different intensities. The remaining number of trees per ha was respectively 160 for the heavily thinned plot (H), 243 for the medium thinned plot (M) and 397 for the lightly thinned plot (L). A fourth plot of 0.15 ha was left uncut as a control (C) with 700 trees per hectare. The thinning primarily focused on removing the interbreed species, dying and damaged trees, and trees of very low stem quality. Branches were left on the site to decompose naturally. More detailed information about the forest site and the forest management has been reported previously (Jamnická et al., 2007; Kellerová, 2009; Barna et al., 2010; Janík et al., 2011; Barna and Bosela, 2015).

During the calibration period (1989–2003) stem diameter at breast height (DBH) was measured annually using a diameter tape with a precision of 1 mm. Individual trees and measurement positions were clearly marked to minimize measurement errors. Tree height (h) was measured three times over the calibration period using a hypsometer (Silva, Clino Master, Sweden in 1989 and 1995; Vertex, Haglöf, Sweden in 2003). For all other years *h* was interpolated from these measurements. DBH and *h* were always measured for each individual tree. The volume (v) of stems and branches was estimated using national volume regression equations based on DBH and *h*. These equations were derived for 12 tree species from the large database assembled in the Czech and in the Slovak Republics (Petráš and Pajtík, 1991). Stem biomass was obtained from the calculated stem volume and the wood density of beech (Pajtík et al., 2009).

2.2. Climate data

For the 1989–2003 calibration period, daily temperature, precipitation and wind speed data were obtained from the meteorological station in the village of Sliač (5 km from the forest site). Nitrogen wet deposition was measured at the site by 10 funnel-shaped collectors established on the forest floor of each plot. NO_3 and NH_4 depositions were then obtained by spectrophotometry. For more details about the sampling method see Janík et al. (2014) and Dubová and Bublinec (2006). Past CO_2 concentrations were obtained from the global values published by Tans and Keeling (2014). Incoming radiation for the site was estimated using NOAA's JavaScript solar position calculator re-coded for Microsoft Excel (Pelletier, 2014).

In view of the limited spatial extent of the forest site under study, we followed the recommendation of Lindner et al. (2014) and used a regional (RCM) rather than a general (GCM) circulation model for making climate predictions. Different RCMs were run using the initial and boundary conditions provided by GCMs (Giorgi, 2006) to generate higher resolution meteorological fields. Because of this higher resolution, RCMs can resolve smaller scale features, such as topography and physical weather processes (Wang et al., 2004). Ten high-resolution daily RCMs were used, all disseminated within the framework of the European ENSEMBLES project (Van der Linden and Mitchell, 2009) and based on the same A1B scenario of IPCC (Moss et al., 2008). The A1B greenhouse gas emission scenario provides a balanced emphasis on all energy sources responsible for greenhouse gas emissions. At the ENSEMBLES data portal 30 models were available driven by the A1B greenhouse gas scenario. A total of 23 model output sets fulfilled the criterion of a sufficiently high spatial resolution (25 km × 25 km), but only 14 output sets covered the entire 1951–2100 period. Two other output sets were removed because they used the same RCM–GCM combination as another one, but with high- and low-sensitivity RCM settings. From the remaining 12 models one was not available at the website and another one contained too many data gaps at the end of the simulation period. A list of the 10 remaining model combinations (RCM–GCM) is provided by Dobor et al. (2015). Note that although the representative concentration pathways have already been adopted by the IPCC for its Fifth Assessment Report (AR5) in 2014, only GCM results were accessible at this time. Time series of maximum temperature ($T_{\max}$), minimum temperature ($T_{\min}$), precipitation and wind speed were selected for the closest grid point to the meteorological station from a 25 km × 25 km horizontal resolution grid. Statistical bias correction was applied to site measurements for the period 1961–2009 using the cumulative distribution function fitting technique (also known as the quantile mapping/fitting or histogram equalization), at monthly time intervals. For precipitation, both the amount and the frequency were corrected. Future atmospheric CO_2 concentrations for the model simulations where also adopted from the A1B scenario of IPCC. Future global radiation was estimated with the MT-CLIM model (Mountain Microclimate Simulation Model (Hungerford et al., 1989; Thornton and Running, 1999), which adequately estimated the daytime temperature and global radiation. Details of the method and its limitations were described previously by Moss et al. (2008) and Dobor et al. (2015).

Nitrogen deposition was kept equal to the average monthly value over the period 1989–2003 for each plot (20–25 kg ha^{-1} yr^{-1}) over the whole prediction period (2003–2100). The level chosen was slightly lower than, but close to, the optimal nitrogen deposition for beech, 28 kg N ha^{-1} yr^{-1} (Kint et al. (2012). No nitrogen deposition trends were observed, neither over years nor over seasons during the calibration period. This was concluded from an automated time series forecasting software provided by SAS statistical program (version 9.1, SAS Institute Inc., Cary, NC, USA). Predictions of nitrogen emissions and depositions depend on decisions with regard to land use, to agriculture, to energy policy, etc., as well as on the only partly known feedbacks between changes in the carbon and nitrogen cycles (Lamarque et al., 2011; van Vuuren et al., 2011; Ciais et al., 2013).

2.3. Forest model types

2.3.1. Empirically-based model SIBYLA

SIBYLA (acronym for Simulator of Forest Biodynamics) is an individual tree, distance-dependent and climate-sensitive growth model (Fabrika and Dursky, 2005, 2006). SIBYLA uses the coordinates, DBH and *h* of every single tree in a stand with the possibility of including different species with different growth rates. In this study the growth, the inter-tree and inter-specific competition and the mortality sub-models were used. The growth and competition sub-models were adopted from the SILVA growth simulator (Pretzsch and Kahn, 1998; Pretzsch et al., 2002) that worked as follows. Species-specific responses of tree increment to climatic and soil variables were based on dose–response functions (Fabrika and Pretzsch, 2013). This made the sub-model suitable for climate impact studies (Fabrika, 2007; Hlásny et al., 2011, 2014). Growth increment was then modified by competition pressure. Competitive interactions between trees and among species were described using a competition index based on positions and dimensions of surrounding trees and the light cone principle (Pretzsch, 1995; Bosela et al., 2013). The mortality was simulated via a sub-model of tree survival probability and using the threshold of stand density. The mortality sub-model has been described previously (Ďurský et al., 1996; Ďurský, 1997). To make the SIBYLA model representative of central Europe, it was calibrated using a large-scale database of forest monitoring and inventory data from Slovakia.

For the site-specific calibration of each of the four forest plots in this study, soil and climate variables measured at the site at the beginning of the calibration period were used to initialise the model. Simulations were then performed for the entire calibration period (1989–2003). The calibration was done for each year using a regression function of the residuals (differences between measured and simulated values) versus the simulated increments. The regression coefficients were then used to correct the simulated increments. The measured DBH and *h* values from the four plots were used for the calibration period. After calibration, an ad hoc variance reproduction procedure was applied based on Gaussian probability functions, in which stochastic variance was artificially created to include possibly unknown or unconsidered factors in the simulation process (Fabrika and Pretzsch, 2013). This resulted each time in 11 prognoses for each of the plots. They represented the source of variance 'STARTSET' for SIBYLA.

2.3.2. Process-based model ANAFORE

ANAFORE (acronym for ANAlysing FORest Ecosystems) is a climate-sensitive, eco-physiological PBM that uses a bottom-up approach to simulate forest growth. Processes at the leaf, the tree and the stand scales are modelled in half-hourly (carbon and water fluxes), daily (all carbon pools) and yearly (wood quality, forest growth and management) time steps, respectively. The model contains among others: (i) a detailed tree carbon allocation mechanism differentiating between transport, structure and storage carbon pools; (ii) a refined stem structure; (iii) a sub-model of labile carbon in the tree; and (iv) a detailed soil sub-model. In ANAFORE tree mortality was defined by the percentage of trees dying when the carbon balance became negative. An extensive and detailed description of the model has been published previously (Deckmyn et al., 2008).

A total of 146 species-specific physiological parameters could be optimized in ANAFORE to calibrate the model for the specific conditions of the particular forest plots of this study. An initial attempt to calibrate ANAFORE using a Bayesian optimization method (van Oijen et al., 2005) produced no reduction in parameter uncertainty. ANAFORE was therefore calibrated by selecting, independently for each plot, 11 parameter sets out of a minimum of 20,000 runs. This selection was made according to the accuracy of the simulated time series with respect to the measured DBH data over the calibration period.

All the required input variables for each of the two models as well as the possible output variables, with their respective spatial and temporal scales, are summarized in Table 1.

2.4. Simulation design

We considered the following variables influencing the total variance of the model results, always referred to as the sources of uncertainty:

i. FMTYPE (Forest model type): two forest model types were used, an EBM (SIBYLA) and a PBM (ANAFORE).
ii. MANFOR (management of the forest): four forest study plots were subjected to different thinning intensities in 1989: H, heavily cut; M, medium cut; L, lightly cut; and a control, C, i.e. no thinning.
iii. CLIMMOD (climate model): 10 RCM results were bias-corrected and used for the simulations up to 2100. All of the RCMs were run based on the A1B SRES scenario of IPCC.

Table 1
Synoptic description of the main characteristics of the empirically based SIBYLA and the process-based ANAFORE models.

Input	Spatial resolution	Temporal resolution	Contents, remarks
ANAFORE			
Stand	Stand	Initial	Site information (long., lat., slope), cohort information
Species	Tree/cohort	Initial	Number of species (up to 10)
Tree	Tree/cohort	Initial	Dimensions, carbon content in pools
Branch	Tree/cohort	Initial	Separate information about branches for each whorl
Soil biota	Stand	Initial	Information about mycorrhizae, saprotrophic fungi and soil microbes
Soil physics	Stand	Initial	Maximum volumetric water content and water potential, ph, thickness, texture
Soil organics	Stand	Initial	Thickness according to litter biomass and a constant organic matter density
Element concentration and fraction	Stand	Initial	Carbon and nitrogen contents divided in fractions of size and availability in each layer
Management	Stand	Year	Thinning timing and rules, rotation cycle
Climate	Stand	Half hour, day or month[a]	Incoming solar radiation, temperature, humidity deficit, wind speed, precipitation, CO_2, nitrogen deposition
Wood grading	Tree/cohort	Initial	Classes of wood quality (european standards)
Log quality assessment species	Tree/cohort	Initial	Four categories for which maximum norms can be given for 10 parameters (european standards)
SIBYLA			
Stand[b]	Tree	Annual	Depends on data available (species, vertical layer, density, age, site index, etc.)
Tree	Tree	Annual	Diameter at breast height, height, crown dimension, crown depth
Soil	Stand	Annual	Soil moisture and nutrient content in simple categories
Climate	Stand	Annual	Temperature, temperature amplitude, length of growing season, precipitation
Management	Stand/tree	Annual	Different management options
Output	**Spatial resolution**	**Temporal resolution**	**Contents, remarks**
ANAFORE			
Stand	Stand	Day	Wood biomass, root biomass, height, maximum leaf area index, soil carbon
Stand scale fluxes	Stand	Day	Gross primary production, netto primary production, heterotrophic respiration, soil respiration, evaporation
Tree output	Tree cohort	Day	Number of trees, carbon allocation (day), carbon content per pool (year), height, basal area, dimensions
Fluxes	Tree cohort	Half hour	Water and carbon fluxes
Phosphorus (P)	Stand	Day	Organic P, minimum P, P uptake by mycorizhae, P uptake by tree, P transfer by mycorizhae, total tree P, carbon:P in organic layer
Soil	Stand	Day	Carbon, nitrogen, p, water, carbon:nitrogen ratio
Nitrogen uptake	Tree/cohort	Day	Available nitrate, nitrate transfer by mycorizhae, available ammonia
Harvest	Tree cohort	Year	Standing and transported carbon, nitrogen all pools, harvested number of trees
Monetary	Stand	Year	Yield, particulate matter, water, carbon, nitrogen, prices
Particulate matter	Tree cohort	Day/year	Deposited, re-suspended, removed, on leaf particulate matter concentration, precipitation, evaporation, throughfall, water on leaf, wind speed above trees, canopy leaf area index
Wood	Tree/cohort	Day	Stem sapwood, stem heartwood, branches sapwood, branch heartwood
SYBILA			
Stand	Stand	Annual	Mean height, mean diameter, wood biomass, root biomass, foliage biomass, chemical content, biodiversity of tree species, forest density and other wood production characteristics
Tree output	Tree	Annual	Height, diameter, wood biomass, root biomass, foliage biomass, chemical content, timber type

[a] Climate data input in daily or monthly time steps are downscaled by the model to half hourly time steps.

[b] Depending on data availability the modeller can choose to use either stand-level or tree-level input data. If only stand-level data are available, the model generates tree-level data (coordinates, diameter at breast height and height distribution) to be used in the simulations.

iv. TIMEWIND (time window): three 15-year time windows were used for the simulations, i.e., 2019–2033, 2049–2063 and 2079–2093. The simulations for each TIMEWIND always started at the same developmental stage of the forest plots. TIMEWIND reflects the contribution of time (in a climate change context) to the total variance and the changes in the relative contributions of the other sources of variance over time. We preferred this splitting method as long term simulations could lead to misinterpretations caused by the change in relative contributions of the sources of uncertainty over time and by the changing interactions among them.
v. STARTSET (starting set-up of the model): 11 model starting sets for each plot and for each model separately were used. In SIBYLA, stochastic variations per plot were taken from the variance reproduction method described earlier. These stochastic variations were used to mimic the biological variability. For each plot in ANAFORE, the 11 parameter sets were produced by the model calibration.

Both models were used to simulate stem dry mass (in kg per tree), always for a period of 15 years, and for each combination of the three TIMEWINDs, the two FMTYPEs, the 10 CLIMMODs, the four MANFORs and the 11 STARTSETs. All combinations of the different categories of each of these sources of uncertainty constituted a total of 2640 different model runs, each with a different simulation design.

The variance decomposition of the RCM results of climate predictions for $T_{\min}$, $T_{\max}$ and precipitation included two sources of uncertainty:

i. RCM: the same 10 RCMs were used in the quantification of uncertainty in the forest model results. In this case they were not used as a source of variance of growth rate predictions, but in the context of the climate predictions.
ii. INTVAR: internal variability of the climate variable.

2.5. Statistical analysis

Variance decomposition of the forest model results was realized by performing an analysis of variance (ANOVA) with the average annual stem biomass increment (ASBI; in dry mass of an average tree) over the 15 years of simulation as the response variable for each of the simulation designs. The analysis was first made for the dataset including results of both FMTYPEs together (complete dataset) and subsequently for ANAFORE and SIBYLA, individually. The studied sources of uncertainty were FMTYPE, CLIMMOD, MANFOR, TIMEWIND and STARTSET. After the ANOVAs for the main effects of FMTYPE (complete dataset), CLIMMOD, MANFOR and TIMEWIND only, their interacting effects were also added as covariates. Two different approaches were thus used. In the first approach these interactions were ignored and their effect was entirely included in the residual error of the model. In the second approach significant two-way interactions were retained. STARTSET (nested in MANFOR) was only added as a covariate in an additional ANOVA analysis and was in all former analyses treated as a completely random source of variance, i.e. part of the residual error.

In all the analyses the fraction of the total variance explained by each source of uncertainty was calculated by dividing the Sum of Square Error (SSE) of the main effect as well as of the potential interactions by the total SSE of the response. The variance explained by the different sources of uncertainty plus the residual error made up 100% of the variance.

Afterwards, the dependence of the ASBI results on the simulation design was studied to obtain information about the differences in results between both FMTYPES in relation to changes in the simulation design (input). The average ASBI was calculated within each category of the sources of uncertainty CLIMMOD, MANFOR and TIMEWIND for both FMTYPEs separately. The correlation coefficients for category averages of consecutively CLIMMOD, MANFOR and TIMEWIND between both FMTYPES were computed. All the above-mentioned statistical analyses were done in the statistical SAS/STAT® registered software (version 9.1, SAS Institute Inc., Cary, NC, USA).

An additional variance decomposition was performed on the RCM climate variable predictions. As all RCMs used the same scenario (A1B), only the model uncertainty and the internal variability were estimated for climate predictions from 2000 until 2100. The averaged climate model results, computed as the annual average of all RCMs were expressed as changes compared to the average of the reference period 1971–2000 and were fit with a fourth-order polynomial using ordinary least squares calculations. A reference period of 30 years was used in line with the definitions of climate by the World Meteorological Organization. The RCM predictions were compared to the polynomial (fitted for the averaged climate model results) and the variance of the differences was calculated per decade; then these variances were averaged through the RCM models. The model uncertainty was defined as the variance of the different models in a given decade. The residual error of the analysis was attributed to the inherent randomness of climate (INTVAR). The fractions of the total variance explained by RCM and INTVAR were calculated and reported as percentages of the total variance.

3. Results

3.1. Quantification of uncertainty in biomass increment predictions

The total variance of ASBI in the complete dataset, i.e., the dataset including both FMTYPEs, was 382.4×10^3 (std. dev. 618). The main effect ANOVA and the two-way interaction ANOVA models explained 74.9% and 86.2% of the total variance, respectively. These ANOVA models provided the SSE values for the calculation of the fractions of the total variance explained by each of the sources of uncertainty, i.e., FMTYPE, CLIMMOD, MANFOR and TIMEWIND, their eventual interactions and the residual error.

The largest part (39.9%) of the total variance of ASBI in the complete dataset was explained by FMTYPE. This was followed by MANFOR (22.2%) and then by TIMEWIND (12.0%). The contribution of CLIMMOD in the explanation of the total variance was small (0.84%; Fig. 1a). There were significant interaction effects between FMTYPE and MANFOR, between FMTYPE and TIMEWIND, and between CLIMMOD and TIMEWIND (Fig. 1b). These interaction effects accounted for 6.4%, 2.7% and 0.35% of the total variance of ASBI, respectively. The residual error accounted for 25.1% of the total variance in the main effect model and for 13.8% of the total variance in the two-way interaction model.

For the ANOVA model including only ASBI data from ANAFORE, 72.0% of the variance was explained by the main effect model and slightly more (76.8%) by the two-way interaction model (Fig. 1b). For SIBYLA the explained variance was higher, ranging from 89.0% for the main effect model to 95.6% for the two-way interaction model. The total variance of the responses of ANAFORE was 10 times larger than the total variance of the responses in SIBYLA (209.7×10^3 against 20.18×10^3). TIMEWIND was a more important source of variance for SIBYLA than for ANAFORE (36.3% against 23.3%). Nearly half of the variance was explained by MANFOR for both models (48.7% for SIBYLA against 47.4% for ANAFORE). The residual error, was smaller for SIBYLA (11.0%) than for ANAFORE (28.0%).

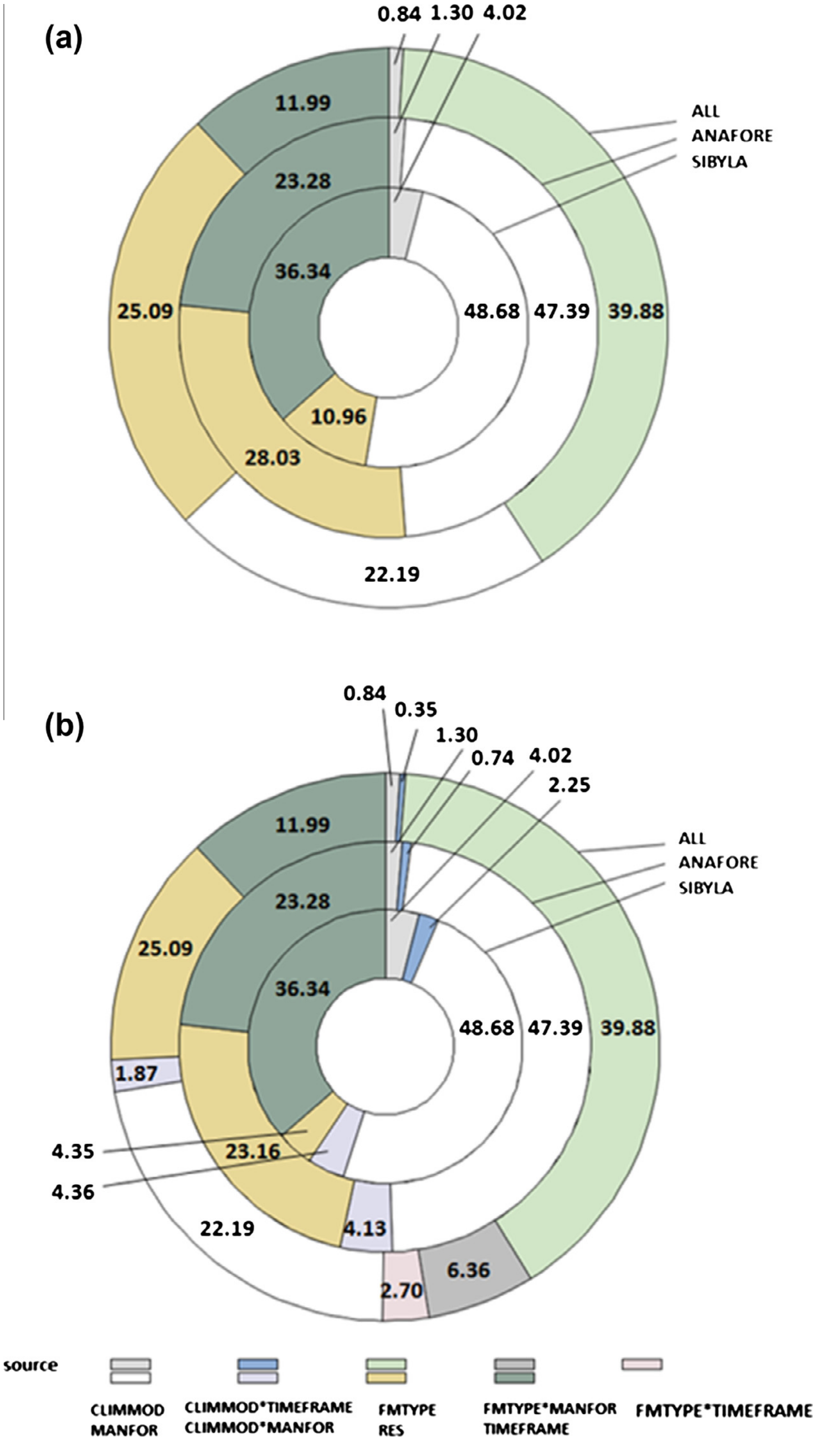

Fig. 1. Variance decomposition of average annual stem biomass increment results (ASBI; kg tree^{-1} yr^{-1}) expressed as percentage (%) of the total variance explained per source of uncertainty, for: (a) only the main effects of each source; and (b) the main effects and the two-way interactions.

For the ANAFORE model there were statistically significant interactions between CLIMMOD and MANFOR (4.1%) and between CLIMMOD and TIMEWIND (0.74%). For SIBYLA these interactions were also significant and accounted for 4.4% and 2.3%, respectively. The residual errors of the ANOVA model were reduced to 23.2% for ANAFORE and to 4.4% for SIBYLA after inclusion of these linear two-way interactions.

The residual error included the variance coming from non-significant two-way interactions and by potentially higher order interactions. In the case of ANAFORE the variance also resulted from the deterministic uncertainty from the different STARTSETS. In the case of SYBILA there was a small stochastic part of the residual error caused by the stochastic processes by which mortality and biological variation of the growth increment (reflected in STARTSERT) were modelled in each run separately.

After inclusion of the main effect of STARTSET and its two-way interactions with TIMEWIND and MANFOR in the ANOVA model for ANAFORE, an additional 15.2% of the total variance of ASBI was explained. The ANOVA model explained 92.6% of the total variance. The high variability caused by STARTSET was expected since the individual parameters from the selected STARTSETs were spread over a large range of their prior distribution (before calibration).

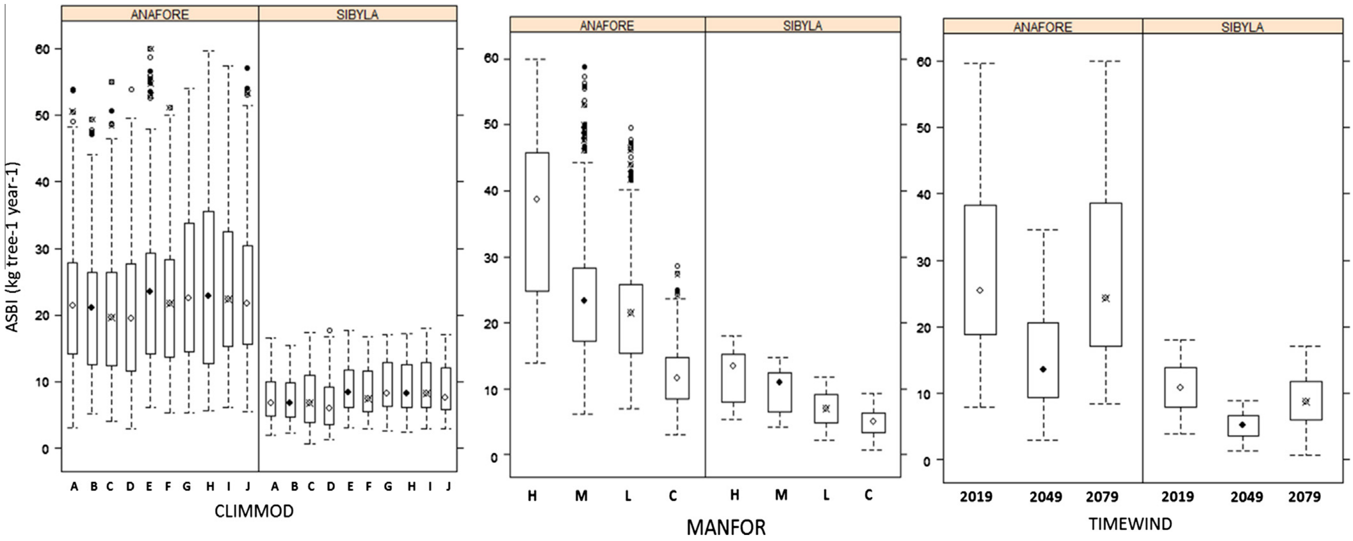

Fig. 2. Boxplots of the predicted annual stem biomass increment (ASBI; kg tree^{-1} yr^{-1}) for the combinations of forest model types, FMTYPES, with: (left) regional climate model (CLIMMOD); (middle) forest management (MANFOR) and (right) time window of the predictions (TIMEWIND). The two forest models used were ANAFORE and SIBYLA.

For SIBYLA the STARTSET effect, here reflecting the use of stochasticity in the tree growth predictions, was not significant.

3.2. Effect of simulation design

For both FMTYPES the effect of the simulation design on ASBI, in particular the effect of the interactions between FMTYPES and CLIMMOD, between FMTYPES and MANFOR, and between FMTYPES and TIMEWIND are shown in Fig. 2. In relative terms, the effect of the simulation design on ASBI was similar for both growth models, as evidenced by the significant correlations between both FMTYPES with correlation coefficients of 0.978 ($p < 0.0001$), 0.969 ($p = 0.0313$) and 0.939 ($p = 0.2240$), respectively, for the category averages of CLIMMOD, MANFOR and TIMEWIND. However, the interaction effects between two of these sources of uncertainty – MANFOR and TIMEWIND – with FMTYPE were significant sources of uncertainty in the ANOVA of the complete dataset (Fig. 1b). This means that in absolute values, the effect of the simulation design was not the same for both FMTYPES.

3.3. Quantification of uncertainties for regional climate predictions

The decadal evolution of the predicted $T_{\max}$, $T_{\min}$ and precipitation, expressed as change compared to the average of the reference period 1971–2000, depended on the RCM used (Fig. 3). For $T_{\max}$ and $T_{\min}$ the percentage of the variance explained by the internal variability was small during the entire prediction period from 2000 to 2100. It decreased from 16.5% to 6.8% for $T_{\max}$, and from 10.2% to 7.9% for $T_{\min}$. The remaining variance was explained by the use of the 10 RCMs changing from 83.5% to 93.2% for $T_{\max}$, and from 89.8% to 92.1% for $T_{\min}$. In absolute values, the total variance of the $T_{\max}$ predictions increased from 0.35 °C to 0.85 °C, and the total variance of $T_{\min}$ increased from 0.40 °C to 0.52 °C.

For precipitation, the fraction of the total variance explained by the internal variability decreased from 32.5% to 16.0% over the prediction period. The fraction of the total variance explained by the use of different RCMs increased from 67.5% in the decade 2000–2010 to 84.0% in the decade 2090–2100. The total variance of the predicted change in precipitation over the different RCMs was 275.85 mm in the decade 2090–2100, compared with 119.19 mm in the decade 2000–2010.

4. Discussion

A major part of the variance of ASBI was explained by FMTYPE. This is explained by the large absolute differences in ASBI results between both FMTYPES and the large uncertainty in the ASBI results of the process-based model ANAFORE. PBMs and EBMs significantly differ in the way that uncertainty is generated and they do this at each place in the model environment were uncertainty is generated (Walker et al., 2003). First, the 'context uncertainty' of the model has to be considered. Although PBMs and EBMs represent the forest system by the incorporation of external climatological variables, state variables (defining the initial forest situation) and eventually the consideration of forest management measures, the system boundaries of both model types are different. For example, ANAFORE defined the soil system in great detail, while SIBYLA didn't. On the other hand, SIBYLA defined the forest structure by describing each individual tree, and thus by including inter-tree and inter-specific interactions.

Secondly, differences in uncertainty were generated by the discrepancy between the inherent structure of the models and reality. In EBMs such as SIBYLA the 'structure uncertainty' lies in the restrictions of the empirical relationships and their integration into the model. These empirical equations are based on data that are not necessarily representative of the entire population and/or of other local conditions (Korzukhin et al., 1996). For SIBYLA the regression functions for some of the sub-models were partly based on data from Germany (Pretzsch, 1995; Pretzsch et al., 2002). For PBMs, the structure uncertainty primarily results from the limits in representing physiological processes and the feedbacks between them (Girardin et al., 2008). They can be considered as simplifications of the real processes and thus imperfect representations of reality. Both model types contain several known, but also a lot of unknown, uncertainties in their structure.

Thirdly, uncertainty differences came with the input data (input uncertainty) and the way they were used in the models. Several of the climate variables were introduced into both models with the same uncertainty, generated by the climate predictions. Other climate variables differed between the models or were not introduced in the same way, thus creating different uncertainties. The differences in climate effects on model results were enhanced by the way in which they were used afterwards (the model structure

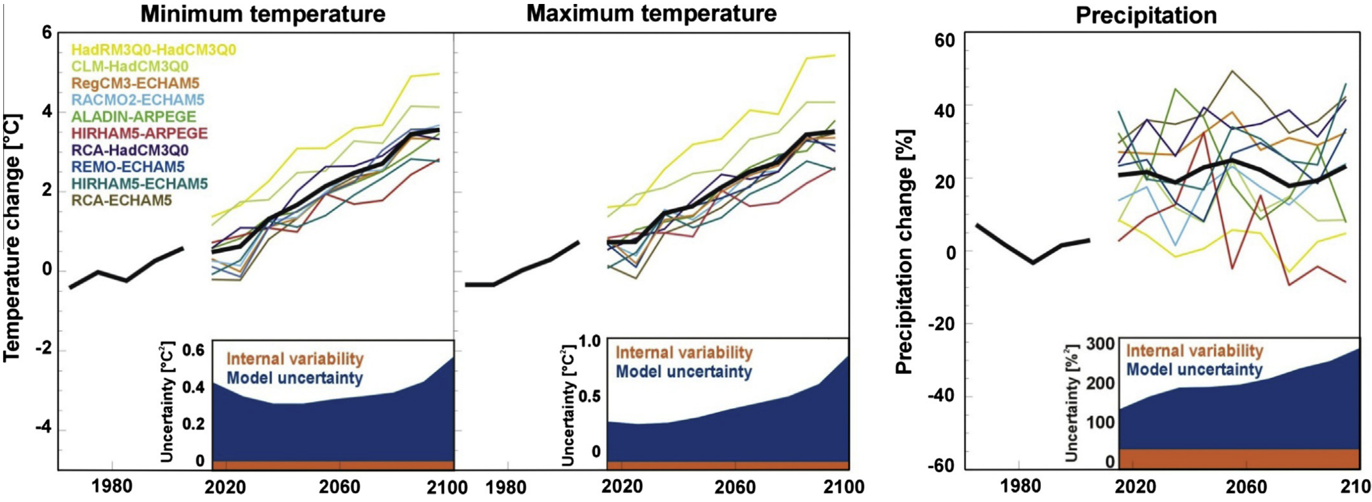

Fig. 3. Regional climate model predictions for minimum temperature, maximum temperature and precipitation, all expressed as changes according to the average of the reference period for climate predictions 1971–2000. The model uncertainty and the internal uncertainty are shown as insets in each plot.

uncertainty). State variables were imported differently in both models, leading to differences in their effect on the uncertainty. With poor information about the state variables, there is a lot of unknown uncertainty, not reflected in the results. In the context of comparing a PBM and an EBM the 'parameter uncertainty' is also a very important cause of differences in model result uncertainty. In PBMs the parameter uncertainty is determined by the multivariate distribution of the parameters (van Oijen et al., 2013). For ANAFORE the parameter uncertainty was reflected in the post-calibration parameter space and could be described statistically. On the other hand EBMs are deterministic in nature. Parameter uncertainty is often represented by the confidence intervals for the input regression functions, which is not the true uncertainty representative of the population. It was thus impossible to quantify the real parameter uncertainty of the SIBYLA model. The parameter uncertainty becomes more important as the site conditions deviate more strongly from the calibration conditions. All the aforementioned uncertainties together are reflected in the final 'model uncertainty'.

Another important source of uncertainty in the ASBI results was MANFOR, the management that resulted in different forest densities prior to the forest growth simulations. Since the four forest plots were exposed to nearly identical environmental conditions, it was possible to estimate the importance of this source of uncertainty. The potential of a forest to withstand slowly changing stresses and acute stress events depends on its natural and human-induced history as well as on its actual density and composition (Lindner et al., 2014). Also, the way in which models cope with mortality becomes more important when forests deviate from their actual equilibrium state (Hlásny et al., 2014). Tree-specific models are very useful to take the exact forest structure into account. PBMs have the advantage that the simulated forest responds much more realistically to climate change. Small, but sometimes drastic interactions between forest structure and climate change might not be captured by either or both models.

Notwithstanding the conclusion that input climate predictions are an important source of uncertainty in ecological impact studies (Olesen et al., 2007; Ruffault et al., 2014), the use of different RCMs did not introduce much variance in the forest model results. By deliberately limiting the climate scenarios to local variants of scenario A1B, the uncertainty from climate scenarios was not fully reflected in this study. Additional sources of unknown uncertainty, not captured in the variance decomposition, could have changed the absolute and relative importance of the sources of uncertainty. Although tree growth varies as a function of nitrogen deposition in a non-linear way (Magnani et al., 2007), we did not include any nitrogen deposition scenario in the study. Further, no climate extremes were included in the predictions. The uncaptured and unknown uncertainties depend on the forest model used and on the choices of sources of uncertainty to be included in the variance decomposition.

The similar relative effect of the studied sources of uncertainty on ASBI results for the EBM and the PBM is encouraging, however, caution is needed. To make growth predictions that apply outside the range of the environmental conditions of calibration, the tree physiological processes must be modelled realistically. In all aspects of modelling, there are inherent risks in extrapolating empirical relationships outside the environmental conditions of the calibration data set. However, in the context of this study ANAFORE was too complex, in other words, over-parametrized for the data available. The significant interaction effects of STARTSET with both TIMEWIND and MANFOR in the ANOVA model confirmed this. Furthermore, ANAFORE has been developed for newly planted young forests; we observed an overestimation of the growth rate when simulating the adult forest plots of the present study. The accuracy, the context and the structure of the model have to be aligned with the management questions and the range of environmental conditions over which the model should be applied (Battaglia and Sands, 1998). This emphasizes the need for intensive collaboration between forest managers and modellers in defining the best model for answering specific questions. The model requirements for input and calibration data as well as their spatial and temporal scales have to be matched to the data available, with a focus on providing answers to the practical questions under specific environmental and management conditions. Purely PBMs or EBMs, or hybrid models could all be useful.

Future research on forest growth predictions should be designed to enable better risk evaluation by decision makers and forest managers. This research would benefit from: (i) open-access databases containing a large range of forest and environmental variables measured at different spatial and temporal scales to enable correct model calibration and validation. The concept of 'supersites' is useful for calibrating parameter-rich models; (ii) ongoing efforts at comparing model structures and their sensitivity to (interacting) external driving variables; (iii) proper communication about the sources of uncertainty, about the quantity of these uncertainties and about the place in the model where these uncertainties are generated.

5. Conclusions

A decomposition of the total variance in forest model results indicated that the type of model employed, i.e., empirical or process-based, makes the largest contribution to the uncertainty in the final model result. Although different simulation designs had similar relative effects on the estimated annual stem biomass increments for both the empirical and process-based models, the absolute differences in the estimates between model types were large. Further, the process-based model results were accompanied with an uncertainty that was 10 times larger than those from the empirical model. The initial values of input state variables made a large contribution to the uncertainty of forest model results. This highlights the risk in forest management when using forest models to guide decisions.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.10.048. These data include Google maps of the most important areas described in this article.

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Research article

Environmental impact assessment and monetary ecosystem service valuation of an ecosystem under different future environmental change and management scenarios; a case study of a Scots pine forest

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ABSTRACT

For a sustainable future, we must sustainably manage not only the human/industrial system but also ecosystems. To achieve the latter goal, we need to predict the responses of ecosystems and their provided services to management practices under changing environmental conditions via ecosystem models and use tools to compare the estimated provided services between the different scenarios. However, scientific articles have covered a limited amount of estimated ecosystem services and have used tools to aggregate services that contain a significant amount of subjective aspects and that represent the final result in a non-tangible unit such as 'points'. To resolve these matters, this study quantifies the environmental impact (on human health, natural systems and natural resources) in physical units and uses an ecosystem service valuation based on monetary values (including ecosystem disservices with associated negative monetary values). More specifically, the paper also focuses on the assessment of ecosystem services related to pollutant removal/generation flows, accounting for the inflow of eutrophying nitrogen (N) when assessing the effect of N leached to groundwater. Regarding water use/provisioning, evapotranspiration is alternatively considered a disservice because it implies a loss of (potential) groundwater. These approaches and improvements, relevant to all ecosystems, are demonstrated using a Scots pine stand from 2010 to 2089 for a combination of three environmental change and three management scenarios. The environmental change scenarios considered interannual climate variability trends and included alterations in temperature, precipitation, nitrogen deposition, wind speed, Particulate matter (PM) concentration and CO_2 concentration.

The addressed flows/ecosystem services, including disservices, are as follows: particulate matter removal, freshwater loss, CO_2 sequestration, wood production, NO_x emissions, NH_3 uptake and nitrogen pollution/removal.

The monetary ecosystem service valuation yields a total average estimate of 361–1242 euro ha^{-1} yr^{-1}. $PM_{2.5}$ (<2.5 μm) removal is the key service, with a projected value of 622–1172 euro ha^{-1} yr^{-1}. Concerning environmental impact assessment, with net CO_2 uptake being the most relevant contributing flow, a loss prevention of 0.014–0.029 healthy life years ha^{-1} yr^{-1} is calculated for the respective flows.

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Both assessment methods favor the use of the least intensive management scenario due to its resulting higher CO_2 sequestration and PM removal, which are the most important services of the considered ones.

1. Introduction

To ensure an environmentally sustainable future for mankind, we must better manage our human/industrial system by reducing its environmental impact caused by emissions of harmful compounds and resource extractions and by industrial remediation of inflicted environmental damage (e.g., soil sanitation). However, we can also manage ecosystems in a manner such that they also indirectly aid us in achieving these sustainability efforts, e.g., provision more renewable resources, in the best way possible.

In addition to the influence of mankind on ecosystems through its direct actions, e.g., harvest and management practices, changing environmental conditions (caused by mankind and nature) such as climate change, which is important to account for, and their interactions with mentioned management practices also have an influence (FAO, 2012). Future environmental conditions are however not exactly known. In this regard, different environmental change scenarios can be drawn, and some long-term scenarios were specifically depicted by the Intergovernmental Panel on Climate Change (IPCC) (IPCC, 2014, 2000).

To unravel the most sustainable ecosystem management scenario, one should estimate what the sustainability impact will be of the ecosystem under these different scenarios in combination with different environmental change scenarios. Because the endpoint is to predict the effect of human actions in the future, it is worth modeling ecosystems according to different management and environmental change scenarios. Furthermore, the combination with approaches that assess the sustainability (or an aspect of it) is more and more needed. In this study, the focus is on environmental sustainability, considering the effect on mankind and nature (see Fig. 1 for an overview).

The main goal of this study is to further the science in the field of environmental sustainability assessment of an ecosystem under different management and environmental change scenarios. This will be exemplified through a case study of a forest, more specifically a Scots pine stand. Different aspects to which improvements are made are addressed in the following subsections: “Environmental sustainability assessment approaches” (Section 1.1), “Predicting future environmental change” (Section 1.2) and “A case study of a specific forest ecosystem” (Section 1.3).

1.1. Environmental sustainability assessment approaches

A particular ecosystem has various interactions with their environment (mankind and the rest of nature), ranging from biomass harvest to recreation, that define their sustainability. The ideal approach to address the environmental sustainability of these interactions results in a single, purely objective (i.e. without needing to involve subjective weighting of different aspects) and tangible (e.g. not using points) outcome. However, such an approach is still non-existent, and we will therefore apply two prominent conceptual approaches.

The first is the ecosystem service approach. As is well described in the Millennium Ecosystem Assessment reports (2005), ecosystem services represent the direct and indirect contributions of ecosystems to humans' well-being (De Groot et al., 2012). Much research is being performed on the mapping, assessment and (monetary) valuation of ecosystem services (Brown and Fagerholm, 2015; Crossman et al., 2013; Maes et al., 2013; Zulian et al., 2014), developing a quantitative basis for the estimation of ecosystems' value to mankind and thus facilitating policy support and decision-making. We interpret an ecosystem service as a property, function, process or a collection of these factors of an ecosystem that provide a benefit to mankind. Ecosystem services are furthermore subdivided into different categories: provisioning (e.g., food, water), regulating (e.g., removal of pollutants, pollination, etc.), supporting (that support other services, e.g., nutrient cycling, primary production, etc.) and recreational/cultural services (Millennium Ecosystem Assessment, 2005). Other classifications also exist, but, according to De Groot et al. (2010), “we should accept that no final classification can capture the myriad of ways in which ecosystems support human life and contribute to human well-being”. Here, we will not focus on ecosystem services that relate to social human well-being. In addition to services, ecosystems also provide disservices, e.g., spreading of infectious diseases, crop damage by pests, emission of volatile organic compounds and allergic reactions to pollen (Dunn, 2010; Escobedo et al., 2011; Lyytimäki and Sipilä, 2009). Because these affect human well-being negatively, they should also be accounted for (Lyytimäki, 2015; Lyytimäki and Sipilä, 2009)

One can account for these different aspects of an ecosystem through a set of indicators and then compare their values. To this end, a multi-criteria analysis (MCA) methodology could be eventually used to identify the preferred management scenario (Cinelli et al., 2014; Hails and Ormerod, 2013; Langhans et al., 2014; Wolfslehner and Seidl, 2010). Some studies compare the scenarios using raw indicator outcomes without the use of an additional MCA methodology (Lasch et al., 2010; Temperli et al., 2012).

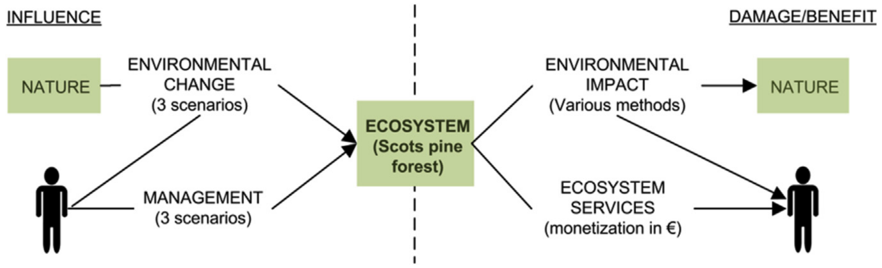

Fig. 1. Overall scheme of the influence of mankind and nature on an ecosystem and the subsequent indirectly induced damage and benefit to themselves. As a case study, we set up a framework to quantify these relationships and effects for a Scots pine forest using different scenarios and methods, shown between brackets.

In this case, the selection of the best scenario is generally based on implicit subjective weighting of the indicator values. Such an approach might be reasonable if only a few indicators are considered, but it remains nonetheless strongly based on subjective opinions. One can also make use of principal component analysis to aid judgment, though this does not result in a single outcome (Duncker et al., 2012). To obtain a more broad opinion on a community scale, the opinion/weighting of indicators by stakeholder groups, e.g., environmental organizations, can be included. An additive utility models can also be used in which stakeholder priority settings are converted into mathematical relationships used to obtain a single numerical outcome, as done by Fürstenau et al. (2007). Similarly, Seidl and Lexer (2013) use a complex framework partially based on a weighting of selected indicators done by some stakeholder groups. A single score can be obtained for both of these methods, but the outcome depends on the subjective priorities/weighting of the stakeholder groups. The authors of the respective studies (Fürstenau et al., 2007; Seidl and Lexer, 2013) conclude that the differences between stakeholder group preferences in fact lead to different outcomes in terms of pinpointing the best management practice. No single (objective) outcome could hence be presented to the reader; no better scenario could be exactly pinpointed. Accordingly, there is a need for methodological development that results in a single or a small set of outcomes based on more/only objective calculations. Furthermore, the aggregated outcomes of the applied multi-criteria analysis methods have no units (they are represented as 'scores' or 'points'), expressing no real tangible quantity and presenting an unclear message regarding the extent of the impact on human well-being of a scenario (choice). If no tangible value is at all attributable to a single MCA outcome, it is difficult to grasp the value of ecosystem services for human well-being, which is relevant in ecosystem service valuation. In this article, the valuation of ecosystem services is therefore put forward through a monetization approach, i.e., valuing ecosystem services in monetary amounts (Baveye et al., 2013; Broekx et al., 2013; de Groot et al., 2012; La Notte et al., 2015; Liekens et al., 2013b; TEEB, 2010). This is not an analysis on financial or economic feasibility/profit, or a cost-benefit analysis of a selected scenario, hence e.g. including management costs, such as that performed by Garcia-Quijano et al. (2005) for climate mitigation through CO_2 uptake. It must be remarked that monetary valuation is not purely objective, though it delivers a tangible overall value and no normalization of services is needed.

Second, Environmental impact assessment can be considered, adding more information on the environmental sustainability of an ecosystem (Fig. 1). In this case, the goal is to quantify the impact of a production system on natural resources, human health and ecosystems due to the extraction of resources and the release of pollutant emissions (de Haes et al., 1999; ISO, 2006). This is commonly applied to human/industrial systems, such as product life cycles, while not typically to ecosystems. For example, Garcia-Quijano et al. (2005) use such an approach to assess the land use impact of different forest management practices. An important aspect of this approach is that it also considers the final impact on nature, whereas ecosystems service assessment focuses only on the eventual benefit to mankind (Fig. 1). This approach is even more objective and also presents the outcome in tangible units, though possibly not in a single one. MCA might thus still be needed to obtain a single outcome if more than one output unit is obtained. The advantage of using an environmental impact assessment approach is that it provide a first screening of the environemntal sustainability of the system potentially in less and tangible units, facilitating more correct judgment by stakeholders that is later needed for MCA-approaches. Schaubroeck et al. (2013) noted that, in the environmental impact assessment of an integrated system of forest and wood processing, the forest ecosystem could have the most important share of impact. These authors also used and provided a framework that allows one to better assess environmental impact by including the uptake of harmful compounds (e.g., CO_2) and illustrated the importance of accounting for this uptake. The respective framework is also used in this study. Good management of ecosystems can thus be most important. In this study, we do not include the industrial system, i.e., we do not account for alterations in environmental impact due to a change in the industrial processes associated with a different management approach. However, these impacts do exist, as clearly shown in the case study of Rugani et al. (2015). In our case study, this is most likely negligible, as shown by Schaubroeck et al. (2013), and therefore not accounted for. Note that other approaches exist to aid stakeholders in selecting the most sustainable management scenario: criteria and indicators (Van Cauwenbergh et al., 2007), decision support systems (Gilliams et al., 2005) and knowledge-based systems (Baelemans and Muys, 1998). However, one should make many subjective choices to pursue these, and no overall tangible outcome can be obtained when addressing multiple criteria.

1.1.1. *Ecosystem services*

An important aspect to address, as illustrated for forests by the literature review (Table S1), is that more relevant services should be considered (see Section 2.5) in a more realistic manner and through a sound approach to better pinpoint the best management strategy under quantified changing environmental conditions (Smith et al., 2013). The most important additional service considered here is particulate matter, responsible for severe damage to human health after inhalation (European Environment Agency, 2013; Kim et al., 2015), removal from the air, a relevant service for a forest ecosystem (Nowak et al., 2014; Schaubroeck et al., 2014) and also possibly for any terrestrial ecosystem, using the modeling framework of Schaubroeck et al. (2014). Moreover, it is important to generally discuss and improve the assessment of pollutant generation/removal as an ecosystem service. In the assessment of such a (dis)service, one should take into account the inflow (or outflow) of pollutants as well. However, the presence of nitrate in ecosystem leachate is currently considered a disservice because of its eutrophication potential (eutrophication indirectly damages ecosystems and human well-being through various pathways, even human health as presented in a report by the World Health Organization (2003)), without taking into account the inflow of eutrophying nitrogen agents (Broekx et al., 2013; Duncker et al., 2012; Liekens et al., 2013b). A solution is presented in this work by considering the ecosystem service equal to the impact of the inflow minus the impact of the outflow, exemplified in nitrogen removal by the respective forest ecosystem. In addition, groundwater recharge is conventionally addressed as a service provided by an ecosystem (Broekx et al., 2013; Duncker et al., 2012; Liekens et al., 2013b). This viewpoint can be questioned, especially because water use will be most likely higher for certain ecosystems, e.g., forests, than for other land uses due to the higher capacity of those ecosystems to evapotranspire (Calder, 2007; Maes et al., 2009). Consequently, it might be more logical to consider freshwater loss as an ecosystem disservice. This is further addressed in Section 2.5.

1.2. *Predicitng environmental change*

Environmental change scenarios can be improved. Most studies only focus on the change in CO_2 concentrations and climate-related characteristics, such as temperature and precipitation (see Table S1). However, other environmental parameters are also of high relevance, e.g., nitrogen deposition related to the ecosystem service of nitrogen pollutant removal or generation, as included in the case study. Moreover, another important aspect of predicting environmental conditions is interannual variability. Environmental change scenarios provide long-term predictions of how the climate will change on average. However, the climatic conditions at each period in time, e.g., for a year, are not exactly predictable because they may still vary due to natural variation, e.g., year 2020 might be colder than year 2019 even though the temperature is predicted to rise on average. Focusing on only weather conditions (precipitation, temperature and irradiation), the uncertainty of near-future predictions is in fact very dependent on this natural interannual variation, see Fig. 11.8 of the IPCC report (2014). It is therefore definitely important to include an interannual variation because, for example, initial forest growth is sensitive to weather conditions (Cunningham et al., 2006; Dzwonko and Gawroński, 2002; Taeger et al., 2013a, 2013b). In this study, an approach for this is presented, while including alterations in the following environmental change parameters as much as possible: temperature, precipitation, nitrogen deposition, wind speed, particulate matter concentration and CO_2 concentration.

1.3. A case study of a specific forest ecosystem

One of the most relevant terrestrial ecosystem types is the forest ecosystem. Forests covered 31% of the total land area in 2010 (FAO, 2010) and provide valuable goods and services to mankind, such as the provisioning of wood or climate change mitigation, e.g., sequestering carbon dioxide (Pan et al., 2011). We therefore focus on this ecosystem type in this study; however, the conceptual approaches are applicable to any ecosystem type, and the case study results are also interesting for similar research on other vegetative terrestrial ecosystem types. To the best of our knowledge, five different similar studies (including the influence of environmental change and management) on specific forests have been performed to date (Duncker et al., 2012; Fürstenau et al., 2007; Pizzirani et al., 2010; Seidl and Lexer, 2013; Temperli et al., 2012), as comprehensively reported in Table S1 of the Supplementary File.

Many new studies focus on the general quantification/mapping of ecosystem services using very robust, generic models across landscapes, delivering valuable data on ecosystem services on a regional level (Boumans et al., 2015; Brown and Fagerholm, 2015; Villa et al., 2014; Zulian et al., 2014). However, there is still a need for thorough detailed studies of ecosystem service supply under different scenarios of environmental change and management, e.g., using high-quality models with the high data demand, on specific sites because the quality of such (ecosystem service) assessments and valuation of the latter studies can be questioned. Such a detailed assessment is presented in this work.

2. Materials and methods

2.1. Site description

The forest ecosystem analysed here is a managed Scots pine (*Pinus sylvestris* L.) forest stand, referred to as 'Scots pine stand', located in the forest 'De Inslag' in Brasschaat, Belgium (51°18′33″ N, 4°31′14″ E). The original Scots pine stand has been extensively studied. For more information, read the works of Schaubroeck et al. (2013, 2012). The regional climate is temperate maritime with a mean annual temperature of 9.8 °C and a mean annual precipitation of 750 mm (Nagy et al., 2006). The soil is loamy sand and moderately humid, with distinct humus and iron B horizons. The groundwater table is usually at a depth of 1.2–1.5 m (Baeyens et al., 1993). A more detailed description of the soil is given by Neirynck et al. (2002) and Janssens et al. (1999). This forest ecosystem was selected because it is a thoroughly studied stand (Schaubroeck et al., 2013, 2012) for which there is a large amount of data, and because Scots pine is an abundant species in European forests (Skjøth et al., 2008; Tröltzsch et al., 2009).

2.2. Model selection

Models were developed to predict general forest growth. For an overview of the types and models applied in the other studies mentioned in Table S1, see the Supporting information Section B. Here, we applied the hybrid model ANAlysis of FORest Ecosystems model (ANAFORE) that was introduced by Deckmyn et al. (2008) and later updated with a soil sub-model (Deckmyn et al., 2011). The model is discussed more in detail in Section B of the Supplementary file. Half-hourly, daily or monthly values of temperature, precipitation, radiation, wind speed, humidity and CO_2 and the stand inventory, forest management and soil characteristics are inputs. ANAFORE is a high detailed parameter-rich model and is therefore less suitable if not enough parameter data are available (van Oijen et al., 2013). However, this is not an issue in this case because the model was already applied and validated for the Scots pine stand considered here (Deckmyn et al., 2011, 2008).

Schaubroeck et al. (2014) integrated the assessment of particulate matter (PM) removal on a half-hourly basis into the ANAFORE model and applied it to the Scots pine stand studied here. This particular submodel was also used in this study to assess $PM_{2.5}$ (PM with a diameter < 2.5 μm) and $PM_{2.5-10}$ removal. The input requirements needed to run it are illustrated by Schaubroeck et al. (2014). The parameter values of Schaubroeck et al. (2014) for $PM_{2.5}$ removal by a Scots pine forest are used and are also applied for $PM_{2.5-10}$ removal.

For the PM removal submodel, the calculation of wood area, which is an important variable for the interception of rain, was improved. See Section C of the Supplementary file for a full description.

To conclude, the ANAFORE model was selected because of the following reasons: (1) it models soil processes (Deckmyn et al., 2011); (2) it is a detailed process-based model (Deckmyn et al., 2008); (3) for a process-based model, it quantifies relatively many ecosystem services and goods, mostly in a detailed manner (Table S1); (4) it has been updated with a model on particulate matter removal (Schaubroeck et al., 2014); and (5) it has been applied and parameterized for the studied site (Deckmyn et al., 2008).

2.3. Management scenarios

The studies described in Table S1 test the management scenarios within a broad spectrum, from no to intensive management, to select the optimal type of management for the forest (Duncker et al., 2012; Fürstenau et al., 2007; Pizzirani et al., 2010) or in light of a specific research question (Seidl and Lexer, 2013; Temperli et al., 2012). Here, the three tested management scenarios are intensive to check whether different outcomes can be obtained by the framework, even at that level of detail, i.e. for quite similar scenarios.

For all scenarios, the considered management of the Scots pine stand is an 80-year rotation period, starting from 10000 one-year-old trees planted per hectare after a clear felling of the current pine forest in 2010 until the next clear cut in 2089. The initial conditions are those after a virtual clear-cut of the existing 80-year-old forest in 2010. The carbon amounts in the soil are those given by Gielen et al. (2013) and are mentioned in Table S2 of Schaubroeck et al. (2014). The distribution over the soil layers is retrieved from a previous run of ANAFORE on the same site. Two-year-old saplings were planted. To initialize the soil conditions after a clear cut in

2010, a preparatory model run was performed for a full length of pine rotation. We consider only one tree cohort in the ANAFORE model, which is reasonable because it is a planted forest.

In all scenarios, after 14 years, a cutting occurs in which 30% of the trees are harvested. The subsequent thinning is different between the scenarios. For LOW management, no thinning occurs. For MID and HIGH management, thinning is performed every 5 years, the applied frequency in yield tables for Scots pine in this region (Jansen et al., 1996), starting from year 21. For MID management, half of the wood increment over 5 years is harvested. For HIGH management, all of the increment is harvested. Random trees are cut when thinning. This is a simplification because different thinning procedures exist, e.g., thinning from taller or shorter trees, but a mixture of these procedures is often applied in actual forest practices. Only wood from stems and large branches is harvested when thinning. Roots, needles and small branch residues are left behind in the forest.

2.4. Environmental change scenarios and their parameter values

Three of the discussed studies, shown in Table S1, use different environmental change models to assess different scenarios (Fürstenau et al., 2007; Seidl and Lexer, 2013; Temperli et al., 2012). Two only consider the increase in temperature and precipitation. In addition to these two variables, Fürsternau et al. (2007) also considered an increase in CO_2. Pizzirani et al. (2010) only considered the increase in biotic threats. In this study, monthly values of weather conditions (temperature, precipitation and radiation) are used as model inputs, and yearly values are used for the others.

Simulations were performed from 2010 to 2089 with three different environmental change scenarios that capture the possible trends in environmental changes: one assuming no change as a reference, the current (CUR) scenario, and two alternative future scenarios. The latter two are roughly based on two possible socio-economic incentives and their effect on environmental change. The severe (SEV) scenario is based on an evolution in which the current environmental policy is considered, implying a more economic-growth-oriented vision. The other future scenario, called moderate (MOD), reflects a development in which more measurements are taken to provide greater socio-environmental sustainability.

Another matter to address when specifying environmental change scenarios is whether there will be a convergence of different communities, i.e., similar climate-related policies among the world-wide communities (IPCC, 2000). Here, we consider a heterogeneous/non-convergent world for both MOD and SEV because we are dealing with more local policies and the implementation of environmental policies still differs among communities, e.g., compare the climate policy of the U.S. with that of Europe (Hayes and Knox-Hayes, 2014). The environmental change scenarios differed in 7 out of the 8 meteorological and environmental variables driving the model: air temperature, precipitation, CO_2 concentration, NO_y deposition, NH_x deposition, wind speed and airborne particulate matter concentration (more specifically that of $PM_{2.5}$ and $PM_{2.5-10}$). The environmental variable for irradiation was considered not to vary among the scenarios because future irradiation changes are expected to be very minor in Belgium (Campioli et al., 2012). The scenarios are aggregated out of other similar scenarios from different references because no single reference provided values for all considered parameters and, furthermore, we wanted to use site-specific values. For an overview, see Table 1. The environmental parameter values differ on a yearly basis, except for precipitation and temperature, which also differ on a seasonal basis.

The considered changes in temperature, precipitation and wind speed, shown in Table 2, were obtained for the moderate (MOD) and severe (SEV) scenarios for the region of study until 2090 based on the scenarios G+ (equivalent to B family) and W+ (equivalent to A family), respectively, of the Royal Dutch Meteorological Institute (Demarée, 2008; van den Hurk et al., 2006). On average, a warmer climate with wetter winters and drier summers compared to the current climate was predicted for the moderate and even more for the severe scenario. For precipitation, this is not considered on an average yearly basis because the projected yearly changes are small compared to the internal variability (i.e., smaller than one standard deviation of the estimated internal variability), see Fig. 11.12 in IPCC (2014), and, specific for Europe, model results do not agree on a yearly corresponding change in precipitation in response to CO_2 increase (IPCC, 2014). Wind speed only influences particulate matter removal and evapotranspiration of water and is forecasted to increase in the G+ (moderate) and W+ (severe) scenarios. All these relative changes in percentages are applied assuming a linear increase over time, e.g., for wind speed increase, a factor of 0.0364 (moderate) and 0.0727 (severe) per year can be derived for the moderate and severe scenarios, respectively.

For CO_2 concentrations, the current scenario concentration was set constant at 390.103 ppmv (IPCC, 2001). Future CO_2 projections for moderate (B2) and severe (A2) scenarios foresaw a gradual CO_2 increase up to 585 and 762.5 ppmv, respectively, in 2090 based on averages of the reference scenario in models ISAM and Bern-CC (IPCC, 2001) (Fig. 2).

Future projections of nitrogen deposition and particulate matter (PM) concentrations (Fig. 2) are based on a report of the Flemish Environmental Agency (FEA), in which different socio-economic scenarios are applied to predict respective future environmental changes in Flanders, Belgium, until 2030 (Van Steertegem, 2009). For the moderate scenario, the ‘Europa’-scenario was selected, in which environmental change is based on meeting specific European environmental policy directives (Amann et al., 2008) applied to Flanders, which is in line with an increase in socio-environmental sustainability.

For the severe scenario, the ‘reference’ scenario was selected, which is a business-as-usual approach. The FEA-calculated specific future prediction values are valid for the location of the Scots pine stand for the years 2010, 2015, 2020, 2025 and 2030. Linear interpolation was used to obtain values for the years between latter ones, and values after 2030 were considered as remaining constant. These trends in evolution were applied using recalibration based on local measurements/determinations of nitrogen deposition and PM concentrations in the year 2010, illustrated by the following example: new prediction 2015 = (prediction FEA 2015)/(prediction FEA 2010) × (measurement 2010).

The total nitrogen deposition to the soil in 2010 is considered to be 40 kg N ha^{-1} yr^{-1} with a share of 0.21 NOy-N and 0.79 NHx-N, valid for the period 1992–2007 for the Scots pine stand (Neirynck et al., 2008). The effect of changing vegetation on the dry deposition of PM and thus on the nitrogen deposition is not considered because this was only responsible for 20% of the total nitrogen deposition (Neirynck et al., 2007). The FEA and IRCEL, the Belgian Interregional Environment Agency, provided a yearly concentration for 2010 of 24.55 μg m^{-3} $PM_{2.5-10}$ and 16.77 μg m^{-3} $PM_{2.5}$ (with a resolution of 3*3 km), for which the methodology of obtainment is explained by Schaubroeck et al. (2014).

To model PM removal, the half-hourly precipitation and PM concentration need to be known (Schaubroeck et al., 2014). For 2010, these values were measured for precipitation and were calculated by IRCEL and FEA for PM as addressed above. Half-hourly precipitation and hourly PM values for other years were obtained via recalibration using the yearly values, e.g., half-hourly precipitation values of 2011 = (half-hourly precipitation values of

Table 1
The aggregated climate scenarios and the scenarios used to model the respective parameters, of which the original names are mentioned (e.g., ‘G+’).

	Moderate (MOD)	Severe (SEV)	Values	Reference
Temperature, precipitation, & wind speed	G+	W+	Table 2	(van den Hurk et al., 2006)
CO_2 concentration	A2	B2	Fig. 2	(IPCC, 2001)
N deposition (NH_x and NO_y) & PM air concentration ($PM_{2.5}$ & $PM_{2.5-10}$)	Europe	Reference	Fig. 2	(Van Steertegem, 2009)
Overall similar IPCC scenario	A2	B2	/	(IPCC, 2000)

Table 2
Considered changes for 2100 compared to 1990 in precipitation, temperature and wind speed for the two future scenarios, based on the work of van den Hurk et al. (2006). The seasons are defined as follows: 'winter' stands for December, January and February and 'summer' stands for June, July and August.

Environmental change scenario	Moderate	Severe
Original name	G+	W+
Temperature		
Global air T (applied to spring and autumn)	+2 °C	+4 °C
Winter average T	+2.3 °C	+4.6 °C
Summer average T	+2.8 °C	+5.6 °C
Precipitation		
Winter average precipitation	+14%	+28%
Summer average precipitation	−19%	−38%
Wind speed		
Average wind speed	+4%	+8%

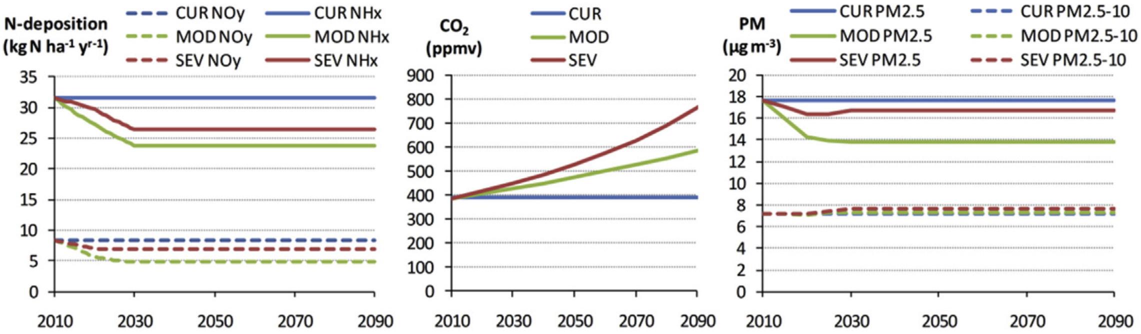

Fig. 2. Nitrogen (N) deposition, CO_2 and airborne particulate matter (PM) values over time for the current (CUR; blue), moderate (MOD; green) and severe (SEV; red) environmental change scenarios. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2010) × (yearly precipitation 2011)/(yearly precipitation 2010). This is not calculated using monthly values for precipitation instead of yearly values because unrealistic results could be obtained due to greater variation between months than between years. Note that every year has similar rain and PM patterns as the reference year 2010. Humidity is set constant at a high value of 0.7 because the climate of the Scots pine stand is humid.

2.4.1. *Interannual variability of weather conditions*

Only interannual climate variability of future climate uncertainty was included. This was performed practically via a new approach, exemplified by the case study. If one assumes that the current scenario is close to that of the previous 10 years (1999–2008), 80 random year samples (with monthly radiation, temperature and precipitation) may be taken out of this pool to obtain one random period of 80 years as the weather input for a run from 2010 to 2089. For example, for one sample, the weather conditions of year 2011 are similar to those of year 2000, and those of year 2012 are similar to those of year 2006, etc. The weather values for the period 1999–2008 were obtained from local measurements (Kint et al., 2012). Fifty random periods were thus created to serve as the weather input for the model runs of the current scenario. Taken together, this created a natural variation in weather conditions. The annual environmental changes in temperature and precipitation (Table 2) per scenario were superseded to obtain the weather inputs for the two future scenarios.

2.5. *Ecosystem services and their monetary valuation*

Ecosystem services are variable over time and space (Lyytimäki and Sipilä, 2009). For example, a forest may reduce runoff to a nearby river, lowering the risk of flooding, but this could lead to a water shortage later on in another region that stores water from this river in a reservoir. Assessments of these services may thus be very case-specific and should therefore be considered for fixed time and space boundaries in practice if applicable.

Only ecosystem services provided during the forest management period were accounted for. The area benefiting from the services varied between the services, from local (water recharge) to global (global warming potential). We first selected ecosystem (dis) services and the processes or aspects responsible for them, which could be directly attributed to the ecosystem. A service should, after all, be the specific result of a function or activity of the forest. In practice, for a regulating service in pollution remediation, these are processes that lead to the enhanced or active uptake of polluting compounds and/or the processing of them to forms that are not/ less harmful. Beyond this, our selection of ecosystem (dis)services was also restricted to those for which monetary values were available. In addition to this criterion, data should be available or modeled, by ANAFORE in our case, to account for a (dis)service. Table 3 lists the ecosystem (dis)services considered in this study.

In the literature reviewed in Table S1, wood production, because it has long been considered the primary function of forests, and biodiversity are accounted for by all 5 studies in a certain manner. Carbon sequestration is considered by three of the studies and groundwater recharge by two. In our study, we considered the following services: wood production, carbon sequestration, water evapotranspiration, $PM_{2.5}$ and $PM_{2.5-10}$ removal, NO_x emissions, NH_3 processing and nitrogen pollution/removal. Biodiversity of the forest itself and alterations were not assessed according to the

Table 3
Ecosystem (dis)services considered for the forest ecosystem with their monetary valuation, and the characterization factors for environmental impact assessment based on values from ReCiPe version 1.08 (2009), Alvarenga et al. (2013) and Pfister et al. (2009). Calculation of the service is performed via modeling using ANAFORE (Deckmyn et al., 2011, 2008) or via data retrieval. Negative monetary values are attributed to disservices in the strict sense. Nitrogen (N)-removal for water purification may also be a disservice if there is a depletion of the soil N stock. DALY: disability-adjusted life years; PM: particulate matter; PO: photochemical oxidant.

Monetary valuation of ecosystem (dis)services							Environmental impact assessment	
Ecosystem (dis)services		Calculation		Monetary valuation			/	
Ecosystem (dis)service (type)	Description	Source	(Additional) calculation	Value(s)	Type	Source	Impact categories	Characterization factors
Production of wood (provisioning)	The amount and quality of stem wood produced and harvested	Modeled		Price of standing stem wood (euro m^{-3}) for different circumferences	product price	Experts forestiers	/	
Sequestration of CO_2 (regulating)	Quantity of CO_2 stored as carbon in the forest	Modeled		20 euro ton^{-1} CO_2	Avoided abatem-ent cost	(Aertsens et al., 2013)	Global warming	1.4E-06 DALY kg^{-1} CO_2 7.93E-09 species*yr kg^{-1} CO_2
Processing of NH_3 (regulating)	Processing of gaseous NH_3 after uptake from air	Data	51.44% of NH_x-N deposition (Neirynck et al., 2007)	30 euro kg^{-1} NH_3	Avoided damage cost	(De Nocker et al., 2010)	Marine eutrophication	Dissolved in water: 1 kg N eq. kg^{-1} N gaseous or particulate 0.092 kg N eq. kg^{-1} NH_3
Emission of NO_x (disservice)	Emission of NO_x to the air	Data	5.29% of N deposition (Neirynck et al., 2007)	0.6 euro kg^{-1} NO_x[a]	Avoided damage cost	(De Nocker et al., 2010)		0.039 kg N eq. kg^{-1} NO_x 0.087 kg N eq. kg^{-1} NH_4^+ 0.028 kg N eq. kg^{-1} NO_3^-
Water purification/ pollution via N-removal/ emission (regulating)	The net amount of eutrophication potential (kg N eq.) of the forest (see Section 2.5)	Data & Modeled	kg N eq. input − kg N eq. output (based on the values of marine eutrophication)	5 euro kg^{-1} N[b]	Avoided abatem-ent cost	(Broekx et al., 2013)	Terrestrial acidification PM formation PO formation	1.42E-8 species*yr kg^{-1} NH_3 3.25E-9 species*yr kg^{-1} NO_x 8.32E-5 DALY kg^{-1} NH_3 5.72E-5 DALY kg^{-1} NO_x 3.9E-8 DALY kg^{-1} NO_x
Enhanced removal of particulate matter (PM) (regulating)	The amount of PM present in air that is taken up by the foliage and ends up in the soil	Mod-eled	See chapter 3	150 euro kg^{-1} $PM_{2.5}$; 25 euro kg^{-1} $PM_{2.5-10}$	Avoided damage cost	(De Nocker et al., 2010; Liekens et al., 2013b)	PM formation	2.6E-04 DALY kg^{-1} PM
Loss of freshwater (disservice)		Mod-eled	rain − infiltration = evapotranspiration + runoff[c]	−0.075 euro m^{-3} H_2O Tax for water extraction	product price	(Broekx, 2013)	Freshwater consumption	0 DALY m^{-3} −2.52E-9 species*yr m^{-3}
/							Resource use	278 GJex ha^{-1} yr^{-1}
/							Land occ.	1.2E-4 species*yr ha^{-1} yr^{-1}

[a] This service includes the indirect effect on the ozone level.

[b] Broekx et al. (2013) give a low, 5 euros, or high, 74 euros, kg^{-1} N removed from water. Expert knowledge of Prof. Dr. Ir. Siegfried Vlaeminck indicates 5 euros as the correct value.

[c] Runoff is negligible for the Scots pine stand because it has almost no slope.

following reasons: (1) forest biodiversity and the differences among scenarios will be small for a planted and intensively managed forest and (2) there is a lack of knowledge with which to value/monetize its benefit towards human well-being (Cardinale et al., 2012). See Section J of the Supplementary material on the current debate about the consideration of biodiversity as an ecosystem service. Stored nutrient amounts and cultural/recreational services were also not considered in the present ecosystem service valuation. Accordingly, the total amount of nutrients already stored in an ecosystem is considered by some as an ecosystem service, e.g., the carbon stock (Broekx, 2013; Duncker et al., 2012; Ninan and Inoue, 2013). However, if services provided by an ecosystem over a period of time are quantified, only the increase or depletion during that time period and the maintenance of the stock should be accounted for. The previously stored nutrient amounts, such as that of carbon and nitrogen, are the result of sequestration before the studied time period, which is thus outside of the system boundaries. Finally, recreational/cultural services were not part of environmental sustainability, and there are several issues in their quantification to substantiate their exclusion from this study (see further argumentation in Section J of the Supplementary file).

To value ecosystem services, monetary values may be attributed to them (Baveye et al., 2013; de Groot et al., 2012). Specific to the region of Flanders, such values have been developed by the Flemish Institute for Technological Research (Broekx et al., 2013; Liekens et al., 2013b) and are used herein. Economic values can be attributed to ecosystem services via different approaches (La Notte et al., 2015). For provisioning services, this is possibly their straightforward normal market price, if it is a merchantable product. Contingent valuation or choice experiments using public surveys, leading to willingness-to-pay for a service, represent other types of approaches, typically used for recreational/cultural services (Liekens et al., 2013a). For regulating services, a first calculation option is the avoided damage cost, and the second option is the avoided abatement cost. Note that the variety of methods induces different outcomes for a certain service and thus variability in its monetization (Kumar et al., 2013). Consequently, it is often infeasible to use a single approach consistently, leading to inevitable uncertainty in the outcome. In fact, the selection of the monetization approach will induce just a share of the associated uncertainty, as a lot of it comes into play for the monetary valuation of ecosystem services as thoroughly discussed by Boithias et al. (2016). Other methods to monetize ecosystem services are not addressed here. For disservices, the negative value of the opposite service is considered. Negative monetary values should be regarded as the cost mankind must pay to negate this disservice. Table 3 shows the monetization approaches used for the different (dis) services considered. Because monetization of ecosystem services specific for Flanders is already performed by mentioned authors (Table 3), their presented values, and the selection of monetization approaches have been mainly used as such. We agree with their arguments regarding why certain monetization approaches have been selected for the respective (dis)services. Note that these authors were often restricted in their selection by the available amount of data and information. For some specific services, we had to select the approach and associated monetary values ourselves. For wood production, we selected market pricing, as is commonly done (Broekx et al., 2013; Duncker et al., 2012; Fürstenau et al., 2007; Pizzirani et al., 2010) and is explained later. Regarding air pollutants, we were consistent and selected the ‘avoided damage cost’ approach as applied for particulate matter and argued by Liekens et al. (2013b). Because monetary values may vary from year to year, 2010 was chosen as the reference year because it is the first year of the management period.

We elaborate more on the considered services in the following text. Furthermore, we explain why some considered services or approaches presented in the literature are not taken into account in our study. The provisioning of freshwater through seepage is accounted for in some studies as a service provided by forests (Fürstenau et al., 2007; Ninan and Inoue, 2013). This could be questioned because it is the complete hydrological cycle that produces rain falling on land that may end up as available freshwater. Attributing this service solely to a terrestrial ecosystem, such as a forest, is not correct. It is not the case that, without the ecosystem, there would be no groundwater recharge. The land ecosystem may, however, influence the fate of freshwater through its influence on runoff, evapotranspiration and infiltration and could thus locally/regionally influence the available stock of freshwater. Runoff and evapotranspiration may in fact lead to a potential loss of freshwater locally because there is less decrease in local groundwater reservoirs. Loss due to evapotranspiration has been noted previously (Jobbágy and Jackson, 2004; Maes et al., 2009). Note that if runoff ends up in another natural freshwater reservoir, it may not be lost. Additionally, on a larger scale, evaporated water could return again as freshwater at another location (Keys et al., 2012). In the studied Scots pine forest, the landscape is flat, and the soils are permeable; surface runoff is thus not significant. It is also situated in an area where a relevant share of infiltrated water later ends up as freshwater through human/industrial groundwater extraction (Broekx, 2013). Though water scarcity is not an urgent issue in the region, it might be in the near future due to depletion of groundwater reserves (note that Flanders is importing approximately 20% of its drinking water), as recently reported by the Flemish government (Rekenhof aan het Vlaams Parlement, 2014). Additionally, if the groundwater table is high enough, tree roots may be able to directly take up ground water, and thus potential freshwater, in addition to rain percolating through the soil (Dawson, 1996; Jobbágy and Jackson, 2004). This was clearly demonstrated by a study on another Scots pine stand with sandy soil in the same region (Belgian Campine), in which the water table contributed, at a certain point, up to 98.5% of the water uptake by vegetation (Vincke and Thiry, 2008). If we only consider the local benefit, evapotranspiration could be regarded as a regulating ecosystem disservice, acting only as a loss of freshwater. This will be accounted for in this study. Duncker et al. (2012) only considered runoff and neglected evapotranspiration. The prevention of erosion and reduction of the impact of flooding through water retention (Stürck et al., 2014) by ecosystem services are not relevant because the Scots pine stand is not located in an area where this is important (Broekx, 2013). However, evapotranspiration has a cooling effect on the surface, counteracting the temperature increase induced by an increase in greenhouse gases (Bonan, 2008). It is, however, difficult to quantify the monetary value of the ecosystem service provided through this cooling effect, and it is therefore not considered here. Moreover, evapotranspiration acts as a supporting service for ecosystem functioning and thus other services (Maes et al., 2009; Muys et al., 2011). To account for all the supported services provided through evapotranspiration is yet again a hard nut to crack and consequently not done here. Overall, consideration of freshwater-related services is site-specific. Our approach can still be questioned, though it is reasoned why it is favored for this site, because further research is needed to take into account all (aspects of) water-related ecosystem services (Muys et al., 2014).

Water may not be provided directly by an ecosystem, though its composition may be altered. (Water) purification is an important ecosystem service that has been put forward many times (Duncker et al., 2012; Ninan and Inoue, 2013). Specifically, there is a water input in the ecosystem with a certain pollutant content, e.g., nitrate, and, after leaving the system, its content may be reduced/the water quality may be improved. In this paper, only nitrogen content is considered under the heading of water quality. To only account for the quality of the water leaving the system is incomplete, because the occurrence of pollutants already present in the initial input, rainfall and deposition is not considered. Broekx et al. (2013) and Liekens et al. (2013b) do however only consider the amount of nitrate-nitrogen leaving the system as a disservice. In fact, the forest ecosystem must cope with the total nitrogen input from rainfall and dry deposition, and the service provided is the amount that does not end up in the water, increasing the water quality. This service is provided by the ecosystem via the uptake of input nitrogen into biomass, converting it into primarily non-harmful dinitrogen gas via microbial processes. A disservice may be the extra presence of N in water flows through depletion of the nitrogen stocks.

In addition, the damaging effect depends not only on the amount of nitrogen but also on the forms, e.g., nitrate, in which this amount is present. By only focusing on the eutrophication potential, which is relevant when considering water purification, of the nitrogen compounds, we may convert all flows to kg N equivalents according to their midpoint eutrophication potential using the values of an impact assessment methodology (given in Table 3) and subsequently sum them. For nitrogen compounds in water flows, this factor is simply the amount of nitrogen per compound, e.g., 0.78 kg N kg^{-1} NH_4^+. For nitrogen in gaseous fluxes and particulate matter deposition, these values are lower due to their lower potential to end up in water flows (Goedkoop et al., 2009). Because the uptake of these fluxes is influenced by the forest, this is more suitable. Ultimately, through enhanced dry deposition via plant surfaces, the forest may aid in bringing N compounds from air into water and thus actively contribute to eutrophication. After obtaining the single summed value in kg N equivalents, we may convert it to a monetary amount by multiplying by 5 euro kg N^{-1}, as mentioned in Table 3. To accurately calculate this value, the composition of nitrogen compounds must be known. For each environmental change scenario, the total amount of NH_x-N and NO_y-N inputs are already given (see Section 4 of Materials and Methods). Based on the values of Neirynck et al. (2007), specific component amounts can be obtained. NH_x-N consists of dry-deposited NH_3—N (51.44%) and NH_4^+-N (17.06%) and wet-deposited NH_4^+-N (31.50%). NO_y-N consists of wet-deposited NO_3^--N (42.64%) and dry-deposited NO_3^--N (25.58%), HNO_2–N (21.71%) and HNO_3–N (10.08%). The dry-deposited amounts of HNO_2–N and HNO_3–N are considered to be NO_3^--N amounts, as in the work of Schaubroeck et al. (2013). The nitrogen leaving the system is considered to be 100% NO_3^- via drainage and there is also the gaseous emission of NO_x, 5.29% of the N deposition (Neirynck et al., 2007).

Two services regarding air purification or pollution by nitrogen compounds are also considered: the net emission of NO_x and the uptake with subsequent net processing of NH_3; this is based on the values given in previous paragraph. These flows are net flows, implying that both input and output are indirectly accounted for.

Through harvest, wood is provided to mankind. The price for the ecosystem service of wood provisioning is that of the market price per cubic meter of standing wood (€ m^{-3}) prior to harvesting as a function of its circumference (cm) at 1.5 m. These values are obtained from the Belgian federation of forestry experts (Fédération Nationale des Experts Forestiers, 2013). Price data for Scots pines from the year 2010 are used here. See Section D of the Supplementary file for these values and further discussion.

2.6. Environmental impact assessment (methodologies)

To assess the environmental impact of the forest ecosystem through resources and emissions, the framework of Schaubroeck et al. (2013) is applied, and an overview of impact methods and values is presented in Table 3. In this framework, the absorption of harmful compounds, e.g., CO_2, by the forests is a negatively valued impact, reflecting the effect of remediation. The impact on three areas of protection is considered: natural systems/ecosystems, human health and natural resources (de Haes et al., 1999). Similarly, the ReCiPe 1.08 method (Goedkoop et al., 2009) was selected to assess the impact of emissions and land uses on ecosystems, expressed as diversity loss (species*yr), and human health, expressed as disability-adjusted life years (DALY), i.e. number of years of healthy life lost. The characterization of the effects are explained in the ReCiPe report (Goedkoop et al., 2009). For example, the effect of global warming, thus temperature increase induced by greenhouse gas emissions, on human health is assessed through an increase in malnutrition (via decrease in agricultural production), malaria and diarrhea (both diseases which occur more if temperature rises), cardiovascular diseases (linked to an increase in number of days with extreme temperature), coastal and inland flooding (due to increase in precipitation and sea level rise). These are not all the indirect effects of global warming on human health and are quite rough estimations. Regarding the impact category of marine eutrophication, eutrophication in coastal and marine waters where a share of the freshwater and its associated nitrogen compounds end up, no quantification of endpoint diversity loss is yet available, though this effect is acknowledged (Goedkoop et al., 2009). Hence, this is simply expressed as kg N equivalents. Furthermore, the impact of the net loss of freshwater, mainly through evapotranspiration, on human health and ecosystem/species diversity is also assessed via the methodology of Pfister et al. (2011, 2009) in which the local and marginal impacts of the consumption of freshwater of lakes, rivers or aquifers is assessed. For this aspect, specific values for Belgium were used and are given in Table 3. For the impact on human health, the value is 0 DALY m^{-3} because the methodology of Pfister et al. (2009) for developed countries such as Belgium assumes that the loss of freshwater is easily dealth with (by purchasing it from other countries), which can be questioned given our discussion in Section 2.5.). The only resource deprived from nature by the intensively managed hence non-natural forest ecosytem is the growth of natural vegetation that could not grow during the time of occupation. This is assessed as the deprivation of natural net primary production (NPP), expressed in exergy and modeled via a global vegetation model (Haberl et al., 2007), using the cumulative exergy extraction from the natural environment (CEENE) methodology (Alvarenga et al., 2013; Dewulf et al., 2007) based on the same reasoning of Schaubroeck et al. (2013). The CEENE characterization factor for land occupation at the exact location (defined by its coordinates) of the Scots pine stand is 278 GJ_{ex} ha^{-1} yr^{-1} (Alvarenga et al., 2013). Because the natural NPP production is induced by the combination of biotic and abiotic conditions (such as rain and sunlight), these are also indirectly accounted for as resources.

The outcome of the overall environmental impact assessment is represented by a set of four values that represent damage to human health (DALY), ecosystems (species*year), marine eutrophication (kg N equivalents) and resources (CEENE). Because a single value was not obtained and cannot be aggregated in a scientifically sound manner (Schaubroeck et al., 2015a), the scores from these indicators need to be interpreted together.

3. Results & discussion

3.1. Case study

The difference in gross forest flows, such as carbon dioxide sequestration, is not the primary focus of this article, but interesting findings can still be drawn from them. This is discussed in Section E of the Supplementary file. The presented modeled values deviate considerably, which illustrates the influence of the natural variation of weather effects, and may thus be considerable in terms of ecosystem growth and its delivered services overall. Additionally, our result emphasizes the relevance of considering the right initial soil conditions (here just after a clear-cut) and using a forest growth model that includes a soil module (Deckmyn et al., 2011), which was not used in the other studies mentioned in Table S1 except that of Seidl and Lexer (2013).

3.1.1. Monetary valuation of ecosystem services

The interpretation and comparison of monetized ecosystem services is more straightforward because these services are all presented in one tangible unit. The profile over time of the provisioning of services is highly similar for all 9 scenario combinations, one of which is presented in Fig. 3. A total positive monetary balance is obtained only after 4–5 years, with a cumulative positive balance over 10–11 years, i.e., only then the Scots pine stand is estimated to provide a beneficial overall service to mankind, according to our results. This is due to the high CO_2 losses and nitrate leaching in the early years, explained in Section E of the Supplementary file. After this period, almost all services maintain a linear increase except CO_2 sequestration, which decreases in slope, and wood harvest, which occurs in steps associated with harvest operations over time. Clear-cutting at the end of the management period is responsible for an important share of the monetary value of this service, leading to the steep increase at the end.

In Fig. 4 (bottom), the results are presented for the 9 different combinations of scenarios, ranging from 361 to 1242 euro ha^{-1} yr^{-1}. By far, the most important service in terms of monetary value is $PM_{2.5}$ removal, with 622–1172 euro ha^{-1} yr^{-1}. When not considering this service, the total balance would be negative for all scenarios. Next in line is CO_2 sequestration (168–371 euro ha^{-1} yr^{-1}). $PM_{2.5-10}$ removal, NH_3 removal, and wood production all have a yearly average of approximately 100–200 euro ha^{-1} yr^{-1}. The largest disservice is the loss in freshwater through evapotranspiration by the Scots pine stand, circa 440 euro ha^{-1} yr^{-1}. Regarding nitrogen, there is a net pollution, meriting 220 euro ha^{-1} yr^{-1}. However, these last two services essentially do not vary between the different scenarios. The emission of NO_x is a negligible disservice, with a value lower than 5 euro ha^{-1} yr^{-1}.

The differences between the environmental change scenarios (60 euro ha^{-1} yr^{-1} less for the severe and 289 euro ha^{-1} yr^{-1} less for the moderate scenarios, on average, than the 939 euro ha^{-1} yr^{-1} for the current scenario) are not large and can be mainly attributed to the discrepancy in PM removal and to a lesser degree to NH_3 removal (and to the other services to a small extent); both of these discrepancies can be allocated to the differences between the lower input/airborne concentrations of these pollutants in the future scenarios compared to the current one. Essentially, less 'pollution' corresponds to a lower possibility for a forest to remove pollutants and to a lower provisioning of the respective services. Note, however, that nitrogen also serves as a nutrient, and a complete depletion in the nitrogen input can be detrimental.

Concerning management scenarios, CO_2 sequestration, PM removal (induced by LAI differences, as discussed in Section E of the Supplementary file) and wood provisioning are most differentiated and thus largely responsible for the differences between these scenarios. Overall, compared to the MID management scenario, the LOW scenario is estimated to have a 1.25–1.30 times higher total monetary value and the high scenario a 1.71–1.92 times lower value of ecosystem services, favoring the lowest amounts of thinning. The difference in CO_2 sequestration is forecasted to be the largest, relatively, and PM removal and wood provisioning are similar in their relative differences. Selection of the management scenario is estimated here to have (and can have) a considerable impact on the services delivered by a forest. If one only regards the provisioning of wood, the same trend is only visible to a much lesser extent (see Figure S6 of the Supplementary file). Regarding all services, the LOW management scenario is preferred. Certain tradeoffs and synergies might exist between the services, which are discussed in Section G of the Supplementary file.

3.1.2. Environmental impact assessment

The environmental impact assessment is expressed in four units: disability-adjusted life years (DALY), species diversity loss, kg N equivalents (marine eutrophication) and cumulative exergy extraction from the natural environment (CEENE). DALY and species diversity loss are shown in Fig. 4. Because CEENE is only quantified per hectare, 278 GJex ha^{-1} yr^{-1}, there is no difference in this unit between the scenarios. Concerning the impact on human health, a clear positive effect is estimated in all cases, 0.014–0.029 DALY ha^{-1} yr^{-1} equal to 5.0–10.6 days ha^{-1} yr^{-1} prevented by the forest ecosystem. Over a complete management cycle, this represents a prevention of 1.1–2.3 disability-adjusted life years ha^{-1}. The largest contributor is the uptake of CO_2 of at least 85%. The rest is attributed to PM removal. Concerning the impact on the biodiversity of natural systems by the considered forest, there is an estimated loss in biodiversity mainly due to the intensive management of the forest. The predicted loss is 1.2 E–04 species*yr ha^{-1} yr^{-1}, which is the diversity loss induced by the non-natural nature of the planted Scots pine stand: the general difference in biodiversity between a natural system and an intensive forest, such as the Scots pine stand, in Europe (Goedkoop et al., 2009). As already reasoned in Section 2.6, the discrepancy in biodiversity among the scenarios will be low and, therefore, the same biodiversity loss is assumed for each scenario. Additionally, freshwater loss likely leads to a minor loss of diversity. CO_2 uptake partially counteracts this biodiversity loss (with 46–101%) by preventing diversity loss on a large scale, normally induced by atmospheric CO_2. Regarding (marine) eutrophication, also leading to a projected diversity loss but only expressed in kg N, the range is very narrow between the scenarios: 43.2–47.2 kg N ha^{-1} yr^{-1}, with the LOW scenario having the lowest values. However, this shows that the forest would have a negative impact on its environment concerning (marine) eutrophication because the forest aids in bringing airborne particulate nitrogen into the leached freshwater via dry deposition. However, the quantified diversity loss does not completely cover the damage to the ecosystem (quality) because some impact categories are not yet expressed in terms of diversity loss, such as marine eutrophication.

Here, CO_2 sequestration and PM removal are the most important fluxes and also differ considerably between management and, to a lesser extent, between environmental change scenarios. For each aspect, the LOW management scenario comes out on top in this assessment approach.

3.1.3. Implications for the case study

In our case study, the LOW management scenario is predicted to

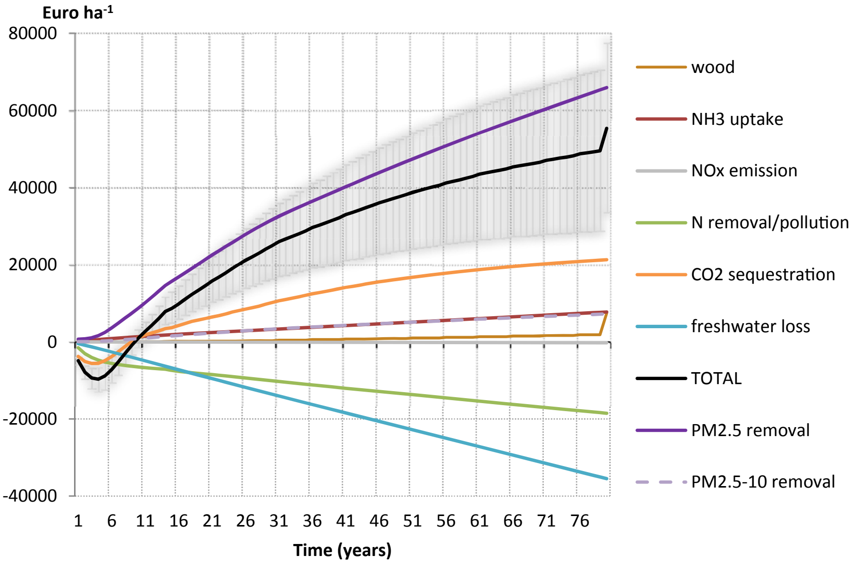

Fig. 3. Ecosystem services provided by the Scots pine stand for the moderate environmental change scenario with MID management, presented in monetary values and cumulative over time. The standard deviation induced by the natural variation in weather conditions is represented by grey shading for the total.

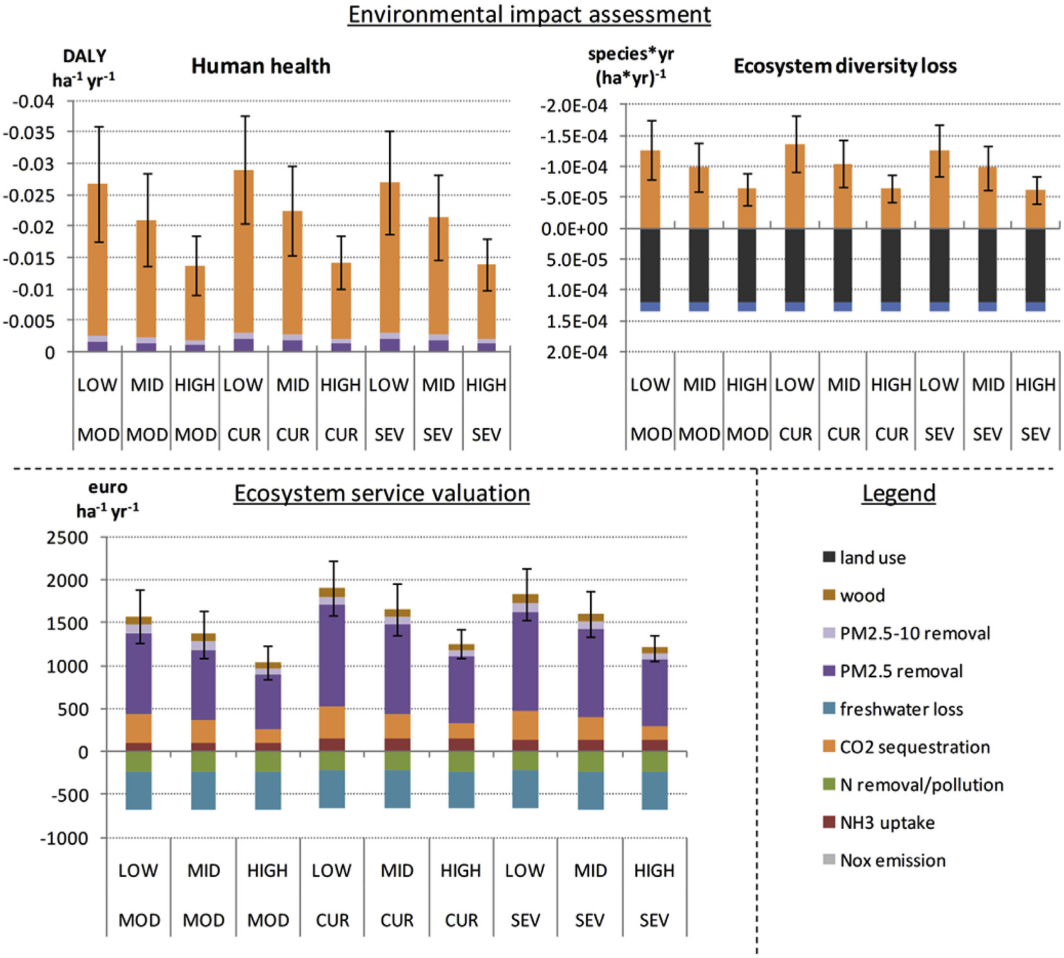

Fig. 4. Comparison of the results of the 9 different combinations of management (low, mid and high) and the three different environmental change scenarios: current (CUR), moderate (MOD) and severe (SEV). Yearly averages of the environmental impact assessment and monetary valuation of ecosystem services are given. The environmental impact assessment expresses the impact on human health as disability-adjusted life years (DALY) and the impact on ecosystems as ecosystem/species diversity loss; that of resource consumption is constant at 278 GJex ha^{-1} yr^{-1} and the difference in eutrophication impact is only discussed in the text. The standard deviation induced by the natural variability of weather conditions (precipitation, irradiation and temperature) (see Section 2.4) is depicted with error bars for the total values.

be the best according to both approaches. However, this is only based on a selected amount of ecosystem services/flows and not all of the relevant ones (see Section 2.5). Therefore, the total values do not represent the total impact nor the value (of all services) of the forest. First, forest trees can deliver different biomass products, e.g., wood, roots. When only considering wood as a product, the impact and the provided services of the forest can be fully allocated to the wood produced, with repercussions on the environmental impact profile. This is further discussed in Section H of the Supplementary file.

The specific Scots pine stand had an approximate selling price of 16,000 euro ha^{-1} in 2010 (price retrieved from the owner, the Agency for Nature and Forestry). Considering the same ratio of rental and selling price as in the nearby city of Brasschaat yields a rental price of 143.6 euro ha^{-1} yr^{-1}. This is approximately a factor 2.5–8.6 lower than the value calculated here that is provided to mankind by the forest through ecosystem services, illustrating the current estimated undervaluation of these services by society.

3.2. Discussion of methodological approaches

The differences in values between the monetary ecosystem service valuation and the environmental impact assessment highlight the distinctions between these methods and also acknowledge that results may vary according to the applied environmental sustainability assessment method. The most important differences for the case study are as follows: PM removal is by far the most important for ecosystem service valuation, but CO_2 sequestration is most important for environmental impact assessment; biomass (wood) production is not accounted for in the latter case, and biodiversity loss is not considered an ecosystem service. Straightforward comparison of the different outcomes is difficult as these are different types of approaches. A possible reason for the higher importance of PM removal for the monetary valuation of ecosystem services is that monetization of this service is specifically developed for Flanders, a very densely populated area within Europe and thus more harm is caused by PM. Human health damage by PM in ReCiPe is characterized on a European level. Moreover, ReCiPe does not distinguish between the difference in health damage between $PM_{2.5}$ and $PM_{2.5-10}$, even though research pinpoints that this is the case (De Nocker et al., 2010); however, Perrone et al. (2013) argue this matter. Furthermore, the endpoint for ecosystem damage is assessed as species diversity/richness, which directly covers only one aspect, information. As discussed in Section 5 of the Materials and Methods, the value of biodiversity is not yet quantified. Theoretically, an increase in richness does not ensure a change in ecosystem processes (de Souza et al., 2013). An improvement would be to assess the functional diversity (de Souza et al., 2013). In the ReCiPe methodological guidelines, however, authors have already noted that the damage to ecosystems also addresses the disruption of mass and energy fluxes, in addition to information (Goedkoop et al., 2009). Interestingly, other authors have explored this issue with approaches based on changes in mass and energy or in exergy fluxes, storage and dissipation (Maes et al., 2011; Schaubroeck et al., 2012; Silow and Mokry, 2010).

However, ecosystem services and environmental impact assessment clearly overlap (see, for example, Table 3) and are increasingly integrated. For example, the uptake of harmful compounds considered by the framework of Schaubroeck et al. (2013) and used in this study is based on regulating ecosystem services. In fact, in that framework, more than just an ecosystem service is accounted for because the beneficial effect on ecosystems is assessed in addition to that on human health. In our study, this was accounted for by using the midpoint characterization of marine eutrophication to convert all N-flows into kg N equivalents in the ecosystem service valuation. Novel environmental impact assessment methodologies have been developed to assess the potential damage on (the provisioning of) ecosystem services (Arbault et al., 2014), mostly for different land uses (Koellner and Geyer, 2013; Saad et al., 2013). However, an essential issue should not be forgotten: the conceptual difference between ecosystem services and environmental impact assessment is that the first only considers the final benefit to mankind but the latter accounts for the total environmental impact. Note that ecosystem services can also be expressed using environmental impact assessment characterization factors and that there is also a potential to express environmental impact assessment results in monetary values (Pizzol et al., 2015). A solution to resolve this limitation of ecosystem services assessment is to redefine its concept to ultimately consider the well-being of both humans and nature. However, this limitation might be irrelevant becaus Schaubroeck (2014) and Schaubroeck et al. (2015b) argue that sustainability is an anthropocentric concept, making humans' well-being the only finality; nevertheless, the indirect impact on mankind via an effect on nature should be accounted for in sustainability assessment. Considering that this is also an ethical issue, the development of a clear objective universal approach is not straightforward.

3.3. *Monetization of ecosystem services, the holy grail?*

In this study, monetary valuation of ecosystem services was performed. Although it allows placing a single value on all services provided, an economic value does not (completely) represent/capture the real value, the benefit to mankind, and the given value depends on the socio-economic framework used to obtain it, e.g., avoided damage, as discussed by La Notte et al. (2015). Baveye et al. (2013) reviewed different scientific opinions on this matter. Consequently, there is still a need to express ecosystem services in a unit that better represents their real value (Baveye et al., 2013). However, given the economics-oriented society in which we live, monetization makes the concept more tangible (Quine et al., 2013). Monetization is adequate to simply compare different alternative scenarios that influence the supply of ecosystem services (Kumar et al., 2013), as in the present study. Today, monetization is necessary to easily account for ecosystem services in our society. Using these values, one may readily consider ecosystem services as economic products. As a step further, one could thus financially reimburse landowners for the services provided by their land through payment for ecosystem services (PES). If we additionally consider these services as tradable entities without fixed prices, different market mechanisms are set loose on the prices that alter them over time. However, it is not guaranteed that these changes in economic price represent changes in the fundamental value of the service to mankind, such as the volatility of the carbon emissions market (Chevallier, 2011). Governments or institutions should control, potentially even fix, these prices. Inversely, this might induce rent-seeking. In this particular accounting/policy method of fixing prices, a difference should be discerned between services that improve the quality of life of the total (global) community, such as climate change, or that of local/regional communities (Kumar et al., 2013). Several of the potential downfalls induced by PES and the necessary regulation for their restriction are discussed in detail by Kronenberg and Hubacek (2013).

In addition, issues related to economic mechanisms such as discounting remain, as exemplified in this paragraph. Consider fixed prices and that the services are provided over a certain period of time. On the market, the profit Y earned in the future after T years has a lower value X in the present due to the possibility to earn Y-X money through investment in the financial markets with similar risk based on a certain discount rate R. Herein, X is the net present value (NPV), calculated as $Y/(1+R)^T$. Again, this can be regarded as a variation in price and thus value. Changes based on percentages inherently distort the value ratios between the services over time; an identical service has a higher price and 'value' in 2010 than in 2011, which implies that the benefit to future mankind is less important than to the current population. However, the unit values of services will change over time due to various factors, and not considering discounting implies that the welfare of the current generation is negligible for long-term future predictions, which is questionable. Many pros and cons can be formulated for discounting; see the specific work of Hepburn and Koundouri (2007) on this issue in the field of forest economics. We considered results without price discounting ($R = 0\%$) in this manuscript, but NPV results with a constant discount rate of 2 and 4%, as done by Fürstenau et al. (2007), have been obtained. The same primary conclusions are drawn with those discount rates as those without discounting, as shown and discussed in Section I of the Supplementary file. In practice, the 'ecosystem service' concept could replace more general ecosystem management principles, e.g., the 'sustainable forest management' principles, as a framework for management selection, although they should co-exist for now because not all ecosystem services have been (e)valuated well enough (Quine et al., 2013). In addition to its advantages mentioned in Section 1.1, valuation through monetization clearly also has its drawbacks compared to MCA methods. This valuation dilemma could, to a certain extent, be resolved by valuating ecosystem services using environmental impact characterization, resulting in an aggregated set of objective tangible values wherever possible, keeping in mind the difference in finality discussed in the previous Section. However, then MCA might still be needed to obtain a single outcome. In general, there is no one ideal approach yet though lessons can be learnt out of the existing ones and integration must be researched.

3.4. *Influence of space and time boundaries*

As previously noted, the temporal and spatial boundaries influence the results of our assessments. Ideally, all impacts and benefits in space and time should be included. However, for practical reasons, boundaries are set, e.g., the global warming potential is assessed over only 100 years, while the effects of emissions might persist longer. A second important point is that, for freshwater loss in Belgium, the human health impact is 0 DALY m^{-3} according to Pfister et al. (2009). Because of the very high human development index (>0.88) for Belgium (Pfister et al., 2009), the malnutrition vulnerability induced by a loss in agricultural crops is set equal to zero, since Belgium can easily buy water from elsewhere. From a marginal and local perspective, this is acceptable (ceteris paribus principle), but, if large quantities are withdrawn, this will always have a direct effect and will result in a loss in agricultural products on the global market (as water from elsewhere is bought); this may thus affect human health, though possibly not locally. Furthermore, water scarcity may become an important issue in Flanders in the near future (Rekenhof aan het Vlaams Parlement, 2014). Evapotranspiration may also lead to an increase in valuable precipitation on downhill agricultural lands (Keys et al., 2012). These boundaries should be considered and possibly broadened through further research. As discussed by Schaubroeck et al. (2013), the time aspect, e.g., the amount of time carbon dioxide is stored, and the regional differentiated aspect of impact/effect need to be better integrated/included in ecosystem service valuation.

4. Conclusions

The environmental sustainability assessment of ecosystem management needs further improvement regarding the following aspects: quantification/modeling of ecosystem flows/services, the influence of future environmental change on their quantities and valuation of the damage and benefit of these flows/services. In this study, we improved several aspects in a general manner and exemplified these through application to a Scots pine forest ecosystem. In general, the following aspects were improved: freshwater loss through evapotranspiration is considered as a disservice (note that this consideration is site-dependent), the inflow is compared to the outflow to better quantify pollutant removal/generation services and interannual climate variability is accounted for in environmental change scenarios. We modeled the Scots pine flows and ecosystem services under different environmental change and management scenarios. Because of the highly detailed process-based modeling effort, the following ecosystem services could be quantified in a relatively high qualitative manner: particulate matter (PM) removal, freshwater loss, CO_2 sequestration, wood production, NO_x emissions, NH_3 uptake and nitrogen pollution/removal. To the best of our knowledge, the considered environmental change scenarios are the most elaborated to date due to the consideration of (site-specific) changes in temperature, precipitation, nitrogen deposition, wind speed, PM concentration and CO_2 concentration.

Two environmental sustainability assessment approaches were applied: environmental impact assessment and monetary ecosystem service valuation. These approaches result in outcomes that are more tangible and less subjective than those of multi-criteria decision analysis (with stakeholder opinion). Note however that monetization also has its drawbacks (see Section 3.3). Though the monetary ecosystem service valuation is quite commonly applied, we used values specifically obtained for the region, but questioned the use of economic value to characterize ecosystem services. Hence, environmental impact assessment, in combination with MCA if no single outcome is obtained, might be reasonable good alternative and also characterizes the final damage and benefit to other ecosystems, in addition to mankind, on which the effect is only considered for ecosystem service valuation. However, addressing consensus on the integration between these approaches is the next step, as the endpoint (the well-being of both humans and nature or only of humans) of any environmental sustainability assessment approach is still debatable.

In this study, the monetary valuation highlights the likely importance of services provided by the forest, with a total estimated yearly average of 361–1242 euro ha^{-1} yr^{-1}. $PM_{2.5}$ (<2.5 μm) removal is the key service, with a projected value of 622–1172 euro ha^{-1} yr^{-1}. These total values do not represent the total impact or the value (of all services) of the forest because not all aspects are considered. Concerning the environmental impact assessment, with net CO_2 uptake being the most relevant contributing flow, a loss prevention of 0.014–0.029 healthy life years ha^{-1} yr^{-1} is calculated.

Both assessment methods favor the use of the least intensive management scenario because it results in higher CO_2 sequestration and PM removal induced by a higher leaf area index. Although the current focus in the literature is often on assessing as many ecosystem services as possible for large areas, the present case study clearly demonstrates the relevance and important new findings of the thorough study of a specific ecosystem. There are, however, still many prominent limitations to various aspects of this study. It is, after all, a prospective modeling effort, and its outcome should be regarded as an estimation. Further research to improve the assessment is imperative.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jenvman.2016.03.005.

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Modelling water and ^{36}Cl cycling in a Belgian pine forest

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INTRODUCTION

Understanding the role of trees as biological pumps cycling radionuclides in forests is essential in order to elucidate the potential sinks of radionuclides in the forest ecosystem and the effect of climate variation on contaminant distribution.

In an accidental release of radionuclides, following atmospheric deposition, the primary source of tree contamination is direct interception of aerosol by the canopy, followed by further translocation from foliar surfaces to structural components of the tree. After the initial exposure period, the dominant process is the recycling caused by the self-cleaning of the canopy by precipitation wash-off (throughfall) and litterfall (which returns radionuclides to soil after decomposition) as well as re-entry by root uptake of the radionuclides that have migrated into the soil profile. The internal translocation within vegetation is probably low compared with exchange (uptake/return) between the soil and the forest vegetation. In more routine situations, and/or especially when the contamination is located below ground, the transfer processes from the saturated zone to the plant become critical, then root uptake followed by vertical transport and the recycling of radionuclides from trunk to leaves and back to soil. The source term in this case is always present, and there is a dynamic balance between input from below the tree and the return processes to the ground, with annual oscillations caused by the vertical moving of the water table with the seasons. The number of processes involved and associated uncertainties require simplification of the problem if the model is to serve as a practical aid in radiological assessment.

In 2005, a research programme was initiated which focused on a Scots pine forest on sandy soil from an area of Mol (Belgium), situated above a shallow water table (Vincke and Thiry, 2008). Hydrological monitoring (climate, through-fall, moisture, tree transpiration and water table variations) was continuous throughout the year. A compartmental model for chlorine cycling was developed for this forest stand (Van den Hoof and Thiry, 2012). From here we developed a new 1-dimensional layered water table model based on Darcy and capillarity flow rather than explicitly resolving the highly non-linear Richards equation (Richards, 1931). We coupled such model to a vegetation model representing a Scots pine in which the equations of xylem and phloem transport, transpiration, translocation and litterfall/organic decomposition are provided. We tested the model against the results of the field study and matched the water fluxes in the steady state to the ^{36}Cl model. The ultimate goal of this work is to integrate the model with a biosphere approach for human impact assessment, developing an assessment tool sufficiently complex to be realistic but sufficiently simple to be practical.

MATERIALS AND METHODS

Even when represented within a 1-dimensional model, soil hydrology is not so easily considered, and the model needs to be finely adjusted to achieve a water balance between the volumetric water content of the soil column layers, the net recharge, surface water inflow/outflow, evaporation from soil and transpiration from plants. It assumes a quasi-steady-state of water (laminar) flow, whereupon the higher kinetic terms of Richard's equation can be neglected and hydraulic conductivity is approximately constant.

A model was set-up in the *ModelMaker* 4 software (Rigas, 2000) (Fig. 1) using the Gear integration method (Gear, 1971). The main parameters are given in Table 1. A 'tipping-bucket' approach is used whereby different soil layers in a 10 m soil column gradually fill-up as adjacent layers become saturated. The volumetric water content in each layer can fluctuate between a minimum, defined by the soil field capacity, and a maximum, defined by the soil porosity, until the resulting water table occupies the whole soil column, leading to runoff.

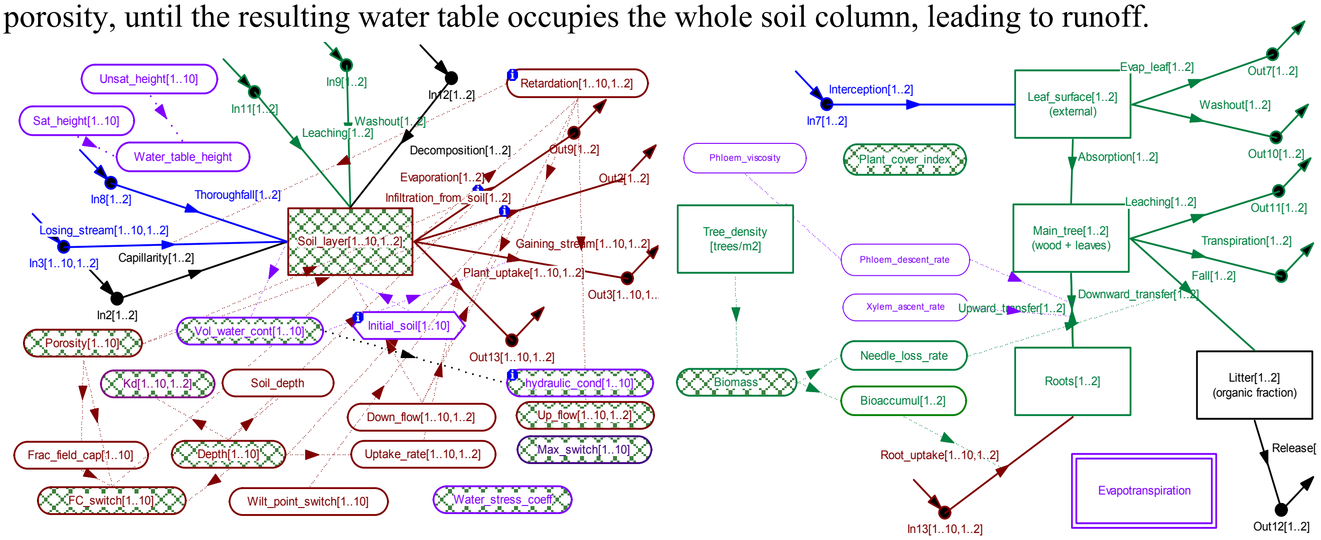

Figure 1: Conceptual model including compartments (rectangles), variables (rounded rectangles), definitions (polygons), flows (arrow lines) and influences (dotted arrow lines)

Table 1: Model parameters

Parameter	Symbol	Value
Allometric factor a for tree biomass	a, b	0.152 kg, 2.234 (Xiao and Ceulemans, 2004)
Amplitude of energy radiation	Rn-G	237.3 J m^2 s^{-1} (Ceulemans et al., 2003)
Diameter of tree at breast height	DBH	0.2897 m (Van den Hoof and Thiry, 2011)
Extinction coefficient from Beer's law	γ	0.526 (Brission et al., 1992)
Forest stand density	Σ	3.59×10^{-2} m^{-2} (Van den Hoof and Thiry, 2011)
Fractional field capacity of sandy soil	ξ	0.19 (Brakensiek et al., 1984; Schroeder et al., 1994)
Fractional needle mass	N_m	0.22 – 0.36 (Pausas, 1997; Xiao and Ceulemans, 2004)
Leaching, decomposition and needle fall rates	$k_{63,}$ k_{dec}, k_{64}	4.93×10^{-5} d^{-1}, 4.22×10^{-3} d^{-1} , 5.27×10^{-1} d^{-1} (Pausas, 1997; Van den Hoof and Thiry, 2012)
Phloem drag coefficient	χ	0.5 (Nonweilwer, 1975)
Plant absorption, intercption & washout	$k_{76,}$ $f_{int}^{p,}$ w_f	0.15, 0.29, 0.85 (Van den Hoof and Thiry, 2012)
Ratio below/above ground biomass	κ	0.26 (Xiao and Ceulemans, 2004)
Hydraulic conductance	H_c	0.710 m d^{-1} (typical for sand)
Root depth & extinction coefficient	h_{root}, b	1.4 m (Vincke and Thiry, 2008), 2 d^{-1} (Li et al., 1999)
Runoff coefficient	r_c	0.1 (ODOT, 2005)
Soil bulk and particle density	ρ_0, ρ_{soil}	1880, 2650 kg m^{-3} (Baes and Sharp, 1983)
Sorptivity constant (undisturbed soil)	S	3.79×10^{-2} m $d^{-1/2}$ (Fuentes et al., 2010)
Pine tree density & tree height	ρ_{tree}, h_{tree}	700 kg m^{-3} (Ketterings et al., 2001), 35 m (Rushforth, 1981)
Xyleem density & viscosity	ρ_{xyl}, η_{xyl}	1.08×10^3 kg m^{-3} (Lane, 2012), 1.68×10^2 kg m^{-2} d^{-1} (Hölttä et al., 2006)

Downward water migration through the soil was modelled by Darcy's law and upper capillary transport is described by Newton dynamics' equation for a viscous non-compressible liquid, assuming quasi-steady Poiseuille flow, approximated by Phillip's law (1957). Though the model is 1-dimensional, the effect of a nearby river is modelled by a simple losing or gaining stream with lateral flow calculated using Darcy or Torricelli flows, respectively.

Plant root water uptake was represented by an exponential root water uptake model (Li et al., 1999), with the total root uptake rate balanced against the total evaporation demand and provision for soil drying (wilting point) or waterlogging (anaerobiosis, using a water stress coefficient). Vertical transport is modelled as the ascent of xylem across a hydraulic potential gradient (Poiseuille equation) and the descent of the phloem – a 20% sucrose solution (Saupe, 2009) along an osmotic pressure gradient. The model calculates the combined effect of soil evaporation and plant transpiration using the Penman-Monteith equation (Monteith and Unsworth, 2007). Evaporation and transpiration are separated using a plant cover index, which according to Beer's Law is a function of the leaf area index.

The model apportions precipitation to different parts of the plant by the relevant interception, washout, absorption and leaching factors. Litterfall is assumed to be continuous, using an annually averaged, moisture-corrected needle mass turnover rate. Return of radionuclides to the soil is modelled by a constant decomposition rate. The model incorporates a simple logistic model for stand density, quantifying the effect of water availability on tree density.

From a hydrological point of view, Cl is usually considered to be a conservative element; hence the K_d is virtually 0 and there should be in principle no retardation in soil transport. However, the model provides a generic retardation approach linked to a K_d function of volumetric water content (Perez-Sanchez et al., 2012) applied to both infiltration and capillarity flows. We also assumed that radionuclide transfer from soil, and subsequent circulation within the tree, follow the water fluxes multiplied by the radionuclide concentrations in water and corrected by a selectivity coefficient S_c (Casadesus et al., 2008). Based on analogue chemistry, S_c for ^{36}Cl would arguably be equal to 1 but this coefficient was adjusted for each compartment to match the previous ^{36}Cl model.

RESULTS AND CONCLUSIONS

Previous research (Vincke and Thiry, 2008) quantified water table cycling in Scots pines in sandy soil located in Mol. Continuous monitoring in 2005 (climate, throughfall, moisture, tree transpiration, water table variations, real-time LAI and root counting) reveals a shallow water table. Pine transpiration was estimated to be < 1.85 mm d^{-1}, 25% of PET. Understory evaporation was estimated as 18 – 20% of total ET. The soil water reserve is found at 2.5 m, with extractable water table at 1.45 m below surface. The contribution of the water table to forest transpiration was 61% (98.5% in dry periods), signalling its potential as a contaminant source in dry periods where the predominant water transport direction is upwards. Although the capillary flow through the soil was not measured, upward flow rates of more than 2 mm day^{-1} are common, and values range from 0.5 to 8 mm day^{-1} (Raes and Deproost, 2003).

The model successfully predicts the main observed trends in evapotranspiration in comparison with the average monthly PET values for grass and coniferous tree-covered surfaces based on the climatological data for Mol (Belgium) in the period 1984-88 (Mallants, 2005), as shown in Fig. 2. The use of real irradiance data taken on a daily basis somewhat improves on the sinusoidal expression used to predict monthly irradiance. The model also successfully predicts the mean soil water content of ~ 25%, as evidenced in Vincke's study, and that most of the water is stored in the roots, followed by the rest of the plant and leaf outer surfaces. The water table height below ground is predicted to fluctuate between 2.1 and 2.6 m (paper states water table floor 1.8 – 2 m). Pine transpiration is calculated to be < 1.2 mm/day (expected < 2 mm/d). At peak periods transpiration is ~ 15% of PET compared with 20% in the study. The predicted maximum capillarity flow of 0.4 mm per day is compatible with estimations.

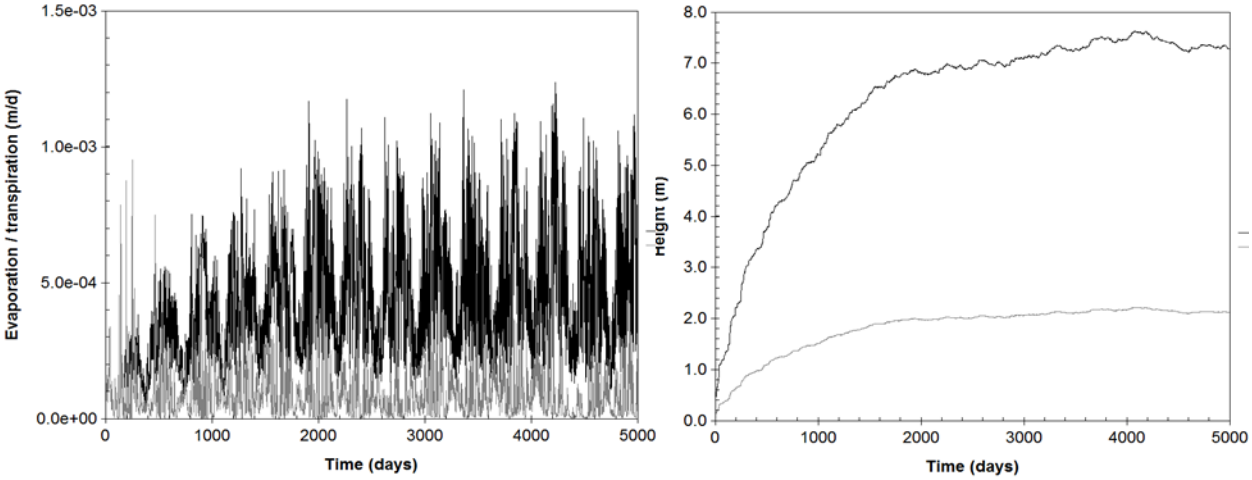

Fig. 2: (a) Model-predicted evaporation (black) and transpiration (grey) – (b) Water table (black) and capillary front (grey) heights (simulation starting from empty compartments)

At the time of writing there is on-going validation of the model following its coupling to a previous stand-alone ^{36}Cl model (Van den Hoof and Thiry, 2012), and the solution for a constant water table is consistent with the predictions of that original model.

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