



Can tree species richness attenuate the effect of drought on organic matter decomposition and stabilization in young plantation forests?

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ABSTRACT

Changes in precipitation due to climate change are likely to influence soil organic matter (SOM) decomposition and stabilization. In forests, increased tree species diversity could modulate the effects of drought on SOM decomposition and stabilization. We addressed this issue by a decomposition study under simulated drought (through precipitation reduction at Zedelgem, Belgium) and natural drought (ORPHEE, southern France) in young experimental plantations (tree species richness 1 to 5). In Zedelgem, the study focused on tree species richness around oak and beech trees. Two tea bag indices (TBI) – decomposition rate (k) and stabilization factor (S) – were calculated by measuring the decay of green and rooibos tea in soils. Overall, TBI's were higher in Zedelgem than at ORPHEE. In Zedelgem, k increased with tree species richness under drought around oak, indicating that tree species richness modulated the effects of drought on decomposition. Under beech, k decreased with drought while no effect of tree species richness was detected. S increased with drought under both oak and beech, without any effect of tree species richness. In ORPHEE, we did not detect any tree species richness effect on both TBIs. S decreased significantly, while k was marginally reduced under drought. The higher S under drought in Zedelgem and under control in ORPHEE suggests that the carbon sequestration potential under climate change would be dependent on the environmental context. Further, in young plantations, high species richness may modulate the drought effect on SOM decomposition, but not on stabilization.

1. Introduction

Soil organic matter (SOM) transformation (decomposition and stabilization) is an important ecological process regulating nutrient cycling and ecosystem carbon (C) balance. As main controlling factors include temperature and water availability (Aerts, 1997; Swift et al., 1979), this process is likely to be affected by the predicted changes in precipitation patterns under climate change. For Europe, climate models predict a decrease in mean annual precipitation in the temperate region, associated with more frequent extreme climatic events such as heavy precipitation and severe droughts (EEA, 2017; Kovats et al., 2014). In Belgium, the total amount of precipitation may remain unchanged by the end of this century, but up to 50% decrease in summer precipitations and an increase in winter precipitations are expected (Baguis et al., 2010; Brouwers et al., 2015). Resistance and resilience of forest ecosystems to these changes can be influenced by forest management decisions, such as the choice of tree species and the association of different tree species in forest mixtures (Grossiord et al., 2014a;

Lebourgeois et al., 2013). Better knowledge on responses of SOM transformation to reduced precipitation in relation to tree species richness is therefore essential to our understanding of forest ecosystem functioning under future climatic conditions.

SOM decomposition refers to the breakdown of complex biological material into simpler molecules (Juma, 1988), whereas SOM stabilization refers to the integration of SOM into the soil matrix, resisting further breakdown (Paul, 2016). Interactions between climate, litter quality and decomposer community determine SOM transformation rates (Aerts, 1997; Swift et al., 1979). Soil moisture influences SOM transformation directly by altering the abiotic conditions and indirectly through changing litter quality and decomposer community (García-Palacios et al., 2016). Drought can reduce SOM decomposition through a moisture-induced reduction in soil microbial activity (Sanaullah et al., 2012; Saura-Mas et al., 2012; Walter et al., 2013). Heterotrophic respiration, i.e. the CO_2 produced by microbial decomposition of SOM, accounts for 58–76% of total ecosystem respiration (Curiel Yuste et al., 2005). Therefore, any alteration of SOM dynamics could alter the total

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ecosystem C balance. For instance, it has been shown that drought could change the forest ecosystem C balance from sink to source (Ciais et al., 2005; Misson et al., 2009).

Unlike decomposition, information on the effect of soil moisture on SOM stabilization is limited. The recalcitrant part and a portion of labile components of SOM become stabilized in the soil during the decomposition processes (Prescott, 2010). Along with litter quality, physical and chemical site properties can influence SOM stabilization rates (Berg and Meentemeyer, 2002) and processes (Castellano et al., 2015; Paul, 2016; Poeplau et al., 2015; Sollins et al., 1996). Environmental conditions reducing SOM decomposition rates are expected to enhance stabilization (Keuskamp et al., 2013). Therefore, the response of SOM transformation to future environmental conditions will be crucial to ecosystem C sequestration.

Any forest management (e.g. mixed forests) that influences stress resistance could reduce the negative impact of reduced precipitation and soil moisture changes on SOM transformations. European forest management is moving from monocultures to mixed forests for better adaptation to multiple risks (Jactel et al., 2017). Species rich forests are more stable and productive (Jucker et al., 2014), provide diverse ecosystem services (Isbell et al., 2011), better resistance to herbivory and disease (Jactel and Brockerhoff, 2007; Pautasso et al., 2005), and have higher biological diversity (Hartley, 2002) than monocultures. Mixing of functionally dissimilar species enhances ecosystem services (Hättenschwiler, 2005; Lange et al., 2015; Ratcliffe et al., 2016; Thakur et al., 2015), although species identity can override the diversity effect (Dawud et al., 2016; Vivanco and Austin, 2008). Tree species composition is a key determinant of the microenvironment under the canopy and of litter quality (Berg and Meentemeyer, 2002; Prescott, 2010, 2002). As a result, belowground processes such as SOM decomposition are likely to be different in species rich forests vs. monocultures (Gessner et al., 2010). Although, mixing of functionally different tree species may enhance decomposition rates (Bastianoni et al., 2015; Scherer-Lorenzen, 2008), the response to soil moisture change remains uncertain. Diverse forests are often more resistant to abiotic stresses due to complementary effects and asynchronous stress responses (Scherer-Lorenzen, 2014) but to what extent they perform better under drought is still controversial (Forrester et al., 2016). In particular, drought resistance of mixed species forests seems to vary between biomes (Grossiord et al., 2014b).

In this study, we used the well established tea bag approach to study SOM transformation (Djukic et al., 2018; Keuskamp et al., 2013) in two tree diversity experiments. We estimated two tea bag indices (TBI), the decomposition rate (k) and the stabilization factor (S). S is interpreted as the inhibiting effect of environmental conditions on the decomposition of the labile fraction and it is indicative of long term C storage, while k represents the short term dynamics of new input (Keuskamp et al., 2013). By using tea bags, we could focus on the effects of a changing microenvironment on decomposition and stabilization, without the effects of litter quality (Hättenschwiler, 2005; Setiawan

et al., 2016) and home-field advantages (Ayres et al., 2009). The specific objective of this study was to investigate the combined effects of drought and tree species richness on SOM transformation in two young forests with contrasting site properties. The study was performed at the Zedelgem site of the FORBIO experiment (Verheyen et al., 2013) on a sandy-loam soil in the temperate climate of Belgium, and at the ORPHEE experiment (Castagneyrol et al., 2013) on a sandy soil under the oceanic climate of southern France. We hypothesized that i) k would be lower and S would be higher under drought, and ii) tree species richness would have a positive effect in mitigating the effect of drought on both TBIs.

2. Materials and methods

2.1. Study sites

The study was conducted within two tree diversity experiments where precipitation was manipulated. Subplots within FORBIO - Zedelgem (Belgium) were subjected to experimental drought through precipitation exclusion (hereafter “drought”), whereas some plots in ORPHEE (France) were subjected to experimental irrigation (hereafter “control”), the other being subjected to natural summer drought (hereafter “drought”). Both sites belong to the worldwide Tree Diversity Network (<http://www.treedivnet.ugent.be/>, Verheyen et al., 2016).

2.1.1. Zedelgem

Zedelgem is part of the Belgian FORBIO experiment (Verheyen et al., 2013). The site is close to the North Sea (51°9' N 3°7' E) with a mean annual precipitation of 855 mm and an average temperature of 10.5 °C (1981–2010; RMI, Royal Meteorological Institute, Belgium). During the study in 2015, precipitation was 43 mm (June), 60 mm (July), 136 mm (August) and 90 mm (September). Soils have been classified as relatively dry sandy soil (Zbh/Podzol) to moderately wet loamy sand (Sdp/gleysol) (Verheyen et al., 2013). The site was previously used as agricultural field, before being planted in winter 2009–2010. The plantations follow a synthetic community approach using a fixed species pool of five site-adapted and functionally dissimilar tree species (*Betula pendula* Roth., *Fagus sylvatica* L., *Quercus robur* L., *Tilia cordata* Mill., and *Pinus sylvestris* L.). In Zedelgem, the 42 plots (42 m × 42 m) were composed of five monocultures, all five possible four-species combinations and a random selection of five two- and five three-species combinations. All combinations were replicated twice, with two additional plots of oak provenance trials. Within mixed-species plots, trees were planted in monoculture patches of 3 × 3 trees with a distance of 1.5 m between the trees (Fig. 1). The details of the plantation have been described elsewhere (Verheyen et al., 2013).

Oak and beech were selected for the drought experiment, given their importance in European forestry. Basic soil properties (0–5 cm) under these species are shown in Table 1. In April 2015, three drought (precipitation reduction) and three control subplots (3 m × 3 m) were

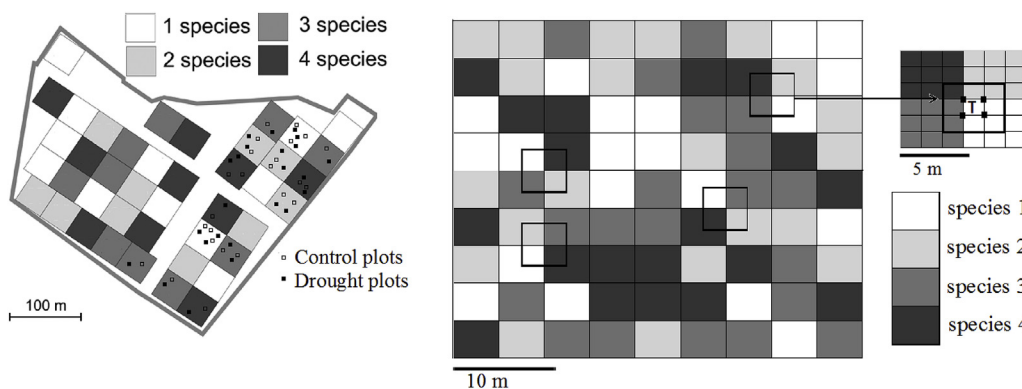


Fig. 1. Left: the 42 plots (42 m × 42 m) of the FORBIO experiment at Zedelgem, and location of drought and control subplots. Right: close-up of a four species richness plot with monoculture patches (3 × 3 trees) of each species. Subplots were placed at the intersection of the four tree species corresponding to the plot's species composition. The black dots inside the subplot (top right) indicate the placement of tea bags. T: target central tree (beech or oak).

Table 1

Basic soil properties (0–5 cm) at Zedelgem and ORPHEE. Values are mean \pm SEM, n = 3.

| | Zedelgem | | ORPHEE |
|-----------------------|------------------|------------------|------------------|
| | Beech | Oak | |
| pH (H ₂ O) | 6.38 \pm 0.04 | 6.14 \pm 0.05 | 4.30 \pm 0.13 |
| SOM (%) | 3.90 \pm 0.07 | 3.91 \pm 0.08 | 11.10 \pm 0.14 |
| Carbon (%) | 1.71 \pm 0.08 | 1.74 \pm 0.07 | 5.55 \pm 0.07 |
| Nitrogen (%) | 0.15 \pm 0.007 | 0.14 \pm 0.006 | 0.19 \pm 0.002 |
| C/N ratio | 11.24 \pm 0.24 | 12.22 \pm 0.19 | 28.40 \pm 2.10 |

installed around central oak or beech trees in all the species richness levels (Fig. 1) within the north-eastern part of the site. There were thus 12 (4 richness levels \times 3 replications) drought and 12 control subplots for each oak and beech. In the 2 to 4 species plots, drought subplots were placed at the intersection of the monoculture patches, with the central tree being surrounded by one to three different species (Fig. 1). Precipitation was reduced by installing a rainout shelter, according to the methods of Yahdjian and Sala (2002) and Gimbel et al. (2015). The rainout shelters consisted of PVC gutters (\sim 12 cm wide) placed at an interval of \sim 25 cm to intercept precipitation. For drainage, a 20 cm slope was created by placing the gutter at a height of 0.95 m from the ground at the upper side and 0.75 m at the lower side (Appendix, Fig. A1). Intercepted water was channelled to the downward side of the subplot (6 m away). The gutters covered approximately 50% of the subplot area, i.e. intercepting half of the precipitation, as predicted (Yahdjian and Sala, 2002). The amount of intercepted precipitation was assessed once, by placing rainfall collectors under and outside the rainout shelter in monoculture, two species and three species plots. The shelters excluded about 45–55% of total precipitation from the subplots. In addition to the drought subplots, three subplots of same size with reverse gutters (no interception) were established in the beech monoculture for monitoring a potential change in soil temperature due to the rainout shelter between the control and drought subplots (hereafter “reverse subplots”). The Zedelgem site is flat, and horizontal water movement is negligible.

2.1.2. ORPHEE

The ORPHEE experiment is located in south-western France, 40 km south of Bordeaux (44°44' N, 00° 46' W, <https://sites.google.com/view/orpheexperiment/home>). Mean precipitation and temperature in the study area were 876.3 mm and 12.75 °C between 1996 and 2016. The year 2015 was one of the driest (688.5 mm) and warmest (13.35 °C) of this period. The soil in the study area is a nutrient-poor sandy podzol, with a water table depth varying from 0 to 2 m (Appendix, Fig. A2). The soil is characterized by low pH and high SOM and C content (Table 1). The experiment was established in 2008 on a former plantation of maritime pine (*P. pinaster*). Five native species (*B. pendula*, *Q. robur*, *Q. pyrenaica* Wild., *Q. ilex* L., and *P. pinaster* Ait.), commonly found in the study area, were planted in experimental plots creating a tree species richness gradient from monocultures to five species mixtures. The soil was ploughed and fertilized with phosphorus and potassium before planting.

The whole area was divided into eight blocks, with 32 plots (20 m \times 20 m) in each block. Plots were randomly assigned within blocks and separated by a distance of 3 m. The 32 plots corresponded to all possible 31 combinations of one to five species, with an additional replicate of the five species plot (Fig. 2). Each plot was planted with 10 rows of 10 trees (100 trees/plot). Tree species were mixed according to a substitutive design that kept an equal tree density in the plots. Individual trees from different species were planted in a regular alternate pattern within the plot so that a tree from a given species had at least one neighbour from each of the other species (Castagneyrol et al., 2013).

The area is characterized by low precipitation during the growing season, resulting in natural drought conditions (Appendix, Fig. A2). To avoid summer droughts, half of the blocks were irrigated every night between May and October through a sprinkler system from 2015 onwards (Castagneyrol et al., 2017). The amount of water added was ca 42 m³ per night and per block, corresponding to 3 mm night⁻¹ per plot (checked by means of a rain gauge). This volume was calculated from regional climatic data (evapotranspiration) to avoid any soil water deficit in the irrigated blocks during the entire growing season (Appendix Fig. A2). Thus, the irrigated blocks in ORPHEE were treated as “control” and the blocks subjected to natural precipitation were treated as “drought” treatments.

2.2. Soil temperature and moisture measurements

In Zedelgem, soil temperature at 5 cm depth was measured hourly from April to October 2015 in three drought, three control and in three reverse subplots, using two temperature sensors (DS1922L-F5 iButtonshop.nl, Dikkum, The Netherlands) per subplot. Top soil volumetric water content (0–5 cm) was measured hourly in three drought and three control subplots from August 20, 2015 to onwards, using ML2 thetaprobe (Delta-T Devices Ltd., Hoddesdon, UK) and DL2 data logger (Delta-T Devices Ltd. UK). Both soil temperature and moisture were measured in beech monocultures, and sensors were placed mid-way between the central (oak or beech) and the corner tree, close to the tea bags (see below). Although soil moisture could be influenced by the type of mixtures, due to difference in water use efficiency of the tree species, we assume that this difference might be small in this young plantation. Further, our objective was to assess the effects of 50% precipitation reduction and soil moisture measurements in the beech monocultures indicate the potential effect of this reduction on soil moisture content.

Soil moisture was not continuously measured at ORPHEE during the decomposition period. The soil gravimetric water content was measured in August 2016 in two soil cores taken between 20 and 40 cm depth in selected monocultures of pines, pedunculate oak and birch, and all corresponding two- and three-species mixtures, resulting in seven plots per block, covering a large gradient of canopy closure and tree height heterogeneity (Castagneyrol et al., 2017). The two soil samples were pooled in hermetic plastic bags and stored in portable fridges before being brought to the laboratory where samples were immediately weighed. The samples were dried at 105 °C for 72 h and reweighed. Gravimetric water content was estimated as the proportion of water in fresh samples. We assumed that the difference in soil moisture in 2015 would have been similar, as the irrigation system was identical.

2.3. Tea bag preparation and incubation

Tea bags with woven nylon mesh (Lipton green tea, EAN: 87 22700 05552 5; Lipton rooibos tea, EAN: 87 22700 18843 8, mesh size, 280–300 μ m) were used in this study following the protocol described by Keuskamp et al. (2013). Each tea bag was labelled and weighed to four decimal places (g) prior to burial in the soil. Five green and five rooibos tea bags were opened and tea was dried separately at 70 °C for 48 h to determine the moisture content of tea. The average moisture content of these five tea bags was used for subsequent moisture correction of all tea bags. The weight of 10 strings, 10 labels and 10 empty tea bags without labels were measured separately. The mean weight of empty bags and labels was subtracted from the weight of each tea bag to obtain the actual initial weight of the tea.

In Zedelgem, four green and rooibos tea bags were buried in each of the drought and control subplots (Fig. 1) at 5–7 cm soil depth in mid-June, 2015. Tea bags were buried using a hand trowel to keep the disturbance to the soil and the ground vegetation minimal. These tea bags were placed in the midway between the central tree and the corner trees. A total of 96 tea bags (4 richness \times 3 replications \times 2 treatments

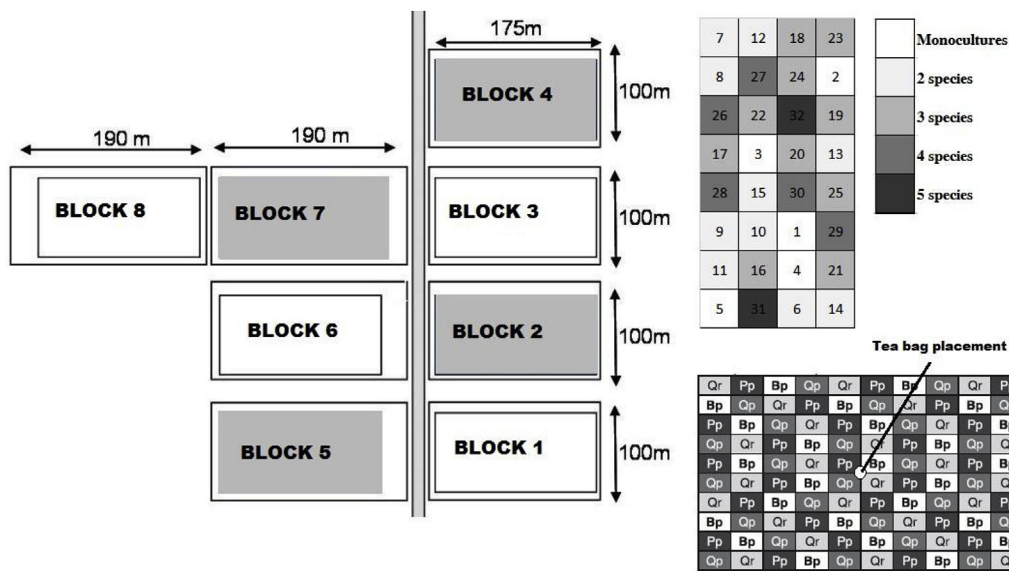


Fig. 2. Left: eight blocks at ORPHEE, grey blocks were irrigated daily during the summer. Right: The 32 plots within a block with different species richness and a close-up view of a four species richness plot with the location of tea bags.

(control, drought) \times 4 tea bags) of each kind were buried around oak and beech trees. The means of the tea bag indices (TBI) of the four tea bags of each plot were calculated and used in the statistical analysis (see below).

In ORPHEE, plots with tree species richness from one to four, one green and one rooibos tea bags were buried in the centre of the plots in the first week of July 2015 (Fig. 2). In plots with five species richness, in order to capture the influence of all species, two green and rooibos tea bags were buried in the central area of the plots. The mean value of the two tea bags of the same type was used in the statistics. In total 272 tea bags [(30 (1–4 species) plots \times 8 blocks \times 1 tea bag) + (2 (5 species) plots \times 8 blocks \times 2 tea bags)] of each kind were buried in ORPHEE.

Tea bags were retrieved from ORPHEE after 90 days and from Zedelgem after 100 days of burial and they were stored separately in labelled envelopes. Tea bags were then thoroughly shaken to remove adhering soil and other debris, dried at 70 °C for 48 h and shaken again to remove the adhering soil. The label (if remained) of the tea bag was removed, and bags were weighed. Then the mean weight of empty tea bags (see above) was subtracted from each tea bag weight to obtain the final weight of tea after decomposition.

2.4. Calculation of tea bag indices

The two types of tea have contrasting decomposition properties—rooibos and green teas are characterized by slow and fast decomposition rates, respectively. These contrasting properties allow to calculate tea bag parameters from a short term decomposition study (Keuskamp et al., 2013). Two TBI's, decomposition rate (k) and stabilization factor (S), were calculated for each pair (green and rooibos) of tea bags using the formulas proposed by Keuskamp et al. (2013):

$$S = 1 - \left(\frac{ag}{Hg} \right)$$

$$ag = 1 - \frac{\text{final weight of green tea (g)}}{\text{initial weight of green tea (g)}}$$

$$k = \frac{\log \left(\frac{ar}{(wt - (1 - ar))} \right)}{t}$$

$$ar = Hr \times (1 - S)$$

$$wt = \frac{\text{final weight of rooibos tea (g)}}{\text{initial weight of rooibos tea (g)}}$$

where,

ag = decomposed fraction of green tea,

ar = predicted labile fraction of rooibos tea,

t = incubation time of tea bags (days),

wt = fraction remaining of rooibos tea.

For calculating k and S , the recommended hydrolysable fractions ($Hg = 0.842 \text{ g g}^{-1}$ for green tea; $Hr = 0.552 \text{ g g}^{-1}$ for rooibos tea) were used (Keuskamp et al., 2013).

2.5. Statistical analyses

All data were analysed using R (version 3.1.1, R Development Core Team, 2014). Data from Zedelgem and ORPHEE were analysed separately, as type of treatment and species richness levels were different. In Zedelgem, the mean value of each TBI for each plot was calculated by averaging the four values of the plot, and used in the analyses. The k data from both sites were log transformed to meet the normality assumption. Data were analysed using mixed effect models (*lmer* function of *lme4* & *lmerTest* package) (Bates et al., 2015; Kuznetsova et al., 2016). In Zedelgem, the effect of drought and tree species richness (1, 2, 3, 4) on TBI were analysed separately for oak and beech, as there was a significant three-way interaction between central tree (oak or beech), treatment (drought, control) and tree species richness. In the mixed model, k or S was used as response variable with treatment (control, drought) and species richness as fixed effects, and species composition as a random effect. The composition was defined as the combinations of species present in the plots, and a composition vector was created by the concatenation of tree species (names) present in each plot. For ORPHEE, k or S was used as response variable in the mixed model while species richness (1, 2, 3, 4, and 5) and treatment (control, drought) were used as a fixed effect, and block: treatment and composition as random effects. For both datasets, fixed effects were tested both as the main and interaction effect. When the interaction effect was not significant, it was removed from the model. Marginal R^2 (variance explained by fixed effects) and conditional R^2 (variance explained by both fixed and random effects) were calculated according to Nakagawa and Schielzeth (2013) (R, MuMIn package, r.squaredGLMM). Visual

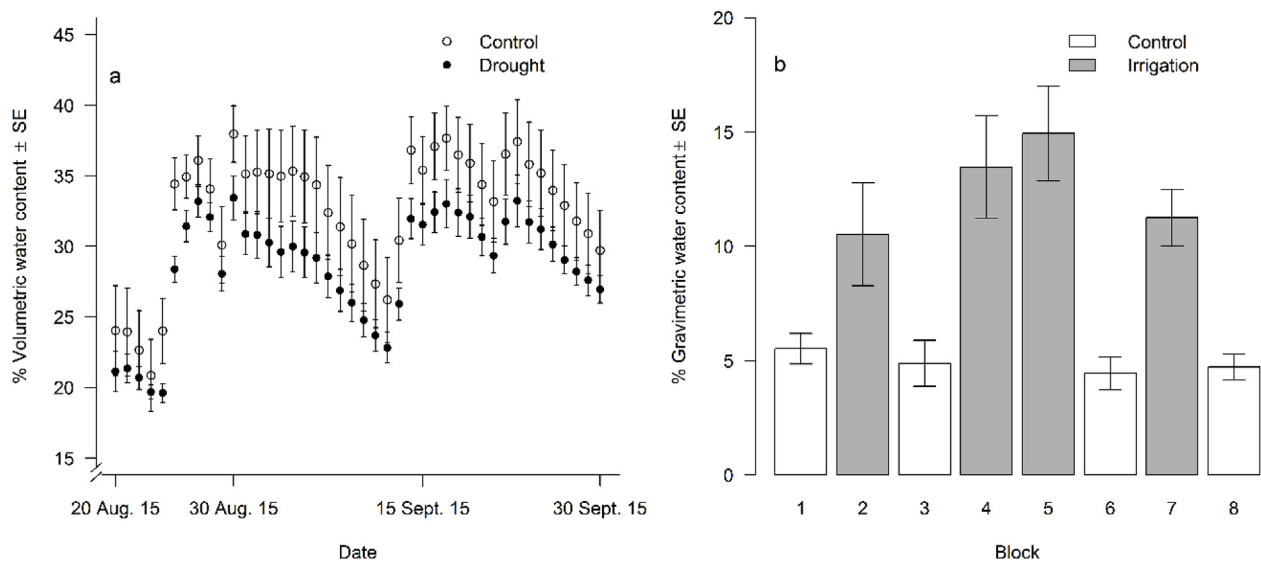


Fig. 3. Soil moisture content at Zedelgem and ORPHEE; a) Zedelgem, daily average soil volumetric water content in control and drought subplots in 0–5 cm soil from August 20 to September 30, 2015 ($n = 3$, error bars = SEM), b) ORPHEE, mean soil gravimetric water content per block in August 2016. Means and standard errors were calculated regardless of the specific composition of plots ($n = 7$). Note that irrigated plots in ORPHEE later treated as “control” while control plots were treated as “natural drought”.

inspection of residual did not reveal any obvious deviations from homoscedasticity or normality.

Response ratios were calculated separately for each site to compare the relative effects of drought on k and S . Within sites, the values of k and S for each species and richness level (Zedelgem) and composition level (ORPHEE) were divided by the mean value of the respective control plots. The response ratio was thus a unit-less metric of a relative change, compared to control.

3. Results

3.1. Soil temperature and moisture

In Zedelgem, during the decomposition study (April to October 2015), the mean daily soil temperature varied between 14 °C and 18 °C with no significant difference between drought, control and reverse subplots (data not shown). The daily mean soil volumetric water content (0–5 cm) varied from 20% to 37% (Fig. 3). Average soil volumetric water content in control subplots ($32.5\% \pm 0.7$) was 4% higher than in the drought subplots ($28.5\% \pm 0.6$) during the study. In the drought blocks of ORPHEE, gravimetric soil water content was about 5%, whereas in control (irrigated) blocks, water content was above 12% (Fig. 3). Across all blocks, the average gravimetric soil water content in drought plots ($4.89\% \pm 0.36$) was about 7% lower than in control plots ($12.54\% \pm 1.0$).

3.2. Decomposition rate and stabilization factor

Both decomposition rate, k , and stabilization factor, S , were lower in ORPHEE than in Zedelgem (Fig. 4). k in Zedelgem was between 0.007 and 0.014 $\text{g g}^{-1} \text{d}^{-1}$ and S was between 0.18 and 0.27. In ORPHEE, k ranged between 0.006 and 0.009 $\text{g g}^{-1} \text{d}^{-1}$ and S ranged between 0.06 and 0.10 (Fig. 4). Both k and S were less variable in ORPHEE than in Zedelgem.

3.3. Zedelgem

For k , the models explained ca. 30% of the total variance, with ca. 23% explained by the fixed factors and ca. 7% explained by the random factor (composition) (Table 2). Under oak, there was a significant

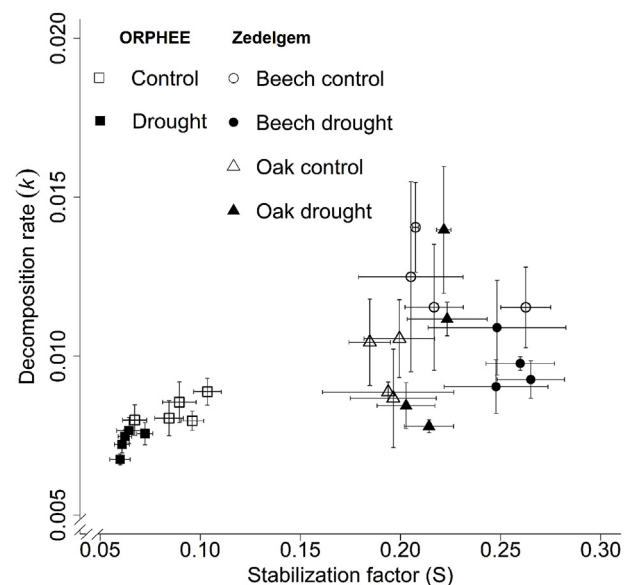


Fig. 4. Mean stabilization factor (S) vs mean decomposition rate (k) at Zedelgem and ORPHEE. Error bars represent SEM.

interaction between tree species richness and treatment for k (Table 2, Fig. 5a). Tree species richness did not change k in control subplots (slope estimate \pm se: 0.03 ± 0.06 , $t = -0.44$, $p = 0.6$), while k increased with tree species richness in drought subplots (slope estimate \pm se: 0.14 ± 0.06 , $t = 2.46$, $p = 0.03$). Under beech, k was significantly lower in drought than in control subplots (Table 2, Fig. 5b), with no significant effect of tree species richness.

For S , under oak, the random effect explained 33% of total variation ($R^2 = 0.45$), while under beech, the random effect was not significant ($R^2 = 0.18$) (Table 3). Both under oak and beech, S was significantly higher under drought than control subplots with no effect of tree species richness (Table 3, Fig. 5c and d). Response ratios indicated a 10% decrease in k under beech and no change under oak, and a 13.6% increase in S due to drought across all plots in Zedelgem.

Table 2

Effects of tree species richness and drought on decomposition rate (k) under oak and beech in Zedelgem. ($\text{lmer}(\log(k) \sim \text{richness} + \text{treatment} + (1|\text{composition}))$).

| Variables | Estimate | Std. error | t value | p |
|---|----------|------------|---------|-------------|
| Oak | | | | |
| Intercept | −4.596 | 0.164 | −27.90 | 0.00 |
| Richness | −0.026 | 0.058 | −0.44 | 0.67 |
| Drought | −0.371 | 0.205 | −1.80 | 0.09 |
| Richness: drought | 0.170 | 0.075 | 2.27 | 0.04 |
| Random effects (as standard deviation) ~ 1 composition | | | | |
| Intercept | 0.071 | | | |
| Residual | 0.205 | | | |
| R ² m | 0.24 | | | |
| R ² c | 0.32 | | | |
| Beech | | | | |
| Intercept | −4.395 | 0.129 | −34.02 | 0.00 |
| Richness | −0.010 | 0.043 | −0.24 | 0.82 |
| Drought | −0.222 | 0.082 | −2.70 | 0.02 |
| Random effects (as standard deviation) ~ 1 composition | | | | |
| Intercept | 0.063 | | | |
| Residual | 0.201 | | | |
| R ² m | 0.23 | | | |
| R ² c | 0.30 | | | |

Bold indicates p value was less than 0.05.

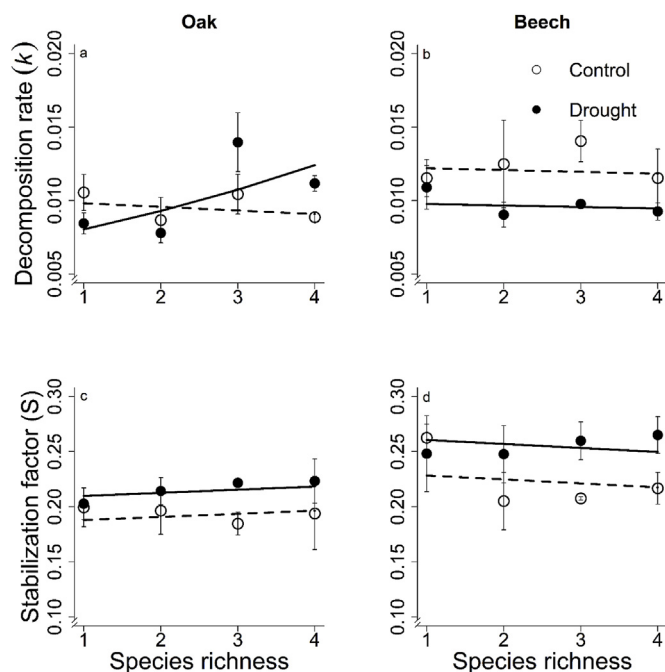


Fig. 5. Changes in decomposition rate (k) and stabilization factor (S) under different treatments (control and drought) and with tree species richness in Zedelgem; a & c) Oak, b & d) Beech. Error bars represent SEM, $n = 3$. Regression lines (mixed models) shown for control (dashed) and drought (solid) treatments.

3.4. ORPHEE

Total variation explained by the models was 10% and 34% for k and S , respectively (Table 4). S was significantly higher in control plots (0.09 ± 0.003) than in drought plots (0.06 ± 0.002). There was a tendency for k being higher in control plots (0.008 ± 0.0002) than in drought plots (0.007 ± 0.0001), but this difference was only marginally significant ($p = 0.07$; Table 4).

There was no effect of tree species richness on k or S , regardless of the drought treatment (Table 4, Fig. 6a and b). Response ratios indicated ca 8.3% decrease in k and a 24.2% decrease in S due to drought

Table 3

Effects of tree species richness and drought on stabilization factor (S) under oak and beech in Zedelgem. ($\text{lmer}(S \sim \text{richness} + \text{treatment} + (1|\text{composition}))$).

| Variables | Estimate | Std. error | t value | p |
|---|----------|------------|---------|-------------|
| Oak | | | | |
| Intercept | 0.185 | 0.023 | 7.93 | 0.00 |
| Richness | 0.002 | 0.007 | 0.36 | 0.72 |
| Drought | 0.021 | 0.009 | 2.24 | 0.04 |
| Random effects (as standard deviation) ~ 1 composition | | | | |
| Intercept | 0.018 | | | |
| Residual | 0.023 | | | |
| R ² m | 0.12 | | | |
| R ² c | 0.45 | | | |
| Beech | | | | |
| Intercept | 0.232 | 0.019 | 11.84 | 0.00 |
| Richness | −0.003 | 0.006 | −0.54 | 0.59 |
| Drought | 0.032 | 0.014 | 2.17 | 0.04 |
| Random effects (as standard deviation) ~ 1 composition | | | | |
| Intercept | 0.00 | | | |
| Residual | 0.03 | | | |
| R ² m | 0.18 | | | |
| R ² c | 0.18 | | | |

Bold indicates p value was less than 0.05.

Table 4

Effects of tree species richness and drought on decomposition rate (k) and stabilization factor (S) across all plots in ORPHEE. ($\text{lmer}(\log(k) \sim \text{richness} + \text{treatment} + (1|\text{block:treatment}) + (1|\text{composition}))$; $\text{lmer}(S \sim \text{richness} + \text{treatment} + (1|\text{block:treatment}) + (1|\text{composition}))$).

| Variables | Estimate | Std. error | t value | p |
|---|----------|------------|---------|-------------|
| Decomposition rate | | | | |
| Intercept | −4.811 | 0.050 | −96.01 | 0.00 |
| Richness | −0.004 | 0.013 | −0.35 | 0.72 |
| Drought | −0.104 | 0.048 | −2.14 | 0.07 |
| Random effects (as standard deviation) | | | | |
| Intercept (1 composition) | 0.02 | | | |
| Intercept (1 block:treatment) | 0.05 | | | |
| Residual | 0.22 | | | |
| R ² m | 0.05 | | | |
| R ² c | 0.10 | | | |
| Stabilization factor | | | | |
| Intercept | 0.087 | 0.008 | 10.44 | 0.00 |
| Richness | 0.002 | 0.002 | 0.87 | 0.39 |
| Drought | −0.028 | 0.008 | −3.44 | 0.01 |
| Random effects (as standard deviation) | | | | |
| Intercept (1 composition) | 0.008 | | | |
| Intercept (1 block:treatment) | 0.010 | | | |
| Residual | 0.027 | | | |
| R ² m | 0.18 | | | |
| R ² c | 0.34 | | | |

Bold indicates p value was less than 0.05.

across all plots.

4. Discussion

European forest ecosystems are expected to be exposed to more frequent and severe droughts as a result of climate change (Allen et al., 2010; Kovats et al., 2014; Park Williams et al., 2012). A lower SOM decomposition rate (k) under drought conditions has been reported globally (Parton et al., 2007; Zhang et al., 2008), and in numerous studies for several ecosystems; i.e. grasslands (Sanaullah et al., 2012; Walter et al., 2013), woody species of the Mediterranean basin (Saura-Mas et al., 2012), temperate forests (Gabriel and Kellman, 2014) and Mediterranean forests (Santonja et al., 2017). We found a decrease in the decomposition rate under beech for the drought treatment in Zedelgem, and a marginally significant decrease under drought in ORPHEE. Response ratios showed a 10% decrease in the decomposition rate under beech in Zedelgem and an 8.3% decrease in ORPHEE. A

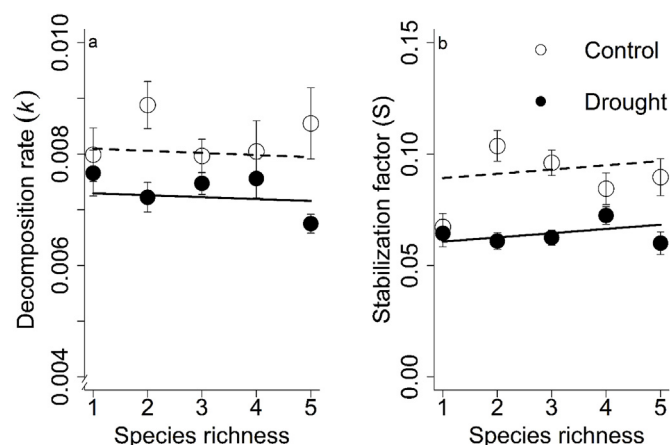


Fig. 6. Changes in a) decomposition rate (k) and b) stabilization factor (S) with tree species richness and under different treatments (control and drought) in ORPHEE. Error bars represent SEM, n = vary for species richness, range = 8–40. Regression lines shown for control (dashed) and drought (solid) treatments.

slower decomposition rate under drought can be explained by decreased microbial activity (Lee et al., 2014; Manzoni et al., 2012; Schimel et al., 2007) and reduced enzyme activity (Sardans and Peñuelas, 2005).

The tea bag method also allows to evaluate the long term C sequestration potential of an ecosystem by measuring the stabilization factor, S (Keuskamp et al., 2013). During decomposition, stabilization of a fraction of the labile compounds into recalcitrant compounds depends on environmental factors (Berg and Meentemeyer, 2002; Prescott, 2010). S is expected to be higher under drought conditions (Keuskamp et al., 2013), but we found different responses of S to drought at the two sites. As expected, S was higher in drought subplots under both oak and beech at Zedelgem. In contrast, at ORPHEE, S was lower in drought plots compared to control plots. Hence, results indicate a higher C storage potential in soils subjected to drought in Zedelgem, but also in the irrigated (control) ORPHEE soils. The higher S under control in ORPHEE is surprising and contrasting with the expectations. It remains difficult to identify the exact mechanism regulating SOM stability (Lutzow et al., 2006), but our result might be explained by the environmental context of each site, specifically the regulatory roles of soil water availability and soil type in ecosystem functioning (Ratcliffe et al., 2017). SOM stabilization is determined by the interaction of organic molecules with other substances and the accessibility of organic molecules to microorganisms and enzymes (Paul, 2016; Sollins et al., 1996). Under dry conditions, the activity of soil microorganisms (Manzoni et al., 2012) and enzymes (Sardans and Peñuelas, 2005) decreases, which could have limited their interaction with SOM in ORPHEE. The stabilization process is also influenced by the physico-chemical characteristics of the site (Six et al., 2002) through the entrapment of SOM within soil micro-aggregates (Plaza et al., 2013; Six et al., 2002). Loamy soils are generally better for SOM stabilization than sandy soils (Hagedorn et al., 2003). Under the very dry conditions (~5% gravimetric water content in drought plots) of the sandy ORPHEE soil, the physico-chemical bond between the easily degradable organic material and the soil might be too weak to promote stabilization. On the contrary, in control plots, irrigation could have increased the accessibility and interaction of the organic material with microorganisms and enzymes. This could have improved the physico-chemical protection of the organic material and thus increase stabilization.

Tree species diversification has been suggested to increase the resistance and resilience of forest ecosystems to stress and improve ecosystem functioning. Here we found a first indication that increasing tree

species richness could offset the reduced decomposition rate induced by drought. This supports findings of Ratcliffe et al. (2017), who reported that the complementary effects of tree species mixing in driving ecosystem functioning increased under drier condition. However, this effect was only detected under oak in the more humid climate of Belgium, but not under beech nor under the drier climate in southern France.

Main drivers of SOM decomposition include the resource quality, physico-chemical environment and decomposing organisms (Swift et al., 1979). In our study, by using standard decomposition material (tea bags), we focused on the tree species richness and reduced precipitation effects on the decomposition process through changes in the physico-chemical and biological microenvironment. Thus the initial litter quality was excluded as confounding factor for explaining the decomposition rates in our study. However, the overall quality of the litter returning to the soil (Hättenschwiler, 2005) can improve soil quality (Carnol and Bazgir, 2013; Poca et al., 2015; Prescott, 2010). Also, mixed litters decompose faster than single species litters (Gessner et al., 2010; Handa et al., 2014; Jacob et al., 2010; Vivanco and Austin, 2008; Vos et al., 2013) influencing soil chemistry and the decomposing organisms (Prescott and Grayston, 2013). Additionally, a positive effect of tree species richness on decomposition of standard material (cellulose strips) has been reported across European forests (Joly et al., 2017). The positive relationship between k and tree species richness in drought treatments under oak may be explained by such improved soil conditions through the diversity of litter and root exudates provided by the surrounding tree species inducing a complementarity effect. Mixing of functionally dissimilar species has a synergistic effect on soil microorganisms and may improve the microenvironment (Prescott and Grayston, 2013; Scherer-Lorenzen, 2008). Also, soil microbial communities depend on tree species identity (Gunina et al., 2017; Sommer et al., 2017). Thus, tree species mixtures may provide a higher microbial diversity and a larger potential range in the degradation of substrates. Further, our results provide support for the hypotheses that the species diversity can stabilize ecosystem processes in response to disturbances and variation in abiotic conditions (Gamfeldt et al., 2013; Tilman et al., 2014), within the biodiversity-ecosystem functioning debate (McCann, 2000; Nielsen et al., 2011) and that complementarity may be more important in more stressful environments (cf. stress-gradient hypothesis of Bertness and Callaway, 1994).

However, this tree species effect was not observed for ORPHEE, nor under beech or control conditions under oak for Zedelgem. This absence of a tree species richness effect may be due to site conditions (Ratcliffe et al., 2017) and/or age of the plantations. With increasing age, stands with specific species composition and richness develop a distinct microenvironment affecting decomposition (Joly et al., 2017). Also, soil processes like SOM accumulation, C and N mineralization gradually increase with forest age (Rahman et al., 2017). In addition, this was a short term study conducted during summer which did not capture the seasonal variation in decomposition. Thus, the effect observed in this study could vary in different seasons and might intensify over time.

As suggested by Keuskamp et al. (2013), the TBIs showed clearly distinct values between ecosystems, with lower values in the southern, relatively dry, sandy ORPHEE soils. TBI values in ORPHEE were lower than the range of values reported by Keuskamp et al. (2013) for European forests. The TBI values in Zedelgem were within the range of published values for temperate ecosystems. k and S are expected to increase and decrease, respectively, with mean annual temperature and precipitation (Keuskamp et al., 2013). Lower precipitation, site quality and land use history before plantations could be, at least partly, responsible for the lower TBIs in ORPHEE compared to Zedelgem. The ecosystem functioning of European forests depends on forest types, geographic region and climatic conditions (Ratcliffe et al., 2016). The ORPHEE site was a pine forest, while Zedelgem had been under agricultural use for several decades before the plantations. Agriculture practices are characterized by high pH, regular ploughing and

fertilization with a shorter SOM turnover rate. Also, previous land use strongly influences soil C and N mineralization after afforestation (van Leeuwen et al., 2017). Furthermore, ORPHEE plantations are located on a sandy soil, with low water holding capacity that might result in lower biological activity and lower decomposition rates.

To conclude, we found that tree species richness could attenuate the drought effect on SOM decomposition in young plantation forests. This effect was found under oak, indicating that admixing species to oak could be beneficial in the context of climate change. Our results also indicate that the SOM stabilization rate would respond differently to a precipitation change, depending on the local environmental context. This context dependency of SOM transformation could be tested in a long-term decomposition study to allow for the seasonal variability. Our study demonstrated the usefulness of TBIs for comparing decomposition characteristics of different sites and assessing the effects of experimental treatments through a short-term study.

Author contributions

Study conception and design: MMR, MC and KV.

Appendix

Acquisition of data: MMR, BC and HJ.

Analysis and interpretation of data: MMR, BC and MC.

Drafting of manuscript: MMR and MC.

Critical revision: MMR, MC, KV, BC and HJ.

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Fig. A1. A 3 m × 3 m rainout shelter in the Zedelgem site of FORBIO (Belgium). PVC gutters (~12 cm) were placed at an interval of about 25 cm. A 20 cm slope was created by placing the gutter at a height of 0.95 m from the ground at the upper side and 0.75 m at the lower side. A 6 m long gutter was placed at the lower side to channel the intercepted water far away from the plot.

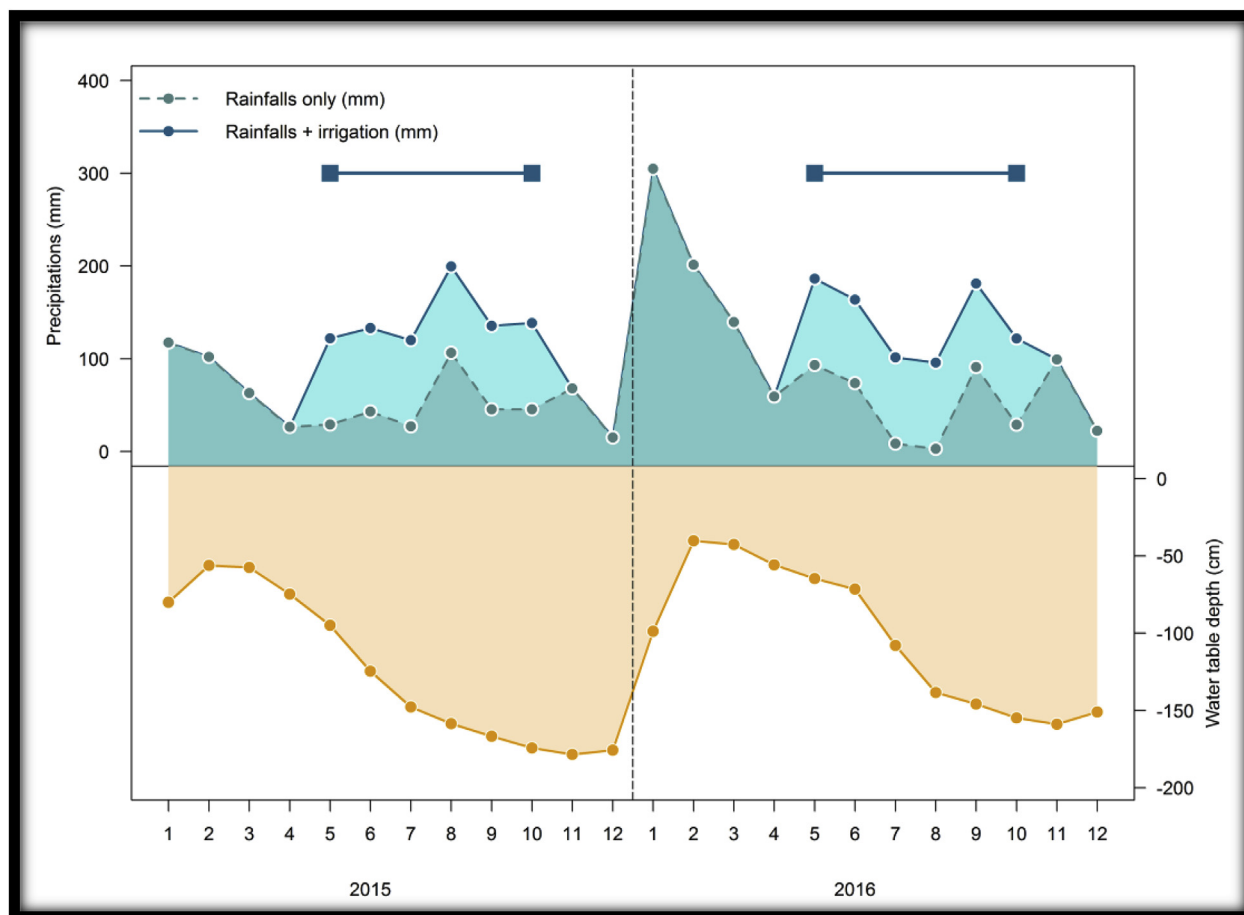


Fig. A2. Comparison of natural rainfall, irrigation and water table depth. Rainfall and water table depth were measured monthly (1 January to 12 December) in a pine plantation close to the ORPHEE experiment (France). Irrigation was 3 mm per night and was summed across days and added to the natural rainfall. The irrigation period is indicated by the two horizontal lines in the upper panel.

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