Research paper

Productivity, stand dynamics and the selection effect in a mixed willow clone short rotation coppice plantation

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A B S T R A C T

Short Rotation Coppice (SRC) is a promising method of biomass production for energy purposes, but there have been concerns about the low diversity of these stands, including the risk for pest outbreaks. Mixing different clones has been advised as a way to tackle this problem and improve yields through positive diversity effects. Recent research into the relationship between biodiversity and ecosystem functioning supports these recommendations, but also raises worries about mechanisms that may confound results, such as a selection effect due to dominant clones outcompeting weaker ones. However, the few available studies on diversity effects in SRC plantations did not allow the disentangling of the mechanisms at play.

We used data from an experimental SRC site, which incorporated three Swedish Salix clones in a row-based mixing design. Productivity was expected to be greater in mixtures and we attempted to elucidate whether this was due to a complementarity or a selection effect. We found that complementarity effects were generally larger than selection effects, yet the total diversity effect on yield was not significant. Leaf surface temperature measurements indicated that drought stress was unlikely to be the factor underlying this distorted diversity productivity relationship. We also found that a less-productive clone (Gudrun) had a different stem biomass distribution when in monoculture, which may have repercussions for the quality of the harvested product and points at a so far less recognized potential benefit of mixing.

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1. Introduction

The use of woody biomass for energy production has been a mainstay throughout the history of human civilization and only in recent, industrial times its importance has plummeted in favor of fossil fuels [1,2]. Questions concerning the continuity of the supply of these fossil carbon stocks [3,4] and the impact on the environment of their liberation has led to renewed interest in alternative sources of energy [5], including woody biomass [6]. The recent interest in developed countries for dedicated production systems of woody biomass for energy can be linked to these concerns [7].

Short Rotation Coppice (SRC) is a silvicultural system developed for efficient production of woody biomass. Fast-growing woody species are planted in high density, harvested in short cycles of 2–5 years and replaced when productivity starts to decrease. SRC incorporates some of the agricultural developments of the 20th century, such as science-based breeding of varieties, mechanized field management and the (limited) use of agro-chemicals [7]. Management of SRC sites is extensive when compared to other cultivation systems for energy production, which often operate in cycles of one year or less. Fertilization is less important as relatively few nutrients are removed with the biomass, which is harvested after leaves are shed [8]. The only important management
intervention during growth is weeding in the first year after planting, sometimes using herbicides [9,10]. In addition to the relatively low intensity of management, SRC systems possess greater structural diversity than annual crops, resulting in a generally greater associated (functional) biodiversity [11–13]. SRC can also provide other ecosystem services next to biomass production, such as phytoremediation [11].

Despite the successful trials of SRC that have been undertaken across the globe [12,14,15], some issues still threaten its ecological and economical sustainability. One of these is the low diversity of these cultures, in particular because often genetically identical high-yielding clones are used [7]. A lack of diversity results in increased pest pressure in agricultural systems [16,17], which are used [7]. A lack of diversity results in increased pest pressure in agricultural systems [16,17], which typically operate at a temporal scale of less than one year. SRC systems have longer harvest cycles and individual plants are intended to last up to seven such cycles [9], which increases the risk and associated costs of devastating disturbances such as pests or droughts. It is also not as easy or desirable — ecologically or financially — to treat woody (energy) crops with pesticides.

Recent research suggests that introducing mixtures of genetically distinct clones in SRC could be an effective measure to address these risks. The past two decades, evidence has been found in multiple ecosystems of a positive relationship between (genetic) diversity and ecosystem functions such as productivity [18–20]. This field of research is now known as Biodiversity and Ecosystem Functioning (BEF). Several mechanisms were proposed to explain these results, including facilitation, complementarity and the selection effect. Facilitation is the interaction between species where at least one species benefits and neither of them is harmed by the presence of the other [21]. Complementarity allows more diverse systems to make more efficient use of resources, as long as the niches of some of their species differ sufficiently [22]. Finally, the selection effect may occur because the probability of dominant species being present increases as the number of species present increases [23–26].

Only few studies have been undertaken on clonal mixtures in SRC plantations, mainly in the UK [27] and in Northern Ireland [28,29]. These studies found that clonal mixtures of willow (Salix sp.) tended to be more productive [29] and less susceptible to pests [27] than monoculture stands of the clones the mixtures were composed of. These findings might be explained by the mechanisms described in BEF literature [22]. Facilitation could mitigate the impact of pests through associational resistance: differences in susceptibility to pests among clones reduce the overall biotic pressure in the plantation, for instance because it takes longer for pests to spread [30]. Complementarity, e.g. through differences in shade tolerance, could increase the system’s efficiency of resource use [31]. In the study by McCracken. et al. [29], nested mixtures of five, ten, fifteen and twenty clones were compared with the monocultures of their constituent clones. Relatively poor yields of three out of the five clones that were present in all these mixtures could explain the positive diversity effect they found when comparing the five-way mixture with the three others as a selection effect. Comparisons with monocultures cannot be considered accurate, if some of the clones are virtually eliminated as the mixed treatments age and the high-yielding (dominant) clones quickly fill the gaps left this way — as was observed in the study.

In our study, we aimed at evaluating whether multiclone SRC plantations had higher productivity, and whether this higher productivity was due to complementarity effects, rather than or in addition to selection effects. We set up an experimental SRC plantation in which the contributions of the different willow clones to the overall yield could be separated. Furthermore, we determined possible other effects of mixing clones by comparing the stand dynamics of mixtures and monocultures. Conventional sampling methods to assess productivity and soil characteristics were complemented with thermal imagery obtained with an Unmanned Aerial Vehicle (UAV) at the end of a long dry period. The thermal maps were used as indirect estimator of transpiration levels and drought stress severity [32] of the different plots.

2. Materials and methods

2.1. Study site

In March 2010, an experimental Short Rotation Coppice (SRC) plantation was established in Zezelgem, Belgium (51°15’ N, 3°13’ E). The study site has a temperate maritime climate with a mean annual rainfall of 855 mm and air temperature of 10.5 °C (1981–2010, KMI Belgium). Four small former agricultural fields with a sandy soil were combined into an area of 2.28 ha. Before planting, the soil of the site was surveyed. The pH (KCl, 4.8) was below the optimal zone for willow, while the K and Mg content were at the lower end. Therefore, the site was treated with dolomite lime (3 t ha⁻¹) and fertilized with manure (cattle, 23 t ha⁻¹). In the first year after planting, manual weed management was performed three times, based on previous research and management guidelines [9,10]. The site was not cut back after the first growing season, because of the high cost of harvest in the region the site was located.

The site was planted with Swedish willow clone cuttings and saplings of indigenous species. We will focus on the willow clones only, which comprised half of the site. Willow clones have been used in SRC plantations for some time now and breeding stations in Sweden and in the UK have produced varieties with SRC as a specific focus [7]. Swedish clones gave better results than locally-adapted varieties at former SRC experiments in Belgium (Enerpedia.be, in Dutch). The three clones planted at our study site were Tordis, Klara and Gudrun. Gudrun is a clonal variety of Salix dasyclados, whereas Tordis is a hybrid of Salix viminalis and Salix schwerinii clones. Klara is a hybrid with a complex lineage, including clones of S. viminalis, S. dasyclados and S. schwerinii. Gudrun is advertised for its low susceptibility to frost, leaf rust (Melampsora sp.) and leaf beetles (Phratora sp.), Tordis for its tolerance to dry soils and Klara for its frost tolerance and high yield. More information on these clones (including their full pedigrees if known) can be found in the Willow Varietal Identification Guide from Teagasc, Ireland and AFBI, Northern Ireland [33].

The three clones were planted in a full factorial mixing design, i.e. all seven possible combinations of the three clones were present. All the diversity treatments were replicated, which resulted in fourteen different plots distributed over two blocks (Fig. 1a). The spatial distribution of the plots was decided randomly, although each block contained seven different clone combinations. The mean plot size was 33 m × 12 m. Room was left for one access path between the two blocks and machine-turning strips around them. The Swedish planting scheme was used. This scheme consists of double rows of trees, roughly parallel to the north—south axis at our site, with planting distances of 1.5 m between the double rows and 0.75 m between the two rows of a double row. Within each row, the planting distance between the cuttings was about 60 cm (Fig. 1b). This pattern resulted in a planting density of almost 15,000 cuttings per ha and a total of 6 double rows per plot. Mixing was (double) row-based, so that the double rows in a plot contained only one clone.

2.2. Data collection

In late August—September 2011 and in December 2013, subplots of 6.75 m × 3 m were set up in twelve of the fourteen plots (Fig. 1).
Every subplot contained three double rows and an estimated total of 30 planted cuttings. Because the planting distance of 60 cm inside a row varied at times, deviations from this number did not necessarily reflect mortality. A subplot always had a double row adjacent to it that was still a part of the plot it was in. Subplots were also at a distance of at least the tree height from the access paths and turning strips (Fig. 1a). In mixtures of two clones, each clone was present in one of the three rows in one subplot and in two rows in its replicate (Fig. 1b). As some trees were harvested for biomass determination, the subplots of 2013 were not at the same location as those of 2011.

The two most eastern plots (Fig. 1a) were not measured as the overall survival and vitality of the clones was low. In addition, one of the plots—a Gudrun monoculture—had to be replanted in 2011 and the other—a mixture of Gudrun and Tordis—was too small to enable the use of buffer rows. For these two treatments, we installed two subplots in their replicates (Fig. 1a).

In every subplot, the diameter (average of two perpendicular measurements at 20 cm above ground level) of each stem taller than 170 cm or with a diameter larger than 20 mm was measured. We indicated which stems belonged to the same stool. In 2011, the height of each stem was measured using a 7 m measuring pole and the dominant height per double row was calculated as the average height of the 5 highest stems. We could not do this in 2013 as the trees had grown too high. Instead, we used a Vertex hypsometer (Vertex III and Transponder T3, Håglof) to measure the height of one canopy-forming stem per double row.

In 2011 and 2013, one stem in every double row of every subplot was harvested for a total of 42 stems each year. To ensure a minimal degree of diameter variation for the harvested stems of each clone, we randomly allocated one of three diameter classes to each double row in advance. The 42 harvested stems were weighed in situ (accuracy of 0.05 kg). To determine dry weight, a subset of 9 stems—one for each clone and diameter class—was dried at 70 °C until constant weight.

In 2011, a mixed sample of the top 20 cm of the soil was taken in every subplot, composed of 10 subsamples taken randomly throughout the subplot. The soil samples were dried at 40 °C until constant weight, sieved at mesh size 2 mm and then analyzed for pH-H2O, pH-KCl, total P, Olsen P, N percentage by weight and C percentage by weight. pH was assessed using a glass electrode (Orion, model 920A) after extraction of 14 ml soil in a 70 ml H2O or 1 M KCl solution. Total P content was measured according to the colorimetric malachite green procedure [34] after wet, acidic digestion of a 0.2 g sample with an equimolar mixture of HClO4, HNO3 and H2SO4 in Teflon reservoirs for 4 h at 150 °C. Bio-available, inorganic phosphate (Olsen P) was assessed using the same procedure, after shaking a 2 g sample with 0.5 M NaHCO3 at a pH of 8.5 for half an hour. C and N fractions were determined making use of elementary analysis (Variomax CNS, Germany). Also in 2011, the terrain height in the four corners of every plot was measured using a precision GPS (resolution up to 2 cm). Establishing the elevation within the plots was generally not possible as the closed canopy blocked the GPS signal.

On August 2nd and 23rd of 2013, flights were performed with a UAV, the AT8 octocopter of AerialTronics (Scheveningen, The Netherlands), equipped with a thermal and a visual camera. A pre-programmed waypoint flight was used to fly each block in two parallel scan lines at about 50 m altitude. The visual camera (Canon S110, Canon, Japan) was programmed with CHDK to log continuously every 0.5 s. The thermal camera, a Flir SC305 (FLIR Systems, Inc., Wilsonville, OR, USA) has a resolution of 320 × 240 pixels, a thermal accuracy of ±2 °C and a thermal sensitivity of 0.05 °C; equipped with a 10 mm lens, it has a field of view (FOV) of 45° × 34°. The camera is controlled through in-house developed Python-based software from an on-board linux computer (Olimex), logging continuously every 2–2.5 s.

For further analysis, visual images only from the August 2nd flight were used, as a hardware problem during the second flight rendered its visual images unusable. Thermal images were used from the August 23rd flight, however, as there was significantly less wind that day and hence these images were much sharper than those of August 2.

The GPX-logfile from the UAV was used to estimate the GPS position and altitude of the UAV of each visual image. AgiSoft PhotoScan Professional (AgiSoft LLC, St Petersburg, Russia) was used to mosaic the visual images and a georeferenced orthophoto was extracted. The thermal images were converted to canopy temperature images as described by Maes et al. [35]. Due to the relatively low resolution, low overlap and limited contrast between the images, the thermal images could not be mosaicked properly with AgiSoft. Thermal images were therefore overlaid on the visual map in ArcGIS (ESRI, Redlands, Ca, USA) using the Georeference Tool and later mosaicked to form a thermal map. The thermal map covered the entire experiment except for a small gap in a Gudrun-Klara mixture (Fig. 2).
2.3. Data analysis

To estimate standing biomass and productivity, we established allometric relationships between stem diameter (D, mm) and dry biomass (DM, kg) for every clone and separately for the two measuring years by fitting power relationships with the loglinear regression formula \( DM = aD^b \) [36]. We then estimated the dry biomass for every stem and summed these values into standing biomass per stool, per double row and per subplot. The latter two values were transformed into productivity in dry tonnes per hectare per year (t DM ha\(^{-1}\) yr\(^{-1}\)), a metric regularly used in SRC literature [14,15,37].

To explain potential variations in productivity caused by abiotic factors, we performed a Principal Component Analysis (PCA) with the soil variables and the GPS-determined terrain height. We also included a spatial variable that indicated the relative position of the plots from west to east, as there was a visible loss of vitality along this gradient, particularly in 2011. We then used linear regression to look for relationships between subplot productivity (t DM ha\(^{-1}\) yr\(^{-1}\)) and the first two principal components. We also incorporated the planted fraction of Gudrun as a second variable, because initial surveys led us to expect that this clone was considerably less productive than the other two.

To derive corresponding data from the thermal image, subplots of equal size and orientation as described in the previous section were drawn using ArcGIS (Fig. 2), with each subplot corresponding to ca. 718 pixels. These digital subplots were placed as close as possible to the location of the subplots during field measurements in 2013, except for the Gudrun-Klara mixture in the first block due to a thermal data gap (cf. 2.2). Average values and standard deviations of leaf surface temperature were determined for each subplot. Differentiation between double rows was not possible because these elements could not be consistently identified. The average values were related to the field measurements of productivity as well as to soil and spatial variables using linear regression, again including the Gudrun fraction as an additional variable.

Diversity effects were assessed for multiple characteristics other than productivity. This analysis was performed at the double row level rather than the subplot level, because clonal identity effects were expected. The number of stools (S) in a double row was used as a proxy for survival, although the deviations in planting distance may confound this relationship. As the plantation was still in its first rotation and the stools were not cut back after the first year to induce multiple stem formation [as in Ref. [29]], we could assume that different stools originated from different cuttings. An indicator for apical dominance was estimated by calculating the ratio between the total number of stems (N) and S. Averages of S, N and N/S were calculated at the double row level. The evenness (EV) of stool biomass for each double row was calculated as:

\[
EV = -\sum_{i=0}^{S} \frac{p_i \ln(p_i)}{\ln(S)}
\]

with \( p_i \) the fraction of the total biomass for the \( i \)th stool and \( S \) the number of stools in the double row. Lower values of \( EV \) indicate an imbalance of stool biomass within the subplot and suggest that some stools are not doing well and/or other stools are taking advantage of the gaps.

The significance of the diversity effect was tested using two-way ANOVA with clone as the second factor. We incorporated the interaction term, as diversity effects can be clone-specific. Tukey’s Honest Significant Difference test (HSD) was used if significant factors had more than two levels or interactions were significant. Because the mixtures with three clones would distort the balance of the dataset and thus undermine the applicability of Tukey’s HSD, they were combined with the two-clone mixtures into one single level. Analyses were performed for productivity (Y), dominant height (H), number of stools (S), number of stems (N), N/S and the evenness of biomass (EV).

To differentiate the complementarity (CMP) and selection (SEL) effects, we calculated the diversity effect on productivity in the mixed subplots using the method of Loreau & Hector [38]. These effects can be calculated for each mixed subplot using the following equations:

\[
\Delta R_Y = R_Y_{Oi} - R_Y_{Ei} = \frac{Y_{Oi} M_i}{M_i} - \frac{Y_{Ei} M_i}{M_i} = Y_{Oi} - P_{Ai}
\]

\[
CMP = N\Delta R_Y M
\]

\[
SEL = N\text{cov} (\Delta R_Y, M)
\]

\( R_Y_{Oi} \) is the observed relative productivity for clone \( i \) in a mixed subplot, calculated by dividing the observed productivity of this clone in this subplot \( (Y_{Oi}) \) by \( M_i \), the average observed productivity of clone \( i \) in monoculture subplots (both in t DM ha\(^{-1}\) yr\(^{-1}\)). \( R_Y_{Ei} \) is the relative expected productivity of clone \( i \) in mixture based on monoculture performance, or simply the proportion of the area planted with this clone \( (P_{Ai}) \). CMP and SEL are calculated by taking the average and the covariance of the \( \Delta R_Y \) and the \( M_i \) values for all \( N \) clones present in the mixture.

All statistical analyses were performed using the statistical package R 3.1.0 [39].

3. Results

3.1. Productivity

The allometric relationships between diameter and dry biomass held up very well in both years \( (\text{adj } R^2 > 0.985, \text{Fig. 3}) \). Gudrun showed a consistently lower biomass for equal diameters than the other two clones. The relationship for Tordis was similar in both years. The other two clones showed divergent patterns between years, overestimating Klara biomass and underestimating Gudrun biomass if the relationships from 2011 would be extrapolated to 2013 (data not shown).
Fig. 3. The allometric relationships between stem diameter and dry biomass of the three clones in 2011 (a) and 2013 (b). The parameter estimates and adjusted R² values can be found in the embedded tables.

Fig. 4. Productivities in 2011 (a) and 2013 (b). The bars denote the three sampled double rows in the subplots, whereas the curve indicates the average productivity of the three double rows in each subplot.
Gudrun had significantly lower productivity (Fig. 4; Table 1) and was lower in height (Table 1) than the other two clones. One subplot with Klara and one of the three-clone mixtures, both in the first block, were notably underproductive in both years, while the Klara row in the first Gudrun-Klara mixture was a strong and consistent over-productive outlier. The replicates of the Gudrun-Klara mixture with two Klara rows was poorly productive in 2011, but not in 2013. The productivity differences between the subplots were relatively larger in 2011 than in 2013, as can be seen in the slopes of the subplot average curve in Fig. 4.

### 3.2. Soil variables and leaf temperature

The first two axes of the PCA of the soil variables explained together 66% of the total variance. The first axis (40%) was strongly correlated with total P, Olsen P, terrain height, C% and N%. The second axis (26%) was correlated with pH (KCl: -0.87, H2O: -0.76) and the spatial variable (0.64). The first axis showed no relationship with productivity. The second axis scores did show a pattern where lower pH and more eastern subplots were less productive, but they were not significantly related to subplot productivity in 2011 (p = 0.25) or 2013 (p = 0.07) when the fraction of planted Gudrun was included in the model.

Leaf temperatures decreased from west to east in the site (Fig. 2). This spatial relationship was significant (p = 0.01, Fig. 5a) and not due to an effect of the planted Gudrun fraction (p = 0.16). In 2013, productivity tended to increase with leaf temperature (Fig. 5b) rather than decrease, though this relationship was only marginally significant (p = 0.08). Again, no effect of Gudrun (p = 0.17) was observed. The Gudrun-Klara mixture in the most eastern part of the second block had the lowest leaf temperatures. The Gudrun monocultures had the highest variance in leaf surface temperatures.

### 3.3. Diversity effects

Although the difference was never significant, the productivity of any clone was generally higher in mixture than in monoculture – except for Gudrun in 2013 (Table 1). Gudrun had a greater number of stems per stool (N/S) in both years, which was also reflected in its total stem count (N) in 2013 but not in 2011. In 2013, the monocultures of Gudrun showed a significantly higher stem count and lower evenness of biomass (EV) than all the other treatments. To better understand this result, we compiled the stem biomass distribution of Gudrun for this year (Fig. 6). There were much more small stems in the monocultures (stem biomass less than 0.5 kg) and this effect was compensated in terms of standing biomass by more intermediate stems in the mixtures (biomass between 1 and 2.5–3 kg). The largest stems (>5 kg) all occurred in the monocultures again. Gudrun showed a relatively similar pattern (data not shown) in 2011, except that the largest stems were then in the mixtures.

The diversity effect as calculated with the method of Loreau & Hector [38] was generally positive, with the notable exception of one three-clone mixture (1GKT) in both years and one Gudrun-Klara mixture (2GK) in 2011 (Table 2). As one monoculture of Klara (1K) had an unusually low productivity (cf. 3.1), the analysis of diversity effects was repeated omitting the data from this subplot. The average diversity effect diminishes for both years this way, even becoming negative in 2011 (Table S1). The selection effect tended to be negative in 2011 and positive in 2013. The complementarity effect was generally larger in 2011 than in 2013 and always larger than the selection effect, as can be seen in the ratio of their absolute values (Table 2). When the Klara monoculture was omitted from the dataset (Table S1), the complementarity effect was still larger than the selection effect for most subplots. However, the median of the ratio’s decreased, suggesting an increase in the relative contribution of the selection effect.

### 4. Discussion

#### 4.1. Productivity variability

Gudrun has been reported to have a slow initial growth, which eventually catches up with those of other clones [14,33]. We observed that Gudrun’s productivity shortfall was lower in 2013, which seems to corroborate this. Tordis was less variable in its productivity than the other two clones (Fig. 4). This could be due to its genetic characteristics, as it is one of the clones promoted for drier areas by its producer. If drought conditions occur unevenly throughout the plantation, less drought-tolerant clones such as Klara and Gudrun would show greater differences in their productivity. The extreme outlier of Klara in one double row (Fig. 4) suggests that Klara has potential for very high productivity in optimal circumstances. Klara also grew taller than Tordis in the subplots where it did well.

An explanation for the low productivities in some plots could not immediately be found in soil and terrain data. The pH-KCl was 5.7 at the lowest which is still within the optimal range for willow [40]. A spatial link might explain the poor productivity of the first Klara monoculture, in particular in the face of the neighbouring plots to the east that were not sampled in part due to their poor vitality (Fig. 1) and the decreasing leaf temperature trend from west to east (Fig. 5a). However, a spatial link does not explain the consistent productivity shortfall of the three-clone mixture in block 1. The absence of any major pest (leaf beetle, Phratora spp.) or pathogen (rust, Melampsora spp.) of willow in the plantation (pers. obs.) suggests that an abiotic cause is the most likely driver of these low productivities.

Drought could be a potential explanation: whereas Tordis (promoted as a drought-tolerant clone) was consistent in its productivity, Gudrun (discouraged on dry soils) showed low values. However, leaf temperatures were not negatively related to...
productivity, which would be expected if drought stress was the cause of lower productivities. This may be due to a lack of drought stress at the time of measuring leaf surface temperatures and does not rule out the occurrence of drought stress during drier parts of the growing season. However, August 2013 was an unusually dry month in the region where the site is located and the weather was dry in the days leading up to the UAV flight (KMI, Belgium). It is possible that greater productivity is related to greater rates of transpiration, which will deplete soil water more quickly under dry conditions and therefore result in faster stomatal closure, increasing leaf surface temperatures. However, even if this is the case, it would still imply that drought stress is not the limiting factor of productivity over the course of the plantation’s four growing seasons.

Productivities for Klara and Gudrun fell within the expected range as based on previous trials if the poorly yielding plots were ignored. The Flemish research organization Inagro sets its expected productivity for SRC in Flanders at 12 t DM ha\(^{-1}\) yr\(^{-1}\) after three growing seasons.

![Fig. 5. a) Subplot average leaf surface temperatures from west to east. An index of 1 refers to the most western plots; of 6 to the most eastern plots that were measured (cf. also Fig. 1a). b) Subplot average leaf surface temperatures plotted against 2013 productivities.](image)

![Fig. 6. The distribution of stem biomass for Gudrun in 2013. The biomass classes on the x axis are indicated by their upper boundary. The interval size is 500 g.](image)

| Diversity effects according to the method of Loreau & Hector (2001). \(\Delta RY_i\) is the difference in relative observed and expected productivity for clone i. The first clone in each two-clone mixture is the one with two out of three double rows. K is Klara, T is Tordis and G is Gudrun. CMP is the complementarity and SEL the selection diversity effect; both are in t DM ha\(^{-1}\) yr\(^{-1}\). The ratio between the absolute values of CMP and SEL is listed to indicate their relative contribution. The sum of both CMP and SEL is also listed to indicate the total diversity effect. |
|---|---|---|---|---|---|
| | \(\Delta RY_i\) | CMP | SEL | Ratio | Total |
| 2011 | | | | | |
| 1KT | K | 0.08 | 1.77 | 0.01 | 174 | 1.78 | 0.08 | 0.68 | −0.19 | 3.56 | 0.49 |
| | T | 0.17 | 1.77 | 0.00 | 2038 | 2.72 | −0.03 | −0.24 | 0.09 | 2.78 | −0.15 |
| | G | 0.45 | −0.31 | 11.9 | 3.41 | −0.17 | 0.46 | 2.91 | 0.62 | 4.66 | 3.53 |
| 2KT | K | 0.19 | 2.72 | −0.31 | 11.9 | 3.41 | −0.17 | 0.46 | 2.91 | 0.62 | 4.66 | 3.53 |
| | T | 0.20 | 2.72 | 0.00 | 2038 | 2.72 | −0.03 | −0.24 | 0.09 | 2.78 | −0.15 |
| | G | 0.45 | −0.31 | 11.9 | 3.41 | −0.17 | 0.46 | 2.91 | 0.62 | 4.66 | 3.53 |
| 1GK | K | 0.29 | 3.72 | −0.31 | 11.9 | 3.41 | −0.17 | 0.46 | 2.91 | 0.62 | 4.66 | 3.53 |
| | G | 0.01 | −1.21 | −0.46 | 2.64 | −1.67 | −0.10 | 1.43 | 0.34 | 4.25 | 1.76 |
| 2GK | K | 0.24 | 3.72 | −0.31 | 11.9 | 3.41 | −0.17 | 0.46 | 2.91 | 0.62 | 4.66 | 3.53 |
| | G | −0.01 | −1.21 | −0.46 | 2.64 | −1.67 | −0.10 | 1.43 | 0.34 | 4.25 | 1.76 |
| 1GT | T | 0.09 | 2.21 | −0.15 | 1.92 | 1.06 | 0.08 | 0.51 | 0.30 | 1.67 | 0.81 |
| | G | 0.24 | 1.70 | −0.30 | 5.61 | 1.39 | 0.08 | 0.60 | −0.32 | 1.91 | 0.29 |
| 2GT | T | −0.06 | 2.21 | −0.15 | 1.92 | 1.06 | 0.08 | 0.51 | 0.30 | 1.67 | 0.81 |
| | G | 0.00 | 2.21 | −0.15 | 1.92 | 1.06 | 0.08 | 0.51 | 0.30 | 1.67 | 0.81 |
| 1GKT | K | −0.11 | 2.21 | −0.15 | 1.92 | 1.06 | 0.08 | 0.51 | 0.30 | 1.67 | 0.81 |
| | T | −0.06 | 2.21 | −0.15 | 1.92 | 1.06 | 0.08 | 0.51 | 0.30 | 1.67 | 0.81 |
| 2GKT | G | 0.05 | 2.21 | −0.15 | 1.92 | 1.06 | 0.08 | 0.51 | 0.30 | 1.67 | 0.81 |
| | K | 0.16 | 2.21 | −0.15 | 1.92 | 1.06 | 0.08 | 0.51 | 0.30 | 1.67 | 0.81 |
| | T | 0.15 | 2.02 | 0.29 | 6.94 | −6.28 | 2.31 | 0.07 | 1.86 | 0.31 | 3.82 | 2.17 |
| Median | Average | 1.50 | −0.27 | 1.23 | 0.60 | 0.21 | 3.90 | 0.81 |
years, based on their own trials (cf. Enerpedia.be, in Dutch), which is close to the average this site attained (Table 1). Findings from Sweden, Ireland and the UK are also within this range [9,14]. Yet, the age of a plantation is crucial in comparing its yield with other sites; in our experiment, growth in 2010–2011 strongly differed from growth in 2012–2013. The average annual productivity roughly doubled from the first two to the last two years, implying that three times as much biomass was produced in the last two years. Hence, it might be expected that yearly average yields would be lower for a three year period.

4.2. Clone-specific analysis

Gudrun’s deviant characteristics compared to the other clones were most pronounced in 2013, with the exception of productivity (Table 1). The total stem count was not different between clones in 2011, which can possibly be explained by the criteria used for including a stem in our measurements. Very small stems were not measured in both years, but as time progresses more stems will attain the minimum diameter and height.

A lower evenness of biomass was found in the monocultures of Gudrun in 2013 (Table 1) as well as a greater amount of both small and large stools (Fig. 6). The variance in leaf surface temperature was also highest in the Gudrun monocultures (data not shown). A possible explanation for this phenomenon could be that in our plantation, Gudrun generally suffered from greater mortality or more instances of poor vitality regardless of any non-additive diversity effect in the form of facilitation or complementarity [22]. This would distort the evenness of biomass locally, as still fit stools compensate for their less fortunate neighbours and hence unevenness increases in two ways: fit stools grow larger, less fit stools stay smaller. This mechanism can be expected to be more common in monocultures even if survival/vitality was not noticeably different between monocultures and mixtures, as Gudrun double rows will be surrounded by similarly deficient rows in monocultures but not in mixtures. Willows grow fast enough for such compensation between rows to be already apparent after four years of growth [41], though possibly not after two years (cf. the ΔRYi values as discussed in section 4.3) explaining why this phenomenon could not be found in 2011.

This mechanism of unevenness through generally poor vitality also explains why the most massive Gudrun stems were found in monocultures in 2013, though this is not necessarily true for the overall greater stem number. It is possible that this latter effect is related to the poor growth of Gudrun, resulting in less inhibition of lateral growth through shading and less apical dominance in monocultures. It is unclear what implications such a diversity effect on stand dynamics could have for SRC systems. Stem diameters play a role in the choice of harvesters and harvest optimization techniques, as well as the quality of the final product. Smaller stems may be more optimal for modified forage harvesters, as they are less likely to jam the header [42]. Larger stems generally have a lower bark fraction and hence a lower ash content, which improves fuel quality and decreases nutrient losses [43].

4.3. Complementarity and selection effect

The selection effects were generally smaller than the complementarity effects (cf. the ratios in Table 1). This relationship persisted when the data of the Klara monoculture were omitted (Table S1). Klara edged out Gudrun in their more productive mixtures in 2013 (cf. the ΔRYi values in Table 1), which means that Klara’s generally greater productivity increases its specific productivity in mixture at the expense of Gudrun’s. However, this selection effect does not seem to completely or even significantly explain the differences between observed and expected productivity (Table 1). Hence, we might conclude that the diversity effect cannot be explained by the presence of a more productive clone.

Some selection effects were negative, primarily in 2011. A negative selection effect means that a clone that is less-productive in monoculture yields relatively more in a mixture than the more productive other clones present in that mixture. Hence, in such a mixture, the clones do not behave as would be expected from their dominance hierarchies based on their monoculture performance. Competition between double rows (and thus clones) was probably less strong or even absent in 2011, when the plantation was just at the end of its second growing season. The mixture that was most extreme in terms of productivity (1GK) reflects this in its ΔRYi values (Table 1), which were positive for both clones in 2011 but had diverged substantially in 2013.

5. Conclusion

The objective of this research was to identify diversity effects on productivity in a SRC stand and to assess the role of a selection effect. We found indications of a diversity effect on productivity that was not caused by a selection effect, but this effect was not significant due to unexplained variance in productivity. When taking a closer look at the stand characteristics of the studied systems, diversity effects were found for a less productive clone in 2013. Such effects might be expected even in the absence of a non-additive diversity effect on productivity and can still have real impacts on system qualities, such as harvest efficiency or quality of the harvested product. Future research should attempt to keep within-treatment variation as low as possible, necessitating a larger research site or data from multiple sites. Longer time series including harvest years are also recommended, as biotic pressure is expected to be highest just after this traumatic event. Finally, clonal diversity gradients should be widened to more different clones with larger differences in their lineage, as advised by the Willow Best Practice Guide [9].

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.biombioe.2016.02.013.

References

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