



Research paper

Tree genetic diversity increases arthropod diversity in willow short rotation coppice



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ABSTRACT

Demand for bioenergy has rapidly developed in recent decades, resulting in expansion of bioenergy cropping systems such as willow short rotation coppice (SRC). Increasing the number of willow genotypes in SRC can potentially enhance species diversity in the associated arthropod community, which may promote ecosystem functions within plantations. However, the ecology of SRCs and their effects on biodiversity have only rarely been investigated. Therefore, to study the role of plant genetic diversity (GD) in SRC, we established a replicated common garden experiment comprising genetic monocultures and mixtures of two, three and four different *Salix* genotypes used in commercial SRC. We sampled arthropods and examined the effect of GD across trophic groups, to test if the use of genotype mixtures increases arthropod richness and abundance. Species richness of total arthropods and of herbivores increased significantly with increasing GD, regardless whether data were pooled per plot or analysed on tree level. However, effects varied among willow genotypes as positive correlations between GD and different trophic groups were genotype-specific. We show that establishing and managing commercial willow SRCs with a mixture of varying genotypes can help to increase arthropod diversity within a bioenergy system that is a promising renewable energy source.

1. Introduction

Short rotation coppice (SRC) is a promising bioenergy system: willows (*Salix* sp.) or other fast-growing tree species are cultivated in plantations and above-ground biomass is harvested in typical rotation periods of 3–5 years [1]. Such perennial bioenergy crops can, compared to annual bioenergy crops and conventional agriculture, provide environmental benefits, such as soil carbon storage and fertility [1,2]. Given their relatively low levels of disturbance and agrochemical input, combined with high plant cover and structural complexity, SRC systems can improve habitat quality and support associated biodiversity [3], especially when established in intensive agricultural landscapes [4,5]. However, bioenergy plantations are generally established as monocultures [6,7], which may limit their potential to support biodiversity compared to more diverse plant communities.

Arthropods are key organisms in terrestrial ecosystems that provide crucial ecosystem functions and occupy a central position in food webs [8,9]. Traditionally, most arthropods were viewed as pests in cropping

systems. However, it is now established that moderate herbivore densities may improve nutrient cycling and primary productivity [10,11] and that predators can regulate food webs by top-down control [12,13]. A diverse arthropod community can thus be beneficial for a plantation and the surrounding landscape [14].

Ecological theory predicts [12,15] and field data show [13] that habitats with more plant species support a higher diversity of associated arthropods. Although those effects can be particularly large in plant communities consisting of diverse evolutionary lineages [16,17], there is evidence that intraspecific genetic diversity (GD) can, compared to species diversity, have similar [18] or even stronger positive effects [19] on arthropod diversity. In willows, leaf traits can vary among genotypes [20], increasing the heterogeneity of resources for arthropods in genotype mixtures. Management recommendations for willow SRC recommend planting multiple genotypes to preclude pest and disease outbreaks such as rust infestation [21–23], but as growth habits also vary among genotypes, many commercial SRCs are planted with single genotypes to ease monitoring and harvesting [7].

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Nevertheless, beyond biological control, synergies of increased GD on arthropod diversity are likely, but have, to the best of our knowledge, not been studied in SRC systems.

Several mutually non-exclusive bottom-up mechanisms may explain relationships between plant (including GD) and arthropod diversity [24]: at the plant community level, higher arthropod diversity could, for example, result indirectly from enhanced productivity in more diverse plant communities causing higher arthropod abundances ('more individuals hypothesis' [25,26]) and directly from an increased heterogeneity of the available resources ('resource specialisation hypothesis' [15,27]). Increased resource heterogeneity can also be related to arthropod diversity on individual plants, for example when a diverse neighbourhood facilitates efficient resource use by and spill over of arthropods among plants ('associational susceptibility' [28,29]). For herbivores this type of effect may vary with host specialisation [30], but can also differ among trophic groups [19,31,32]. Since herbivores depend directly on plants for food, they are theoretically more strongly related to plant GD than predators, which can be more indirectly related to GD, e.g. via GD-induced changes in the herbivore community affecting trophic interactions [33,34].

To test the influence of GD on associated arthropods in willow SRC, we established a replicated common garden experiment manipulating GD. As traits vary among different willow genotypes [20], we assumed *a priori* that increased GD enhances local habitat heterogeneity. Thus, we hypothesised that (1) arthropod abundance and species richness are positively related to GD through bottom-up effects (*sensu* [27]). Furthermore, we expected (2) stronger effects on herbivores compared to predators.

2. Material and methods

2.1. Study site

ECOLINK-Salix is a willow SRC experiment that was established in March 2014 and is integrated into TreeDivNet, a global network of tree diversity experiments [35]. Designed to investigate the effects of GD on ecosystem functioning, it is replicated in Freiburg (southwest Germany), Rostock (northeast Germany), and Uppsala (Sweden). The current study was conducted at the 'Freiburg Experimental Ecology' field research area (abbreviated FREE; 48°01'N, 7°49'E, elevation: 240 m). The climate is oceanic (Cfb following Köppen climate classification), with a mean annual temperature of 11.8 °C and 858 mm of annual precipitation (averages from 1990 to 2015). The sandy-loamy soil is a rather shallow (~40 cm) Cambisol with high gravel content and is partly anthropogenic disturbed. Until the late 20th century the land was used as a military area, after which grassland developed that was periodically grazed by sheep. More details on the research area can be found in Wein et al. [36].

The common garden experiment uses a randomized block design with three replicates of 15 plots of 9.6 × 9.6 m. A diversity gradient of 1, 2, 3 and 4 genotypes was established adopting a replacement-series-design, i.e. keeping the number of tree individuals per plot constant (Fig. 1). The four genotypes 'Björn' (hybrid *S. schwerinii* × *S. viminalis*), 'Jorr' (*S. viminalis*), 'Loden' (*S. dasyclados*) and 'Tora' (hybrid *S. schwerinii* × *S. viminalis*) vary in relatedness, were acquired from the Svalöf-Weibull breeding programme [37] (see Table 1 for details and Fig. A1 in Supplementary Material for illustrations) and are commonly used in commercial SRC. In each plot, trees were planted in 12 rows of 12 individuals each, with an offset every second row, resulting in a hexagonal planting pattern with equal distances of 0.8 m between individuals (Fig. 1). In the two genotype plots, single genotypes alternate regularly; in the three and four genotype plots the arrangement was randomized, with the constraint that individuals of the same genotype should not be directly adjacent to each other within rows (see Fig. 1). During the time of sampling in the second growing season, the willows were well established and most individuals had reached heights above 2 m.

2.2. Sampling

Arthropods were sampled once per tree during daytime from 27 May to 16 June 2015 when local ambient temperature was above 20 °C, the vegetation was dry, and wind and resulting tree sway was minimal. During periods of high temperatures between 12:00 and 15:00 sampling was avoided. Trees were shaken manually but vigorously and all specimens falling on a round beating tray (72 cm diameter) were collected using aspirators and soft insect forceps. To minimize effects from neighbouring plots and to include a sufficient number of individuals from all genotypes within each plot, sampling was conducted in a central core area that varied in size depending on plot GD. In plots with one and two genotypes the core area was the central 4 × 4 raster of trees, in plots with three and four genotypes the central 6 × 6 and 8 × 8 trees were respectively sampled. Occasionally, trees were missing from the central core area or were too small (height < 0.5 m). In these cases, we sampled individuals of the same genotype adjacent to the core area. One plot with two genotypes was excluded from the sampling because an incorrect genotype was planted during establishment (Fig. 1). Altogether, 1088 trees in 44 plots were sampled once.

Arthropods were preserved in 70% ethanol and identified to the highest taxonomic resolution possible (species or morphospecies, hereafter referred to as species for simplicity; see Supplementary Material Table A1 for the full list and Tables A2 and A3 for an overview) using published identification keys to the central European fauna (e.g. Ref. [38]). Species were assigned to herbivores or predators based on natural history of the higher taxonomic classification (e.g. order or family). For example, spiders and parasitoid wasps were classified as predators while caterpillars, cicadas and aphids were classified as herbivores. Species (mostly Diptera) that could not be assigned to either group with certainty were not further classified (species: 17.5%; individuals: 6.5%).

2.3. Statistical analyses

Data were analysed using R 3.2.2 [39]. Given it is possible to analyse the data at the level of the single tree (i.e. tree level) or at the level of the plot (i.e. plot level) most analyses were performed at both levels. Sampling efficiency was evaluated for the full dataset (plot and tree level) and for genotype-specific subsets (individual level) using jackknife1 species richness estimators and sample-based species accumulation curves (1000 permutations) in the R-package 'vegan' [40].

Data were analysed for total arthropods, and for subsets of only herbivores and only predators to examine differences in the responses of trophic groups to GD. First, linear mixed-effect models in the R-package 'lme4' [41] were calculated to test for effects of willow GD on arthropod species richness at plot level (*sensu* 'resource specialisation hypothesis' [27]). As the number of sampled tree individuals differed with GD (see sampling 2.2), all richness data were rarefied ('rarefy' command in 'vegan') to rule out biases of unequal sampling. The 'rarefy' command randomly draws communities of a standardized size from an entity with equal abundances (see Ref. [18]). The size of the rarefied communities was defined as the lowest number of (pooled) arthropods found per plot and trophic group (all arthropods: 22; herbivores: 14; predators: 4). To test if GD relates to the share of predators among arthropods, the proportion of predators was analysed using the rarefied richness data of predators and herbivores (i.e. excluding unclassified arthropods). *P*-values for linear mixed-effect models were calculated with approximated degrees of freedom after Kenward and Rodger using the R-package 'pbkrtest' [42].

Second, generalized linear mixed-effect models (GLMMs) in 'lme4' were used to investigate effects of willow GD on arthropod species richness and abundance at tree level for the full data set and for genotype-specific subsets. In contrast to rarefied richness data that are numeric and normally-distributed, raw richness and abundance data are counts and thus Poisson-type models were used. Similarly to the

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