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# Stand age characteristics and soil properties affect species composition of vascular plants in short rotation coppice plantations

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## Abstract

Woody biomass plantations on agricultural sites are an attractive source of biomass for bioenergy, but their effects on local biodiversity are unclear. This study's objective was to evaluate the influences of light availability, plantation age, and soil properties on phytodiversity in short rotation coppice (SRC) plantations. Ground vegetation mapping, irradiance measurement (PAR), and surface soil analyses were conducted in 15 willow and poplar SRC plantations in Central Sweden and Northern Germany. We performed different multivariate statistical methods like cluster analysis (CA), principal component analysis (PCA), and canonical correspondence analysis (CCA) in order to analyze species composition and the influence of irradiance, age, and soil properties on phytodiversity. CA revealed highest species composition similarities in SRC plantations in close proximity. PCA identified humus quality/essential plant nutrients, plantation age/irradiance effects, soil acidity and shoot age as the four principal components of the recorded parameters. The ground vegetation cover was negatively correlated with the plantation age component and positively with the nutrient component. With an increase in the plantation age component, a shift in species composition was proven towards more forest habitat species, more nutrient-demanding species, and increasing occurrence of indicator species for basic soils. Applying Ellenberg indicator values, basic soil indicator species corresponded in occurrence to increasing nutrient availability. However, species richness was not related to any of our studied site variables. Judged from CCA, species composition in SRC plantations was influenced by plantation age/irradiance, and nutrient availability; soil acidity and shoot age had no significant influence. Young poplar and willow SRC plantations showed greatest variation in photosynthetically active radiation (PAR). Our findings suggest that phytodiversity in SRC plantations depends mainly on plantation age and thus shifts over time.

**Keywords**

biodiversity, poplar (*Populus sp.*), willow (*Salix sp.*), species composition, photosynthetically active radiation (PAR), irradiance, multivariate analysis

## Introduction

In the near future, bioenergy is predicted to be one of the key strategies for reducing greenhouse gas emissions and substituting fossil fuels (Faaij 2006, Cocco 2007). Renewable energy comprised approximately 10.3 % of the EU gross energy consumption in 2008 and, by 2020, an increase to 20 % is foreseen. To date, Sweden consumes the highest proportion of renewable energy in relation to the final energy use of the EU-countries. Sweden aims to increase the proportion of renewable energy to 49 % of its total energy consumed by 2020 whereas, for Germany, 18 % is targeted (all statements: Eurostat 2010).

Berndes et al. (2003) reviewed 17 studies of the future global use of biomass for energy and pointed out that, in most cases, woody biomass plantations are considered the most crucial source of biomass for energy. Wood and residual wood contributed 3.9 % of total primary energy consumption in EU-27 in 2007 (EEA 2010). The amount of wood suitable for energy purposes from forests will not sustain the increasing demand (Hofmann 2010; Kloos 2010). Short rotation coppice (SRC) plantations are regarded as one of the most promising options for contributing towards the European targets to increase the amount of renewable energy (EEA 2006; Styles and Jones 2007). The above-ground shoots in a SRC plantation are harvested during winter on a cutting cycle of usually 3 yr for willow SRC and 3-7 yr for poplar SRC (Karp and Shield 2008), and the rootstock or stools remain in the ground after shoot harvest with new shoots emerging the following spring (Weih 2009). In general, the planted crops remain viable for 15-30 years (Aylott et al. 2008). Therefore, several cutting cycles can be maintained during the life time of a SRC plantation, and shoot age (within cutting cycle) may differ greatly from plantation age. From SRC plantations, energy from biomass can be produced with little net addition of $CO_2$ to the atmosphere (Volk et al. 2004), which makes SRC plantations one of the most energy efficient carbon conversion measures to reduce greenhouse gas emissions (Styles and Jones 2007). Predominant SRC crops are willow (*Salix sp.*) and poplar (*Populus sp.*), planted at high densities on former arable lands. Due to the expected increase in demand for wood from SRC plantations, it is important to know how they affect the environment, and what factors influence the biodiversity in SRC plantations. Using this knowledge for the establishment and management of SRC plantations, environmental benefits and increased biodiversity may be achieved in agricultural areas. This is especially of interest given the significant role intensive agriculture plays in the world-wide loss of biological diversity (McLaughlin and Mineau 1995; Tilman et al. 2001; Geiger et al. 2010).

Publications of previous surveys have shown that, as a perennial crop, willow and poplar SRC plantations can contribute positively to phytodiversity in agricultural areas (e.g. Delarze and Ciardo 2002; Weih et al. 2003; Cunningham et al. 2004; Augustson et al. 2006; Britt et al. 2007; Kroiher et al. 2008; Fry and Slater 2009; Rowe et al. 2011; Baum et al. 2009; Baum et al. 2012). Predominantly common species are recorded with only few endangered ones (Burger 2006; Kroiher et al. 2008; Vonk 2008, exception: Delarze and Ciardo 2002). Light is often identified as one of the major factors influencing species diversity in SRC plantations with plantation age, tree canopy (Gustafsson 1987, 1988; Heilmann et al. 1995; Delarze and Ciardo 2002; Cunningham et al. 2004; Kroiher et al. 2008; Fry and Slater 2009; Archaux et al. 2010; Baum et al. 2012) and crop planted (Heilmann et al. 1995). Most authors detected a species number increase during the first two years of growth followed by a subsequent decrease (Heilmann et al. 1995; Delarze and Ciardo 2002; Cunningham et al. 2004; Fry and Slater 2009). Due to intensive weed control prior to plantation establishment, ground vegetation cover is low after the establishment of SRC plantations, but then increases during at least the subsequent four years (Cunningham et al. 2004) after which a decrease for longer rotation times is expected (Gustafsson 1987). Furthermore, species composition changes over time from pioneer and ruderal species, typical for open vegetation, to woodland species (Delarze and Ciardo 2002; Britt et al. 2007; Kroiher et al. 2008; Baum et al. 2012). A transition from annual to perennial species has been observed (Cunningham et al. 2004; DTI 2006; Fry and Slater 2009). Further factors influencing species diversity are the surrounding landscape (Gustafsson 1987, 1988; Stjernquist 1994), soil seed bank (Gustafsson 1987, 1988, Stoll and Dohrenbusch 2008), former use (Gustafsson 1987, 1988; Stjernquist 1994; Stoll and Dohrenbusch 2008; Wróbel et al. 2011) as well as soil conditions such as soil moisture and soil nitrogen (Archaux et al. 2010; Wróbel et al. 2011).

The objective was to evaluate the influences of light availability, stand dynamics in terms of plantation and shoot age, as well as soil properties on phytodiversity in SRC plantations. We recorded vegetation, measured irradiance (photosynthetically active radiation, PAR) and conducted soil analyses on 15 Swedish and German willow and poplar SRC plantations. We hypothesized that (1) temporal stand dynamics (by means of plantation age, shoot age and irradiance constrains) are greatly influencing phytodiversity of SRC ground vegetation, and (2) soil parameters for plant nutrients and soil acidity are important co-factors affecting species composition due to different plant requirements. We expect a) a maximum in phytodiversity in middle aged SRC plantations, because of the availability of shaded and non-shaded habitats. With increasing plantation age, we assume b) a shift in species composition towards more forest species due to lower irradiance and c) towards more nutrient-demanding species due to nutrient accumulation in undisturbed soils.

## Materials and methods

### Location and site conditions

The ground vegetation of 15 German and Swedish SRC plantations was investigated in 2009. The eight Swedish willow stands surveyed are located in the Uppland province. Seven SRC plantations are situated in Northern Germany in the states Brandenburg, Saxony and Lower Saxony. Poplar plantations occur at the Cahnsdorf site in Brandenburg and the Thammenhain site in Saxony. In Lower Saxony three of the four sites comprise willow stands (Bohndorf I, II, III), while the Hamerstorf site contains willow and poplar. The poplar and willow SRC plantations varied in age, rotation regime and clones (Table 1). Four Swedish SRC plantations were treated with sewage sludge applied as fertilizer at the time of SRC establishment (sites Åsby, Djurby, Hjulsta II and Lundby II). All willow plantations and the poplar plantation Cahnsdorf were planted in double rows. We chose SRC plantations for which we had sufficient information regarding plant material and management history. A different number of poplar and willow sites were chosen, since (1) no poplar site was available in Sweden and (2) a different number of poplar and willow sites in Germany with above mentioned information were available.

Mean annual temperatures at the German sites were higher (about 8.5 °C) than the Swedish sites (about 5.5 °C). During growing season (May-September), mean temperature was 15 °C at the German sites and 13.5 °C at the Swedish sites. The German sites received more precipitation (annual precipitation: 640 mm; during growing season: 60 mm) than the Swedish sites (annual precipitation: 530 mm; during growing season: 55 mm; data base: long-term recordings from 1961-1990, German Weather Service (DWD 2010); Swedish Meteorological and Hydrological Institute (SMHI 2011)).

The German study sites consisted of sandy soils, whereas the Swedish soils were more cohesive with high clay contents. Soil pH-values (Table 2) characterized the sites as acidic till slightly acidic with focus on moderately acidic conditions (pH values of 5.0-6.0; AK Standortkartierung 2003). The C/N ratios represented a high humus quality (AG Boden 2005) and were lower at the Swedish than at the German sites. C-content, as well as N-content, was low at the German sites and moderate at the Swedish sites (BMELV 2006). However, the phosphorous supply at the German and Swedish sites was high and very high, respectively (Landwirtschaftskammer Nordrhein-Westfalen 2011). The low C/P ratios point to high mineralisation rates of organic matter (AK Standortskartierung 2003). Effective cation exchange capacity ranged from 'low' to 'high' (AK Standortskartierung 2003), with values at the German sites were lower than the Swedish sites. The base saturation was predominantly higher for the Swedish sites than the German ones. Base saturation above 80 % is considered very base-rich to base saturated (AG Boden 2005).

## Vegetation sampling

The growing season starts approximately one month later in Central Sweden than in Northern Germany. Thus, vegetation sampling was conducted from May until July in Germany and from July until August 2009 in Sweden to accommodate similar vegetation phenology in the two distinct regions. The vascular plants in the ground vegetation layer were recorded on eight Swedish willow SRC plantations, four German willow and three poplar SRC plantations. At each site, 1600 m$^2$ were mapped.

**Table 1.** Study sites: Overview of abbreviations, crops, ages and previous uses. D: Germany, S: Sweden

| | | | Geographical location | | Size | | Last | Cutting | | | Plants |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Abbreviation and site** | | **Country** | **N** | **E** | **(ha)** | **Establ.** | **harvest** | **cycle** | **Crop** | **Previous use** | **(per ha)** |
| AS | Asby | S | 59°59'07" | 17°34'57" | 8.2 | 1996 | 2008 | 4 | Willow: 'Tora' | Arable land | 12500 |
| BD I | Bohndorf I | D | 53°10'33" | 10°38'52" | 1.2 | 2006 | 2009 | 2 | Willow: 'Tordis', 'Inger' | Grassland | 13000 |
| BD II | Bohndorf II | D | 53°10'31" | 10°37'53" | 1.5 | 2008 | - | 1 | Willow: 'Tordis' | Grassland | 13000 |
| BD III | Bohndorf III | D | 53°10'18" | 10°37'37" | 1.7 | 2007 | - | 1 | Willow: 'Tordis' | Grassland | 13000 |
| CD | Cahnsdorf | D | 51°51'30" | 13°46'05" | 1.6 | 2006 | 2008 | 2 | Poplar: 'Japan 105' | Arable land | 10000 |
| DJ | Djurby | S | 59°41'20" | 17°16'34" | 2.3 | 1990 | 2006 | 5 | Willow: 'L78101', 'L78021' | Arable land | 12500 |
| FF | Franska försöket | S | 59°49'10" | 17°38'28" | 0.7 | 1994 | 2007 | 5 | Willow: 'Anki', 'Astrid', 'Bowles Hybrid', 'Christina', 'Gustaf', 'Jorr', 'Jorun', 'Orm', 'Rapp', 'Tora', 'L78021' | Arable land | 18000 |
| HS I | Hjulsta I | S | 59°31'55" | 17°03'00" | 3.0 | 1995 | 2008 | 4 | Willow: 'Jorr' | Arable land | 12500 |
| HS II | Hjulsta II | S | 59°32'01" | 17°02'54" | 6.2 | 1995 | 2008 | 4 | Willow: 'Jorr' | Arable land | 12500 |
| HTP | Hamerstorf: *Populus* | D | 52°54'35" | 10°28'06" | 2.1 | 2006 | - | 1 | Poplar: 'Hybrid 275', 'Max 4', 'Weser 6' | Grassland | 2500 |
| HTS | Hamerstorf: *Salix* | D | 52°54'34" | 10°28'06" | 1.8 | 2006 | - | 1 | Willow: 'Tora', 'Tordis', 'Sven', 1 unknown | Arable land | 13000 |
| KT | Kurth's trial | S | 59°48'29" | 17°39'25" | 1.2 | 1993 | 2007 | 4 | Willow: 'L81090', 'L78021' | Arable land | 17500 |
| LB I | Lundby I | S | 59°40'42" | 16°57'18" | 1.2 | 1995 | 2005 | 3 | Willow: 'L78021' | Arable land | 12500 |
| LB II | Lundby II | S | 59°40'44" | 16°57'43" | 9.5 | 2000 | 2005 | 2 | Willow: 'Tora' | Salix (died), before 1995: Arable land | 12500 |
| TH | Thammenhain | D | 51°26'31" | 12°51'12" | 10.5 | 1999 | - | 1 | Poplar: 'Max 4', 'Graupa' | Set aside/arable land | 2000 |

**Table 2.** The pH and element concentrations of the mineral top soil (10 cm depth, N=4 (except HTP and HTS: N=2). std.: standard deviation, CEC: effective cation exchange capacity, BS: base saturation, Al + Fe: exchangeable aluminium and iron ions. For site abbreviations, see Table 1

| | **pH** | | **pH** | | **C/N** | | **C** | | **N** | | **P** | | **C/P** | | **CEC** | | **BS** | | **Al + Fe** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | **($H_2O$)** | | **(KCl)** | | **ratio** | | **(‰)** | | **(‰)** | | **(mg/100g)** | | **ratio** | | **(mmol$_c$/kg)** | | **( %CEC)** | | **( %CEC)** | |
| | **Ø** | **std.** | **Ø** | **std.** | **Ø** | **std.** | **Ø** | **std.** | **Ø** | **std.** | **Ø** | **std.** | **Ø** | **std.** | **Ø** | **std.** | **Ø** | **std.** | **Ø** | **std.** |
| BD I | 6.4 | 0.3 | 4.9 | 0.4 | 12.5 | 2.0 | 10.68 | 2.09 | 0.85 | 0.06 | 18.6 | ± 6.1 | 65.14 | 33.89 | 40.4 | 14.2 | 87.0 | 14.8 | 10.8 | 14.8 |
| BD II | 6.4 | 0.2 | 5.3 | 0.1 | 12.0 | 0.4 | 10.25 | 4.42 | 0.85 | 0.35 | 29.8 | ± 5.3 | 33.42 | 9.87 | 43.1 | 14.9 | 94.2 | 1.5 | 3.8 | 1.7 |
| BD III | 6.2 | 0.1 | 5.4 | 0.1 | 13.5 | 1.7 | 10.85 | 2.41 | 0.80 | 0.08 | 25.2 | ± 1.8 | 43.65 | 12.75 | 41.1 | 8.5 | 94.9 | 1.1 | 3.0 | 0.7 |
| CD | 6.5 | 0.1 | 5.9 | 0.1 | 14.5 | 1.9 | 7.45 | 0.97 | 0.53 | 0.13 | 40.6 | ± 3.3 | 18.30 | 0.86 | 35.8 | 4.2 | 92.6 | 2.9 | 6.7 | 3.0 |
| HTP | 6.7 | 0.1 | 5.7 | 0.2 | 13.9 | 0.7 | 11.75 | 0.35 | 0.85 | 0.07 | 25.5 | ± 2.6 | 46.33 | 6.13 | 38.3 | 6.3 | 96.3 | 0.3 | 2.6 | 1.0 |
| HTS | 6.8 | 0.0 | 5.7 | 0.1 | 13.7 | 0.2 | 8.20 | 0.14 | 0.60 | 0.00 | 38.8 | ± 1.7 | 21.18 | 1.31 | 52.4 | 8.4 | 97.2 | 0.6 | 1.5 | 0.4 |
| TH | 6.3 | 0.1 | 5.0 | 0.3 | 13.6 | 1.3 | 10.13 | 0.76 | 0.75 | 0.10 | 32.8 | ± 1.5 | 30.97 | 3.14 | 40.1 | 14.9 | 93.1 | 2.1 | 4.0 | 1.6 |
| AS | 5.3 | 0.2 | 4.1 | 0.1 | 12.6 | 0.7 | 25.28 | 11.13 | 2.05 | 1.00 | 70.0 | ± 13.5 | 35.71 | 14.26 | 69.5 | 19.9 | 78.3 | 4.5 | 20.1 | 4.1 |
| DJ | 6.6 | 0.0 | 5.4 | 0.1 | 10.8 | 0.5 | 30.88 | 3.87 | 2.85 | 0.37 | 82.3 | ± 7.2 | 37.70 | 5.37 | 278.1 | 23.2 | 98.4 | 2.4 | 1.5 | 2.4 |
| FF | 6.1 | 0.1 | 4.7 | 0.1 | 12.1 | 0.9 | 13.98 | 2.54 | 1.15 | 0.13 | 80.1 | ± 2.8 | 17.40 | 2.71 | 110.4 | 11.9 | 96.6 | 0.7 | 2.6 | 0.7 |
| HS I | 6.7 | 0.4 | 5.5 | 0.7 | 12.0 | 0.4 | 15.00 | 2.46 | 1.25 | 0.19 | 65.9 | ± 3.0 | 22.77 | 3.50 | 154.7 | 73.6 | 98.7 | 0.9 | 1.0 | 0.8 |
| HS II | 7.2 | 0.3 | 6.2 | 0.6 | 11.1 | 0.4 | 15.25 | 0.52 | 1.38 | 0.05 | 69.5 | ± 4.0 | 21.99 | 1.27 | 186.1 | 16.3 | 99.3 | 0.1 | 0.4 | 0.0 |
| KT | 6.4 | 0.1 | 5.1 | 0.1 | 10.7 | 0.6 | 25.08 | 2.07 | 2.35 | 0.26 | 75.6 | ± 9.4 | 33.30 | 1.92 | 226.9 | 84.5 | 99.6 | 0.2 | 0.3 | 0.1 |
| LB I | 6.2 | 0.0 | 5.0 | 0.2 | 11.2 | 0.5 | 28.80 | 3.97 | 2.58 | 0.45 | 79.8 | ± 4.9 | 36.32 | 6.34 | 247.3 | 32.3 | 99.2 | 0.3 | 0.6 | 0.2 |
| LB II | 6.5 | 0.1 | 5.3 | 0.0 | 12.0 | 0.6 | 38.95 | 10.35 | 3.23 | 0.70 | 70.2 | ± 4.1 | 55.54 | 13.89 | 296.2 | 20.3 | 98.4 | 1.2 | 1.5 | 1.2 |

This area was first subdivided into four 400 $m^2$ sample areas, each of which was again subdivided into 36 plots of 11 $m^2$, that the resulting 144 plots were recorded per site (exception: HT: 72 willow (HTS) and 72 poplar (HTP) plots; TH: 132 plots due to tree felling in two of the sample areas one day before mapping). For each plot, a species list and species percentage cover was compiled for the tree and ground vegetation layer. The percentage cover was recorded in 5 % intervals following the scale from Londo (1975); if cover was less than 5 %, the scale was subdivided into 1 % categories. At a cover below 1 %, we differentiated between two to five individuals (0.2) and one individual (0.01) according to the Braun-Blanquet's (1928) scale. The nomenclature follows Rothmaler (2002).

## Soil sampling

Soil sampling was conducted in March and April 2010 in Germany and in May 2010 in Sweden. On each of the four sample areas (400 $m^2$) per site, four shuffle samples of topsoil (10 cm depth) were taken and merged into one composite sample per 400 $m^2$ area.

The composite samples were air-dried and sieved to 2 mm. Each measurement was conducted twice. For the carbon and nitrogen determination, the samples were dissolved at 1000 °C. The water content was determined to derive the correction factor F, which is necessary for converting the element content in the air-dried soil to absolute dry soil (Eq. (1), HFA 2005). This allowed a better comparability and was used for the pH, CEC elements and phosphorus:

$$F = \frac{(100 + WG)}{100}$$

where F= correction factor, WG= water content (%).

For the determination of water content, pH in $H_2O$, and pH in KCl methods from HFA (2005) were applied (A2.1, A1.1.2 and A1.1.4, respectively). CEC and phosphorus were analyzed by methods described in König and Fortmann (1996) (AKE1.1, DAN1.1, respectively).

## Irradiance measurement

Radiation was measured during the vegetation mapping in summer of 2009 under a homogeneous cloud cover or, if this was not possible, at sunset or at sunrise. The measurements were taken with a LI-COR® radiation sensor model LI-1400, which measures the photosynthetic active radiation (PAR, 400-700 nm wave length).

One logger was positioned outside the SRC in an open field, and measurements were made every second and mean radiation recorded every 30 seconds, in addition to the minimum and maximum for this period. A second logger was placed within the SRC and operated manually to measure irradiance at ground vegetation height at the middle of each plot (144 measurements per site; exceptions: FF: N=135 due to hardware failure, TH: N=132 due to tree felling, HTP and HTS: N=72 due to size). Radiation in the open field was set as 100 %. The data collected in the SRC were calculated in relation to the open field value for the corresponding 30 second interval.

## Data analysis

Red Lists were used for the estimation of endangered species. For all sites located in Lower Saxony, the Red List for the region "lowlands" was applied (NLWKN 2004). The Red Lists for Saxony (SMUL 2009), Brandenburg (MUGV 2006) and Sweden (Gärdenfors 2005) were used for the particular sites.

Cluster analysis (CA) was performed with XLSTAT (version 2011.2.06) for presence-absence data. The cluster-algorithm "complete linkage" was applied, and the Sørensen coefficient chosen as similarity measure for creating the dendrogram.

Principal Component Analysis (PCA) with data standardized by z-transformation was conducted using SAS 9.2 (procedure PROC FACTOR, METHOD=PRINCIPAL, ROTATE=VARIMAX). Before performing the PCA calculations, the aptitude of the variables pH (in KCl), C, N, P, Al, Fe, Mn, K, Na, Mg, Ca, PAR, shoot age, and plantation age was tested via communalities. We kept all variables that contributed to more than 0.70 to the overall communality.

Pearson's product moment correlation analyses and quadratic regression analyses were conducted to determine whether the four factors resulting from the PCA correlate with species number, ground vegetation cover, Ellenberg indicator values and the qualitative and quantitative proportion of forest species. The mean Ellenberg indicator values (Ellenberg et al. 2001) for nitrogen (N), soil reaction (R) and moisture (F) calculated per 1600 m$^2$ (N=144, exception: HTP and HTS: 800 m$^2$, N=72) are partially qualitative: the qualitative indicator spectra of the plots (11 m$^2$) were used for calculating the 1600 m$^2$ area mean, so that the frequency of a species and its Ellenberg indicator value were included. Thus, an overestimation of rare species, which is possible when only qualitative data is used, was prevented, and the dependency on growth, which may arise if only quantitative data is used, was also avoided. High vegetation cover does not only depend on local site characteristics but also on the specific growth habits (Ellenberg 2001). The qualitative and quantitative proportion of forest species was calculated per plot and averaged per site as described prior for the Ellenberg indicator values. The quantitative forest species proportion includes the species percentage cover. The classification of forest and non-forest species was done according to Schmidt et al. (2011).

Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) were performed with CANOCO® 4.54. The function "down-weighting of rare species" was chosen. The DCA (not shown) and CCA results generally corresponded, which showed that the essential environmental factors were captured. For the CCA, the principal components gained from the PCA were used as environmental factors explaining the variation in vegetation composition of the sites.

## Results

### Species composition and abundance

In total, 237 vascular plant species were recorded in the SRC ground vegetation layer, of which 83 % are perennials. Species number in Sweden (163) was higher than in Germany (152). *Cirsium arvense* (creeping thistle) and *Taraxacum officinale* (common dandelion) were found at all 15 sites; *Elymus repens* (couch grass) and *Urtica dioica* (common nettle) at 14, *Dactylis glomerata* (orchard grass) and *Agrostis capillaris* (common bent) at 13 sites. Other common species were *Galium aparine* (cleavers), *Poa trivialis* (rough bluegrass), *Poa pratensis* (common meadow-grass), *Myosotis ramosissima* (early forgetmenot) and *Alopecurus pratensis* (meadow foxtail). Of those species found, 56 % were found at only one or two sites. On average, 95 % of the species per study site had a maximum cover of 5 %. Percentage species cover was similar across all sites. In contrast, the percentage cover of *Urtica dioica* (common nettle) was 59 % at a three-year-old Swedish willow site (DJ). A total of 18 of the 237 species had a cover above 5 %, including ten grasses. According to the relevant Red Lists, no endangered species were found at any recorded SRC, and only few uncommon species were recorded. In Swedish SRC plantations, these were *Luzula luzuloides* (forest wood-rush, site AS), *Odontites vernus* (red bartsia, LBI, LBII), *Rubus caesius* (European dewberry, HSI), *Rumex obtusifolius* (broad-leaved dock, FF) and *Sagina nodosa* (knotted pearlwort, HSI, HSII). They all occurred infrequently. Uncommon species recorded in German SRC plantations were *Filago arvensis* (field cudweed, CD, BDII) and *Hieracium aurantiacum* (orange hawkweed, BDII). Of the recorded species, 42 % were classified as forest species and 11 % as forest specialists. Mean species number per plot varied by a factor of 2.4 and was lowest at the willow SRC Kurth's trial and highest at the willow SRC Lundby I (Table 3). The species number per site (1600 m$^2$) varied 1.8 fold. Highest PAR values and variations were recorded in the poplar SRC plantations Cahnsdorf and Hamerstorf and in the willow SRC Bohndorf I. In general, PAR was lower in Swedish SRC plantations than in German ones.

The cluster analysis dendrogram with present/absent species data separated two distinct major groups: the German and the Swedish sites (Fig. 1). The poplar sites (CD, TH, HTP) were more similar to some of the willow SRC plantations than to other poplar SRC plantations. The nearby sites HSI vs. HSII, LBI vs. LBII, and HTP vs. HTS were very similar.

**Table 3.** Species numbers per SRC-site (1600 m², exceptions: HTP, HTS: 800 m²), mean species number per plot (N=144, exceptions: HTP, HTS: N=72) and relative irradiance (PAR). P=*Populus*, S=*Salix*, sp. no.: species number. For site abbreviations, see Table 1

| | German SRC-sites | | | | | | | Swedish SRC-sites | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Site** | **BD I** | **BD II** | **BD III** | **CD** | **HTP** | **HTS** | **TH** | **AS** | **DJ** | **FF** | **HS I** | **HS II** | **KT** | **LB I** | **LB II** |
| Crop | S | S | S | P | P | S | P | S | S | S | S | S | S | S | S |
| Cutting cycle age (yr) | 0 | 1 | 2 | 1 | 3 | 3 | 10 | 1 | 3 | 2 | 1 | 1 | 2 | 4 | 4 |
| Plantation age (yr) | 3 | 1 | 2 | 3 | 3 | 3 | 10 | 13 | 19 | 15 | 14 | 14 | 16 | 14 | 9 |
| Mean sp. no./plot | 11.1 | 14.5 | 7.9 | 11.0 | 8.4 | 11.9 | 7.4 | 11.3 | 8.3 | 8.1 | 10.4 | 9.3 | 7.0 | 16.7 | 14.4 |
| Sp. no./site | 56 | 73 | 48 | 55 | 31 | 50 | 40 | 70 | 41 | 60 | 67 | 62 | 47 | 65 | 62 |
| PAR (mean, %) | 61.2 | 38.5 | 11.1 | 75.7 | 60.5 | 24.1 | 10.5 | 19.5 | 13.6 | 4.2 | 11.9 | 16.6 | 2.4 | 25.7 | 11.6 |
| PAR (SD, %) | 27.3 | 16.1 | 3.2 | 30.7 | 31.2 | 18.5 | 11.0 | 15.0 | 3.3 | 2.3 | 7.0 | 7.0 | 1.1 | 19.2 | 7.3 |

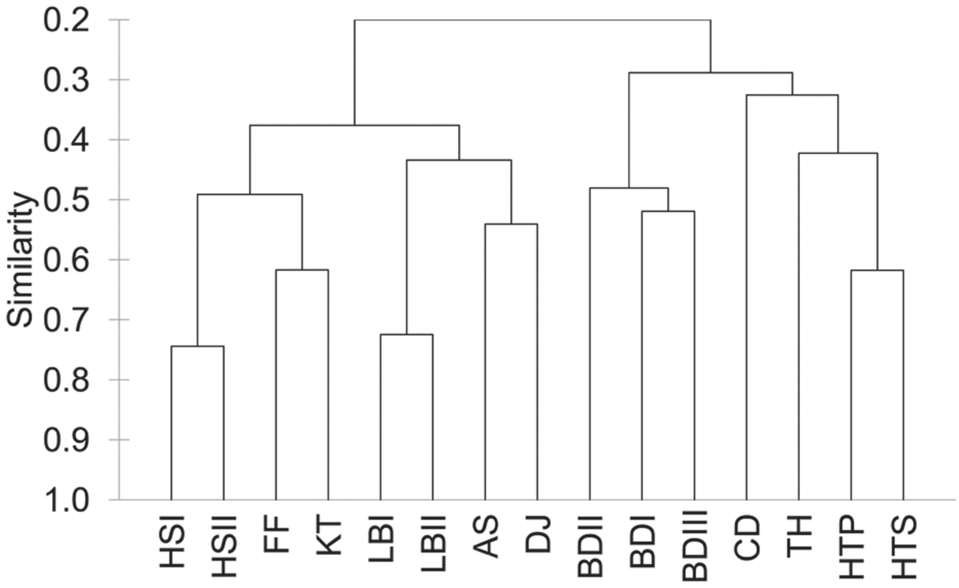

**Figure 1.** Cluster analysis of species composition of the ground vegetation. Present/absent data. Cluster-algorithm: complete linkage; similarity measure: Sørensen coefficient. N per site=144, except TH: N=132, HTP: N=72, HTS: N=72. For site abbreviations, see Table 1

## Environmental and internal factor influences

We analyzed the influence of environmental factors as well as of stand-internal factors on ground vegetation composition and structure. These factors were the concentration of carbon (C), nitrogen (N), phosphorous (P), potassium (K), sodium (Na), magnesium (Mg), calcium (Ca), aluminium (Al), iron (Fe), manganese (Mn), as well as pH (KCl) value, irradiance (PAR), and shoot age and plantation age, latter as internal factors. For structuring and simplifying these variables, PCA was applied and resulted in four principal components. CCA was conducted to show correlations between environmental and internal parameters expressed by the factors gained from PCA and variation in vegetation structure.

Table 4 shows the standardized variables included in the principal component analysis. The first principal component was highly positively loaded by soil concentrations of carbon (C), nitrogen (N), calcium (Ca), iron (Fe), magnesium (Mg), sodium (Na), and negatively loaded by manganese (Mn) concentration. Thus, the first principal component was identified as the humus quality, nutrient and lime component and is called 'nutrient component' in the following. The second component was highly positively loaded by concentrations of calcium (Ca), potassium (K), phosphorus (P), SRC plantation age, and negatively loaded by irradiance (PAR). This factor displayed a 'plantation age component' that includes also an increasing absence of soil disturbances. Latter aspect promotes the accumulation of organically bound nutrients (K, P concentration) in the top soil. The third principal component was highly positively loaded by pH and highly negatively loaded by aluminium (Al) concentration, and hence represented a 'soil acidity component'. Factor 4 was highly positively loaded by manganese (Mn) concentration and shoot age representing the effect of the age within cutting cycle and is called 'shoot age component'. The German site Thammenhain showed the highest shoot age (10 years) along with high Mn concentration value, which might in part explain the strong overall correlation between these two variables.

The ground vegetation cover increased with increasing factor 1 values (nutrient component) and decreased with increasing factor 2 values (plantation age component, Table 5). Both qualitative and quantitative forest species proportion in SRC plantations ascend with increasing factor 2 values. The Ellenberg indicator value for nitrogen

**Table 4.** Communalities of the variables and rotated factor pattern of the principal component model. Highlighted bold: value factor loading >0.5 or < -0.5. Expl. var.: variance explained by each factor. Age: SRC plantation age

| Variable | Communality | Factor 1 | Factor 2 | Factor 3 | Factor 4 |
|---|---|---|---|---|---|
| pH (KCl) | 0.874 | -7 | -9 | **-91** | -20 |
| Al | 0.912 | -5 | -4 | **92** | -25 |
| C | 0.943 | **87** | 38 | 22 | -3 |
| N | 0.946 | **85** | 44 | 18 | -5 |
| Ca | 0.952 | **75** | **58** | -22 | -6 |
| Fe | 0.718 | **84** | -2 | -13 | -2 |
| K | 0.937 | 19 | **92** | -21 | -12 |
| Mg | 0.876 | **82** | 39 | -20 | 3 |
| Mn | 0.830 | **-58** | -18 | -3 | **68** |
| Na | 0.797 | **85** | 22 | 14 | 9 |
| P | 0.902 | 49 | **78** | 9 | -23 |
| PAR | 0.784 | -14 | **-78** | -15 | -37 |
| Age | 0.908 | 35 | **87** | 16 | -3 |
| Shoot age | 0.796 | 14 | 4 | -2 | **88** |
| Overall | 12.180 | | | | |
| Expl. var. | | 4.907 (40.3%) | 3.736 (30.7%) | 1.982 (16.3%) | 1.556 (12.8%) |

**Table 5.** Linear correlations between principal components and vegetation characteristics. Species no.: species number, Ground cover: ground vegetation cover, F_qual/ F_quan: qualitative and quantitative forest species proportion, Ellenberg N, R, F: Ellenberg indicator values for nitrogen (N), soil reaction (R) and moisture (F). Highlighted bold: significant correlations. N=15

| | Factor 1 | | Factor 2 | | Factor 3 | | Factor 4 | |
|---|---|---|---|---|---|---|---|---|
| Pearson | r | p | r | p | r | p | r | p |
| Species no. | 0.09 | 0.75 | 0.11 | 0.70 | 0.31 | 0.27 | -0.31 | 0.26 |
| Ground cover | **0.52** | **0.04** | **-0.53** | **0.04** | 0.28 | 0.30 | -0.04 | 0.89 |
| F_qual | -0.11 | 0.68 | **0.75** | **<0.01** | 0.11 | 0.70 | 0.23 | 0.41 |
| F_quan | -0.18 | 0.52 | **0.67** | **<0.01** | -0.02 | 0.95 | 0.12 | 0.67 |
| Ellenberg N | 0.28 | 0.31 | **0.70** | **<0.01** | -0.02 | 0.93 | 0.26 | 0.35 |
| Ellenberg R | **0.57** | **0.03** | **0.59** | **0.02** | -0.26 | 0.35 | 0.01 | 0.97 |
| Ellenberg F | -0.23 | 0.42 | -0.04 | 0.90 | 0.16 | 0.57 | 0.15 | 0.60 |

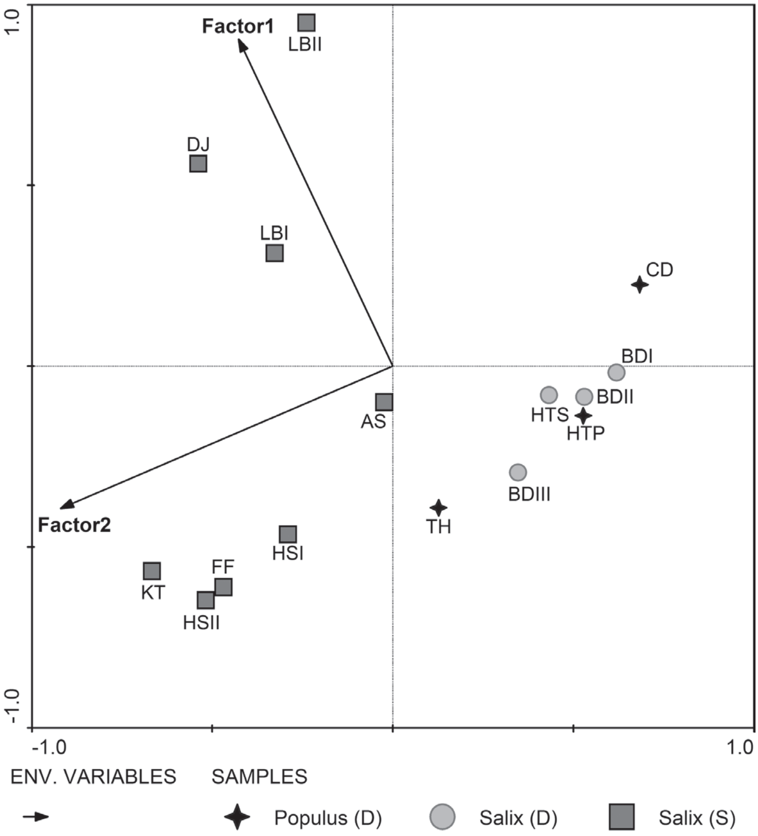

**Figure 2.** CCA ordination diagram of SRC plantation's ground vegetation layer in relation to the main components gained by PCA. Factor 1: plantation age component, factor 2: nutrient component. Sum of all eigenvalues: 3.785, eigenvalue axis 1: 0.530 (species-environment correlation: 0.972), eigenvalue axis 2: 0.344 (species-environment correlation: 0.954, percentage variances of species-environment relation of the first axis: 60.7 %. Legend: letters in brackets: D: Germany, S: Sweden. Sig.: significant, n.s.: not significant. For site abbreviations, see Table 1

was positively related to factor 2. The Ellenberg indicator value for soil reaction rose with increasing factor 1 (nutrient component) and increasing factor 2 values. Species number and the Ellenberg indicator value for moisture were not linearly correlated with the factors revealed by the PCA. No quadratic relationships between factors and variables were found.

Based on species percentage cover and the factors received by PCA, CCA showed that differences in species composition among SRC plantations were mainly due to plantation age (factor 2; first axis: r=-0.89, p=0.002) and nutrient availability (factor 1; second axis: r=-0.86, p=0.04). Factor 3 (soil acidity component) and factor 4 (shoot age component) contributed not significantly to the ordination (p=0.210 or p=0.176, respectively). The Swedish and German sample areas showed clear differences (Fig. 2): The German sites differed mainly due to factor 2 between each other. In contrast, the Swedish sites diversified because of both factors. In general, the German sites had lower factor 2 values than the Swedish sites (exception: ten-years-old site TH), while most Swedish sites had higher factor 1 values than the German ones.

## Discussion

### Age characteristics and soil properties influence species composition

Species composition in SRC plantations differed greatly as cluster analysis showed. This was also found in South and Central Sweden by Gustafsson (1987). We found mostly similar species compositions in SRC plantations in close proximity, indicating that recruitment from surrounding vegetation has an essential influence (Gustafsson 1987). Our results show that species composition in SRC plantations was influenced by environmental parameters: the PCA resulted in four principal components standing for nutrients, plantation age effects, soil acidity, and shoot age. PCA showed that the relative irradiance correlated only with plantation age but not with shoot age. This might be due to the great variety of crop species (cf. Table 1) creating different light regimes for the ground vegetation and due to different rotation numbers: after each harvest the sprouts re-grow from the stool higher branched than before (Ceulemans et al. 1996). In real time series we would expect a decreasing irradiance with increasing shoot age. In CCA, the abundance of species was related to principal components gained from PCA. The CCA supported the influence of the principal components on species composition, whereat the soil acidity component (factor 3) and shoot age component (factor 4) had no significant influence. For the soil acidity component, this may be due to the low variety in acidity between the study sites (cf. Table 2). We would expect the shoot age component being significant for species composition in a real time series.

Of the four principal components gained by PCA, especially plantation age characteristics (expressed by factor 2) greatly influenced species composition correlating with five of the seven variables tested (cf. Table 5). A higher factor 2 value means a higher plantation age, higher P and K contents (due to limited disturbance), higher

Ca contents and lower irradiance available for the ground vegetation. With increasing plantation age effect/factor 2 values, the qualitative and quantitative forest species proportions and the mean Ellenberg indicator values for nutrients and soil reaction of the vegetation increased. This suggests a change in species composition: increasing plantation age and decreasing irradiance goes along with an increase in forest species number and a shift from nutrient-poor to nutrient-rich indicator species, as well as a change from acidic to base indicator species. The species composition shifted from acidic to base indicator species with increasing nutrient availability, too (factor 1). The increase in species proportion typical for forests with increasing plantation age component was slightly more pronounced for forest species number than for forest species cover percentage. Kroiher et al. (2008) found an increase in forest species with increasing plantation age in willow and poplar SRC plantations in Northern Germany. Archaux et al. (2010) confirmed the increase in forest species in 11 to 15-year-old poplar SRC plantations in northern France, but found no significant relationship between age and forest species in two to five-year-old poplar stands. Regarding the shifts in species composition it is important to keep in mind that our results, the results by Kroiher et al. (2008) and Archaux et al. (2010) were not gained from real time series studies but included different old SRC plantations. However, Delarze and Ciardo (2002) conducted a real time series study and their results support the shift in species composition towards more forest species as they found an increase in forest species with increasing shoot age at the expense of ruderals and pioneers which are highly light, warmth, and nutrient-demanding; endangered species were found among them. The role of canopy cover, and its effect on soil temperature was described by Ash and Barkham (1976) for cleared and closed oak-ash-maple-hazel woodland in the UK. In most cases we found higher variations in irradiance (photosynthetic active radiation, PAR) in the poplar than in the willow SRC plantations, where PAR variability was also high in the four-month-old willow SRC Bohndorf I. The relative PAR was generally lower (and the tree cover generally higher; not shown) in Swedish SRC plantations than in German ones. We presume that this was due to different plantation ages: whereas Swedish SRC plantations were up to the fifth cutting cycle, the German SRC plantations had reached the first or the second cutting cycle. After each harvest, willows become denser so that PAR within the stands slightly declines. Soil moisture and soil nitrogen (calculated by Ellenberg indicator values of recorded plant species) were major determinants of plant communities in a study by Archaux et al. (2010) on poplar stands, while choice of clone and stem density had no significant effects but could be explained by the low variation in stem density.

## Ground vegetation cover is greatly affected by plantation age characteristics

In our study, ground vegetation cover increased with increasing nutrient availability (factor 1) and decreased with increasing plantation age component (factor 2). In contrast, Cunningham et al. (2004) found increased ground vegetation cover with shoot age over a four-year study period in willow SRC plantations in the UK, where ground vegetation cover varied considerably between individual sites and also between individual plots within a SRC, with some plots having low ground vegetation cover even after several years of crop growth. Unlike our survey, the study of Cunningham et al. (2004) was a time series within one cutting cycle so that long-term age effects (plantation age) were not taken into account. Gustafsson (1987) could not prove any correlation between tree and ground vegetation cover in Swedish willow stands up to three years old but expected a decrease in ground vegetation cover for longer cutting cycles. According to Heilmann et al. (1995) ground vegetation cover also depends on the crop and/or variety planted: They found a declining cover gradient from *Salix* to the aspen *Astria* to the broad-leafed poplars Muhle Larsen and Rap in three-year-old SRC plantations, and explained this gradient by differences in foliation, growth habit and biomass resulting in a decline in appropriate light conditions along this gradient. In contrast, we found higher PAR in poplar than in willow SRC plantations of the same age. Differences in plantation spacing and architecture, i.e. wide-spaced plantations of single-tree poplar (2500 and 10000 plants/ha, cf. Table 1) vs. narrow-spaced plantations of multi-stem willow (12500-18000 plants/ha), may cause different below-canopy light climate, because multi-stem architecture of narrow-spaced willow probably covers the ground more effectively than single-stem architecture in much wider-spaced plantations of poplar. During the first two years after establishment, Proe et al. (2002) found that coppicing and wider spacing had a reducing effect on PAR (single stems of alder and poplar of 1.0 m (10000 plants/ha) and 1.5 m spacing (4400 plants/ha); multi-stem alder, poplar and willow of 1.0 m spacing), but light interception was similar across all treatments after three years.

## Plantation and shoot age characteristics are unrelated to species number

We found no relationship between plantation age or shoot age and species number (cf. Table 5). In reference to Thienemann's biocoenotic principle stating the more diverse the living conditions the larger the number of species (Kratochwil 1999), highest species number occurs at mean irradiance due to availability of both shaded and non-shaded habitats. Based on time series at one location, an increase in species number during the first years of growth followed by a subsequent decline was reported by Heilmann et al. (1995), Delarze and Ciardo (2002), Cunningham et al. (2004) and Fry and Slater (2009). However, our study was conducted in different SRC plantations distributed across Central Sweden and Northern Germany and thus the influence of the surrounding landscapes on species diversity (Gustafsson 1987, 1988; Stjernquist 1994) may have influenced our result. Archaux et al. (2010) recorded a significantly lower species richness in mature poplar plantations (11–17 yrs) than in young ones (2–5 yrs), but could not clarify whether the relationship between species number and age was linear or curvilinear due to the lack of data for plantations between six and ten years old. Gustafsson (1987) found no correlation between tree cover and species number in Swedish willow stands up to three years old.

### Trivial species dominate the SRC plantations

In our study we found predominantly common perennial species, which is in line with the results by many other authors (Gustafsson 1987; Grünert and Roloff 1993; Heilmann et al. 1995; Weih et al. 2003; Cunningham et al. 2004; DTI 2006; Britt et al. 2007; Vonk 2008; Rowe et al. 2011). Only few species reached higher percentage covers. These were species very often reported as being dominant, like in particular, *Urtica dioica* (common nettle), *Cirsium arvense* (creeping thistle), *Taraxacum officinale* (common dandelion), *Galium aparine* (cleavers) and various grasses like *Elymus repens* (couch grass), *Poa trivialis* (rough bluegrass) and *Poa pratensis* (common meadow-grass) (cf. Gustafsson 1987; Grünert and Roloff 1993; Heilmann et al. 1995; Cunningham et al. 2004; DTI 2006; Britt et al. 2007; Rowe et al. 2011). Unlike some authors (cf. Burger 2006; Kroiher et al. 2008; Vonk 2008), we found no endangered species in our SRC study sites. The highest number of 18 Red List species in SRC plantations, was reported in western Switzerland by Delarze and Ciardo (2002) who suggested that this high number was due to high below-canopy irradiance in low-density poplar plantations.

## Conclusions

We have shown that especially plantation age and irradiance play an important role for plant diversity in SRC plantations but also soil nutrient contents. Influences on species composition and ground vegetation cover were proven. This indicates that diversity in SRC plantations varies over time; within cutting cycles and with plantation age. Thus, it is advised to plant several smaller SRC plantations with different rotation regimes and clones in one area instead of a large one. These measures enhance structural diversity of SRC plantations and foster phytodiversity of agricultural landscapes by providing different light regimes and thus habitats for species with different demands. We found no relationship of plantation age or shoot age on species number implicating that harvesting has no negative influence on species diversity.

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## Appendix

Species list of the study sites. (doi: 10.3897/biorisk.7.2699.app) File format: Microsoft Word Document (.doc).

**Explanation note:** Number of plots containing the respective species is stated. Habitat preferences according to Schmidt et al. (2011): F: forest species, nF: non-forest species, ns: not stated. Abbreviations of sites: AS: Åsby, DJ: Djurby, FF: Franska försöket, HSI: Hjulsta I; HSII: Hjulsta II; KT: Kurth's trial; LBI: Lundby I, LBII: Lundby II, BDI: Bohndorf I, BDII: Bohndorf II, BDIII: Bohndorf III, HTS: Hamerstorf (*Salix*), CD: Cahnsdorf, HTP: Hamerstorf (*Poplar*), TH: Thammenhain.

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