Biodiversity-ecosystem function in a willow biomass production system

Tree productivity, litter decomposition and fungal community

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Cover: Four willow genotypes grown in mixture and their interaction with decomposing litter and fungal community.
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Abstract

The relationship between biodiversity and ecosystem function is an important issue in ecology. Stands of *Salix* (willow) are suitable model systems to study this relationship. *Salix* and other crops are mainly grown in monoculture in agricultural systems. Species or genotypes grown in monoculture share the same functional traits and can therefore be expected to compete strongly for resources. In contrast, different species or genotypes grown in mixed culture vary in their functional traits and may use different niches, leading to reduced competition. Thus, higher diversity in functional traits can increase ecosystem functions such as productivity and litter decomposition. This thesis examined how individual *Salix* genotypes affect community shoot biomass, litter decomposition and fungal diversity when grown in pure and mixed cultures of different genotypes.

Three field sites were established in Central and Northern Europe (Freiburg and Rostock in Germany, Uppsala in Sweden). Within each location, plots were planted with pure and mixed communities of four *Salix* genotypes ('Björn', 'Jorr', 'Loden' and 'Tora') that differ in their morphological and functional traits. In addition to the field study, the two taxonomically and physiologically most distinct genotypes ('Loden' and 'Tora') were grown under two different nutrient treatments in pure and mixed communities in a pot study.

Genotypes exerted different influences on the *Salix* community in which they were grown, although there was no general increase in productivity, decomposition rate or fungal diversity with increasing genetic richness. Among other findings, one genotype ('Jorr') enhanced productivity and litter decomposition when grown in mixed communities. Another genotype ('Tora') had a negative effect on productivity, litter decomposition and fungal diversity when added to a community. 'Tora' benefited from the presence of other genotypes, but under nutrient poor conditions it performed worse in the presence of a competitor. Litter chemistry differed between genotypes, and decomposition showed a distinct pattern between sites. Fungal communities were affected by different drivers including leaf chemistry, soil properties and genotype identity, but not by genetic diversity. The results suggest that the specific functional trait combinations of individual genotypes affect their response to mixture as compared to monoculture and that the attributes of individual genotypes are more important than genetic richness for the ecosystem functions studied here.

Keywords: Short rotation coppice, *Salix*, genetic diversity, genotype complementarity, biomass productivity, litter decomposition, fungal community

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Biodiversitet och ekosystemfunktioner i ett odlingssystem av salix på jordbruksmark: biomassaproduktion, förnanedbrytning och svampsamhällen

Sammanfattning

Sambandet mellan biodiversitet och ekosystemfunktioner är en viktig fråga inom ekologin, och odlingar av salix kan användas som ett modellsystem för att studera sambanden. Både salix och andra grödor odlas främst i monokultur. Arter eller genotyper (sorter) som odlas i monokultur delar oftast samma funktionella egenskaper, och de enskilda plantorna i beståndet förväntas därför att konkurrera hårt om resurserna. I motsats till detta kan en blandning av arter eller genotyper (sorter) variera i sina egenskaper, vilket leder till en minskad konkurrens mellan de enskilda plantorna i beståndet. Därmed kan en högre diversitet öka ekosystemfunktioner som biomassaproduktion och förnanedbrytning. Den här avhandlingen undersökte hur olika sorter av salix påverkade skottbiomassa, förnanedbrytning och svampsamhällena när sorterna växte antingen i renbestånd eller i blandningar. Tre fältförsök etablerades i centrala och norra Europa (Freiburg och Rostock i Tyskland, och Uppsala i Sverige). På varje lokal planterades både monokulturer och blandade bestånd av fyra olika sorter av salix (‘Björn’, ‘Jorr’, ‘Loden’ och ‘Tora’), vilka skiljer sig åt både i morfologi och funktionella egenskaper. Utöver fältförsöken genomfördes också ett försök i odlingslådor där de två mest olika sorterna (‘Loden’ och ‘Tora’) odlades i monokultur och blandade, och med två olika växtnäringsbehandlingar. Inblandning av de olika sorterna påverkade ekosystemprocesserna i bestånden på olika sätt. Flera sorter av salix, dvs. en ökad diversitet, ledde inte generellt till en ökad biomassaproduktion, nedbrytning eller svampdiversitet. När sorten ‘Jorr’ var inblandad i beståndet ökade både produktiviteten och förnanedbrytningen. Sorten ‘Tora’ hade däremot en negativ påverkan på produktivitet, förnanedbrytning och svampsamhällenas diversitet när den fanns med i blandade bestånd. ‘Tora’ drog istället fördel av andra sorter i blandade bestånd, men under näringsbegränsade förhållanden växte den sämre under konkurrens. Förnasammansättningen skilde mellan olika sorter och nedbrytningen var beroende av vilken plats (t.ex. Uppsala eller Freiburg) de odlades på. Svampsamhällena påverkades av flera olika faktorer, som till exempel förnasammansättning, markegenskaper och sortval, men var inte kopplad till sortmångfalden i beståndet. Resultaten visar på att kombinationen av specifika funktionella egenskaper i bestånd av salix påverkar hur de samverkar när de odlas i blandningar jämfört med om de odlas i monokultur. Därför är individuella sorters egenskaper av större vikt än sortmångfalden för de ekosystemfunktioner som undersöktes här.

Dedication

To my grandfather Horst Liebe

Nature does nothing without purpose or uselessly

Aristotle

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I **Hoeber, S.**, Fransson, P., Prieto-Ruiz, I., Manzoni, S. and Weih, M. (2017). Two *Salix* genotypes differ in productivity and nitrogen economy when grown in monoculture and mixture. *Frontiers in Plant Science* 8, 231.

II **Hoeber, S.**, Arranz, C., Nordh, N.-E., Baum, C., Low, M., Nock, C., Scherer-Lorenzen, M. and Weih, M. (2018). Genotype identity has a more important influence than genotype diversity on shoot biomass productivity in willow short-rotation coppices. *GCB Bioenergy* 10(8), 534–547.

III **Hoeber, S.**, Fransson, P., Weih, M. and Manzoni, S. Leaf litter quality coupled to genotype identity drives *Salix* litter decomposition more than litter diversity and climate. (Manuscript)

IV **Hoeber, S.**, Baum, C., Weih, M. and Fransson, P. Plant genotype and diversity as potential drivers of soil fungal community structure and diversity in willow biomass systems. (Manuscript)

Papers I and II are reproduced with the permission of the publishers.

The contribution of Stefanie Hoeber to the papers included in this thesis was as follows:

I Planned and designed the study in collaboration with the co-authors, performed the experimental work, analyzed and evaluated the data together with the co-authors and wrote most of the manuscript.

II Planned, designed, performed, analyzed and evaluated the study in collaboration with the co-authors and wrote most of the manuscript.

III Planned and designed the study in collaboration with the co-authors, performed the experimental work, analyzed most of the data and wrote parts of the manuscript.

IV Planned and designed the study in collaboration with the co-authors, performed some of the experimental work, analyzed and evaluated the data and wrote parts of the manuscript together with the co-authors.

Co-authored articles that are not part of the thesis:

- Weih, M., **Hoeber, S.**, Beyer, F. and Fransson, P. (2014). Traits to ecosystems: The ecological sustainability challenge when developing future energy crops. *Frontiers in Energy Research* 2,17.
- Baum, C., Hrynkiewicz, K., Szymańska, S., Vitow, N., **Hoeber, S.**, Fransson, P.M.A. and Weih, M. (2018). Mixture of *Salix* Genotypes Promotes Root Colonization With Dark Septate Endophytes and Changes P Cycling in the Mycorrhizosphere. *Frontiers in Microbiology* 9,1012
- Djukic, I., Kepfer-Rojas, S., Kappel-Schmidt, I., [...], **Hoeber, S.**, et al. (2018) Early stage litter decomposition across biomes. *Science of the Total Environment* 628, 1369-1394.

1 Background

1.1 Biodiversity-ecosystem function

Biodiversity is defined by the number of species or genotypes in an ecosystem. Functions within an ecosystem often increase with species and genetic diversity, and with similar relative abundance of species (Magurran, 2013; Srivastava and Vellend, 2005). The functions carried out by ecosystems are the result of interactions between organisms and their habitat, where functions can refer to ecosystem properties and ecosystem services (Lecerf and Richardson, 2009). Ecosystem properties can be stocks of energy and material (*e.g.* biomass), fluxes of energy or material processes (*e.g.* production and decomposition) and stability of rates (*e.g.* nitrogen mineralization) or stocks (*e.g.* carbon storage) over time (Kinzig et al., 2001). Ecosystem services derive from ecosystem properties and can provide products (*i.e.* food or biomass for bioenergy) or other benefits such as decomposition of waste, cleaning of water, and aesthetics to increase human wellbeing. Thus, "the joint effects of all processes that sustain an ecosystem" are defined as ecosystem functioning (Reiss et al., 2009). Ecosystem functioning is affected by functional attributes of species or genotypes (their traits) which can locally alter biotic (*e.g.*, competition, predation) or abiotic factors (*e.g.*, microclimate, disturbance, resource availability) (Chapin et al., 2000; Wood et al., 2015).

A diverse community differs in productivity (*e.g.*, in terms of biomass production) and its contribution to ecosystem functions. It can therefore influence ecosystem properties and processes by increasing ecosystem functioning (according to biodiversity-ecosystem function (BEF) theory). More specifically, a trait is a measurable feature of an individual that potentially affects performance or fitness. It can be physical (*e.g.* plant branching pattern), biochemical (*e.g.* plant photosynthetic pathway), behavioral (*e.g.* nocturnal or diurnal foraging), temporal or phenological (*e.g.* flowering time)

(Cadotte et al., 2011). Thus, functional traits are able to regulate the influence of species or genotypes on the environment and their response to the environment, and thereby the fitness of the specie or genotype (Wood et al., 2015). Ecologists are increasingly interested in trait-based community diversity studies rather than species richness or composition (McGill et al., 2006). On managed land, ecosystem functioning and ecosystem services are driven by species or genotypes with different functional traits. Increased diversity in managed ecosystems can either affect ecosystem services directly, due to an increase in human nutrition (in terms of nutritious food) (Remans et al., 2014), or indirectly, through cover crops promoting plant biomass growth and better water quality (Dabney et al., 2001). A sustainable and multifunctional agriculture or silviculture system should deliver several ecosystem services. Aboveground, a sustainable agriculture system should provide yields of food, fiber and fuel, pollination or disease regulation and pest control, while belowground should supply soil retention, supporting carbon sequestration and structure, regulation of soil fertility, nutrient cycling and water cycle and quality. Conservation of biodiversity and human health also plays an important role in a sustainable, multifunctional us of land (Power, 2010; Zhang et al., 2007).

1.1.1 Species and genotype richness

At species level, higher species richness and diversity of traits is frequently accompanied by higher productivity (BEF theory) (Cardinale et al., 2011; Duffy et al., 2017; Hooper et al., 2005; Tilman et al., 2014). However, sometimes species or genotype identity can play a more important role than diversity *per se* (Scherer-Lorenzen et al., 2004). Biodiversity-ecosystem function theory was developed mainly based on model systems such as grassland (Hautier et al., 2014; Hector, 1999; Isbell et al., 2015; Tilman, 2001) and forests (Chisholm et al., 2013; Piotto, 2008; Zhang et al., 2012). In experimental plant communities of grassland, total plant biomass has been reported to either increased with increasing species richness (Hector, 1999; Hector et al., 2010; Tilman et al., 1996) or to decreased (Gross et al., 2014; Hector et al., 2010). Apart from species richness, genetic diversity within plants also plays a significant role in ecosystem functioning (Cianciaruso et al., 2009; Hughes et al., 2008). Genetic diversity can influence plant productivity (Cook-Patton et al., 2011; Kotowska et al., 2010), litter decomposition (Schweitzer et al., 2008), resistance to disturbance (Parker et al., 2010), and the presence and abundance of soil organisms, aboveground predators or herbivory (Chateil et al., 2013; Johnson et al., 2005; Parker et al., 2010; Wimp et al., 2004). Although biodiversity can be beneficial, *e.g.* for productivity or resistance to disturbances, over the past century species richness and genetic diversity have been reduced in managed areas to increase productivity. Currently, most arable fields are cropped with only one genetically homogeneous cultivated species and the number of different species or genotypes cultivated in fields is generally declining on a regional and global scale (Bonnin et al., 2014). In modern arable systems, high-yielding genotypes that are adapted to intensive management practices are generally being selected. However, such practices are far from sustainable, as high amounts of fertilizers and pesticides are used to ensure high yields. In addition, irrigation and intensive management practices tend to degrade soil fertility and the functioning of non-cultivated, natural ecosystems (Barot et al., 2017). Most modern agricultural systems, with high-yielding genotypes cultivated in monocultures, are more vulnerable to changes in climate than diverse agricultural systems (Gaba et al., 2014). In addition, soil tends to be degraded by the intensive agricultural management practices implemented today. Increased species or genetic richness in agriculture could promote yield, yield stability and sustainability and/or reduce soil degradation (Altieri, 1999; Gaba et al., 2014; Kassam et al., 2009).

1.1.2 Diversity effects: The link between genetic diversity and ecosystem functioning

There are two main mechanisms through which species or genotype richness affects ecosystem functions such as biomass productivity or yield. These are: the selection (or sampling) effect and the complementarity effect due to niche differentiation or facilitation (Loreau and Hector, 2001; Tilman et al., 1997). Positive selection effects occur when a highly productive genotype dominates the community in terms of space occupancy or biomass, whereby the community component does not necessarily need to dominate the community completely, a slight selective advantage could be enough to generate dominance (Loreau, 2000). The selection effect emerges in space and time as environmental conditions change between locations (due to soil properties) and time (years due to climate). Thus the species or genotype with the best performance is not necessarily the same between locations and years.

Complementarity effects occur when species or genotypes use different ecological niches or resources in a complementary manner. Thus, complementarity can promote functional trait variation between species or genotypes (Loreau, 1998). The specific complementarity effect of niche differentiation, where co-existing plant species occupy different parts of niche space, can occur when functionally different species and genotypes use resources in different space and/or time, *e.g.* due to differences in canopy or root structure

(Bayer et al., 2013; Craine and Dybzinski, 2013) or differences in the timing of phenological events such as bud burst or bud set (Weih, 2009). Facilitation takes place when one community component enhances the growing conditions of another community component. This can increase community productivity when multiple species or genotypes are present, which can lead to higher production than in their respective monocultures (Loreau, 2000). Increasing community productivity might be a result of selection effects, as a community with multiple functional components (plants) is more likely to contain a well-performing species or genotype at any time. Alternatively, increasing community productivity can be explained by complementarity effects, as diverse communities are more likely to use different niches at any time (Loreau, 2000). In both cases, functional differences between species or genotypes are crucial to achieve a positive effect on productivity, and thus increased yield. However, increasing functional differences within a field do not necessarily result in a positive effect on productivity.

1.1.3 Functional trait diversity and plant competition

In an ecosystem, whether natural or managed, single-species or diverse, there exists always competition for space, light, water or other resources, *e.g.* nutrients (Lambers et al., 2008). In monocultures, plants usually share the same functional traits and thus they flower, grow and root at the same time, while using shared resources. Therefore, competition for resources such as light or nutrients is usually high. When nutrients are limited, genetically diverse managed or natural ecosystems with different functional traits develop different strategies to acquire or allocate nutrients and might perform better in terms of productivity.

In a fertile ecosystem, nutrients are often not limiting, which can lead to increased plant growth, but also increased competition for light (Tilman, 1990). Successful competitors capture resources rapidly to develop new leaves and roots, and have a high morphological flexibility (*e.g.* leaf morphology, orientation or spatial arrangement) and rapid turnover of leaves and roots (Aerts, 1999). Fast-growing plants in fertile environments have roots that allow rapid nutrient uptake and invest in biomass allocation to shoots and leaves, which can lead to a competitive advantage (Caldwell et al., 1996; Jackson and Caldwell, 1996; Lambers and Poorter, 1992). Plants growing rapidly in strongly nutrient-limited ecosystems are often characterized by slow turnover of leaves, long tissue life span, low leaf nutrient concentrations, and strong investment in root biomass to access soil nutrients (Bloom et al., 1985). Thus, higher functional trait diversity could lead to lower plant competition than found between plants grown in monoculture.

1.2 Litter decomposition

Decomposition is a chemical and physical process by which plant litter is reduced to carbon dioxide (CO_2), water and mineral nutrients (Aerts, 1997). In most terrestrial ecosystems, decomposition is a key process in the nutrient cycle and plays a significant role in the global carbon budget (Aerts, 1997; Schimel, 1995). Decomposition is strongly influenced by microbial activity. Microbes produce enzymes that contribute to decomposition, thereby degradation products such as nutrients becomes available to the microbial population. In particular, organically bound nutrients such as nitrogen (N) and phosphorus (P) can be released through decomposition. Organic phosphorus can be released by plants or microbial enzymes and plants can take up inorganic phosphorus forms (Lambers et al., 2008). Nitrogen in leaf litter passes through three different phases: leaching, nitrogen accumulation and nitrogen release. Nitrogen leaches from litter directly after trees shed have their leaves, with the rate of nitrogen release being determined by precipitation or, even more strongly, by freeze-thaw cycles. While nitrogen is being released through leaching, fungal biomass can grow into leaf litter and can transport nitrogen actively into the litter through the presence of mycelium alone (Berg and Laskowski, 2005). In the nitrogen accumulation phase (also called immobilization), nitrogen transport and the amount of nitrogen in the litter increase, reaching values higher than the initial nitrogen amount. The transport of nitrogen into litter can occur either through N_2-fixing microorganisms that are present in the litter or by fungal hyphae that take up nitrogen from surrounding litter, which is more common in temperate and boreal forests (Berg and Laskowski, 2005). Accumulation of nitrogen in litter depends on the quality of the litter (nitrogen-poor or nitrogen-rich) and the extent to which nitrogen is limiting microbial growth. Already during the accumulation phase, nitrogen is released in mineral forms (*i.e.* nitrate (NO_3) and ammonium (NH_3)) from degrading litter. After soluble compounds (phosphorus, nitrogen and carbon) are released, degradation of hemicellulose occurs, followed by degradation of cellulose (Berg and Laskowski, 2005). Degradation of one of the most recalcitrant (resistant or difficult to degrade) substrates, lignin, eventually comes to dominate when the carbohydrates most easily available to microbes have been consumed by microbial communities (Berg and Laskowski, 2005). Lignin degradation is performed by microorganisms such as fungi (or bacteria) that possess specialist enzymatic mechanisms to degrade lignin.

1.2.1 Factors influencing litter decomposition

Litter decomposition rate is mainly driven by microbial activity. As such, it depends on environmental conditions such as climate (moisture or temperature), litter quality (chemical and physical characteristics) and the composition and abundance of soil biotic communities (Aber and Melillo, 1982; Swift et al., 1979). The litter decomposition rate of a litter cohort decreases over time (Aerts, 1997). During the first phase of decomposition, environmental conditions, especially temperature and moisture, have a strong direct effect on litter decomposition (Aerts, 1997), followed by litter chemistry and soil organisms (Lavelle et al., 1993; Swift et al., 1979). However, so far it is unclear which of these factors is the main driver of decomposition. On a global scale, climate and litter quality can affect decomposition (Cornwell et al., 2008; Djukic et al., 2018; García-Palacios et al., 2013; Parton et al., 2007; Prescott, 2010; Swift et al., 1979). Decomposition is usually slower in cold, dry regions than in warm, moist environments such as tropical forests (Parton et al., 2007). High levels of ultraviolet radiation can also affect decomposition (Austin and Ballare, 2010). On a local scale, litter quality and traits (such as leaf toughness, nitrogen and phosphorus content, lignin content, polyphenol concentrations or carbon (C):N ratio) may be good predictors of litter decomposition rates (Aerts, 1997; Bakker et al., 2010; Cortez et al., 2007; Güsewell and Verhoeven, 2006). Nutrient-rich litter with high concentrations of nitrogen, phosphorus and carbohydrates decomposes faster than nutrient-poor, 'low-quality' litter, which tends to contain higher concentrations of complex and more recalcitrant compounds such as lignin, tannins or phenolics (Berg and McClaugherty, 2008). Soil fauna also play an important role in litter decomposition and may be equally important to litter quality. The effect of soil fauna on the rate of decomposition is driven in turn by climate and litter quality (García-Palacios et al., 2013). Hence, the relative composition and relative abundance of soil fauna such as earthworms, nematodes, mites and collembola but also bacterial and fungal communities can drive litter decomposition significantly (Bardgett and Wardle, 2010; Hättenschwiler et al., 2005). Further, the chemical composition of litter differs across sites and decomposition can be affected by edaphic factors. For example, plants that grow in nutrient-poor environments may produce nutrient-poor litter, slowing decomposition (Carreiro et al., 1999). Early stage decomposition can be controlled by climate and the concentrations of major nutrients (*e.g.* N, P, sulphur (S), potassium (K), calcium (Ca), magnesium Mg), manganese (Mn)) (Berg and McClaugherty, 2008), by nematodes and microbial communities (García-Palacios et al., 2016), by the amount of soluble substances (Heim and Frey, 2004), and by soil temperature and pH (Djukic et al., 2012). Decomposition at later stages is driven mostly by climate (moisture, temperature), organic matter quality, nitrogen availability, soil texture, and litter quality, especially its lignin concentration (Prescott, 2005).

1.2.2 Litter diversity

Interactions between litters from various species or genotypes affect decomposition by increasing the number and type of microhabitats and chemical diversity (Hättenschwiler et al., 2005). Litters from different species or genotypes vary in their nutrient content, chemical composition and leaf structure, and thus differ in their capacity to provide resources to microbes (Hansen and Coleman, 1998; Hector et al., 2000). Due to the complementary resource use permitted by mixed litter compared with homogeneous litter, detritivores and microbes are able to optimize their nutrient acquisition (Gessner et al., 2010). This can have an overall impact on decomposition rate and microbial activity, as nutrients can be actively transferred from one litter type to the other (Schimel and Hättenschwiler, 2007).

Fungi can grow into nutrient-poor litter and then compensate for limiting resources by extending their hyphae into nutrient-rich litter. Thus, fast decomposition of nutrient-rich litter with a low C:N ratio can increase decomposition of nutrient-poor litter (Wardle et al., 1997). Nutrients can also be passively transferred via leaching of soluble and carbon compounds. More inhibitory compounds in one litter type can thereby be leached and transferred to another litter type. However, this depends on the mobility of nutrients, as some (*e.g.* phosphorus) are more mobile than others (*e.g.* nitrogen). Diverse litter can improve microclimatic conditions and microhabitats, due to variations in leaf color, size and shape and leaf-surface structure of the mixed litter involved (Wardle et al., 2003). In general, this indicates that increasing litter diversity might increase decomposition due to complementary resource use. However, litter diversity and decomposition can have additive (single-species litter decomposes equally fast to mixed litter) or non-additive effects (Gartner and Cardon, 2004). The decomposition rate of mixed litter can be either higher or lower than that of single-species litter. Among the non-additive effects, synergistic effects dominate, followed by antagonistic effects (Gartner and Cardon, 2004; Hättenschwiler et al., 2005).

1.3 Soil fungal community

Soil fungal communities are crucial for driving biogeochemical processes in soils and act as decomposers and mutualists (Tedersoo et al., 2014). Soil fungi can link aboveground and belowground ecosystem processes by decomposing organic matter, live in symbiosis with plant organisms to obtain photosynthesized carbon from the plant, which triggers nutrient uptake by the fungi (Ortas and Rafique, 2017), and drive carbon cycling as root-associated mediators of belowground carbon transport and respiration (Clemmensen et al., 2013). Fungal communities are globally driven by edaphic and climate conditions, while fungal richness generally increases with latitude (Tedersoo et al., 2014). There are two major fungal groups that are of interest for the work in this thesis. These are saprotrophic fungi and mycorrhizal fungi, which differ in their functional role.

1.3.1 Saprotrophic fungi

Saprotrophic fungi are usually taxonomically basidiomycetes and obtain their energy and nutrients from dead plant tissue and animals. They are able to produce hydrolytic enzymes that can degrade complex cell wall polymers of plants, such as lignin, cellulose, hemicellulose or pectin, to obtain carbon (Baldrian, 2008). Besides degrading wood and other dead plant tissue, litter-degrading fungi can translocate resources such as carbohydrates, mineral nutrients (*e.g.* nitrogen) and water with their mycelia and can reallocate nitrogen in litter from nutrient- and resource-rich to nutrient- and resource-poor regions (Boddy, 1999; Lindahl and Olsson, 2004).

1.3.2 Mycorrhizal fungi

Mycorrhizal fungi are known for their symbiotic relationships with plant roots and have key functional traits for nutrient acquisition by plants (Martin et al., 2001). There are two main types of mycorrhizal fungi (ectomycorrhizal and endomycorrhizal), which enter into different symbiotic relationships with their hosts. To exchange nutrients, the hyphae of the ectomycorrhizal fungi form a sheath around the outside of the plant root and grow between the plant cells. In contrast, the hyphae of the endomycorrhizal fungi enter the plant root cells. Ectomycorrhizal fungi are one of four main functional mycorrhizal types (ectomycorrhiza, arbuscular mycorrhiza, ericoidmycorrhiza and orchid mycorrhiza) belonging to the Basidiomycota or Ascomycota (Barker et al., 1998; Smith and Read, 2008). They dominate boreal and temperate forests where 95 % of short roots form a symbiotic association with ectomycorrhiza (Martin et al., 2001). Ectomycorrhiza predominantly form a symbiosis with tree species (Salicaceae, Dipterocarpaceae, Pinaceae, Fagaceae, Myrtaceae, Betulaceae, Nothofagaceae and some Fabaceae) (Martin et al., 2001; Tedersoo et al., 2010). In forests, major nutrients such as nitrogen and phosphorus become progressively immobilized into accumulating organic layers and access to these resources becomes limited. In such cases, ectomycorrhiza can contribute to tree nutrition through mineral weathering (Landeweert et al., 2001) and mobilization of nutrients from organic matter (Read and Perez-

Moreno, 2003). On the top organic layers, where decomposition occurs and mostly saprotrophic fungi dominate, complex carbohydrates originating from litter (*i.e.* cellulose and lignin) are present. However, ectomycorrhiza have only a limited ability to degrade litter using polyphenol oxidases and to release nitrogen from polymers (*i.e.* cellulose and lignin) (Lindahl and Tunlid, 2015; Read and Perez-Moreno, 2003). In soils, ectomycorrhiza have access to root exudates containing *e.g.* carbon fixed in photosynthesis, which is strongly increased by the presence of the fungi (Hobbie, 2006; Nehls et al., 2010). As a symbiont, ectomycorrhiza provide host plants with nutrients and water, especially when either is limited (Smith and Read, 2008). They form an external mycelium that is important for spreading the ectomycorrhiza and in forming a network to facilitate the transfer of carbon and nutrients between individual hosts (Selosse et al., 2006; Simard and Durall, 2004). Nutrients can be taken up by an increased uptake surface (as hyphae access more volume than roots due to their increased surface) and associated access to a greater soil volume, or by increased nutrient mobilization through ectomycorrhiza using specialist enzymes to take up organic nitrogen and phosphorus, which are unavailable to most plants, or to extract nutrients such as phosphorus, potassium, calcium and magnesium from solid mineral substrate through organic excretion, thereby making them accessible to plants via the ectomycorrhizal mycelium (Wallander and Wickman, 1999).

In contrast to ectomycorrhiza, arbuscular mycorrhiza occur mainly in nutrient-rich or phosphorus-limited habitats such as tropical forests, although some are found in temperate forest, grassland and cropping systems (Smith and Read, 2008; Wang and Qiu, 2006). Arbuscular mycorrhiza are able to take up nutrients (especially phosphorus) from organic material, but are limited in their capacity to degrade organic material enzymatically (Hodge and Storer, 2014). Like the ectomycorrhiza, their main source of energy is photosynthetically fixed carbon, which they invest into thin ‘feeder’ roots that absorb water and nutrients to take up nutrients in mineral form.

1.3.3 *Salix* as a dual mycorrhizal plant

In some tree species, for example members of the families Salicaceae and Myrtaceae and the genus *Quercus*, dual mycorrhizal systems are formed by arbuscular mycorrhiza and ectomycorrhiza, with the latter mostly dominating. In general, dual mycorrhizal plants benefit from synergistic effects and the two mycorrhizal types can complement each other in acquisition of limited nutrients (Tedersoo and Bahram, 2019). Plant colonization by mycorrhizal fungi can be influenced by soil water content, the availability of soil nutrients, site management and the diversity of the vegetation. In this thesis, the dual mycorrhizal genera of different *Salix* (willow) genotypes were studied. *Salix* is usually dominated by ectomycorrhiza in terrestrial systems in northern Europe (Hrynkiewicz et al., 2009), whereas arbuscular mycorrhiza may dominate in flooded areas in response to the flooding (Lodge, 1989). The dominance of either arbuscular mycorrhizal or ectomycorrhizal colonization is not only environmental-dependent, but also genotype-dependent (Baum et al., 2018).

1.3.4 Relationship between host genotype identity, genotype diversity and soil fungi community

The diversity of mycorrhizal fungi contributes strongly to the maintenance of plant diversity and ecosystem functioning (van der Heijden et al., 1998). The functioning of diverse plant communities can be affected by the presence and diversity of decomposers (*i.e.* saprotrophic fungi) and mutualists (*i.e.* mycorrhizal fungi), which can influence the resource acquisition abilities of plants and change the competition between them (Wagg et al., 2014). For example, increasing mycorrhizal diversity can increase the uptake efficiency of organic phosphorus (Baxter and Dighton, 2005).

However, plant responses to fungal community are often genotype dependent (Schweitzer et al., 2008). In particular, mycorrhizal fungal diversity and composition are influenced by size and growth of the host plants (Korkama et al., 2006; Velmala et al., 2012), differences in chemistry of senescent leaves (Lamit et al., 2016), soil properties (Bonito et al., 2019; Tedersoo et al., 2016), nutrient availability (Gallart et al., 2017) and changes in competition between host plant genotypes (Baum et al., 2018).

1.4 Willow short-rotation coppice

Many of the studies performed when developing the biodiversity-ecosystem function theory were carried out in grassland systems (Hautier et al., 2014; Hector, 1999; Isbell et al., 2015; Tilman, 2001) and forest systems (Chisholm et al., 2013; Piotto, 2008; Zhang et al., 2012). In those systems, the diversity-productivity relationship was often explored using interspecific diversity, where taxonomic predictors were used rather than functional traits (Weih et al., 2019). The willow plant material used in short rotation coppice (SRC) is taxonomically diverse and often comprised of hybrid varieties originating from different taxonomic units or species, accommodating great variability in functional traits (Kuzovkina et al., 2008; Weih et al., 2019). As described in section 1.1.2, plants with different functional traits can use different niches, which can improve productivity. Therefore, instead of focusing on purely taxonomic differences between species, as done in many other studies, a selection of different willow genotypes, offering a large variety of different functional traits, was used in this thesis to investigate biodiversity-ecosystem function theory.

Native willows (species of the genus *Salix*) have been traditionally used for multiple purposes, *e.g.* baskets, cooking, boats or even heating, for more than 10,000 years (Isebrands and Richardson, 2014). In order to meet the increasing demand for baskets, cultivation of willows on a small scale started already around 1880. Since the oil crisis in the 1970s, the interest in renewable biomass resources to replace fossil fuels has increased, and with that the demand for renewable energy. In order to satisfy this increasing demand, different sources of renewable biomass are emerging. Among these are second-generation biofuels, which are processed from lignocellulosic biomass derived from various plants including *Miscanthus* or switchgrass, and fast-growing woody crops such as willows (*Salix* spp.) and poplar (*Populus* spp.). Both willows and poplar are cultivated in short rotation coppice (SRC) plantations (Keoleian and Volk, 2005). Willows are planted in high density in SRC and harvested for biomass in cycles of two to five years, with new shoots sprouting after each so-called cutting cycle (Larsson et al., 2007). Besides their fast growth and the potential for high yields, *Salix* species are able to grow on marginal agricultural land or on soil contaminated with heavy metals, where this production system can be used for phytoremediation (Aronsson and Perttu, 1994). With the introduction of *Salix* cultivation in SRC to produce renewable energy, various species have been combined in plant breeding to obtain material with different agronomic (*i.e.* growth, phenology and drought, cold and pest resistance) and physiological traits (*i.e.* phenology, water-use efficiency, cold hardiness, site-adaptability) (Stanton et al., 2014). The main focus in current breeding efforts is on leaf rust resistance and high yield (Clifton-Brown et al., 2018).

Salix SRC is usually planted in monoculture. However, high-yielding monocultures are reported to be more vulnerable than genotype mixtures to pathogens (*i.e.* leaf rust) (Karp et al., 2011) and to herbivory by insects or mammals (Larsson, 1998). Susceptibility to pathogens is one of the strong arguments for growing *Salix* in mixture, rather than monoculture, as a mixture of genotypes with different functional traits pertaining to *e.g.* high resistance to different pathogens, might reduce the overall disease level within the SRC community. When willow mixtures are used for pest control of pathogens such as leaf rust, the genetic diversity of the planting material matters, since a mixture of only different *Salix viminalis* genotypes comes to resemble a monoculture after two cutting cycles (Begley et al., 2009). Compared with diverse use of land for food production, mixed SRC plantations are less problematic to harvest, unless the growth architecture (*e.g.* many small branches, many shoots per stool with many branches) varies dramatically between the genotypes grown.

Based on differences in functional traits such as drought, disease resistance and high yield in specific environments, various *Salix* varieties have been selected for bioenergy production (Kole et al., 2012). Among the varieties bred for biomass production are 'Björn', 'Jorr', 'Loden' and 'Tora'. These four varieties partly belong to different *Salix*- species and differ in their functional traits.

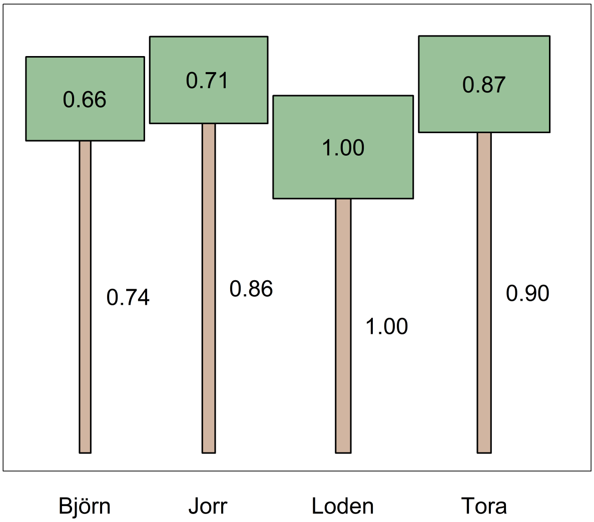


Figure 1: Schematic diagram of leaf area, height and shoot diameter, of the four genotypes studied in this thesis: 'Björn', 'Jorr', 'Loden' and 'Tora' (diagram from Paper II). Values shown besides the 'stem' are normalized shoot diameter and values in the green 'canopy' are normalized leaf area.

1.4.1 Functional trait differences between the genotypes studied in this thesis

In general, phenotypic traits can be measured at the level of individual plants and are defined by morphological, physiological and phenological characteristics, without additional information from the environment (Violle et al., 2007). There is a high variation in different morphological and functional traits in *Salix*. For example, some species or genotypes have high leaf area, but are shorter than other species, while some genotypes have an upright growth habit with long shoots and small leaves.

Although the varieties ‘Björn’ and ‘Tora’ are taxonomically closely related to each other, as they derive from the same parent material (*S. viminalis* x *S. schwerinii*), they differ in their morphological characteristics (*e.g.* stem diameter and leaf area) and functional characteristics (*e.g.* leaf nitrogen concentration). ‘Tora’ is often reported to be one of the highest-producing genotypes, and ‘Björn’ is sometimes reported to be one of the lowest-producing genotypes (Weih and Nordh, 2002) (Figure 1). The pure *S. viminalis* genotype ‘Jorr’ has the highest biomass productivity per unit leaf area (leaf area productivity). The broad-leaved genotype ‘Loden’ (*S. dasyclados*) is characterized by the highest leaf area ratio among the four genotypes studied here, and is the most taxonomically distant from the other three genotypes (Larsson, 1998). These four varieties (or genotypes) were used in this thesis to examine the effects of genotype diversity on biomass productivity, litter decomposition and fungal community development.

2 Aim and hypotheses

The overall aim of this thesis was to investigate how increasing *Salix* genotype diversity affects ecosystem functions related to tree biomass production (Papers I and II), leaf litter decomposition (Paper III) and soil fungal diversity (Paper IV).

The following hypotheses (H1-H3) were tested:

H 1 Biomass production, litter decomposition and fungal diversity are higher in *Salix* mixtures than monocultures, and increase with the genetic richness of the willow community.

H 2 Addition of different *Salix* genotypes to a genotype mixture has different effects on willow community productivity, leaf litter decomposition and soil fungal diversity.

H 3 Addition of taxonomically distinct willow genotypes to a mixture has a stronger effect on productivity, litter decomposition and fungal diversity than addition of taxonomically closely related genotypes.

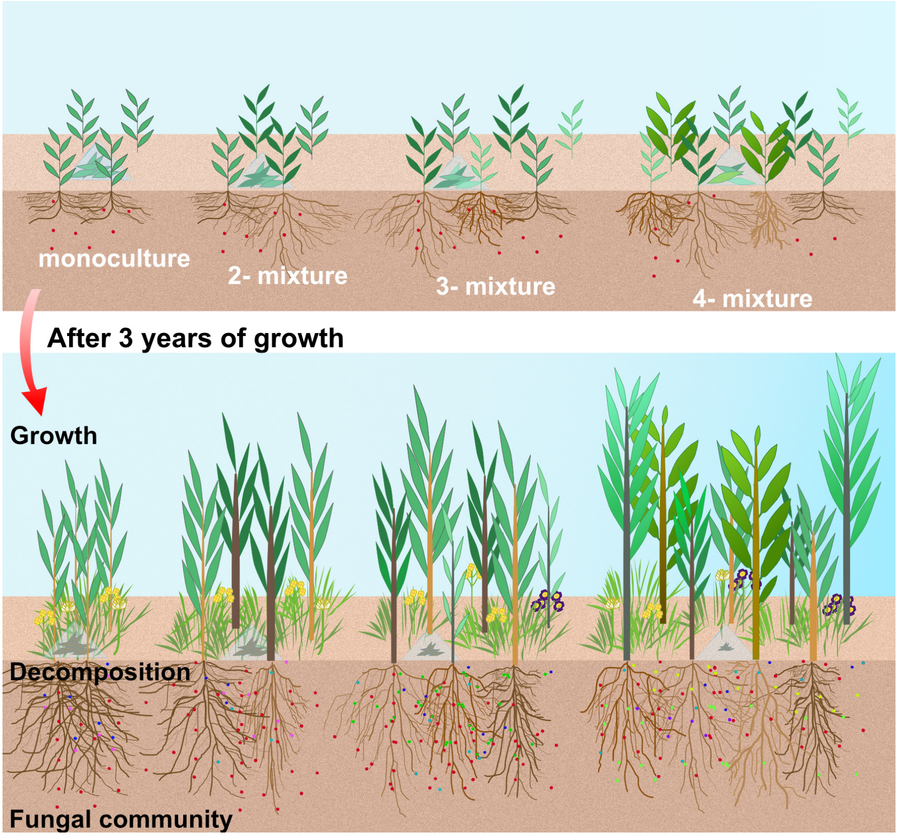


Figure 2: Schematic representation of the overarching hypothesis in this thesis, which was that increasing genetic diversity increases overall community biomass production, litter decomposition and fungal community diversity. Four *Salix* genotypes were grown in monoculture, and in mixture of two, three and four genotypes. Growth, decomposition (using litter bags) and soil fungal community in all diversity treatments were analyzed after one cutting cycle (three years of growth).

3 Material and Methods

The biomass productivity, diversity effects, decomposition and fungal community of the four different *Salix* genotypes (‘Björn’, ‘Jorr’, ‘Loden’ and ‘Tora’) was studied at three field sites located in Sweden and Germany (Papers II-IV). In addition, the biomass productivity and nitrogen economy of two of the four genotypes (‘Loden’ and ‘Tora’) was investigated in detail on a whole-plant basis (including all plant parts) in a pot study that included two nitrogen treatments, one with low and one with high soil nitrogen availability (Paper I).

3.1 Experimental design and plant material

3.1.1 Field trials

In order to compare the growth of the *Salix* genotypes between different latitudes, field trials were established at three different sites: Uppsala, central Sweden (59°49’ N; 17°39’ E), Rostock, northern Germany, (54°02’ N; 12°05’ E) and Freiburg, southern Germany (48°01’ N; 7°49’ E) in spring 2014 (Papers II- IV)(Figure 3).

Each site consisted of a field with three blocks each (one block = one replicate). At the Uppsala and Freiburg sites, four *Salix* genotypes with different phenology and functional traits were grown: ‘Jorr’ (*S. viminalis*), ‘Björn’ (*Salix schwerinii* E. Wolf. x *S. viminalis* L.), ‘Tora’ (*S. schwerinii* x *S. viminalis*) and ‘Loden’ (*S. dasyclados* Wimm.). All genotypes were planted in monoculture and in all possible mixture combinations (two-, three- and four-genotype mixtures), with all 15 combinations (15 plots) replicated three times (in three blocks; total number of plots n=45). Due to space restrictions, at the Rostock site only the two genotypes with the greatest differences in functional traits (‘Loden’ and ‘Tora’) were planted in monoculture and mixture. Each plot consisted of nine subplots and 144 plants (12 rows x 12 plants), planted in a hexagonal pattern (right-hand image in Figure 4). Mixtures with two genotypes were planted in a checkerboard pattern within plots, while mixtures with three and four genotypes were randomly planted.

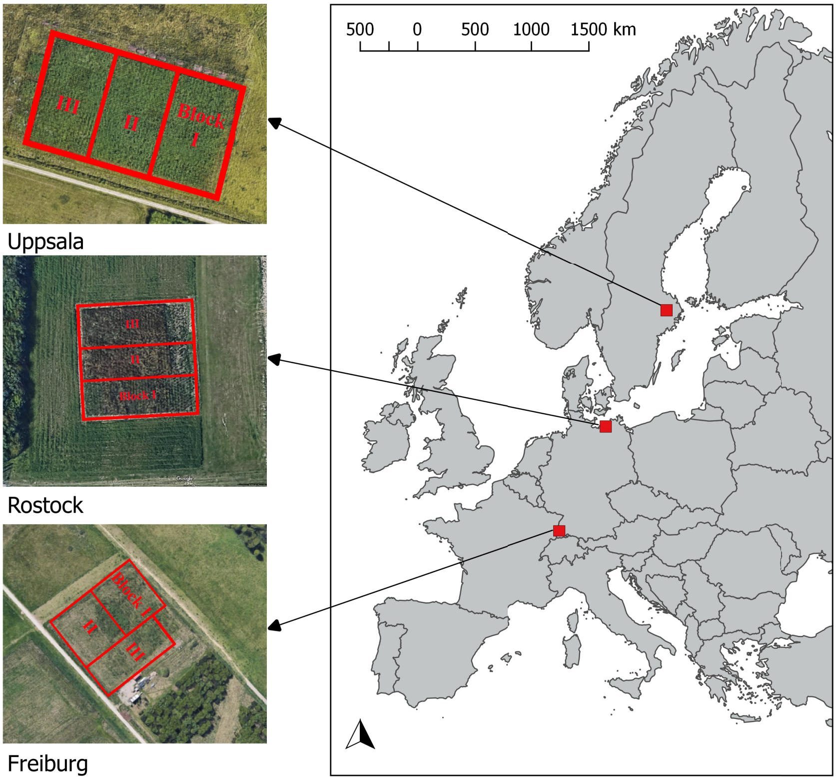
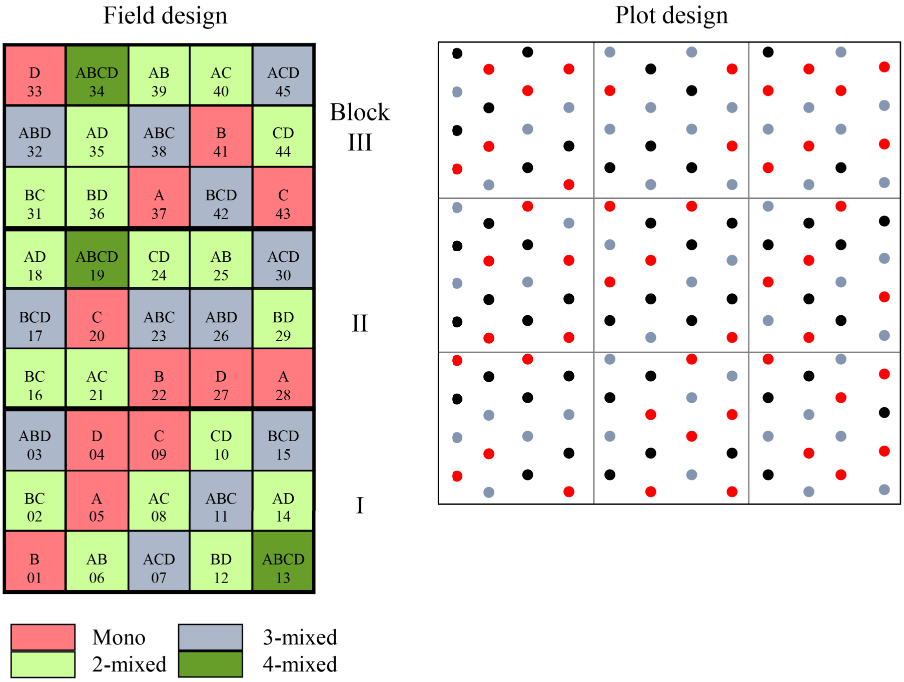


Figure 3: Location and block pattern of the three study sites: Uppsala in central Sweden, Rostock in northern Germany and Freiburg in southern Germany (Papers II and III; Paper IV only Uppsala and Rostock).

3.1.2 Pot study

The pot study was conducted in Uppsala in 2014 (Paper I). As in the field trial in Rostock, only the two genotypes 'Loden' and 'Tora' were planted in monoculture and mixture in the pot study. *Salix* cuttings were cut into 5-cm pieces to minimize the initial nitrogen amount in the cuttings, and randomly selected per genotype for potting. Cuttings were planted in 16.9 L rectangular pots filled with 22 kg washed quartz sand. Each pot contained six plants, planted in a hexagonal pattern to ensure equal distance to neighboring plants (Figure 5). The experiment had a full-factorial block design, where plants were treated with either a high amount of nutrients (F+) or a low amount of nutrients (F-), and with full water supply (well-watered, W+) or limited water supply (water-stressed, W-). In total, the study included 12 treatments



D 33	ABCD 34	AB 39	AC 40	ACD 45	
ABD 32	AD 35	ABC 38	B 41	CD 44	Block III
BC 31	BD 36	A 37	BCD 42	C 43	
AD 18	ABCD 19	CD 24	AB 25	ACD 30	
BCD 17	C 20	ABC 23	ABD 26	BD 29	II
BC 16	AC 21	B 22	D 27	A 28	
ABD 03	D 04	C 09	CD 10	BCD 15	
BC 02	A 05	AC 08	ABC 11	AD 14	I
B 01	AB 06	ACD 07	BD 12	ABCD 13	

Figure 4: (Left) Field design of the trials in Uppsala and Freiburg in a random block design with four *Salix* genotypes (A = ‘Björn’, B = ‘Jorr’, C = ‘Loden’, D = ‘Tora’) growing in various mixtures (monoculture; 2-, 3- and 4 genotype mixtures). (Right) Example of the plot design of the three-genotype mixtures, showing the random plantation scheme.

(W+N+ ‘Loden’, W+N+ ‘Tora’, W+N+ ‘Loden’ + ‘Tora’, W+N- ‘Loden’, *etc.*)(Figure 5) each with four replicates (*i.e.* in total 48 pots), plus two additional pots (one of each genotype) without any experimental treatment for an initial harvest.

3.2 Biomass assessments

3.2.1 Field trials

In winter 2016/2017, after three growing seasons, all field trials were harvested. Within an area of 8.0 m x 3.2 m = 26.24 m^2 in each plot, all plants were cut 10 cm above the ground and shoot fresh weights was measured.

To calculate genotype-specific relationships between shoot fresh weight and shoot dry weight (shoot biomass), stratified sampling of 10 shoots per

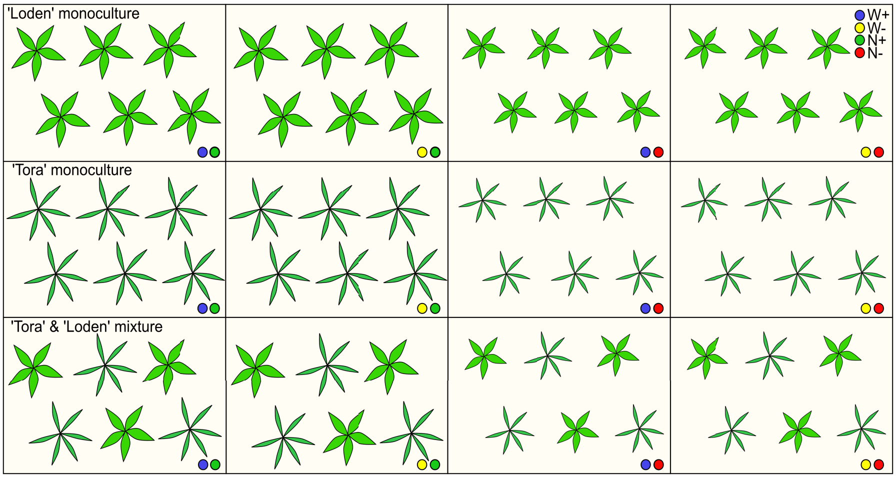


Figure 5: Design of the pot experiment with the *Salix* genotypes 'Loden' (broad-leaved) and 'Tora' (narrow-leaved), planted in monoculture and mixture, and grown under high fertilization (green dots) or low fertilization (red dots) and well-watered (blue dots) or water-stressed (yellow dot) conditions.

monoculture plot was performed (four genotypes x three replicate monoculture plots = 10 shoots x 4 genotypes x 3 blocks =120 shoots). The stratified sampling covered the range of diameters recorded for a specific genotype, from shoots with the smallest to shoots with the greatest diameter. Each of the 120 selected shoots was cut 10 cm above the ground and fresh weight was determined. Shoot biomass was calculated after shoots were dried in an oven at 70°C for 96 hours. Allometric relationships between monoculture and mixture did not differ, and thus stratified sampling was performed only in monoculture plots.

3.2.2 Pot study

In order to analyze the productivity and allocation of plant material, first and final harvests were conducted in each year. The first harvest was carried out in late June, 34 days after start of growth, when plants had just sprouted and had 1-2 leaves. For this harvest, only one pot with six plants per *Salix* genotype was harvested. Just before plants entered the senescence stage, after 120 days of growth in early September, a final harvest was performed of the full treatment design. At both harvests, plants were separated into leaves, shoots, cuttings and roots. Number of leaves was counted and A_{leaf} was measured, as were shoot height, shoot diameter and leaf biomass. In order to calculate aboveground biomass, all leaves and shoots were dried in an oven and weighed. In addition, specific leaf area was calculated by dividing A_{leaf} by total leaf biomass. Root biomass was measured for two replicate pots per treatment. Nitrogen content was determined for all plant parts, pooled per genotype and pot, and total nitrogen content was calculated by multiplying total nitrogen concentration per unit biomass of each plant organ by total biomass of that plant organ and adding together the values obtained.

3.3 Analysis of diversity effects

Net diversity was calculated by using additive partitioning (Loreau and Hector, 2001) to analyze the relationships between aboveground biomass (Paper I) or shoot biomass (Paper II) of the plants grown in monoculture and mixture. Specifically, net diversity effect was assessed using the differences between the observed and expected biomasses in the mixture, where the expected values were based on the individual performances of genotypes when grown in the respective monocultures. The net diversity effect was calculated from the sum of the complementarity and selection effects. If the selection effect of a genotype is positive, the genotype that performs best in monoculture can be assumed to dominate in mixtures. A negative selection effect of a genotype implies that a less well-performing genotype (*e.g.* in terms of biomass) has an advantage in mixtures and thus dominates (Tilman et al., 1997). A positive complementarity effect indicates that a genotype performs better in mixture than in monoculture.

3.4 Analysis of decomposition

In order to analyze leaf decomposition rates for each genotype mixture studied in the field trials, a selected number of plants per plot were covered with tree netting in autumn 2014 to collect leaf litter (Figure 6a). After all leaves had dropped from the trees, the litter was slowly dried at 40 °C, mixed, and subsamples were placed in litter bags. The litter bags were triangular and had a mesh size of 50 µm to allow fungal and bacterial entry, colonization of the contents and decomposition, while excluding plant roots from growing into the bags. The litter bags were filled with plot-specific litter and placed around the central subplot in each plot (Figure 4). Litter bags were recovered after 73-80 weeks and 119-126 weeks and dried in oven at 70 °C for 72 hours (Figure 6b). It was found that very small clay particles had entered the litter bags incubated in Uppsala, and therefore litter mass loss could not be calculated by simply weighing the litter bags. To correct the dry weight loss for clay particles attached to the litter, the decomposed litter was weighed, incinerated in a furnace oven at 550 °C for 6 hours to combust all organic matter, and weighed again. The concentrations of carbon, nitrogen, phosphorus and lignin in the initial litter, and the concentrations of carbon and nitrogen in the decomposed litter, were analyzed per pooled litter sample and per plot.

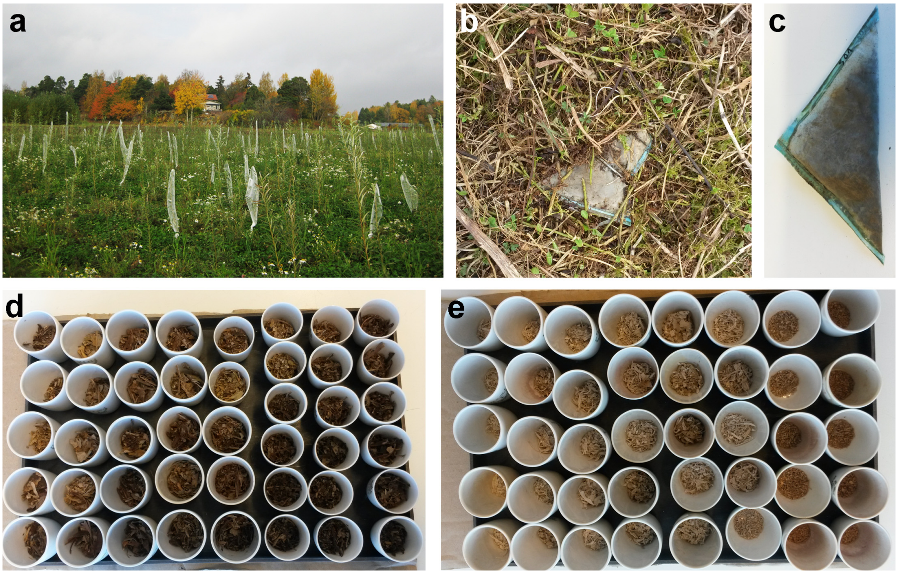


Figure 6: (a) Collection of litter in tree-nets for the decomposition study carried out in field trials, (b) litter bags were filled with dry litter and placed on the ground, (c) recovered litter bag with decomposed litter, (d) ceramic crucibles containing decomposed litter from the litter bags and (e) the same samples after ashing at 550 °C.

3.5 Fungal community analysis

Soil fungal communities were analyzed in soil samples from the field sites in Rostock and Uppsala, using high-throughput sequencing. With the aim of analyzing initial fungal communities in soil, nine soil samples (one per subplot) were collected in spring 2014 before the cuttings were planted, pooled per plot and then frozen at -18 °C or dried rapidly at 50 °C. This procedure was repeated each spring from 2015-2017, to follow annual changes in development of the fungal communities (Figure 7). Seasonal changes in the fungal communities were studied only during the 2016 growing season, using soil samples collected in spring, summer and autumn.

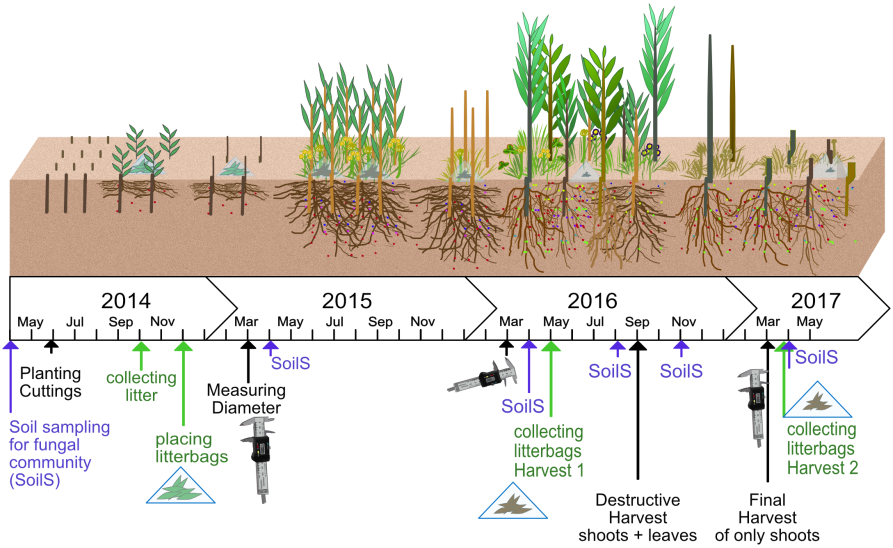


Figure 7: Work flow of the field studies: *Salix* cuttings were planted in spring 2014, grown over three growing seasons and harvested in spring 2017. Throughout this period, shoot diameter and biomass and leaf biomass were measured to determine productivity (black text). Litter was collected and litter bags were placed on the soil surface and later recovered to analyze decomposition pattern (green text). Soil samples were taken to analyze fungal communities in the soil (violet text).

For high-throughput sequencing, plot-pooled samples were freeze-dried and milled to homogenize each sample and break down cell wall material, followed by DNA extraction. In polymerase chain reaction (PCR) analysis, a set of primers (gITS7, ITS4 and ITS4arch) was used to identify fungal species (Ihrmark et al., 2012). Fungal species can be identified through their internal transcribed spacer (ITS) region. In order to identify individual samples, unique identification tags were added to the amplicons. With this method, each fungal community per sample was identified in a pooled high-throughput sequencing approach, followed by bioinformatics analysis.

3.6 Data analysis

In the field trials, shoot biomass data were derived using genotype-specific shoot fresh weight and dry weight (shoot biomass) from stratified sampling (Paper II). The shoot biomass per individual genotype was calculated from the resulting genotype-specific linear regression (shoot biomass= a +b x shoot fresh weight).

3.6.1 Plant nitrogen economy

Plant nitrogen economy in the pot experiment (Paper I) was calculated based on the methodology introduced by Weih et al. (2011) and Weih (2014). Mean plant nitrogen content was calculated based on the nitrogen content in the perennial part of the plant (the cutting) and the nitrogen content in biomass from the first and second harvest.

3.6.2 Decomposition

In the leaf litter decomposition study (Paper III), the fraction of remaining leaf mass was calculated per plot as the ratio between the mean leaf mass remaining when litter bags were harvested and the mean mass of leaves inserted in the litter bags before field incubation.

3.6.3 Statistical analysis

Linear mixed models were used to calculate the effects of fertilization treatment, genotype and genetic richness (Papers I and II). The Shapiro-Wilk test was used to test for normal distribution and scatter plots were used to test for homoscedasticity, followed by analysis of variance (ANOVA) to test for differences between treatments (Paper I at pot level, Papers III and IV at plot level). Two- and three-way analysis of variance (ANOVA) was followed by multiple-comparison Tukey's honestly significant difference (HSD) test to compare treatments. The confidence interval was set at 95 % *i.e.* statistical significance was set at $p<0.05$. Analysis of covariance (ANCOVA), with plant biomass as covariate, was applied to test for differences in root allocation. All statistical and graphical analyses were performed in R (version 3.3.3, R Core Team 2019).

Sequence data for the soil fungal community were clustered, resulting in operational taxonomic units (OTUs), also called species hypotheses

(SHs), and given unique names (Kõljalg et al., 2013). Multivariate analyses (principal component analysis (PCA) and detrended correspondence analysis (DCA)) were performed to visualize the variation in soil fungal communities using SHs. Analyses were conducted for the two sites, Rostock and Uppsala, together and separately. The multivariate analyses were performed in CANOCO (version 5.02, Microcomputer Power).

3.6.4 Genotype-specific community performance, analyzed by Bayesian model

A linear Bayesian model was used to calculate the probability (and range of credible values) of an effect caused by the addition of a specific *Salix* genotype to a community with other *Salix* genotypes. Positive, neutral or negative effects on shoot biomass (Paper II), decomposition or remaining nitrogen (Paper III) or fungal diversity (Paper IV) were analyzed using this approach. Thereby, differences for all possible community combinations, with and without a specific genotype, were estimated and compared. The resulting posterior distributions were derived and mapped. A posterior distribution around 0.5 was considered to have no effect, whereas a posterior distribution close to 0 was interpreted as indicating a strong negative effect and a posterior distribution close to 1 as indicating a strong positive effect.

A second linear Bayesian model was used to estimate the probability of a specific *Salix* genotype to perform better grown in mixture with other genotypes than grown in monoculture (two, three- or four-genotype mixture minus monoculture). Here, posterior distribution close to 1 was taken to indicate that a genotype was likely to perform better in mixture than in the corresponding monoculture, while values close to 0 were taken to indicate the contrary. The models were run in JAGS (Plummer, 2003).

4 Results and Discussion

4.1 Genetic diversity

Based mainly on previous findings in multi-species grasslands and forest stands, willow productivity and other ecosystem processes were expected to increase with increasing diversity of plant community components. It was therefore expected that increasing genetic diversity would result in an increase in shoot biomass production, higher litter decomposition rate (less remaining mass and nitrogen) and higher fungal species richness with increasing diversity level in the willow plantations investigated (see Figure 2). However, the results showed that biomass production (Paper II), litter decomposition including the fraction of remaining nitrogen (Paper III) and fungal species richness, diversity and biomass (Paper IV) did not differ significantly between monoculture and mixtures at plot level at any of the three field sites included in this thesis work (Figure 8).

Rather than the expected increase in productivity and leaf litter decomposition with increasing diversity, shoot biomass production and litter decomposition rate actually decreased in the four-genotype mixture compared with the monoculture and two- and three-genotype mixtures at the Freiburg site. This observed negative effect of mixtures on productivity contradicts previous reports of higher productivity with higher species richness and higher diversity of traits (Cardinale et al., 2011; Duffy et al., 2017). At the Freiburg site, the three-genotype mixtures grew better than the monocultures and two- and four-genotype mixtures. A significant negative complementarity effect suggests that competition could explain the significant decrease in productivity observed of the four-genotype mixture (see Figure 4 in Paper II). At the Uppsala site, mean productivity of the three-genotype mixtures was not different from mean productivity of the monocultures. Two three-genotype combinations produced more shoot biomass than the other two three-genotype combinations (see Figure S1 in Paper II). When various three-genotype mixture combinations that differed greatly in their mean productivity were taken for analysis to calculate mean productivity, this could explain why the reported mean productivity of the three-genotype mixtures was similar to the

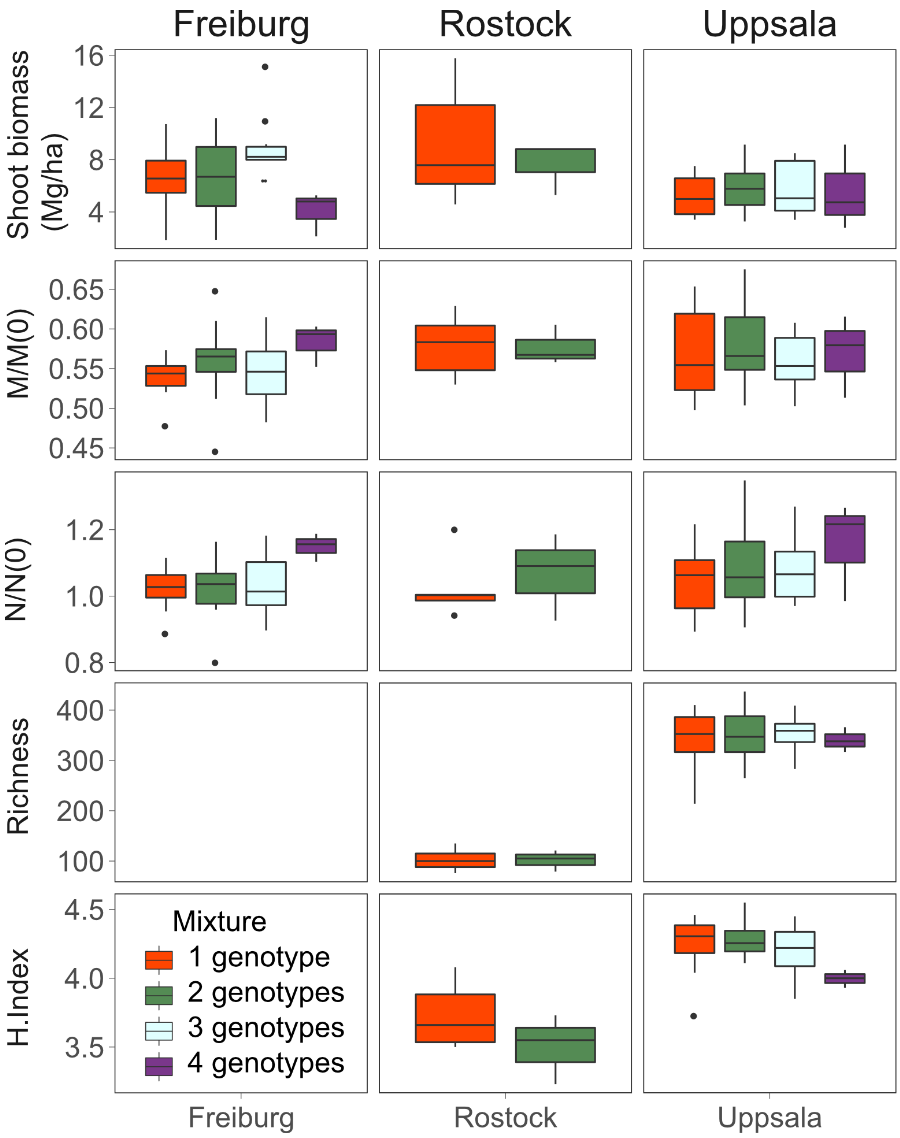


Figure 8: (From the top) Shoot biomass (Mg/ha), fraction of remaining mass (M/M(0)), fraction of remaining nitrogen (N/N(0)), fungal richness and fungal diversity (H. index) across four diversity levels (number of *Salix* genotypes in mixture) and three field trials (Freiburg, Rostock and Uppsala).

mean productivity of monocultures. The four genotypes planted in the field sites differed in their functional traits, what leads to the hypothesis that these genotypes use different niches when grown in mixtures, resulting in a positive complementarity effect. However, no evidence was found of an overall positive complementarity effect when assessed across all field sites. In the pot study (Paper I), a positive complementarity effect of the two-genotype mixture (‘Loden’ and ‘Tora’) was observed only when the plants were grown under low nutrient supply. A positive complementarity effect was also found in the field study performed in Uppsala, but only for the two- and three-genotype mixtures, suggesting that niche differentiation could have occurred at this site. A more pronounced complementarity effect, and thus higher niche differentiation between the genotypes, might appear in the future when the trees have grown larger and interaction between neighboring plants can be expected to be greater. Population structural changes may then lead to dominance of the best-performing species in the community (Loreau, 2000; Tilman et al., 1997).

A more diverse genotype mixture can be expected to provide higher variability in litter quality, with different nutrient and lignin concentrations. Hence, the litter has a higher chance of being degraded by the microbial community (Schimel and Hättenschwiler, 2007). The results of the litter decomposition study (Paper III) contradicted previous studies showing faster decomposition with increasing tree species richness (Gartner and Cardon, 2004; Hättenschwiler et al., 2005; Jacob et al., 2009). Although leaf litter quality traits such as phosphorus and lignin content differed significantly between the four genotypes grown in monoculture, what implies that they provide different resource quantities to the microbial communities, decomposition in the four-genotype mixture decreased. The litter decomposition rate of single-genotype litter differed significantly between the genotypes grown in monoculture in Uppsala, but these differences were not seen when the plants were grown in mixtures (see Figure 2 in Paper III). Detailed comparison of genotype combinations revealed that the decomposition rates in some mixtures were faster than in others. Litter of the fast decomposing genotypes ‘Jorr’ and ‘Loden’ incubated together showed a higher decomposition rate than litter of the combination of slowly decomposing genotypes ‘Björn’ and ‘Tora’ (Figure 9).

Apart from increases in productivity and decomposition, greater heterogeneity in resources and environmental conditions supported by plant-species richness should result in higher soil microbial richness (Hooper et al., 2005; Wardle, 2006), here reported as fungal richness and diversity. Although this expectation seems reasonable and soil fungal richness may be affected by

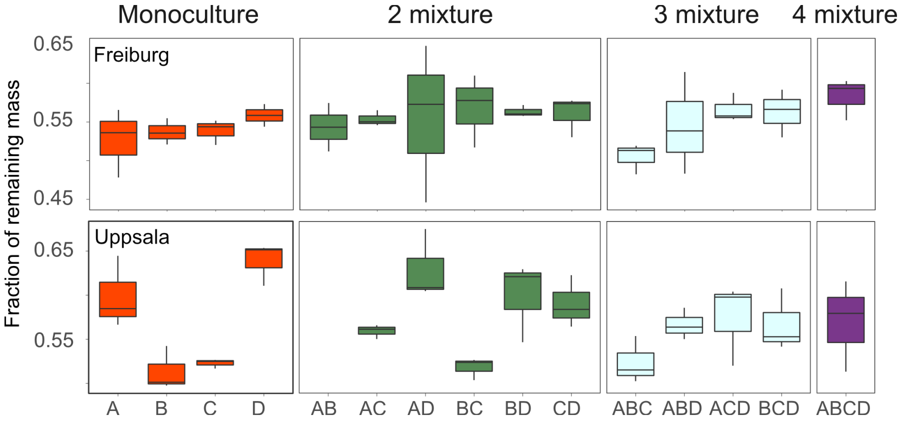


Figure 9: Fraction of remaining mass of all genotypes grown in monoculture and in 2-, 3- and 4-genotype mixtures in Freiburg and Uppsala. Mean stand biomass of the *Salix* genotypes ‘Björn’ (A), ‘Jorr’ (B), ‘Loden’ (C) and ‘Tora’ (D) after three years of growth.

plant diversity (Urbanová et al., 2015), the scientific evidence is contradictory. Plant species richness can drive fungal diversity at local scale (Peay et al., 2013). Yet, abiotic factors can be stronger drivers of fungal community richness than plant species richness (Tedersoo et al., 2014). In this thesis, the distribution of fungal functional groups was similar between monoculture and two- and three-genotype mixtures. The distribution of fungal functional groups even increased slightly with genetic richness of *Salix* plants after three years of *Salix* growth, with a strong increase in ectomycorrhizal fungi in the third year (see Figure S2 in Paper IV). However, in the four-genotype mixture, almost no increase in ectomycorrhiza during the three years of growth was found and the overall fungal diversity showed a negative trend (Figure 8). This is consistent with studies performed in Estonia and Finland, where tree species diversity did not show strong effects on fungal diversity (Tedersoo et al., 2016).

Overall, the simple step of adding one or two genotypes to monocultures, irrespective of the genotypes used, did not alter productivity, decomposition or fungal diversity in the studies described in this thesis. In fact, growing all four selected *Salix* genotypes together had a negative impact on the ecosystem functions investigated. In the following two sections, the genotype-specific effects are explored in detail, in order to evaluate the contribution of the individual genotypes to overall mixture performance.

4.2 Genotype-specific response to biomass production, decomposition and fungal diversity

Within a plant community of multiple species or genotypes, plant identity is important (Scherer-Lorenzen et al., 2004). From an ecological and agronomic perspective, it is interesting to define genotypes that improve ecosystem functions and to identify those that have a generally negative effect. This thesis analyzed whether addition of a specific *Salix* genotype had a positive, negative or no effect on biomass productivity, litter decomposition and fungal diversity.

Genotype differences in biomass production followed the same pattern at the Freiburg and Uppsala sites with respect to addition of a particular genotype to the community of other genotypes. However, for litter decomposition and the fraction of remaining nitrogen, differences emerged between genotypes and sites (Figure 10). In general, the two full-sib relatives 'Björn' (*Salix schwerinii* x *S. viminalis*) and 'Tora' (*S. schwerinii* x *S. viminalis*) had a rather negative impact on biomass production. Considering the similar plant morphology of the two genotypes, their similar effect is perhaps not surprising. Especially their greater average height compared with the other genotypes, may enable them to outgrow the other genotypes when grown in mixture. 'Björn' and 'Tora' also exhibited similar decomposition rates between sites, but had different effects on the overall decomposition rate of litter in the community. Although these genotypes are closely related (Barker et al., 1999), they show different functional traits, especially in leaf nitrogen concentration (Weih and Nordh, 2002). Here, they had different effects on productivity (Figure 6 in Paper II) and litter chemical characteristics and decomposition rate (Table 2 and Figure 2 in Paper III), which in turn can affect the performance of the community.

In general, when present, 'Tora' had a negative effect on the productivity of the plant community, decomposition and fungal diversity (Figure 10). The negative effect of 'Tora' on productivity could be driven by its higher growth compared with the genotypes 'Jorr' and 'Loden' (see Figure 1). 'Tora' benefited from the presence of other genotypes, as it grew better in mixture compared to monoculture, but this could not compensate for its overall negative effect on the average productivity of the communities (Figure 6 in Paper II).

The negative effect of 'Tora' on the decomposition rate (shown as higher fraction of remaining mass in Figure 10) when grown in a mixture could be explained by the low litter quality of this genotype. At local scale, litter quality can drive litter decomposition, as nutrient-rich litter with a high nitrogen and phosphorus content decomposes faster than low-quality litter with higher

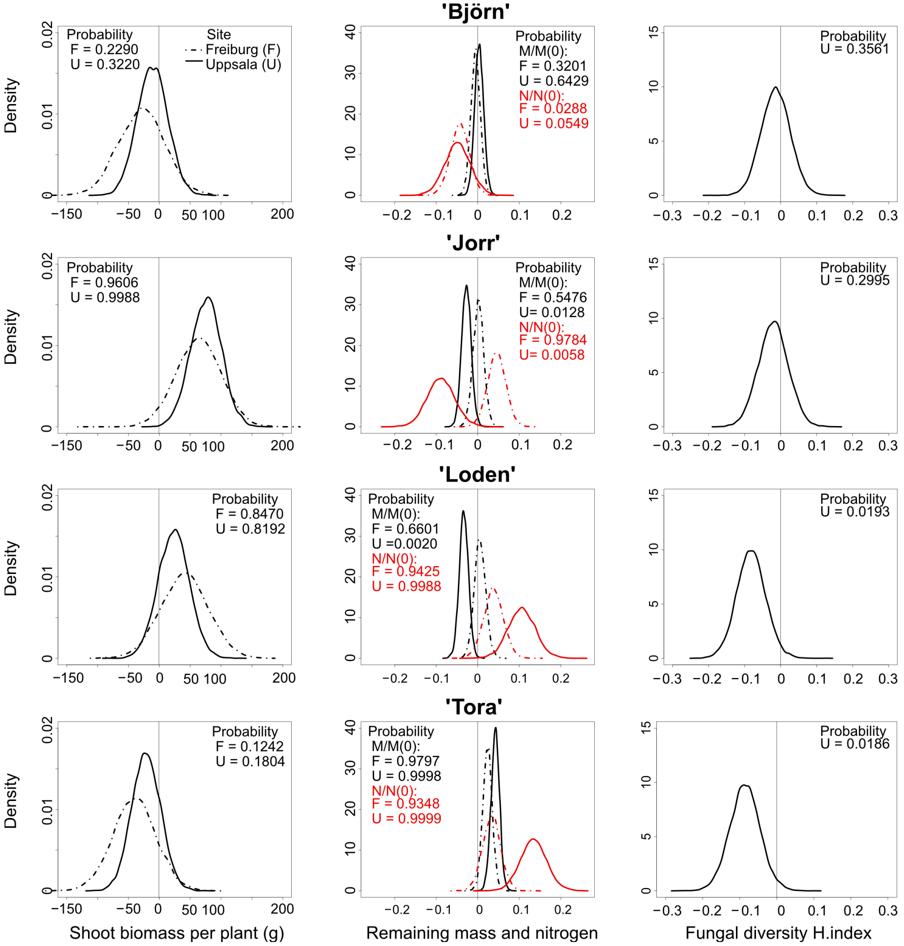


Figure 10: Posterior probability distribution showing the effect of the presence of a specific *Salix* genotype (Björn', 'Jorr', 'Loden' and 'Tora') on mean shoot biomass (left panels), fraction of remaining mass (M/M(0); middle panels, black lines), fraction of remaining nitrogen (N/N(0); middle panels, red lines) and fungal diversity (H. index; right panels). Positive values indicate an increase, negative values indicate a decrease, and the vertical line indicates no average effect of adding a specific genotype to the community. Dotted lines indicate data from the Freiburg site and solid lines data from the Uppsala site. Diagrams modified from Papers II and III, and data used from Paper IV.

contents of complex compounds, for example lignin (Berg and McClaugherty, 2008). In this study, ‘Tora’ produced the slowest decomposing leaf litter among the genotypes, with a high lignin concentration and the lowest phosphorus concentration of all genotypes when grown in monoculture (Table 2 and Figure 2 in Paper III). These properties could potentially slow down litter decomposition of the other genotypes. In contrast, similar decomposition rates and fractions of remaining nitrogen were found for ‘Tora’, ‘Björn’, ‘Jorr’ and ‘Loden’ monocultures grown at the site in Freiburg (Table 2 and Figure 2 in Paper III). According to the Bayesian analysis, there is a very high probability (0.97 in Freiburg and 0.99 in Uppsala) of ‘Tora’ lowering the litter decomposition rate when it is present in willow communities. Other litter characteristics not assessed in this study could explain this finding, for example greater leaf toughness, which would make it more difficult for the microbial community to degrade the leaf litter generated by ‘Tora’. Some studies report a negative relationship between litter decomposition rate and leaf toughness, which in turn can affect nutrient release (Cornelissen and Thompson, 1997; Gallardo and Merino, 1993; Pérez-Harguindeguy et al., 2000).

The negative effect of ‘Tora’ on litter decomposition rate and fraction of remaining nitrogen in communities where ‘Tora’ was present could possibly also be linked to the observed lower fungal diversity of communities containing ‘Tora’. ‘Tora’ could affect other genotypes, and thus fungal diversity, due to its leaf chemistry or belowground components such as root exudates, which can play a role in structuring microbial communities (Schweitzer et al., 2008). Fungal diversity can be driven more strongly by species or genotype identity than by species diversity (Schweitzer et al., 2008). In this study, leaf biomass, litter chemistry, fraction of remaining nitrogen in litter after decomposition, and soil properties such as soil pH, soil nitrogen and soil carbon were significantly correlated with fungal communities. This demonstrates that variations in fungal community might be affected by different drivers. For example, genotypic variation in aboveground plant traits can be linked to soil microbial dynamics (Schweitzer et al., 2004), and ectomycorrhizal fungal communities can be linked to plant biomass (Korkama et al., 2006; Velmala et al., 2012), or leaf chemistry of senescent litter (Lamit et al., 2016). Soil chemical characteristics such as soil pH or soil nutrients have also been found to be strong drivers of fungal communities (Bonito et al., 2019).

The taxonomically distinct genotypes ‘Jorr’ (*S. viminalis*) and ‘Loden’ (*S. dasyclados*) had a positive effect on productivity when added to a community (Figure 10). The positive effect of ‘Jorr’ might be caused by its morphological and phenological traits such as low leaf area and height (Weih and Nordh, 2005), providing other genotypes with more light and space for better growth compared to other genotypes. ‘Loden’ usually has greater leaf area and lower shoot height (Weih and Nordh, 2005), leading to greater canopy stratification. Greater canopy stratification, such as a second canopy layer in mixtures and complementary crown shapes, could enhance canopy filling, in turn increasing productivity when different genotypes are grown together (Ishii and Asano, 2009; Pretzsch, 2014). At the Uppsala site, the genotypes ‘Jorr’ and ‘Loden’ increased decomposition rate when grown together with other genotypes, which is not surprising as the litter of ‘Jorr’ and ‘Loden’ incubated in monoculture decomposed faster (Figure 9; Figure 2 in Paper III). These two genotypes also produced higher quality litter, with high phosphorus and low lignin concentrations which led to faster decomposition rates (Table 2 in Paper III). Thus, litter of ‘Jorr’ or ‘Loden’ could enhance the decomposition of litter originating from other genotypes in the plant community.

In general, this evaluation of adding specific *Salix* genotypes to a community showed that a close taxonomical relationship between community components (for example ‘Björn’ and ‘Tora’) did not necessarily mean that they exerted similar effects on ecosystem processes when present in a mixed community. It is worth pointing out the positive impact of ‘Jorr’ and ‘Loden’ on productivity and decomposition rate when present in a mixed community. One of the most interesting findings in this thesis was the dominant (mostly negative) effect of ‘Tora’ on productivity, decomposition rate and fungal diversity when present in a mixed community. This prompted further studies on how this genotype (and the other genotypes) performed when grown in mixture compared to their monoculture.

4.3 Genotype-specific performance when grown in mixture compared with monoculture

The four *Salix* genotypes studied in this thesis were planted in mixture and monoculture to investigate the competitive or complementary use of resources. Successful competitors grown in fertile ecosystems use their resources efficient to produce aboveground and belowground biomass (Aerts, 1999; Caldwell et al., 1996; Lambers and Poorter, 1992). In nutrient-limited ecosystems, plants tend to invest more biomass in roots (Bloom et al., 1985). The genotypes used in this study differ their functional traits such as relative growth rate, leaf area productivity and nitrogen uptake efficiency, suggesting niche differentiation when the genotypes were planted in mixture. In the pot study, the growth performance and nitrogen economy of the two *Salix* genotypes 'Loden' and 'Tora' were examined under high-nutrient and low-nutrient conditions, to identify potential drivers of niche differentiation when both genotypes were grown in mixture compared with their corresponding monoculture (Paper I). Both genotypes responded with a significantly higher root growth rate to limited nutrient availability, which confirms previous findings for many other plant species (Aerts et al., 1991; Ericsson, 1995). At high nutrient availability, 'Loden' developed more roots when grown in mixture than in monoculture, whereas 'Tora' showed similar performance in both forms of culture (Figure 1 in Paper I).

'Tora' is a genotype with high shoot and root growth rate and high leaf nitrogen concentration compared with 'Loden' (Weih and Nordh, 2002). Therefore, 'Tora' was expected to outperform the slower-growing genotype 'Loden'. In fact, the results showed that 'Tora' performed better in terms of aboveground, productivity and nitrogen economy (nitrogen uptake efficiency and yield-specific nitrogen efficiency) in monoculture compared with mixture in both the high-nutrient and low-nutrient treatments. 'Loden' showed the opposite pattern, performing better in mixture than in monoculture at low nutrient availability (Figure 4 in Paper I). These results indicate that 'Loden' is the better competitor of the two. In terms of leaf nitrogen productivity and leaf area productivity at low nutrient availability (Figure 2 in Paper I), 'Tora' performed better in mixture, whereas 'Loden' performed better in monoculture. A previous study on three *Salix* genotypes suggested that differences between monoculture and mixture become more pronounced after two-four years of growth (Dillen et al., 2016). Thus, it remains to be seen whether 'Tora' performs better than 'Loden' after more growing seasons.

In this context, the growth performance of 'Loden' and 'Tora' in monoculture and in mixtures was evaluated at the three field sites (Freiburg, Rostock and Uppsala) (Figure 7 in Paper II). Differences in productivity (shoot biomass) between the two genotypes in mixture resulted in a distinct pattern across sites. As the pot study showed differences in nitrogen economy between the two genotypes grown in mixture and monoculture, it was expected that these differences would result in a different growth performance pattern across sites. It was found that 'Tora' performed better in monoculture than in mixture with 'Loden' in Rostock, which was the site with the lowest soil nitrogen content and soil organic matter content, what confirms the findings of the pot study under low nutrient availability (Paper I). In Freiburg, the site with the highest soil nitrogen content and soil organic matter content, both genotypes showed higher productivity in mixture than in their corresponding monoculture. In Uppsala, only 'Tora' performed better in mixture.

In general, at both the Freiburg and Uppsala sites 'Tora' grew better in mixture than in its corresponding monoculture, not only together with 'Loden' but also with other genotypes in the two- and three-genotype mixtures. This indicates a competitive advantage of 'Tora' compared with the other *Salix* genotypes. In a nutrient-limited environment, such as at the Rostock site, the growth of 'Tora' in mixture is rather limited.

4.4 Implications for biodiversity ecosystem function research

This thesis provides insights into plant-plant and plant-environment interactions of a *Salix* short-rotation coppice system used to explore the biodiversity-ecosystem function (BEF) theory. In Papers I-IV, ecosystem functions related to productivity, litter decomposition and fungal community were analyzed to explore the performance of genotypes that differ in their functional traits. The first hypothesis (H1), on the importance of genetic richness for productivity, litter decomposition and fungal diversity, was only partly confirmed, as only some specific genotype mixtures improved ecosystem functions. Overall, the results did not supply much supporting evidence for the major hypothesis underlying biodiversity-ecosystem function theory, which states that higher genetic diversity promotes ecosystem functions such as productivity and decomposition (Cardinale et al., 2011; Duffy et al., 2017; Loreau, 2000). Some studies have found that plant identity is more important for ecosystem functions than genetic diversity, due to large differences between species or genotypes in important functional traits (Mokany et al., 2008; Tedersoo et al., 2016; Wardle et al., 2003). This was the basis for hypothesis H2 in this thesis. The results clearly indicate that individual genotypes had a stronger effect than genetic diversity on productivity, litter decomposition and partly fungal community. Under the assumption that functional traits are less similar between taxonomically further related species, co-culture of taxonomically more distinct genotypes should affect ecosystem functions more strongly than taxonomically closely related genotypes (hypothesis H3). This hypothesis was only partly supported by the results obtained in this thesis. This indicates that ecosystem functions are more strongly affected by the use of functionally diverse community components than by a taxonomically close relationship between plants. The results in this thesis also indicate that specific genotype combinations can favor some ecosystem functions, whereas other genotype combinations are less favorable for some ecosystem functions.

5 Conclusions

- The characteristics of the individual *Salix* genotypes studied here were more important than genetic richness for ecosystem functions related to biomass production, litter decomposition and fungal diversity.
- The high-performing genotype ‘Tora’ had an overall negative effect on the performance of mixed *Salix* communities and grew better in mixture than in monoculture, but only under favorable soil conditions.
- Taxonomically closely related genotypes, with similar characteristics in many functional traits, differed greatly in their performance when grown in mixed communities.

6 Future prospects

In this thesis, measurements on plantations were carried out during and after the first cutting cycle. Thus, plants may not yet have had a fully developed root system, which could lead to fewer interactions between genotypes. The effects of genetic richness on productivity or fungal community might thus appear less pronounced. The four genotypes studied differ in their root growth and growth rate (Weih and Nordh, 2005). Thus, higher biomass production in mixtures due to higher resource uptake and stronger niche differentiation (Reich et al., 2012; Sapijanskas et al., 2013) might be expected in subsequent rotations, as shoot growth rate usually increases after the first cutting cycle (Fontana et al., 2016). Therefore, stronger interactions between genotypes competing for resources can be expected, particularly in monoculture, and complementary use of resources in mixtures, especially in those where 'Jorr' and 'Loden' are present. Certain genotypes, such as 'Jorr' and 'Loden', could increase overall shoot productivity as they potentially promote canopy stratification due to their plant morphology and functional traits.

Greater differences in the composition of fungal communities in the future can also be expected, especially in monocultures, as previous studies have concluded that tree identity is of greater importance than host diversity (Korkama et al., 2006; Schweitzer et al., 2008). As ectomycorrhizal communities increased strongly between summer 2016 and shoot harvest in spring 2017, a strong trend for ectomycorrhizal fungi in fungal community composition after the second cutting cycle (planned for spring 2020) can be expected in future studies, and possibly a greater difference in the composition of specific ectomycorrhizal fungi contributing to the fungal community composition.

Future planned harvests will show how fungal community composition has developed in monocultures and mixtures, and may provide insights into specific genotype combinations that improve ecosystem functioning and biomass production.

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