Floristic diversity in Short Rotation Coppice (SRC) plantations: Comparison between soil seed bank and recent vegetation

Sarah Baum*, Martin Weih** and Andreas Bolte***

Abstract

In the near future an increase in Short Rotation Coppice (SRC) plantations is to be expected. The objective was to compare the recent vegetation and the soil seed bank in SRC plantations to reveal the functioning of the soil seed bank for phytodiversity and vegetation structure after reconversion of SRC plantations into arable land. For the analyses, above-ground vegetation surveys and soil seed bank samples of six German and four Swedish SRC plantations were used. Similarity in composition of soil seed banks and recent vegetation was low in terms of species, plant strategy types, species habitat preferences and seed longevity. On average, the proportion of common species of recent vegetation and soil seed bank was 8.4 % (± 6.7 % SD). The recent vegetation was dominated by competitive (c) plant species while in the soil seed banks highest proportions were detected for ruderals (r) and competitors (c). Species with long-term persistent seeds had the highest contribution to both the recent vegetation and the soil seed banks. Grassland species had highest species habitat preference proportion in the recent vegetation. The soil seed banks contained predominantly ruderal species and woodland species were almost absent. Due to the poor coherence of seed bank vs. recent vegetation, we conclude that the site history has only a minor influence on phytodiversity in SRC plantations, suggesting that recent vegetation composition is mainly due to the species pool of the adjacent vegetation and site conditions like below-canopy irradiance and site nutrition.

Keywords: seedling emergence method, reconversion, functional species composition

Zusammenfassung

Floristische Vielfalt in Kurzumtriebsplantagen (KUP): Vergleich zwischen Diasporenbank und aktueller Vegetation

Es wird eine zeitnahe Zunahme von Kurzumtriebsplantagen (KUP) erwartet. Um die potentielle Rolle der Samenbanken im Boden in KUPs für die Phytodiversität und Vegetationsstruktur nach Rückumwandlung in Ackerland abschätzen zu können, wurde in sechs deutschen und vier schwedischen KUPs die floristische Zusammensetzung der aktuellen Vegetation und der Diasporenbank verglichen. Die Ähnlichkeit hinsichtlich der Zusammensetzung der Arten, Konkurrenzstrategien, Lebensraumpräferenzen sowie der Lebensdauer der Samen war gering. Der Anteil der Arten, die sowohl in der aktuellen Vegetation als auch in der Diasporenbank auftraten, lag bei 8.4 % (± 6.7 % SD). In der aktuellen Vegetation dominierten Konkurrenzstrategien (c), in den Diasporenbanken Ruderal- (r) und Konkurrenzstrategien (c). In aktueller Vegetation und Diasporenbank überwogen Arten mit langlebigen Samen. Grünlandarten hatten den größten Anteil der Lebensraumpräferenzen der aktuellen Vegetation. In den Diasporenbanken überwogen Ruderalarten, während Waldarten kaum anzutreffen waren.

Aus der schwachen Übereinstimmung von aktueller Vegetation und Diasporenbank schließen wir, dass die Nutzungsgeschichte einen geringen Einfluss auf die Phytodiversität in KUPs hat, was nahelegt, dass die aktuelle Zusammensetzung vor allem durch den Artenpool der angrenzenden Vegetation und Standortbedingungen wie Unterkronestrahlung und Nährstoffangebot bestimmt wird.

Schlüsselworte: Keimlings-Auflauf-Verfahren, Rückumwandlung, funktionelle Artenzusammensetzung

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1 Introduction

Due to political efforts to reduce greenhouse gas emissions, the proportion of renewable energies has to be increased to 20% in the EU until 2020 (European Commission Climate Action, 2010). One promising option contributing to this goal is woody biomass production in Short Rotation Coppice (SRC) plantations (cf. Berndes et al., 2003). Fast growing tree species like Salix spp. or Populus spp. are planted in high densities on agricultural lands and harvested after two to six years. These tree species have the ability to re-grow from their stools which generally remain viable for 15 to 30 years (Aylott et al., 2008). When agricultural lands are changed into SRC plantations, the ground has to be prepared by ploughing and weed control to ensure the establishment of the planted crop. Since no further measures are necessary, a ground vegetation cover establishes. This can be by living vegetative parts like rhizomes, tillers or alive roots in the soil (Gustafsson, 1987) and from the soil seed banks (Gustafsson, 1987; Stoll & Dohrenbusch, 2008). Plants can also establish by diaspor input from the surroundings (Gustafsson, 1987; Weih, 2009).

Many studies deal with the role of soil seed banks in re-colonization after disturbances (Bakker et al., 1996; Waldhardt et al., 2001; Luzuriaga et al., 2005; Dölle & Schmidt, 2009), restoration (Blomqvist et al., 2003; Matus et al., 2003; Martin & Wilsey, 2006; Bossuyt & Honnay, 2008) and succession (Hill, 1986; Young et al., 1987; Milberg, 1995; Grandin & Rydin, 1998; Faliríka, 1999; Bekker et al., 2000). In general, great floristic differences between above-ground vegetation and soil seed bank are reported for different habitats (e.g. D’Angela et al., 1988; Kitajima & Tilman, 1996; Davies & Waite, 1998; Bekker et al., 2000; Dölle & Schmidt, 2009) due to the ability of seeds to survive in the soil for many years without being present in the recent vegetation (Thompson & Grime, 1979; Hill & Stevens, 1981). Especially weed seeds in agricultural soils are able to outlast long periods and germinate when conditions are suitable again (Brown & Oosterhuis, 1981; Bakker et al., 1996). In contrast, vegetation and seed bank are similar in early successional communities following periodical disturbance, where early successional annual weed species with persistent seed banks dominate (Moore, 1980; Luzuriaga et al., 2005; Dölle & Schmidt, 2009). Persistent seed existence in the soil depends on many aspects like predation, germination requirements, dormancy mechanisms, seed shape, and resistance to pathogens (Thompson et al., 1993).

Despite abundant reports on relationships between soil seed banks and recent vegetation across various habitats, we are aware of only one study on soil seed banks in SRC plantations: Hoffmann (2005) surveyed the soil seed banks in SRC plantations of different poplar clones in northern Hesse (Germany), but made no comparisons with above-ground vegetation. The author found a relationship between planted clone types, light conditions on the soil surface and different species and numbers of individuals in the soil seed banks.

Our study focuses on the differences in germinable seeds in 10 to 20 cm depth and the recent vegetation in SRC plantations and thus on the role of the soil seed bank for phytodiversity in SRC plantations. A great coherence of soil seed bank and recent vegetation would imply different floristic diversity in SRC plantations in dependency on the site history. Further, comparing floristic diversity of the recent vegetation and the soil seed bank provides information about the potential contribution of the soil seed bank to the above-ground vegetation after reconversion into arable land. We address the hypothesis that functional species composition of recent SRC vegetation and soil seed bank differ with regard to strategy types, habitat-specific species diversity, and seed longevity. Thus, we expect weak influence of vegetation elements of former land use on recent vegetation in SRC plantations.

2 Materials and Methods

2.1 Study sites: Locations and site conditions

Soil seed bank sampling and vegetation surveys were conducted on ten study sites located in northern Germany and central Sweden. The German sites are situated in the federal states Brandenburg (site CD) and Lower Saxony (all other sites). Four of them contained willow and two poplar (Table 1).

<table>
<thead>
<tr>
<th>Abbreviation and site</th>
<th>Country</th>
<th>Crop</th>
<th>Established</th>
<th>Last harvest</th>
<th>Rotation no.</th>
</tr>
</thead>
<tbody>
<tr>
<td>BDI</td>
<td>DE</td>
<td>Willow: Tordis, Inger</td>
<td>2006</td>
<td>2009</td>
<td>2</td>
</tr>
<tr>
<td>BDII</td>
<td>DE</td>
<td>Willow: Tordis</td>
<td>2008</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>BDIII</td>
<td>DE</td>
<td>Willow: Tordis</td>
<td>2007</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>CD</td>
<td>DE</td>
<td>Poplar: Japan 105</td>
<td>2006</td>
<td>2008</td>
<td>2</td>
</tr>
<tr>
<td>HTP</td>
<td>DE</td>
<td>Poplar: Hybrid 275, Max 4, Weser 6</td>
<td>2006</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>HTS</td>
<td>DE</td>
<td>Willow: Tora, Tordis, Sven, one unknown</td>
<td>2006</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>HSI</td>
<td>SE</td>
<td>Willow: Jorr</td>
<td>1995</td>
<td>2008</td>
<td>4</td>
</tr>
<tr>
<td>HIJII</td>
<td>SE</td>
<td>Willow: Jorr</td>
<td>1995</td>
<td>2008</td>
<td>4</td>
</tr>
<tr>
<td>LBI</td>
<td>SE</td>
<td>Willow: 78021</td>
<td>1995</td>
<td>2005</td>
<td>3</td>
</tr>
<tr>
<td>LBII</td>
<td>SE</td>
<td>Willow: Tora</td>
<td>2000</td>
<td>2005</td>
<td>2</td>
</tr>
</tbody>
</table>
The four Swedish sites are located in the Uppland province and contained willow clones. Two of the Swedish SRC plantations were treated with sewage sludge before planting the crop (HSII and LBII). SRC plantations were established on arable land (CD, HTS, HSI, HII, LBI, LBII) or grassland (BDI, BDII, BDIII, HTP). We chose SRC plantations for which we had sufficient information regarding plant material and management history.

Mean annual temperatures were higher at the German sites (about 8.5 °C) than at the Swedish sites (about 5.5 °C). During the growing season (May to September) mean temperature for the German sites was 15 °C and 13.5 °C for the Swedish sites.

Precipitation rates were higher in Germany (annual precipitation: 640 mm; during growing season: 60 mm) than in Sweden (annual mean: 530 mm; during growing season: 55 mm; data base: long-term recordings from 1961 to 1990, German Weather Service (DWD, 2010); Swedish Meteorological and Hydrological Institute (SMHI, 2011)). The German study sites were characterized by sandy soils with sandy deposits as parent material. The soils of the Swedish sites are cohesive with high clay contents. The bedrock is predominantly granite or gneiss (site Djurby: greywacke, schist and quartzite).

2.2 Seed bank sampling
A pilot study was conducted in 2009 in order to find the most feasible method for seed bank sampling. In early March, 18 soil samples were taken on two 100 m² plots (one located centrally and one at the edge of the SRC plantation) in a willow SRC in Jamikow/Uckermark (Brandenburg, northeast Germany) from three different depths (0 to 10; 10 to 20 and 20 to 30 cm) with a 8 cm diameter soil corer. Three different volumes were taken per depth: 5, 10, or 15 soil cores (corresponding, 2510 cm³, 5030 cm³ and 7540 cm³ respectively). Soil cores of respective depths and volumes were mixed for each plot and concentrated to the fraction between 0.2 to 2 mm by washing and sieving. This sample concentration leads to an enhanced number of emerging seedlings by applying the seedling emergence method afterwards in comparison to raw samples (Ter Heerdt et al., 1996; Thompson et al., 1997). Approximately 2000 g of sieved soil of each sample were spread in a 28 x 46 cm plant tray on a 3 cm layer of sterilized sandy subsoil. Trays were placed in an unheated greenhouse for five months (April to September), and were covered with gauze to avoid contamination by external seeds. Emerging seedlings were determined, counted and removed creating optimal conditions for further seedling. Seedlings initially undeterminable were transplanted in separate pots where they could grow till they could be identified.

Data analyses of the pilot study showed a dependency of species number and number of individuals on sample depth with highest numbers for 10 to 20 cm depth ($R^2 = 0.47$ or $R^2 = 0.57$, respectively; Figure 1a). Species number and number of individuals were not influenced by sample volume ($R^2 = 0.15$ or $R^2 = 0.04$, respectively; Figure 1b). Of the total number of species recorded for each sampling area (all depths and volumes), 9 % within the SRC and 21 % at the edge of SRC, respectively, were not found in 10 to 20 cm depth. Thus, we decided in the main study to sample the depth of 10 to 20 cm within the SRC and to take nine soil cores (= 4523.9 cm³) corresponding to the number of vegetation survey sub-plots per 100 m² allowing a consistent soil sampling in 2010. Another aspect is that the upper layer is presumably strongly influenced by the recent vegetation (Bakker et al., 1996; Grandin & Rydin, 1998) and deeper layers contain thus more information regarding species of the former use.

Soil samples evaluated in this study were taken at the beginning of 2010 after winter stratification, but before emergence of early spring annuals. The German sites were sampled between the end of March and the beginning of April, the Swedish sites at the beginning of May as the growing season starts approximately one month later in central Sweden.

![Figure 1](image-url)

Figure 1
Pilot study for seed bank sampling: dependency of species number and number of individuals on a) sample depth and b) sample volume. Equations: a) Species no./depth: $y = -0.0442x^2+1.875x-6.1667$, $R^2 = 0.47$, $N = 18$; no. of individuals/depth: $y = -0.58x^2+23.717x-141.5$, $R^2 = 0.57$, $N = 18$; b) Species no./volume: $y = -0.1067x^2+2.1x+2.1667$, $R^2 = 0.15$, $N = 18$; no. of individuals/volume: $y = -0.46x^2+8.1667x+34.167$, $R^2 = 0.04$ $N = 18$. Poly.: Polynomial (square) function.
compared to northern Germany. At each SRC site two plots of 100 m² were sampled. All plots were located within the SRCs to avoid edge effects. In total, there were 12 samples in Germany and eight samples in Sweden with 4523.9 cm³ (= 9 soil cores) each. After mixing and weighing the nine soil cores, composite samples were halved, sieved and spread into plant trays as in the preliminary study in 2009. Samples were halved to avoid thick layers where seeds would have lower chance to germinate due to light deficiency and less suitable temperatures (e.g. Thompson et al., 1997). The trays were placed in the greenhouse for six month from May till November. Samples were disturbed in June and August after a period of no new seedlings by drying out for one week and intermixing. Afterwards samples were watered again to enable as many seeds as possible to germinate.

2.3 Vegetation sampling
The recent above-ground vegetation was recorded in 2009 from May till July in Germany and from July till August in Sweden. At each SRC site the same two plots of 100 m² (10 x 10 m) as for the soil seed bank analyses were sampled. Each 100 m² plot was divided into nine sample sub-plots which were pooled for evaluating the vegetation data. A species list of the vascular plants with percentage covers was created on a scale subdivided into 5 % intervals based on the scale of Londo (1975) for the ground vegetation layer. Below 5 % cover the intervals were 1 % and under 1 % it was differentiated between two to five individuals (0.2) and unique (0.01) referring to the scale of Braun-Blanquet (1928). The nomenclature follows Rothmaler et al. (2002).

2.4 Data analysis
For each plot the density of germinating seedling per m² (from now on named seed density) was calculated by eq. 1:

\[ S = \frac{1}{4.5 \cdot A_c} \cdot n_s \]  

Where \( S \) = seed density (seeds/m²), \( A_c = \) circle area of soil cores: \( A_c = \pi r^2 \) with \( r = 0.04 \) m (\( A_c \) was multiplied by 4.5 as nine soil cores were taken but samples were halved after mixing, see chapter Materials and Methods, section Seed bank sampling) and \( n_s = \) number of germinating seedlings of the sampled plot.

The mean values of species proportions in regard to strategy types, proportions of species habitat preference types and seed longevity were calculated. The plant strategy type classification was done according to Hodgson et al. (1988) with the differentiation: c: competitors, r: ruderals, s: stress tolerators and the intermediate strategy types cr, cs, sr and csr. Species habitat preferences were based on coarse habitat preferences according to Ellenberg et al. (2001), cf. Dölle & Schmidt (2009): arable field (a), grassland (g), ruderal site (r) and woodland (w) species. Some species are assigned to more than one group concerning strategy type classification and habitat preferences. The proportions of these mixed categories were split into the number of their groups. Species seed longevity was determined according the classification scheme by Thompson et al. (1997) who defined three main types of seed longevity: transient (seeds persisting in the soil for less than one year), short-term persistent (seeds persisting 1 to 5 years) and long-term persistent (seeds persisting at least 5 years).

Before mean values of species proportions of strategy types, habitat preferences or seed longevity were compared, residuals were tested for normal distribution with the Shapiro-Wilk test. In case of normal distributed residuals and homogeneous variances (tested by Levene’s test of homogeneity of variance) differences between groups were tested by one-way ANOVA and subsequent multiple comparisons using Tukey’s HSD post-hoc test for unbalanced data considering type I errors. The significance level for all tests was \( p < 0.05 \).

3 Results
3.1 Species of the recent vegetation and their abundances
Recording the recent vegetation resulted in a total of 140 vascular plant species. 79 species were recorded on the Swedish sites and 98 on the German ones. Mean species number per plot (100 m²) was higher in Sweden (29.5, range: 20 to 35) than in Germany (24, range: 13 to 37).

The most frequent species on the German sites was *Elymus repens* (couch grass), found on all sites. *Holcus lanatus* (Yorkshire fog) occurred in 83 % of the plots. *Elymus tetragonum* (square-stalked willowherb) was found in 75 %, *Taraxacum officinale* (common dandelion) in 67 % of the plots. In Sweden, *Taraxacum officinale* occurred in all plots. *Betula pendula* (silver birch), *Dactylis glomerata* (orchard grass) and *Geum urbanum* (wood avens) were found in 88 % of the Swedish plots.

3.2 Species of the soil seed banks and their abundances
In total, 2,077 seeds germinated and were assigned to 43 vascular plant species. 18 species were found in the Swedish SRC plantations and 34 species in the German SRC plantations. The species numbers per plot ranged from 4 to 14 at the German sites and from 2 to 5 at the Swedish sites. Calculated seed density per m² ranged from 354 to 20,336 at the German plots and from 221 to 4,112 at the Swedish plots.

Only few species dominated the soil seed banks: At the German sites, the most frequent germinating species with an occurrence in 55 % of the plots was *Chenopodium album* (goosefoot). *Juncus bufonius* (toad rush) was detected in 40 %, *Trifolium repens* (white clover) in 30 % of the study plots. Most frequent were the seedlings of *Juncus bufonius* which accounted for 28 % of the germinated seeds and seedlings of *Poa pratensis* (common meadow-grass, 13 % of the germinating seeds). Most frequent species at the Swedish sites were *Polygonum aviculare* (common knotgrass), *Brassica elongata* (elengated mustard) and *Convolvulus arvensis* (plot...
bindweed), occurring in 62.5, 50, and 37.5 % of the plots, respectively. The seedlings of Chenopodium polyspermum (many-seeded goosefoot) accounted for 34 % of the germinating seeds, seedlings of Ranunculus repens (creeping buttercup) for 23 %.

3.3 Common species of recent vegetation and the soil seed bank
Out of the 43 soil seed bank species, 21 also occurred in the recent vegetation of the corresponding plot, with Convolvulus arvensis, Holcus lanatus, Trifolium repens (each in 25 % of the plots) and Epilobium tetragonum (20 %) being most frequent.

Per study plot, the cumulative species number of the soil seed bank and the recent vegetation was set to 100 %. The proportion of common species ranged between 0 and 21.7 % and was on average 8.4 % (± 6.7 % SD).

3.4 Functional species composition
The significantly highest strategy type proportions in the recent vegetation of the SRC plantations had the competitors. In the soil seed banks, proportions of ruderals were highest, but their proportion differed not significantly from that of the competitors (Figure 2).

Species with long-term persistent seeds had the significantly highest proportions of the recent vegetation and the soil seed banks (Figure 3). No significant differences in species proportion of long-term persistent seeds were found. Short-term persistent seed species proportions did not differ. Species with transient seeds were only detected in the recent vegetation and differed not between German and Swedish plantations.

In total, recent vegetation was dominated by grassland species (mean: 36 %). Ruderal species proportion was on average 24 %. Woodland and arable field species proportions were significantly lower (13 % or 8 %, respectively). However, in the soil seed bank, ruderal species had the highest proportion (mean: 48 %). 21 % were arable field species, and 18 % grassland species. Woodland species (0.4 %) were almost absent from the soil seed bank.

4 Discussion

4.1 Low similarity of soil seed banks and recent vegetation
Our results show a low similarity of the species composition of the soil seed bank in 10 to 20 cm depth and the recent SRC vegetation. On average, the recent vegetation and the soil seed bank had 8.4 % (± 6.7 % SD) of their cumulative species number in common. Differences in seed banks between SRC sites (e.g. due to different site history) therefore seem not to contribute much to floristic diversity in SRC plantations, and the actual conditions in the plantations (e.g. plantation age, irradiance available for ground vegetation, soil nutrient contents; Baum et al. (2012a)) appear to be more important for phytodiversity than seed bank diversity. Low similarities of the soil seed bank and the recent vegetation were also reported in studies on several land uses other than SRC (cf. Thompson & Grime, 1979: vegetation types dominated by...
woody species, derelict herbaceous, wetland and disturbed vegetation; Fischer, 1987: forest and grassland communities; Bekker et al., 2000: hayfield; Luzuriaga et al., 2005: perennial grassland after ploughing).

Our data are not suitable for time series analyses, but other authors found the variables time, disturbance and light to be important factors influencing ground vegetation: Dölle & Schmidt (2009) found a decreasing correspondence of soil seed bank and recent vegetation for increasing successional stage as well as for decreasing disturbance intensity of former arable fields. Hoffmann (2005) found that different poplar clones providing different light conditions for the ground vegetation influenced species numbers as well as individual numbers of the soil seed banks: conditions of soil seed bank renewal were better under the more light-transmissive Max clones (no differentiation was made between different Max clones) than under Hybrid 275, where less species and individuals germinated in both surveyed soil depths (0 to 5 cm and 5 to 20 cm). As the SRC trees re-grow denser after each harvest (Tubby & Armstrong, 2002), the amount of light reaching the ground decreases and thus germination conditions in terms of light and soil temperature might deteriorate. Further, referring on land use intensity, Waldhardt et al. (2001) presume an exponential depletion of the seed bank of arable land species and their abundance starting around ten years after last cultivation and a nearly exhausted seed bank of arable land species after twenty years.

4.2 Large differences in functional composition of soil seed banks and recent vegetation

The strategy type proportions are indicators for the different disturbance regimes of the past, when the SRC fields were arable land or grassland, and today: while species of the soil seed banks were predominantly ruderals (r strategists) and competitors (c strategists), the recent SRC vegetation was dominated only by competitors (c). Ruderals are typical for habitats with low stress and high disturbance. In this context, stress includes conditions that restrict biomass production like shortage of water, mineral nutrients, light, or suboptimal temperatures. Disturbance refers to destruction of plant biomass by for example man, herbivores, or wind damage (Grime, 1977). The high proportion of ruderals in the soil seed banks may result from cultivar treatments like ploughing, mowing and harvesting at sufficient conditions regarding e.g. water and nutrient supply. Further, ruderals are adapted to highly disturbed habitats in terms of their rapid growth, high seed production and long-term persistent seed banks (Thompson et al., 1997). Competitors are typical for low stress and low disturbance conditions (Grime, 1977). Our study sites were characterized by still high nutrient availability but lower disturbance in comparison to the former land use. These conditions might have favoured competitors.

In yearly ploughed fields as well as in 23 and 36 years old successions on former arable lands, Dölle & Schmidt (2009) found that the proportions of ruderals and competitors were inversely related with more ruderals and less competitors in the soil seed bank than in the recent vegetation. This result goes in line with our findings for the Swedish SRC plantations that showed that the recent vegetation had a higher proportion of competitors but a lower proportion of ruderals than the soil seed bank. In the German SRC plantations, the proportion of ruderals was lower in the recent vegetation than in the soil seed bank, too, but the proportion of competitors did not differ significantly. The strategy type proportions of the German and Swedish SRCs did not differ significantly.

The high habitat-specific diversity in the recent vegetation (on average 36 % grassland, 24 % ruderal, 13 % woodland and 8 % arable field species) shows the great heterogeneity of SRC plantations, suitable for species with diverging ecological demands (Baum et al., 2012b). The habitat-specific species proportions of recent vegetation and soil seed bank were reverse: In the soil seed bank, the proportions of arable field species were 2.6 times higher and the proportions of ruderal species were twice as high as in the recent vegetation. However, proportions of woodland and grassland species were higher in the recent vegetation than in the soil seed bank. This discrepancy shows the difference in lighting conditions between the former land uses without tree cover (arable field, grassland) and the SRC plantations, whereas light conditions were suitable for light-demanding arable field and ruderal species in the former land uses (arable fields, grasslands) and vice versa, conditions were more suitable for woodland species in SRC plantations. Seeds of woodland species are often transient (Thompson et al., 1997) what might explain that they were almost absent from the soil seed banks.

The recent vegetation and the soil seed banks of the SRC plantations were dominated by species with long-term persistent seeds. Especially for the soil seed banks, this can be explained by the finding that the majority of arable weeds have persistent seed banks (Thompson et al., 1998). Specifically in the soil seed banks short-term persistent seeds were found in much lower numbers than long-term persistent seeds. Transient seeds were absent from the soil seed banks. This can be explained by seed longevity that is 1 to 5 years for short-term persistent seeds and less than one year for transient seeds (Thompson et al., 1997). Further, seed characteristics play a role: persistent seeds are small, light and rounded, whereas transient seeds are larger and heavier with a flattened or elongated shape (Thompson et al., 1993; Bakker et al., 1996). Thus, unlike to transient seeds, persistent seeds penetrate more easily into deeper soil layers in general (Poschlod, 1991; Bakker et al., 1996). Transient or short-term persistent seeds might have reached deeper soil layers during the former usage as arable land by tillage but could have lost germination ability because tillage damages short-lived seeds more than persistent ones (Albrecht & Auerswald, 2009). But the main reason for the absence (transient) or low number (short-term persistent) in our study can be explained by their seed longevity with a maximum of five years.
4.3 The possible relevancy of soil seed banks for vegetation composition in the light of succession

In general, the planted crops remain viable for 15 to 30 years (Aytole et al., 2008). After this period, replanting of the crop or reversion of the SRC plantation into arable land is conceivable. In both cases the soil gets mixed due to root removal and seeds from the lower layer can reach the soil surface and are likely to influence vegetation composition. Especially the species grown from persistent seeds in the soil will have the opportunity to characterize the upcoming vegetation. These are predominantly species of frequently disturbed habitats, while plant communities of relatively undisturbed habitats such as woodland and pasture have generally lower seed persistence (cf. Poschlod, 1991; Thompson et al., 1998; Albrecht & Auerswald, 2009). In perennial grasslands Luzuriaga et al. (2005) found low plant densities and slow colonisation rates in sterilised plots indicating the crucial role of seeds and propagules stored in the soil in colonisation of disturbed habitats and only a minor contribution of seed rain. The example from perennial grasslands indicates that the soil seed bank can be of great importance for potential future vegetation (Bakker et al., 1996; Waldhardt et al., 2001), but vegetation structure and development depend also on the new land use and secondary succession processes. In general, initial vegetation is highly determined by early successional species characterized by high growth rate but short life span and high amount of small seeds dispersed over large distances and with long seed viability, while late succession species have low growth rates but long life spans and fewer larger seeds dispersed over shorter distances and with short viability (Huston & Smith, 1987). These differences in seed and plant characteristics between early and late successional species result in vegetation shift over time (i.e. succession) and in initially great but later decreasing importance of soil seed bank for the apparent vegetation. Our results show a poor coherence of seed bank and recent vegetation, probably indicating that the vegetation analyses were carried out at a later successional stage. Thus, we conclude that the site history might have an initial influence on phytodiversity in SRC plantations, but successional processes have taken place between the point in time of SRC establishment and our investigations, suggesting that recent vegetation composition is mainly due to the species pool of the adjacent vegetation and site conditions like below-canopy irradiance and site nutrition.

References


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