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Interactions between drought and shade on the

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walnut-based alley-cropping system

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Keywords

agroforestry ; rainfall manipulation ; tree-crop interaction ; yield components ; Mediterrean area ; climate change

Abstract

In the face of climate change, more frequent drought events are expected in the Mediterranean regions. Alley cropping is an agroforestry practice that represents a promising adaptation strategy to sustain yield productivity under drier conditions. However, the presence of trees limits the productivity of the intercrop by reducing light availability and by competing for soil water resources, which could potentially exacerbate the yield losses due to drought conditions. Furthermore, the effects of co-occurring drought and shade stresses on annual crops are still poorly understood. To tackle this issue, we performed a rainfall manipulation experiment on winter pea (*Pisum Sativum L.*) grown in full sun conditions (agricultural control) and under different levels of shade in a 25-year walnut-based alley cropping system located in southern France. We evaluated first the effect of trees on light and water availability and we then studied the effects of early drought (135 mm excluded from April to the end of May) and light conditions on crop performances and yield components. At 3.5 m from the tree line, light availability was reduced on average by 19% at South and 35% at North of trees over the entire crop cycle and mostly after tree budburst. The impact of trees on soil water content in the crop root zone was weak thanks to the good complementarity of the respective root systems. Under normal rainfall conditions, tree shade decreased pea yield from -25% to -77% compared to full-sun conditions. In case of spring drought, pea yield was decreased by -22% in full-sun conditions. The negative effect of tree shade was reduced and decreased pea yield only by -1% to -47%. Under the most intense shade conditions, pea yield was even higher under drought than in normal rainfall conditions. The analysis of crop dynamics and yield components revealed that the vegetative development of pea ceased under drought to the benefit of biomass allocation toward the reproductive organs. Pea yield was less impacted by tree shade under spring drought because yield elaboration relied less on the success of pod set, sensitive to shade, and more on grain filling, improved in case of early

drought event. This study supports the hypothesis that agroforestry systems may be more resilient in the case of early drought.

Introduction

There is a raising concern about agroecosystems sustainability and food security in the context of climate change (Godfray et al., 2010). While the world population is likely to increase until the end of the 21st century (Gerland et al., 2014), crop yields have been stagnating in many regions of the world during the last decades (Brisson et al., 2010; Calderini & Slafer, 1998; Lin & Huybers, 2012). Although climate change is not the unique cause to observed yield stagnation (Ray, Ramankutty, Mueller, West, & Foley, 2012), there is a large consensus among the scientific community to agree that yield trends and variability are linked to overall climate variability (Moore & Lobell, 2015; Osborne & Wheeler, 2013). Under Mediterranean climates, the more frequent and prolonged drought and heatwave events seriously challenge crop production at the regional level (Ababaei & Chenu, 2020; Cammarano et al., 2019). In response to this challenge, farmers and researchers look for innovative strategies for climate change adaptation (Howden et al., 2007). Diversifying agroecosystems at both national and farm-level may be an adequate solution to sustain and stabilize crop production under increasing climate hazards (Reidsma, Ewert, Lansink, & Leemans, 2010; Renard & Tilman, 2019).

Agroforestry (AF) is a promising agricultural practice for climate change adaptation and mitigation (Altieri, Nicholls, Henao, & Lana, 2015; Verchot et al.,

2007; Wolz, Lovell, et al., 2018). Among the wide diversity of AF designs, alley cropping systems, which combine tree lines and cropped alleys, are gaining attention because they allow conventional mechanized management operations. The introduction of trees inside agricultural fields improves local nutrient budget due to the reduction of nutrient leaching (Wolz et al., 2018), sustains soil organic matter in cropped horizons (Cardinael, Chevallier, et al., 2015; Cardinael et al., 2017; Pardon et al., 2017), sequesters C on the long term in deep soil horizon (Cardinael et al., 2018) and enhances floral and animal biodiversity (Boinot, Fried, et al., 2019; Boinot et al., 2019; Pardon et al., 2019) with potential positive impacts in terms of pest-regulation (Martin-Chave, Béral, & Capowiez, 2019). In addition, alley cropping systems reduce soil evaporation (Jackson & Wallace, 1999; Wallace, Jackson, & Ong, 1999), atmospheric evaporative demand (Kanzler, Böhm, Mirck, Schmitt, & Veste, 2018) and buffer climate extremes (Gosme, Inurreta-Aguirre, & Dupraz, 2016; Inurreta-Aguirre, Lauri, Dupraz, & Gosme, 2018). In a diachronic study in Spain, Arenas-Corraliza, López-Díaz, & Moreno (2018) evidenced a positive influence of alley cropping on barley yield in case of spring heat events, due to an overall reduction of thermal stresses during grain filling.

However, predicting the effects of drought on the functioning of alley cropping systems is particularly challenging because of the complex below- and aboveground interactions between crops and trees (Jose, Gillespie, & Pallardy, 2004; Ong, Black, & Wilson, 2015). From an aboveground perspective, microclimate modification by trees is perceived as an asset for facing drier conditions, but tree shade also becomes a preponderant factor limiting the productivity of the (inter)crop in mature AF systems. From a belowground perspective, the negative effects of competition between trees and crops for soil water resources were revealed by segregating root systems (Jose, Gillespie, Seifert, & Biehle, 2000; Korwar & Radder, 1994; Miller & Pallardy, 2001). But a few studies also revealed positive effects of the spatial complementarity of root systems between trees and crops, especially during dry periods when deep soil water resources are available (Gao et al., 2018; Schwendenmann et al., 2010) and possibly redistributed towards upper horizons (Bayala & Prieto, 2019). According to the stress-gradient hypothesis, the net balance between competition and facilitation in plant communities shifts towards more facilitative interactions under more stressful conditions (Bertness & Callaway, 1994). Nevertheless, this generic hypothesis has been shown partially false depending on the nature and the intensity of the stresses (Maestre, Callaway, Valladares & Lortie, 2009), and under Mediterranean climates, more frequent drought events could also amplify belowground competition under specific circumstances (*e.g.* shallow soil conditions, high tree density), threatening in turn the productivity of the system. In most cases, drought-shade interaction has a strong impact on crop yield in agroforestry because both drought and shade affect plant biomass allocation

differently according to stress timing and intensity. Although annual crops present different tolerance and plasticity to shade (Arenas-Corraliza, Rolo, López-Díaz, & Moreno, 2019), little knowledge exists on the effects of its interaction with drought on the productivity of annual cropped species. The analysis of crop yield and its components allows identifying critical periods during crop cycle and eventual

compensation effects at the plant level (Fischer, 1985). Improving the knowledge of critical periods could help to better understand yield variation in alley cropping systems. In durum wheat, Inurreta-Aguirre et al. (2018) showed that the number of grains per spike varied according to the position relative to tree lines, mostly because of contrasting shade conditions before anthesis (Savin & Slafer, 1991). Studies with shade application during the crop cycle revealed that development stages around flowering are critical for most of the annual crops because a limited supply of assimilates during this stage reduces the number and/or the weight of grains (Kirkegaard, Lilley, Brill, Ware, & Walela, 2018; Lake, Godoy-Kutchartt, Calderini, Verrell, & Sadras, 2019; Lake & Sadras, 2014; Sandaña, Harcha, & Calderini, 2009). While drought magnitude affects the overall plant biomass, drought timing profoundly affects the biomass allocation between vegetative and reproductive organs whether it occurs early or late during the crop development cycle (Wery, 2005). Rainfall manipulation experiments revealed that the harvest index of field pea and barley was improved under early drought events because of a restricted vegetative development but a sustained (or sometimes improved) reproductive development, while late drought events only impacted the reproductive stages (Day et al., 1978; Martin & Jamieson, 1996).

To assess the interactive effects of shade and drought on crop productivity in a mature alley cropping system, we performed a rainfall manipulation experiment and compared full-sun conditions to different shade levels in AF. As a case study crop, we chose winter pea (*Pisum Sativum L*.), a legume crop with indeterminate growth and particularly sensitive to drought conditions (Munier-Jolain, Biarnès,

Chaillet, Lecoeur, & Jeuffroy, 2010). We expected that well-developed trees would alter crop development and yield elaboration essentially through the reduction of light and water availability. We hypothesized that:

1) large walnut-trees strongly reduce light and soil water availability for winter pea compared to a full sun situation due to tree-crop competition

2) early spring drought impacts more strongly the vegetative development of winter pea than tree shade

3) pea yield is less impacted by agroforestry conditions under drought

Material and methods

Study site

The experimental site is located in the South of France (Prades-le-Lez, 43°42'15.9" N, 3°51' 4" E, Figure 1), at the Restinclières Farm Estate, one of the oldest agroforestry research site in Europe. Within the same parcel, two cropping systems are compared: agroforestry (AF) in the southern part and an agricultural control (AC), in the northern part. Although parcel design did not offer a randomized design between AF and AC (which is a known limitation of this experimental site), soil texture was spatially characterized in 2012 (Cardinael, 2015) and revealed overall homogenous conditions between respective cropping systems (Figure S.1). The soil is a deep alluvial Fluvisol (IUSS Working Group WRB, 2007), with a loam texture (41.0% of silt and 41.5% of sand) in the plough layer, and a more clayey texture in deeper horizons (Cardinael, Chevallier, et al., 2015). The soil is 4 to 10 m deep until the limestone bedrock. A water-table connected to the local intermittent river is usually deeper than 6 m, but may rise to 3 m during floods, and disappears in summer when the river stops flowing. The spatial variation of the current tree size probably reflects the soil depth heterogeneity (Figure 1).

Hybrid walnuts (Juglans regia x nigra, cv. NG23) were planted in 1995 at 13 x 4 m spacing on East-West oriented lines, separating cropped alleys. Stand density was 192 trees.ha⁻¹ originally but, in order to limit tree-crop competition, tree density was reduced by half in 2004 after a selective tree thinning. In 2017, tree height averaged 10.9 m, yielding to a mean height-to-alley width ratio of 0.84, reflecting that significant tree-crop interactions prevailed during this study (Dupraz & Liagre, 2008). Tree roots now occupy the entire cropped alleys, as revealed by soil pits. Tree roots explore the soil at least up to 6 m deep (observed through soil coring techniques), but the maximum depth of the root system is unknown. The water table ceiling probably limits it at approximately 6 m depth in winter.

Crop rotation is mainly based on winter crops (Durum Wheat - Winter Barley -Winter Pea) since 1995. In 2018-2019, the experimental field was ploughed on the 11th of December to 30 cm depth and a semi-leafless winter pea variety (Pisum Sativum *cv. Dexter*) was sown. Plant density was standardized at 80 plants.m⁻² in observation quadrats by removing extra plants by hand at the end of winter to avoid any effect related to sowing density. No fertilization was added and only one fungicide was applied right after the beginning of flowering. Weeding was

performed by hand in all quadrats until complete closure of pea canopy was reached.

Experimental design

The rainfall manipulation experiment was conducted in a paired design (with/without rain exclusion) within 8 subplots, distributed over the two cropping systems (4 in AF and 4 in AC) (Figure 2). Each AF subplot comprised two adjacent trees and one of them was randomly chosen for rainfall exclusion. Subplot locations were chosen to ensure that trees had similar diameter at breast height, height, earliness of budburst, pruning management and local tree neighborhood (number of adjacent trees on the same line). Homogeneity of light conditions within the pairs of trees was also controlled by measuring light interception by the canopy with hemispherical photographs. Monitored quadrats were located 3.5 m from the tree line, both North and South, to have comparable intensity of belowground competition between trees and crops.

In total, 40 monitored quadrats (1 m²) were distributed in AC (8) and AF (32). In AF, we took advantage of the East-West orientation of tree lines and the heterogeneity of trees in the plot to measure the impact of contrasting light conditions, *i.e.* in quadrats lying North (very shady) or South (sunnier) of the tree lines and situated in subplots with small or large trees with early or late phenology. The rainfall regime was manipulated using mobile rainout shelters over half of the quadrats.

Rainout shelters design and operation

The set-up of rainout shelters aimed at limiting the artifacts inherent to any rainfall manipulation experiment (Beier et al., 2012). Rainfall exclusions were conducted only for rainfall events forecasted to be more than 10 mm of rain. We did so to i) minimize the impacts of light interception by rainout shelters and ii) avoid any permanent obstacle on the field to ease the technical management of the crop and ensure homogeneity of cropping conditions. Rainout shelters were composed of steel tubes from greenhouse structures and a movable roof made of a translucid tarpaulin (Figure 1). The tube structure was circular and covered 15 m² (diameter of *ca.* 4.5 m). Four rainout shelters were located around each tree and covered a total area of 60 m² (estimated as 60% of the total soil area exploited by a tree). This layout was chosen to reduce the bias that could result from a split-root effect on the tree, with a part of the root system in drier soil (under the shelters) than the other part (outside the shelters).

All tarpaulin roofs were stored in the vicinity of experimental plots and could be quickly assembled just before rain events. During rainfall exclusion, a rain gutter attached to the tarpaulin collected rain into a tank, itself connected to an outlet pipe for water evacuation far from the rain-excluded areas. Monitored quadrats were placed at the centre of each covered areas. We limited edge effects related to external water flows by i) trenching surface soil around rain-excluded areas to avoid inflows from run-off and ii) by setting up a fine-meshed net on the side of rainout shelters to intercept lateral rainfall in windy conditions. Spatial measurements of rainfall and soil water content during the prototyping year of

rainout shelters revealed that edge effects were negligible from 50 cm inwards the border of the rain-excluded area. One quadrat was excluded from the study due to leaking issues in the centre of one rainout shelter during an intense hail event.

Climate context and rainfall manipulation scenario

The study site has a sub-humid Mediterranean climate with an average cumulated rainfall of 853 mm and an average temperature of 14.1 °C over the past 25 years. Rainfall distribution is bimodal, with precipitations mostly distributed over fall and spring. Fall thunderstorms are typical in the region (Vautard et al., 2015) and usually replenish the soil to field water capacity after dry summers. Therefore, the different rainfall regimes were compared between years based on cumulative rainfall from the 1st of September to June (*i.e.* end of harvest period). Cumulative rainfall in rainfed conditions (CTL) reached 628 mm between September 2018 and June 2019, which was just below the median according to the past 25 years (Figure 2). Rainfall events during Fall and Winter were above the median scenario, while conditions became relatively dry over the end of winter and spring. Rainfall exclusion was performed during four rainfall events (>10 mm) from April to May, reducing cumulated rainfall by 135 mm (20% of the total) in rain-excluded (EXC) quadrats. Considering the distribution of cumulative rainfall over the past 25 years, rainfall exclusion performed in EXC mimicked a scenario drier than the 2nd driest year (in 2005, with 574 mm from September to June), with an unusual dry spring (only 75 mm in EXC between the period from the 21st of March to the 21st of June, which is close to the 2nd driest spring observed in 2014, with 69 mm).

During the crop cycle, air temperature was unusually cold for the region, especially during the spring period with both mean and maximal air temperature of 0.7 and 1.3°C below the average. Mean daily air temperature remained below 25°C during the whole crop cycle, preventing crop yield reduction due to flower or seed abortion induced by thermal stress above this threshold (Guilioni, Wery, & Tardieu, 1997; Jeuffroy, Duthion, Meynard, & Pigeaire, 1990).

Environmental monitoring

Local air temperature and relative humidity were measured using HMP 155 probes (Campbell Scientific, USA) at a meteorological station located in AC (near subplot I) (Figure 1). Incident and intercepted rainfall were recorded with a tipping-bucket rain gauge (ARG100, Campbell Scientific, USA) and standardized rain gauges located next to rainout shelters in each subplot.

Light conditions were documented with hemispherical photographs (HPs). To capture the impact of tree canopy dynamics on local light availability, HPs were shot on each quadrat and repeated at three different dates: before tree budburst, at the end of the growth of tree short shoots and at the end of the growth of tree long shoots. HPs were processed with the WinSCANOPY software (Regent Instruments Inc., QC, Canada) and daily PAR radiation [MJ.day⁻¹] were estimated assuming a solar constant of 1370 W.m⁻², a spectral fraction of 0.51, an atmospheric transmissivity of 0.6 and a diffuse radiation fraction of direct radiation of 0.15. For diffuse radiation flux, the model of clear sky was selected.

At each quadrat, composite time series of daily PAR reaching the crop were established by i) considering PAR estimated from a picture of leafless trees before budburst and ii) by applying linear interpolation on PAR estimates according to the time between budburst (or the last picture) and pictures shooting dates. To ensure the validity of the method, 12 additional sensors (PAR-80, Decagon Devices, Pullman, WA) were distributed in AC (4) and AF (8). Sensors were set up in late February until harvest and post-calibrated. Estimations from HPs and measurements from PAR sensors showed good agreement overall ($r^2 = 0.95$), although HPs overestimated slightly cumulated PAR_{inc} in all cropping conditions due to inadequate consideration of daily cloudiness (Figure S.2). Transmittance, defined as the ratio of incoming light in the understory over incoming light in a treeless situation, was computed daily to evaluate shade dynamics. Estimated incident PAR (PAR_{inc}) was cumulated over the whole crop cycle, from sowing to harvest, as a proxy of local light availability.

Soil water content (SWC) measurements were performed using time-domain reflectometers (TDR) sensors (CS650, Campbell Scientific, USA) in AC and AF. TDR probes were installed horizontally at three depths (50; 150; 250 cm) by digging soil pits in four subplots (I, IV, B and H), with sets of sensors under both rainfall regimes. Additional sensors were installed in the plough layer (20 cm) after crop sowing in early January. At sensor set-up, volumetric soil content of the monitored soil layer was independently measured by gravimetry on undisturbed soil samples close to each probe. Theoretical values of field capacity (FC) and permanent wilting point (PWP) were computed using the pedotransfer function proposed by Rawls,

Pachepsky, Ritchie, Sobecki, & Bloodworth (2003). TDR signals were corrected using field measurements from soil cylinders, and signal consistency was visually assessed for every sensor in relation to rainfall dynamics and signal position in comparison to field capacity and permanent wilting point. SWC records at 150 and 250 cm showed only minor fluctuations during this period, and maximal pea rooting depth reached down to 100 cm this year (evaluated at maximal crop development, at the end of May), so only SWC dynamics at 20 and 50 cm were considered in this study.

Crop growth monitoring

Phenological development was evaluated every week according to the BBCH scale (Hack et al., 1992), from emergence to harvest, with an emphasis during the flowering period. Data were summarized according to 3 periods: i) vegetative growth, from emergence to maximal LAI measurement ; ii) flowering period, from the opening of flowers (stage 61) to flower decay (stage 69) and iii) fruit development and seed maturation, from pod set (stage 71) to harvest date.

Non-destructive methods were used to characterize the Leaf Area Index (LAI) dynamics for all quadrats. In the first period (from emergence until pea canopy closure reached 80%), LAI was estimated based on cover rate, using a linear regression ($r^2 = 0.91$, data not shown) between destructive LAI measurements and cover rate measured in other parts of the field. The cover rate was estimated through picture analysis with the ImageJ (version 1.46) software (Schneider, Rasband, & Eliceiri, 2012) and destructive LAI measurements were done by measuring the surface of pea green leaves with the WinFolia software (Regent

Instruments Inc., QC, Canada). Beyond 80% canopy closure, LAI was measured by means of an LAI-2200 Plant Canopy Analyzer (LI-COR Inc., Lincoln, Nebraska) until senescence.

The whole quadrat (1m²) was harvested at pea maturity from the 13th to the 19th of June in EXC and from the 19th to the 21st of June in CTL. On each sample, aboveground total biomass and grain yield were assessed. All biomass samples were oven-dried at 50°C until weight remained stable. At harvest, yield components, *i.e.* the number of pods per plant, the number of seeds per pod and thousand kernel weight (TKW) were recorded at the quadrat level. Additionally, two plants were randomly sampled at harvest near each quadrat (80 plants in total) and for each plant, pods and seeds were collected, counted and weighed per node position. So the determination of yield components was performed at the stand (quadrat) and the individual plant level. Individual plant analysis was included to detect possible ontogenetic change (alteration of flowering or fruiting patterns) across growth conditions.

Data analysis

Statistical analyses were conducted with the R software (R Core Team, 2020) to: 1) evaluate the influence of tree on light and water availability and to 2) investigate the effects of light and water availability on crop yield and to 3) analyze plant biomass allocation between vegetative and reproductive organs (maximal LAI and yield components). Tree effects on light availability were evaluated by comparing the transmittance dynamics and cumulated incident PAR between AF and AC. The effects of trees and rainfall exclusion on SWC were compared according to daily dynamics. For each soil layer, data from individual sensors were averaged either by cropping system (AC against AF ; 4 sensors by modality) or by rainfall regime (CTL against EXC ; 4 sensors by modality).

The effects of light availability and rainfall regime on maximal LAI, yield components, grain yield, straw yield and harvest index were tested using linear mixed models fitted with the lme4 package (Bates, Machler, Bolker, & Walker, 2015). For each target variable, a full model with cumulated PAR_{inc} and rainfall regime as fixed effects was compared to progressively reduced models. Subplots were introduced as random effects to account for effects related to uncontrolled environmental variability among the blocks. Second-order Akaike Information *Criterion* (AIC_c) was computed for each model with the package AICmodavg (Mazerolle, 2020) to correct bias related to small sample size (Hurvich & Tsai, 1991). The final model was retained according to the lowest AIC_c value (Δ AIC_c > 2) and significance of the fixed effects was tested according to the Satterthwhaite's method implemented in the lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2017). In addition to the linear regressions, the bivariate relationships between i) maximal LAI and straw yield, ii) yield components and grain yield and iii) maximal LAI and yield components were evaluated using standardized major axis (SMA) regression with the smatr package (Warton, Duursma, Falster, & Taskinen, 2012).

Finally, curves of yield components at the plant level were compared using paired t-test applied for each reproductive node number to assess if light conditions in AF-S and AF-N induced changes in the fruiting pattern compared to the conditions in AC. Bonferroni correction was applied to adjust the significance level in case of multiple comparisons.

Results

Reduction of light and soil water availability under large walnut trees PAR levels in agroforestry (AF) conditions (Figure 3) featured a gradient of cumulated incident PAR (PARinc), partly explained by quadrat position (North or South) relative to the tree. In agricultural control (AC), sky conditions were pretty clear overall (Figure 3.A.) and cumulated PAR₀ reached 1112 MJ.m⁻² over the cropping period. In AF, cumulated PAR_{inc} was reduced during the cropping period by 19 % (-236 MJ.m⁻²) and 35 % (-439 MJ.m⁻²) at South (AF-S) and North of the tree (AF-N) (Figure 3.C.). Dynamics of light availability exhibited three distinctive periods (Figure 3.B.): i) from December to February, light transmittance was around 75% with only minor differences (2%) between AF-N and AF-S; ii) from March to tree budburst (which occurred from the 17th of April to the 6th of May across subplots), relative light transmittance was 92% in AF-S and 75% in AF-N; iii) from tree budburst to crop harvest (between the 13th and 21st of June), light transmittance dropped by 20% more in AF conditions, and decreased continuously until harvest down to 60 and 40 % in AF-S and AF-N respectively. Overall, 65% of

light reduction was observed during the part of the crop cycle that occurred after tree budburst.

During the cropping period, soil water content (SWC) dynamics of AC and AF differed in shallow soil layers but not in deeper soil layers. At 20 cm depth (Figure 4.A.), SWC did not differ much during the winter period (December to February), as SWC remained around field capacity. From early March to mid-May, SWC in AF became progressively drier in comparison to AC. After mid-May, SWC became less contrasted, and differences were no longer perceptible at harvest. At 50 cm depth (Figure 4.C.), mean sensor signals remained close to the 1:1 line.

Effects of rainfall regimes on soil water content

From sowing to early April, SWC dynamics between CTL and EXC conditions were similar (Figure 4.B and D, blue dots). During spring rainfall events, 135 mm of rain water was excluded in EXC and impacted SWC down to 50 cm depth (Figure 4.B and D, orange and red dots). Differences in SWC dynamics between CTL and EXC rainfall regimes lasted until harvest, although they diminished progressively at the end of the cropping period.

Impacts of light conditions and rainfall regime on winter pea

Crop phenological development was very sensitive to the rainfall regime while light conditions had a weaker influence (Figure 5.A.). The beginning date of flowering (around the 29th of April) was similar in all cropping conditions, although major rainfall exclusion were performed during the preceding month. The flowering duration was shortened by 12 days on average in EXC compared to CTL, and subsequent phenological stages (*e.g.* pod elaboration, grain filling, grain maturation) were observed earlier in EXC. Shade effects on flowering were only observed in AF-N, where flowering lasted longer (up to 14 days). At the end of the crop cycle, harvest dates differed up to 8 days between cropping conditions and rainfall regimes.

At harvest, light conditions and rainfall regime negatively impacted straw and grain yield (Figure 6). Straw yield ranged from 134 to 344 g.m⁻², with a clear difference between CTL (136 to 344 g.m⁻²) and EXC (134 to 206 g.m⁻²). Light conditions (P =0.022) and rainfall regimes (P < 0.001) had a significant impact on the slope and the intercept of the selected mixed model respectively. On the other hand, effects on grain yield were more complex due to the significant interaction observed between light conditions and rainfall regimes (P < 0.001). Pea yield were lower in AF conditions compared to AC in both rainfall regimes but the yield reduction due to the presence of trees was more pronounced in CTL (-25% to -77% yield difference between AC and AF) than in EXC (-1% to -47% between AC and AF). Under spring drought, pea yield was reduced in AC by -22% compared to rainfed conditions while it was relatively improved in AF conditions between +12% (when $PAR_{inc} > 920 \text{ MJ}.\text{m}^{-2}$) and +20% (when $PAR_{inc} < 920 \text{ MJ}.\text{m}^{-2}$). The HI was systematically higher in EXC (HI_{mean} = 0.522) than in CTL (HI_{mean} = 0.428) in all cropping conditions. The interaction between light conditions and rainfall regime on HI was significant (P = 0.002) and reflected that the HI was less influenced by the light gradient in EXC (coefficient of variation (CV) = 6.7%) than in CTL (CV = 14.2%).

Linkages between plant biomass allocation and crop yield

Rainfall regime impacted maximal LAI and yield components of winter pea whereas light conditions influenced yield components only (Table 1). The vegetative development ended on average 10 days earlier (Figure 5.A.) and maximal LAI was reduced by 46% in EXC (P < 0.001) with no effect of light conditions (Figure 5.B.). The number of pods per plant was significantly reduced under shade conditions (P < 0.001), but presented a significant interaction with rainfall regime (P = 0.014). In particular, the number of pods per plant varied along the light gradient in CTL (observed range: 3.7 to 9.9 pods.plant⁻¹; CV = 26.5%), but did not in EXC (observed range: 4.4 to 7.7 pods.plant⁻¹; CV = 15.5%). Overall, spring drought reduced the number of pods per plant by -38% in AC but only by -8% in AF. On the opposite, spring drought had a positive effect on the number of seeds per pod (P = 0.001) and the TKW (P = 0.009). More specifically, TKW was increased on average by +10% in AC and +13% in AF in case of spring drought. Shade conditions decreased the number of seeds per pod (P = 0.026) and the TKW (P < 0.001).

Interdependences between maximal LAI, yield components and crop performances were observed (Table 2). Maximal LAI was significantly correlated to straw yield under all rainfall regimes (overall P<0.001 and R² = 0.74). Among yield components, grain yield was positively correlated with the number of pods per plants (overall P < 0.001 and R² = 0.50) and with the TKW (overall, P < 0.001 and R² = 0.45). Under CTL conditions, the number of pods per plant was positively correlated to grain yield (P < 0.001 and R² = 0.80). For the yield components, a significant relationship was only observed between maximal LAI and the number of pods per plant (P < 0.001 , R² = 0.34 ; Table S.3).

Different fruiting patterns were observed depending on rainfall regime and light conditions (Figure 7). Compared to AC, the number of pods per node and the number of seeds per pods were reduced in CTL at the higher reproductive nodes (*i.e.* later produced, nodes 9,10 and 11) in both AF locations (AF-N and AF-S). Kernel weight was significantly reduced along all reproductive nodes in AF-N, and only for nodes 8 to 11 in AF-S. In EXC conditions, yield component pattern was very similar in all cropping conditions. In comparison with CTL, the number of nodes bearing a pod in EXC was halved and induced a denser distribution of the other yield components toward low (*i.e.* early produced) nodes.

Discussion

Large walnut trees strongly reduce light availability but the impacts on soil water remain limited

Twenty-five years after the plantation of walnut trees in the AF plot, light interception by trees was significant but heterogeneous. Shade is expected to be the most intense close to the tree lines, where yield measurements were performed (Coussement et al., 2018; Pardon et al., 2018). Quadrats located North of tree lines had much lower light availability on average than in the South (Figure 3), as it was expected with East-West oriented tree lines. In a modeling experiment, Dupraz et al. (2018) showed that East-West oriented tree lines under Mediterrean latitudes induce higher spatial variability of incoming light in the alley as compared to North-South oriented tree lines.

The gradient of light reduction observed in AF resulted from structural and phenological heterogeneity of the tree stand. Walnut trees presented heterogeneous crown volumes (Figure 1) and the trees' growth rate was likely impacted by site heterogeneity (*e.g.* soil properties, water table depth) and individual genetic factors. The budburst period differed markedly between subplots, with differences up to 4 weeks between early and late trees (from mid-April to early May). In a deciduous AF system, most of the reduction of available light for winter crops occurs after tree budburst, although the reduction induced by woody parts of the tree (*i.e.* trunks and branches) during the winter period can not be neglected as trees become larger (Figure 3.B and Talbot & Dupraz (2012)). The timing of tree budburst is often mentioned to be a critical point regarding light competition (Dufour, Metay, Talbot, & Dupraz, 2013) as it occurs when PAR₀ radiation increases drastically (Figure 3.A). The earlier the budburst is, the stronger the impact of shade on critical phenological stages like flowering (Figure 5).

In contrast, walnut trees moderately impacted soil water content in the crop root zone, probably due to the good complementarity of tree-crop root systems. During the cropping period, soil water dynamics were very similar between the two cropping systems in deep soil horizons (\geq 50 cm) (Figure 4.C), while soil conditions were drier in AF as compared to AC in the plough layer (Figure 4.A). The reduction

of soil water availability by trees in the crop root zone has been observed in AF with manipulative studies, either by installing physical barriers or by pruning roots (Jose et al., 2000; Korwar & Radder, 1994; Miller & Pallardy, 2001). However, these studies dealt with summer crops, when water requirements of both trees and crops were simultaneously high. In temperate deciduous AF systems with winter crops, a higher complementarity for water resources is expected, either temporally because winter crops can take advantage of fall and winter precipitation when trees are leafless, or spatially because trees can benefit from deeper water resources during summer. At the study site, previous work showed that the distribution of tree root systems shifted towards deeper horizons over the long term as a response to treecrop competition, root destruction by annual ploughing in the upper soil horizon and local soil conditions with substantial water resources in deeper soil horizons (Cardinael, Mao, et al., 2015; Mulia & Dupraz, 2006). Nevertheless, we were surprised by the earliness of the drying trend observed in AF in upper soil horizon, since early March and way sooner than tree budburst. Although tree water uptake begins a few weeks before budburst, during bud swelling (Essiamah & Eschrich, 1986), uptake is generally considered as limited at first and most of the competition for water occurs once leaf canopy is well-developed (around end of May in this site) (Broadhead, 2015). Therefore, further analyses should be performed to investigate whether such trend is related to crop water requirements, soil water dynamics (*e.g.* evaporation, infiltrability) or soil heterogeneity (*e.g.* texture, compaction). Rainfall exclusion performed in spring had, *in fine*, a much stronger effect on soil water availability in the crop root zone than trees (Figure 4).

Spring drought blocked the vegetative development of winter pea while tree shade only had a minor impact

Spring drought reduced pea LAI and straw biomass at harvest. Rainfall exclusion affected pea growth just before the period of maximal leaf expansion (Figure 5), reducing maximal LAI (Table 1) and the number of reproductive nodes of plant profiles (Figure 7). Under drought, vegetative growth of pea ceases due to physiological regulation at cell level (Davies, Tardieu, & Trejo, 1994; Lockhart, 1965), which decreases leaf production and leaf expansion rates (Lecoeur & Guilioni, 1998; Lecoeur & Sinclair, 1996 ; Lecoeur, Wery, Turc, & Tardieu, 1995).

In comparison, tree shade only had a modest impact on vegetative development. Light conditions had a significant but rather weak effect on straw mass (Figure 6) and no effect on maximal LAI (Table 1). Though tree budburst occurred during the period of maximal leaf growth rate (Figure 5), light conditions were quite similar between AF and AC over the vegetative period of winter pea (Figure 3), as tree leaf canopies were still poorly developed. Maximal LAI of legume crops is not very sensitive to shade (Allard, Nelson, & Pallardy, 1991; Meadley & Milbourn, 1971; Verghis, Mckenzie, & Hill, 1999), suggesting that tree shade in such AF system does not affect much the vegetative growth of legume crop. The low sensitivity of leaf development to shade could be explained by C allocation priority towards vegetative organs during maximal leaf expansion. Jeuffroy & Warembourg (1991) showed that, under light reduction, the growing apex of winter pea constitutes a larger C sink compared to the other organs under formation, although sink strength

of the apex decreases progressively to the benefit of newly formed reproductive organs.

The cessation of vegetative development under spring drought strongly decreased pea yield potential in both AC and AF systems. In coherence with the reduction of maximal LAI under drought (Figure 5), the number of reproductive nodes at plant level (Figure 7) and the number of pods per plant at quadrat level (Table 1) were reduced as well. In indeterminate crops such as winter pea, biomass allocation during the end of vegetative development is complex, because leaf expansion, flower emission and pod set occur simultaneously at the plant level (Munier-Jolain et al., 2010). The cessation of the vegetative development under drought decreases the number of reproductive phytomeres (*i.e.* potentially bearing flowers or pods) and affects in turn the yield potential of pea crop, although some compensation effects during seed formation and grain filling can offset partially such yield reduction (Wery, 2005).

The negative effect of drought on pea yield faded with shade

Tree shade impacted less pea yield under drought conditions. Tree shade reduced grain yield in all rainfall regimes but the yield reduction was lower under spring drought (from -1% to 47% compared to AC) than in rainfed conditions (from -25 to -77% compared to AC) (Figure 6.B). In AF, grain yield in the shadiest conditions was even higher under spring drought than in rainfed conditions (+20% where PAR_{inc} < 920 MJ.m⁻²) and contributed to decrease the difference between yields in AF and AC. In terms of biomass allocation, the HI revealed that allocation to grain was particularly improved in case of spring drought along the shade gradient

(Figure 6.C). Similarly, Verghis et al. (1999) also observed on chickpea that the reduction of grain yield due to lower water availability (non-irrigated vs. irrigated conditions) was buffered under shade due to the improvement of both the grain yield and the HI. Though spring drought have a negative impact on pea yield, early drought can improve the HI of pea because pea plant compensates through other yield components in response to the limited vegetative development (Martin & Jamieson, 1996; Wery, 2005). The modification in terms of HI of winter pea also suggested that yield elaboration was less sensitive to tree shade under spring drought.

Spring drought and tree shade reduced both the number of pods per plant but the sensitivity of pod set to shade decreased under drought. In full-sun conditions, spring drought negatively impacted pea yield by stopping the vegetative development and reduced in turn the number of pods per plant (-38% in AC). Tree shade also decreased the number of pods per plant but mostly in rainfed conditions as revealed by the interaction effect (Table 1). Shade conditions around pod set is critical on grain yield and the HI of field pea and other legume crops (Lake et al., 2019; Lake & Sadras, 2014; Sandaña & Calderini, 2012). When light reduction occurs around pod set, higher flower and pod abscission rate reduces the number of pods per plant (Heindl & Brun, 1983; Jiang & Egli, 1993; Verghis et al., 1999). Under drought, the number of reproductive phytomeres of pea plant decreased, but similar pod production levels were sustained under more intense shade conditions (Figure 7). On the contrary, there was a clear decrease of pods for the latterproduced nodes in rainfed AF conditions. In a sink-source framework, flower or

pod abscission is considered as the result of trophic competition between the growing apex, flowers and pods along the nodes (Heindl & Brun, 1983; Jeuffroy & Warembourg, 1991). We interpreted this as a shift from source-limited conditions in AF-CTL (*i.e.* lack of photoassimilates under tree shade to fulfill flowers or pods requirements) to sink-limited conditions in AF-EXC (*i.e.* lower number of flowers or pods but sufficient production of photoassimilates under shade conditions to fulfill organs requirements) during the flowering and pod set period.

Pea seed weight was improved under spring drought in all cropping conditions and contributed to alleviate the negative impact of tree shade on pea yield. Tree shade decreased the number of seeds per pod and TKW, while spring drought had an opposite effect (Table 1). Nevertheless, TKW explained better the variations observed on grain yield than the number of seeds per pod (Table 2), suggesting that grain filling was a more determinant factor than seed set. In AF system, Dufour, Gosme, Bec, & Dupraz (2020) showed that intense tree shade close to tree line could considerably reduce TKW compared to other locations in the alley. Our results suggest that TKW reduction depends on the rainfall regime because of possible compensation effects at the plant level. Although the weight of pea seeds in a given reproductive node is relatively insensitive to light reduction (Sandaña et al., 2009), differences appear among the reproductive nodes due to the progressive increase of the number of sinks and the modification of cropping conditions (Munier-Jolain & Ney, 1998). Spring drought lowered the overall number of reproductive sinks and induced a greater proportion of bigger seeds at plant scale, with only a negligible effect of tree shade (Figure 7). On the contrary, shade

conditions decreased the seed weight along the reproductive nodes of a pea plant grown under rainfed conditions and negatively impacted TKW. Therefore, winter pea fully revealed its reproductive plasticity between the tested rainfall regimes in AF: depending on the potential number of reproductive sinks formed during the vegetative development, pea crop adjusted the number and size of reproductive sinks according to photoassimilate availability (Guilioni, Wéry, & Lecoeur, 2003).

Conclusion

In this 25 year-old walnut agroforestry system, tree shade was the major factor limiting pea yield, while tree-crop competition for water appeared limited. This was attributed to a good complementarity of the tree root system with the intercrop and consequent soil water reserves (*i.e.* deep soil combined with favourable rain regime). Under shade, yield reduction of winter pea was largely explained by the reduced number of pods per plant and reduced seed weight. Under spring drought, the yield potential of winter pea strongly decreased in all cropping conditions because of a reduced vegetative development. In agroforestry, the negative impacts of tree shade decreased under drought because biomass allocation shifted to the benefit of reproductive organs during pod set and grain filling. Under the most intense tree shade, crop yield was even higher under drought than in rainfed conditions. Although this study did not address the productivity of agroforestry at the whole plot scale, this experiment supports the hypothesis that agroforestry systems may be particularly resilient in case of early spring drought, which is an increasing concern with climate change.

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Tables

Table 1. Linear mixed effect analyses to test the effects of resource availability onproxies of vegetative and reproductive development.

| | LAI _{max} | | Nb. pods / plant | | Nb. seeds / pod | | TKW | |
|------------------------|------------------------------------|--------|--------------------------|--------|--------------------------|-------|----------|--------|
| | [m ² .m ⁻²] | | [ind.ind ⁻¹] | | [ind.ind ⁻¹] | | [g] | |
| Fixed Effects | Estimate | Р | Estimate | Р | Estimate | Р | Estimate | Р |
| Cum. PAR (PAR) | 0.001 | 0.210 | 0.006 | <0.001 | 0.001 | 0.026 | 0.085 | <0.001 |
| Rainfall regime (RAIN) | -1.347 | <0.001 | 3.513 | 0.057 | 0.429 | 0.001 | 47.603 | 0.009 |
| PAR × RAIN | - | - | -0.005 | 0.014 | - | - | -0.034 | 0.091 |
| <i>r</i> ² | 0.67 | | 0.48 | | 0.31 | | 0.72 | |

Table 2. Standardized major axis (SMA) regression to test the effect size ofrespective proxies of vegetative and reproductive development on cropperformances.

| Proxies (targeted crop performance) | Rainfall regime | п | r^2 | Р | Slope | Intercept |
|--|--------------------|----|-------|--------|--------|-----------|
| <u>Maximal LAI</u> (Straw yield) | - | 39 | 0.74 | <0.001 | 58.62 | 70.95 |
| | CTL | 20 | 0.57 | <0.001 | 64.07 | 64.07 |
| | EXC | 19 | 0.49 | <0.001 | 48.42 | 48.42 |
| Nb. pods / plant (Grain yield) | - | 39 | 0.50 | <0.001 | 48.43 | -61.27 |
| | CTL | 20 | 0.80 | <0.001 | 51.10 | -110.49 |
| | EXC | 19 | 0.12 | 0.137 | 60.89 | -98.18 |
| <u>Nb seeds / pod</u> (Grain yield) | - | 39 | 0.18 | 0.007 | 153.46 | -281.85 |
| | CTL | 20 | 0.33 | 0.008 | 287.11 | -680.73 |
| | EXC | 19 | 0.20 | 0.055 | 90.42 | -82.93 |
| <u>TKW</u> (Grain yield) | - | 39 | 0.45 | <0.001 | 3.69 | -286.02 |
| | CTL | 20 | 0.52 | <0.001 | 4.54 | -373.51 |
| | EXC | 19 | 0.58 | <0.001 | 3.18 | -237.76 |

Figure legends

Figure 1. Spatial layout of experimental design at parcel A2 at the Restinclières Farm Estate (France)

Figure 2. Rainfall regimes according to cumulative rainfall. Rainfall interception periods are represented with orange filled areas. Vertical dashed lines represent sowing and harvest dates during experiment year.

Figure 3. Light conditions over the cropping period according to available PAR (PAR₀) in agricultural control (AC) (A.), median dynamics of PAR transmittance in agroforestry (AF) (B.) and boxplots of cumulative incident PAR (PAR_{inc}) in AF (C.). Orange areas depict rainfall interception periods and green areas indicate tree budburst period. Horizontal solid line in B. and C. indicates the value of transmittance (100%) and PAR_{inc} (1247 MJ.m⁻²) in AC.

Figure 4. Paired analysis of mean daily soil water content (SWC) [m³.m⁻³] between cropping systems (A. and C.) and rainfall regime (B. and D.) at 20 and 50 cm depth. Dotted line indicates 1:1 line and dashed lines indicate permanent wilting point (PWP) and field capacity (FC) computed according to Rawls et al. (2003). Colors indicate different time period, set as i) 1-month interval for the evaluation of SWC dynamics between cropping systems and as ii) interperiod between major rainfall exclusion (> 20 mm) for the evaluation of dynamics between rainfall regime.

Figure 5. Phenological development of winter pea (A.) and LAI dynamics (B.) according to cropping conditions and rainfall regime. In A., black crosses indicate sowing date, while colored lines of vegetative growth start at emergence. In B.,

confidence curves were computed according to standard error of LAI values pooled per rainfall regime. Orange areas depict rainfall interception periods and green areas indicate tree budburst period.

Figure 6. Linear mixed effects analyses of straw yield (A.), grain yield (B.) and harvest index (C.) in relation with cumulated PAR over the whole cropping period and rainfall regime. Estimates of fixed effects (β) in retained models according to AIC_c value and their significance are provided, as well as pseudo-r². Confidence intervals represent the standard error of the model.

Figure 7. Average profile of the number of pods per node (A.), the number of seeds per pod (B.) and individual seed weight (C.) along reproductive nodes of winter pea according to rainfall regime and three different cropping conditions : agricultural control (AC), South (AF-S) and North (AF-N) of tree lines in agroforestry conditions. Black symbols indicate significant differences between AF and AC conditions according to a paired sample t-test ($\alpha = 0.05$) with Bonferroni correction.













