



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

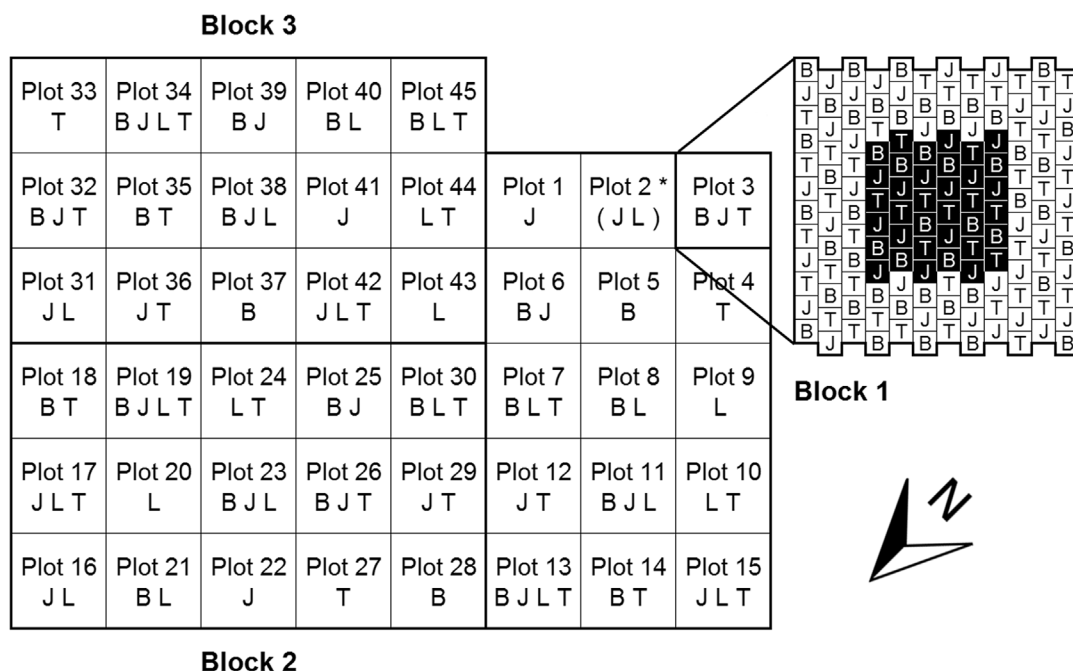


Fig. 1. Experimental setup of the ECOLINK-Salix field site in Freiburg (located at 48°01'N, 7°49'E). The 45 plots are arranged in 3 replicated blocks. Each plot has a size of 9.6 × 9.6 m and contains 12 × 12 Salix individuals. Capital letters (B: Björn/J: Jorr/L: Loden/T: Tora) indicate the mixture per plot. The enlarged section illustrates the planting pattern of a plot with three genotypes, including the sampled core area (black background). In plot 2 a planting error occurred. The originally intended mixture (J L) was mistakenly replaced by (B J).

Table 1

Details on genotypes used in ECOLINK-Salix. Given are the name of the genotype, the original *Salix* species and the Svalöf-Weibull cultivar/genotype number [40].

Genotype name	Species	Cultivar number
Björn	<i>S. schwerinii</i> E.L. Wolf × <i>S. viminalis</i> L.	SW 910006
Jorr	<i>S. viminalis</i> L.	SW 880013
Loden	<i>S. dasyclados</i> Wimm.	SW 890129
Tora	<i>S. schwerinii</i> E.L. Wolf × <i>S. viminalis</i> L.	SW 910007

plot-level analyses, the share of predators was tested. As shares of counts are proportional data, GLMMs with a binomial error distribution were fitted. Analyses of the share of predators excluded trees without arthropods and trees that hosted only unclassified arthropods (neither herbivores nor predators).

The hierarchical experimental design consisting of plots nested in blocks was accounted for in all model structures by treating block as a random effect (with plot nested in block for tree level models). Additionally, mixture identity was included into all tree-level models as a non-nested random effect to account for potential mixture-specific variances. As Poisson and binomial models have a tendency for overdispersion, an observation level random effect (OLRE) was added to all models (following Harrison [43]), whenever this approach eliminated overdispersion. Overdispersion mainly occurred in herbivore abundance data, likely due to high aphid abundances on single trees.

To investigate if species richness and abundance were related (following the ‘more individuals hypothesis’ [26]), we calculated GLMMs with the same random effect structure for the respective correlations between species richness and abundance within trophic groups and genotypes. Effects of GD on predators may be indirect [18], and predator richness and abundance could be affected by GD induced changes in herbivore richness and abundance rather than by GD itself. Therefore, the relationships between herbivore richness and predator richness (and the respective abundances) were also tested using the same model and random effect structures as described above. Separate GLMMs on tree level with the fixed effect genotype identity were used to test if arthropod richness and abundance differed among genotypes.

All *p*-values for comparisons between multiple genotypes were Bonferroni-corrected (R-package ‘multcomp’ [44]).

The replacement-series-design used here and in most other tree diversity experiments results in uneven numbers of sample trees among diversity levels (see also the rarefaction approach used for plot-level analyses). To test if this is influencing the relationship between GD and arthropod richness and abundance on tree level, GLMMs were recalculated with reduced data in which all GD levels were standardized to the same number of trees (termed ‘subsample models’). For each diversity level, the smallest number of trees per diversity level was drawn randomly without replacement. For each model, we generated 250 random subsamples, calculated single models for each subsample and extracted mean model parameters.

To analyse variation in arthropod communities among willow genotypes, non-metric multidimensional scaling (NMDS) in ‘vegan’ was used. Ordinations were two-dimensional and calculated with Morisita-Horn dissimilarities of square-root transformed and Wisconsin-double standardized abundance data pooled for each genotype per plot. Rare arthropod species with less than five individuals were excluded. An analysis of dissimilarity (function ‘adonis’ in ‘vegan’) accounting for the hierarchical design by using block as ‘strata’ was performed (1000 permutations) to test for differences between arthropod communities among the different genotypes.

3. Results

3.1. General community patterns

Altogether, 4580 arthropods belonging to 257 different morphospecies from all major terrestrial arthropod orders were sampled (Tables A1 A2, A3). On 9% of trees ($n = 101$), no arthropods were found. Herbivores from the order Hemiptera (aphids: 1850 individuals, cicadas: 866 individuals) dominated numerically. The most abundant predators were spiders (254 individuals) and parasitic wasps (230 individuals). We collected 176 (68%) species with fewer than five individuals, of which 113 species were singletons. Total herbivore and predator species richness were identical (herbivores: 106 species, predators: 106 species) but total herbivore abundance was six times higher

Table 2

General arthropod data for all genotypes (Total) and separated per genotype. Given are total arthropod abundance, total arthropod species richness, estimated species richness (jackknife1 ± SE), the share of sampled species in the estimated species richness (% sampled) and the number of sampled trees. Data for herbivores (H) and predators (P) are given in parentheses.

Genotype	Abundance	Richness	Jackknife1 ± SE	% sampled	Sampled trees
Björn	1112 (H: 937, P: 128)	114 (H: 54, P: 43)	176 ± 9 (H: 78 ± 5, P: 72 ± 6)	64.9% (H: 69.3%, P: 60.0%)	273
Jorr	1114 (H: 900, P: 131)	126 (H: 51, P: 51)	194 ± 9 (H: 72 ± 5, P: 83 ± 6)	65.0% (H: 70.9%, P: 61.7%)	276
Loden	1156 (H: 915, P: 149)	152 (H: 69, P: 61)	229 ± 11 (H: 97 ± 6, P: 99 ± 7)	66.5% (H: 71.2%, P: 61.9%)	268
Tora	1198 (H: 921, P: 200)	128 (H: 60, P: 46)	184 ± 9 (H: 84 ± 5, P: 64 ± 5)	69.6% (H: 71.5%, P: 72.1%)	271
Total	4580 (H: 3673, P: 614)	257 (H: 106, P: 106)	373 ± 11 (H: 152 ± 7, P: 151 ± 7)	68.9% (H: 69.8%, P: 69.6%)	1088

than total predator abundance (Table 2). Species richness estimation indicated that irrespective of plot or tree-level analyses the sampling contained 69% of the expected species pool present on the willows at our study site (Table 2, Fig. A2 in Supplementary Material). Sampling efficiency for single genotypes and trophic groups was similar.

3.2. Effects of genetic diversity

At plot level, total arthropod species richness increased significantly with increasing GD (Fig. 2, $p = 0.04$, statistical details are given in Table 3), with a prediction of more 16% species in mixtures of four genotypes compared to monocultures. Similarly, an 18% increase of species richness with GD was predicted for herbivores ($p = 0.03$). Predator richness and the share of predators were unrelated to GD.

The positive relationship between GD and species richness of all arthropods and herbivores occurred not only at plot level but also at tree level (Fig. A3, statistical details in Table A4 in Supplementary Material). In plots with four genotypes and in plots with three genotypes (except for Björn), a tree was inhabited by more species when compared to mixtures of two genotypes and monocultures (Fig. 3). Predator richness was unrelated to GD but increased with herbivore richness ($p = 0.02$).

Although the strength of the relationships between GD and arthropod species richness or abundance on tree level varied among genotypes and trophic groups (Table A4), the sign of the relationships was almost always positive, and statistically significant for two of the four investigated genotypes. While herbivore richness (predicted increase from monocultures to four genotype mixtures: 62%, $p < 0.01$)

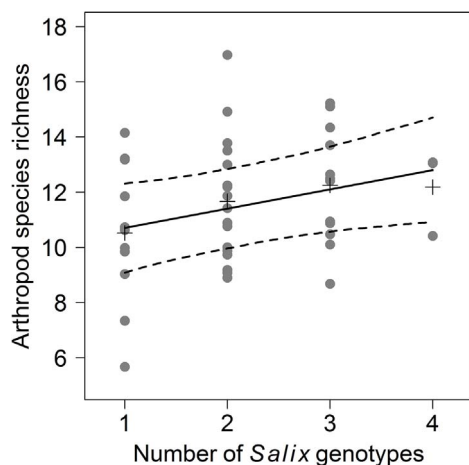


Fig. 2. Relationship between the number of *Salix* genotypes and total rarefied arthropod species richness per plot. Means are indicated with black crosses. Regression lines indicate the prediction (solid line) and the associated 95% CI (dashed lines, 1000 bootstraps) of the corresponding linear mixed model.

Table 3

Results of linear mixed-effect models testing effects of GD. Given are results of the models on richness of all arthropod species (Rich all), only the herbivores (Rich H), only the predators (Rich P) and the share of predators (Share P) per plot. For each model the estimate (± SE), F -value and the p -value of the F -statistic are given. Kenward-Roger approximated degrees of freedom (numerator: left, denominator: right) are reported as subscripts to the F -value. Significant ($p \leq 0.05$) models are indicated in bold. Please see Table A4 (Supplementary Material) for results of analyses on tree level.

Model	Estimate ± SE	F	p
Rich all	0.70 ± 0.33	4.43_(1,40)	0.04
Rich H	0.46 ± 0.20	5.37_(1,40)	0.03
Rich P	0.08 ± 0.06	1.99 _(1,40)	0.17
Share P	−0.01 ± 0.01	1.33 _(1,40)	0.26

and abundance (74%, $p = 0.02$) were positively related to GD on Tora, increases of predator richness (16%, $p = 0.01$) and abundance (20%, $p = 0.01$) were found on Loden (Fig. A4, statistical details in Table A4). For both genotypes (Tora, Loden), total arthropod richness increased significantly with GD (predicted increase: 39 and 44%; $p = 0.05$ and 0.01, respectively). Species richness and abundance for all arthropods and for trophic groups were among all genotypes and for all data tightly related ($p < 0.01$). The share of predators was significantly and positively correlated with GD for abundance data from Loden. Subsample models using a standardized number of trees had always qualitatively similar results, albeit with predominantly higher p -values due to the smaller sample sizes (Table A5 in Supplementary Material).

3.3. Effects of genotype identity

Arthropod abundance and species richness differed among genotypes (Table 2, Fig. A5). Tora was the genotype with the highest total arthropod and predator abundance, of which the latter was significantly higher per tree on Tora compared to either Björn ($p = 0.03$) or Jorr ($p = 0.05$) but not to Loden. Total arthropod species richness was highest on Loden, which was per tree significantly higher compared to Björn and Jorr (both $p < 0.01$).

Arthropod communities varied significantly among genotypes ($F_{(3,90)} = 3.87$, $p < 0.01$, analysis of dissimilarity) and genotype identity explained 11.4% of the variance in community composition. The NMDS-ordination (Fig. 4) shows that the community composition of Loden differed from the other genotypes. Additional analyses of dissimilarity restricted to Björn, Jorr and Tora revealed no significant differences, indicating that Loden had a different arthropod community compared to the other genotypes.

4. Discussion

4.1. Positive effects of willow GD on arthropod diversity

Our study shows that already in the second growing season, higher

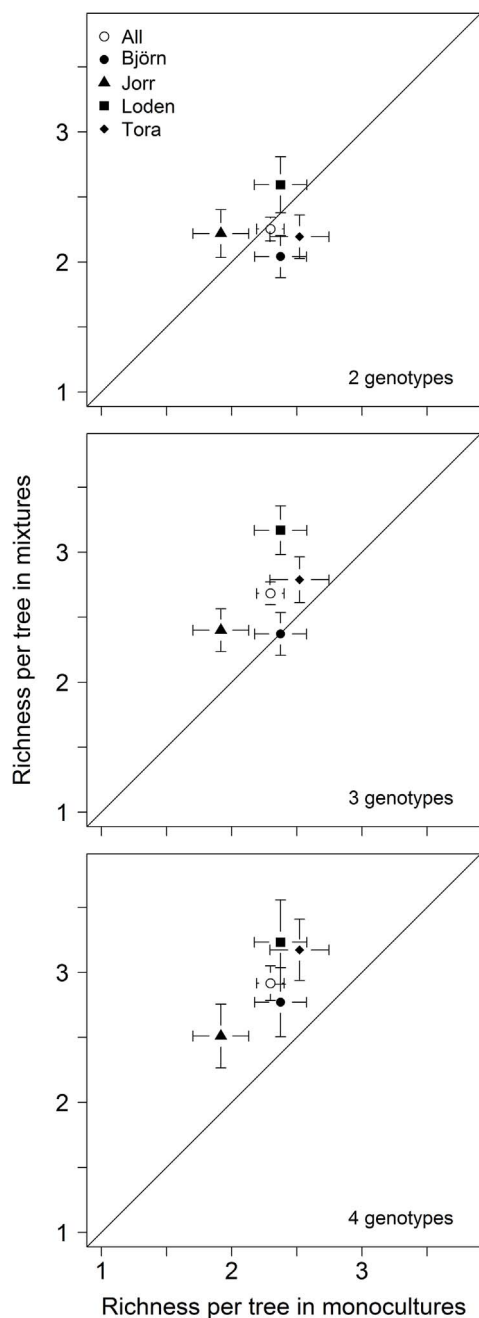


Fig. 3. Total arthropod richness in 2-, 3- and 4-genotype mixtures compared to monocultures. Values are means (\pm SE) arthropod richness per tree for each combination of genotype and diversity level. The diagonal lines represent the 1:1 relationship of arthropod richness in mixtures and monocultures. Values above this line indicate increased richness in mixtures.

GD in willow plantations can increase arthropod species richness. This was the case for both plot and at tree level analyses, providing evidence that genetically diverse SRCs can enhance the diversity of associated organisms within the plantation, as hypothesised (1). Such positive relationships between arthropod richness and GD are known from other experiments with herbaceous (e.g. Refs. [18,19,24]) or woody plants [32], and we extend these findings to a commercial cropping system.

The relationship between GD and associated arthropods was likely induced by a combination of direct and indirect processes. Following ecological theory, higher intraspecific GD will directly increase the variety of microhabitats ('resource specialisation hypothesis' [27]), allowing more species to coexist locally, in our case at plot level. More indirectly, higher GD could also increase abundances due to enhanced

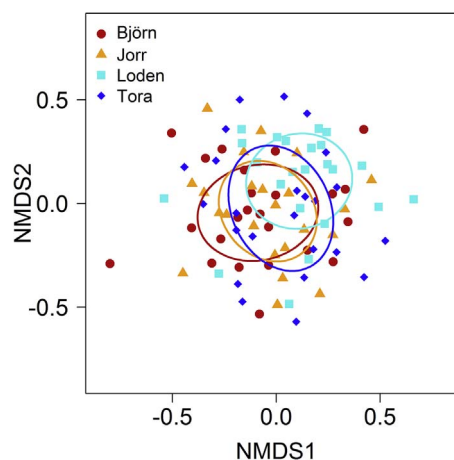


Fig. 4. NMDS-ordination plot (two-dimensional stress = 0.31) based on the Morisita-horn index of abundance data pooled per plot and genotype. Genotype identity is indicated by different symbols and colours. Ellipses indicate 95% CI of axes scores per genotype. Increasing the number of dimensions in the ordination reduces stress, but does not affect the configuration of the first two NMDS axes (function 'protest' in 'vegan', 1000 permutations). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

productivity (e.g. Refs. [18,24]), which increases the probability for having more species per tree individual in mixtures ('more individuals hypothesis' [26]). While we could not directly test for the influence of tree biomass because these data become only available on harvest (after a typical rotation for SRC), there is evidence for an abundance-driven relationship and the highly significant correlations of species richness and abundance support a 'more individuals' mechanism [18,24]. Nevertheless, increased species richness was not only abundance driven, as the influences of GD on total arthropod and herbivore species richness were at tree level much stronger than on the corresponding abundances and persisted at plot level even once for variation in abundance was accounted through rarefaction.

In contrast to the relationship for herbivores, the correlations between predator species richness and GD were not significant. However, at tree level predator and herbivore species richness were positively related, suggesting an indirect bottom-up effect across trophic groups [18,31], which is expected as predators depend on their mostly herbivorous prey that is itself directly influenced by plant GD [31]. Although the share of predators on the willows was largely unrelated to plant GD, the differing results for herbivore and predator richness indicate varying GD effects among trophic groups and support hypothesis (2).

Albeit many species inhabiting SRC are naturally associated with scrubland or early successional woodland and likely common (compare [45]), our results show that SRC with four willow genotypes can increase associated arthropod diversity relative to monocultures, illustrating that genetically diverse SRC have the potential to improve the habitat quality for many arthropods. Usually diversity begets diversity [34] and increases trophic interactions [46]. Thus, higher associated diversity in genetically diverse SRC can benefit the plantation, for example through accelerated nutrient turnover (compare [10,11]), and increased biodiversity in SRC may support ecosystem stability due to food-web complexity ('diversity-stability-hypothesis' [47,48]). In future work the net effect of the greater herbivore diversity on productivity will be clarified by examining the GD-productivity relationship using biomass harvest data and by synthesizing data from the different ECOLINK-Salix sites.

Management recommendations for commercial SRCs already advise the use of genotype mixtures to reduce the risk of disease and pest outbreaks [21,22] and to increase biomass yield [23,49]. Although establishing genotype mixtures may be more costly compared to planting single genotypes and harvesting might be slowed if growth characteristics differ among genotypes, the economic advantages from

genotype mixtures outweigh the challenges [6,23,50]. As we show, in addition to economic benefits, genotype mixtures may also increase the ecological value of SRC as a habitat for associated arthropods and possibly other organisms such as herbaceous plants or small birds. Expanding our study to those organisms is a promising subject for further research. In addition, monitoring should be continued into the future, because SRCs are established as perennial cropping systems and we expect the biodiversity-ecosystem-functioning processes to intensify over time [51].

4.2. Genotype-specific effects of willow GD on different trophic groups

At the genotype level, relationships between the richness and abundance of separated trophic groups were restricted to two of four genotypes, suggesting that specific genotype mixtures in an SRC can be important for achieving positive relationships between GD and arthropod diversity. Similarly, genotype composition is also important for productivity. For some willow genotypes biomass production in mixtures is lower while it is considerably higher for others [49,52].

The increase in herbivore richness on Tora was probably abundance-driven because GD also correlated with herbivore abundance. In more diverse mixtures, herbivores could benefit by feeding on and spilling over among several genotypes (*sensu* [28]), thus increasing energy uptake and performance. Many herbivores have a relatively low mobility and, assuming optimal foraging, such spill over is most likely among directly neighbouring plant individuals. Thus, differences in leaf traits within a plot might explain the positive relationship between GD and herbivores for all genotypes and on Tora [53]. Genotype-specific traits can, for example, influence the relative palatability of an individual of a genotype compared to its direct neighbours and thus explain if positive (associational susceptibility) or negative (associational resistance) relationships between herbivores and GD occur on a genotype [29,30,54]. Unfortunately, we lack site-specific trait data, but genotype-specific differences in defence compounds might possibly be responsible for the higher susceptibility of Tora in mixtures [20,55]. However, herbivores did not prefer Tora in general. Herbivore abundance and richness were similar among genotypes as was arthropod community composition among Björn, Jorr and Tora, which might be a result of the closer relatedness of these genotypes ([56,57], but see Ref. [58]).

From an economic perspective, recommending genotype mixtures to increase herbivore diversity might sound counterintuitive. However, except during outbreaks of single pest species, moderate herbivory facilitated by associational susceptibility can accelerate nutrient turnover and increase primary productivity [10,11], which may increase a SRC's harvestable biomass. In light of the search for sustainable production systems, which do not deplete but sustain natural resources, such biotic interactions that support ecosystem processes, productivity and stability should therefore be valued [1].

As for herbivores, a positive correlation between GD and predator richness and abundance was restricted to a single genotype (Loden). There was, however, no relationship between herbivores and predators on the same genotypes. Contradicting our expectation (2), this indicates a direct and independent effect of GD on predators, which is known from other experiments with trees [32] and herbaceous plants [59,60]. Opposed to herbivores, chemical plant traits are less likely to cause GD effects on predators. Many predators prefer structurally complex habitats [61–63] and might therefore favour Loden, which has different growth characteristics compared to the other genotypes and could enhance within-plot structural heterogeneity in mixtures. This variance in morphology could also have caused the different arthropod community composition and the high total species richness and abundance on this genotype. Using structurally dissimilar genotypes in a willow SRC may increase structural heterogeneity within the plantation and provide microhabitats for predators and other arthropods. Consequently, the use of particular genotypes could, in line with the ‘enemies hypothesis’

[12,61], affect top-down processes and contribute to biological pest control, and simultaneously increase biomass production [64].

5. Conclusions

Considering the important role of arthropods in ecosystems, high arthropod diversity could increase ecosystem functionality in an SRC and the surrounding landscape. This makes genetically diverse SRC plantations a promising tool for biomass production that moderates the often adverse effects monoculture energy crops have on arthropod diversity. As SRC with many genotypes have not only a higher diversity of associated fauna, but at the same time also high yield and resistance against pests and diseases, it is recommended to use multiple genotypes differing in traits when establishing new willow SRC plantations. By doing so, comparatively high biodiversity could be maintained in commercially managed ecosystems.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.biombioe.2017.12.001>.

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