UNIVERSIDAD O····· **DE EXTREMADURA**

TESIS DOCTORAL

Respuesta de variedades de trigo (*Triticum aestivum* L.) y cebada (*Hordeum vulgare* L.) al cultivo bajo arbolado en sistemas agroforestales mediterráneos

María Guadalupe Arenas Corraliza

Programa de Doctorado en Ciencia y Tecnología de los Sistemas Agroforestales

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Conformidad de los Directores:

"La conformidad de los directores de la Tesis consta en el original en papel de esta Tesis Doctoral"

D. Gerardo Moreno Marcos   Dña. María Lourdes López Díaz

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Los doctores D. Gerardo Moreno Marcos (Director), Profesor Titular de Universidad del Departamento de Biología Vegetal, Ecología y Ciencias de la Tierra de la Universidad de Extremadura y Dña. Mª Lourdes López Díaz (Codirectora), Profesora Titular de Universidad del Departamento de Ingeniería del Medio Agronómico y Forestal de la Universidad de Extremadura certifican:

Que la presente Tesis Doctoral titulada "Respuesta de variedades de trigo *(Triticum aestivum* L.) y cebada (*Hordeum vulgare* L.) al cultivo bajo arbolado en sistemas agroforestales mediterráneos", presentada por Dña. María Guadalupe Arenas Corraliza para la obtención del título de Doctor, ha sido realizada bajo su dirección y cumple con los requisitos necesarios para ser juzgada por el correspondiente tribunal.

Y para que conste y surta los efectos oportunos, firman la presente en Plasencia, a 2 de diciembre de 2021.

D. Gerardo Moreno Marcos   Dña. María Lourdes López Díaz

TESIS DOCTORAL

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MARÍA GUADALUPE ARENAS CORRALIZA

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Cuando has trabajado tanto en algo, nunca sabes si has acabado, pero creo que este puede ser un buen punto y aparte.

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RESUMEN

Los efectos del cambio climático, como el aumento de las temperaturas, las olas de calor y las sequías, son cada vez más intensos y frecuentes, especialmente en la zona mediterránea y están perjudicando a la producción de alimentos, entre los que se encuentran los cereales, como el trigo y la cebada. Esto, unido a la creciente población mundial, puede comprometer el abastecimiento de alimento en las próximas décadas y la necesidad de ampliar la frontera agrícola. Sin embargo, la escasez de nuevas tierras de cultivo hace que la producción de suficiente alimento deba conseguirse a través de sistemas agrarios más intensificados y, al mismo tiempo, más sostenibles, lo que se conoce como "intensificación ecológica".

Una de las propuestas más relevantes de la intensificación ecológica son los sistemas agroforestales, que combinan, en una misma superficie, varios estratos productivos (arbóreo, herbáceo y/o arbustivo con o sin ganadería), realizando un uso más eficiente de los recursos disponibles. Además, los sistemas agroforestales constituyen un medio de adaptación al cambio climático (por su resiliencia a eventos climatológicos extremos) y de mitigación del mismo (por el secuestro de carbono en los árboles y suelo), como ya se ha reconocido por diversos organismos internacionales.

Sin embargo, la propia naturaleza de los sistemas agroforestales hace que se produzcan interacciones positivas y negativas entre los estratos vegetales. Ello hace que sea necesario un conocimiento exhaustivo tanto de las especies utilizadas como de las relaciones que se establecen entre ellas, para poder diseñar las combinaciones y los planes de gestión más adecuados que permitan establecer sistemas agroforestales eficientes.

Un tipo concreto de sistema agroforestal es el silvoarable, que combina el estrato arbóreo con un cultivo herbáceo, compaginando así los beneficios a largo plazo del arbolado con la

renta anual del cultivo. El estrato arbóreo suele estar representado por especies caducifolias para la producción de madera o fruto. El estrato herbáceo se compone, normalmente, de cultivos anuales u hortícolas, siendo los más comunes los cereales de invierno, como el trigo y la cebada, puesto que su siembra se realiza en el otoño-invierno y completan la mayor parte de su ciclo durante la parada vegetativa del arbolado caducifolio, minimizando así posibles interacciones negativas.

Dentro de los sistemas silvoarables, uno de los más extendidos en Europa es la combinación de nogal híbrido para la producción de madera de calidad (*Juglans x intermedia*) con cereales de invierno, en su mayoría, trigo blando (*Triticum aestivum* L.). Sin embargo, aunque varios autores han estudiado la interacción de ambos estratos a nivel productivo y radicular, con interesantes hallazgos respecto a la plasticidad radicular del nogal en su combinación con el cereal, poco o nada se ha investigado hasta la fecha sobre la adaptación de la parte aérea del cereal a la sombra impuesta por el arbolado.

A pesar de que una de las premisas fundamentales de los sistemas agroforestales es la protección que ejerce la copa del árbol frente a las altas temperaturas, no se ha reparado lo suficiente en el efecto simultáneo y habitualmente perjudicial que ejerce la sombra sobre los cereales, causante, en la mayor parte de los casos, de la disminución de la producción de grano en este tipo de sistemas. No obstante, aún no se conoce como la disponibilidad de radiación determina el equilibrio entre los efectos positivos y negativos de la sombra del arbolado sobre el cereal, teniendo como hipótesis que los efectos positivos aumentan con la termicidad.

Esta Tesis aborda las complejas relaciones que se generan entre el nogal y el cultivo intercalado de trigo y cebada en el centro peninsular de España. Se estudian las bases fisiológicas de los efectos de la sombra sobre el crecimiento y desarrollo del grano del cereal, así como la respuesta de los rasgos funcionales del cereal a la sombra, conocimiento que permitirá establecer estrategias para la selección de variedades de cereal adecuadas para los sistemas agroforestales en función de las condiciones climáticas y la radicación disponible.

En el primer capítulo, se exploraron los efectos productivos entre el nogal y el cereal (trigo y cebada) en un sistema agroforestal del centro peninsular, durante tres años climatológicos consecutivos, utilizando variedades de cereal ampliamente comercializadas en la zona. Este estudio reveló un efecto cambiante del arbolado sobre el cereal en términos de producción, dependiendo de las condiciones climáticas de cada año. Así, en los años más productivos para el cereal, con abundantes precipitaciones primaverales, el arbolado tuvo un efecto perjudicial para la producción de cereal. Sin embargo, en los años menos productivos, con escasas precipitaciones y ocurrencia de olas de calor, el arbolado tuvo un efecto protector sobre el cultivo, llegando incluso

a aumentar la producción de grano y mejorar su calidad respecto al monocultivo de cereal. El resultado más novedoso de este experimento fue la mejor adaptación de la cebada, anteriormente apenas utilizada en sistemas agroforestales, en comparación al trigo, a las condiciones impuestas por el arbolado. Por otra parte, la presencia del cereal disminuyó el crecimiento en diámetro del arbolado, revelando una fuerte competencia por K entre ambos estratos. Finalmente, el LER (*Land Equivalent Ratio*) del sistema fue superior a la unidad todos los años, mostrando la mayor eficiencia del sistema combinado en el uso de los recursos disponibles en comparación con el monocultivo de cereal y la plantación pura de nogal.

En el segundo capítulo, se abordó el efecto aislado de la sombra en condiciones controladas sobre distintas variedades de trigo y cebada en un entorno de alta disponibilidad lumínica. Este experimento reveló, por primera vez, mecanismos de adaptación a la sombra en trigo y cebada, especies tradicionalmente seleccionadas para condiciones de plena luz. Así, mientras que la cebada mostró una gran aclimatación fotosintética a la sombra (menor punto de saturación de luz y respuestas adaptativas en parámetros de fluorescencia), el trigo desarrolló una adaptación morfológica a nivel de hoja, con menor LMA (*Leaf Mass Area*) en las condiciones de luminosidad reducida. De esta forma, aunque siguiendo diferentes estrategias, ambas especies aumentaron su rendimiento en grano en la sombra en comparación con las condiciones de plena luz. No obstante, existieron grandes diferencias entre las variedades exploradas, lo que abrió el camino para la realización de programas de selección de aquellas mejor adaptadas a las condiciones de sombra para su utilización en sistemas agroforestales.

En el tercer capítulo, tomando como base el ensayo experimental del segundo capítulo, se evaluaron los cambios en diferentes rasgos funcionales del trigo y la cebada en respuesta a los niveles de sombra, valorando aclimataciones fenológicas, morfológicas, fisiológicas y bioquímicas. El estudio mostró diferentes agrupaciones del conjunto de rasgos funcionales en ambas especies según los distintos niveles de sombra estudiados, indicando que los niveles de sombra ejercen un efecto global sobre estos rasgos. Una de las adaptaciones a la sombra más destacada fue el desarrollo más avanzado de ambas especies de cereal en condiciones de sombra, lo que se relacionó directamente con el aumento de producción de grano. Respecto a las variedades, en general, todas las variedades de cebada aumentaron su producción en sombra, mientras que sólo las variedades más tardías de trigo consiguieron incrementar su rendimiento en estas condiciones, revelando, de nuevo, la importancia de la selección varietal del cereal para el cultivo bajo arbolado en sistemas agroforestales.

En el cuarto capítulo, se seleccionaron aquellas variedades que mejor se adaptaron a la sombra en el capítulo anterior para su cultivo bajo arbolado de nogal, con objeto de estudiar otros

posibles efectos, diferentes a la sombra, del arbolado sobre el cereal. El experimento mostró un efecto amortiguador del arbolado sobre las condiciones microclimáticas del cereal. No obstante, dicho efecto no fue suficiente para evitar la disminución de producción de grano en el sistema agroforestal, posiblemente debido a que el año de estudio fue especialmente productivo para los cereales, lo que limita el potencial beneficioso del arbolado para el cultivo, como ya se observó en el primer capítulo. No obstante, el arbolado ejerció un efecto positivo sobre las condiciones de crecimiento del cereal, mejorando rasgos morfológicos y fisiológicos en comparación con el monocultivo. Además, aunque ambos estratos revelaron una competencia por N, el arbolado aumentó la disponibilidad de P para el cultivo, mejorando la ratio N/P en el cereal. Por último, este estudio mostró, por primera vez, que el arbolado modificó el conjunto de rasgos funcionales que determinaron la producción de grano en el cereal, tanto en trigo como en cebada, respecto al monocultivo, lo que tiene importantes implicaciones en los programas de selección basados en la adaptación de rasgos funcionales a las condiciones impuestas por los sistemas agroforestales.

Esta Tesis ha demostrado que el rendimiento de un sistema silvooagrícola de nogal híbrido con cereal de invierno en condiciones mediterráneas puede aumentar la producción de trigo y cebada debido a la mejora en las condiciones microclimáticas y rasgos funcionales claves en el cereal, especialmente en el caso de la cebada. El rendimiento global del sistema fue siempre superior a los rendimientos de arbolado y cereal por separado, destacando la idoneidad de este tipo de sistemas en el contexto actual de cambio climático. No obstante, el balance neto de interacciones positivas o negativas entre ambos estratos dependió en gran medida de las condiciones climatológicas de cada año y de las variedades de cereal utilizadas. Éstas últimas han demostrado gran variabilidad en la aclimatación de sus rasgos fenológicos, fisiológicos, morfológicos y bioquímicos a la sombra, lo que ha provocado aumentos o disminuciones de la producción en condiciones de menor radiación solar. Además, el arbolado ha influido en la dinámica productiva del cereal, afectando a rasgos funcionales determinantes de la producción de grano. Todo esto ha puesto de relevancia la necesidad de programas de selección basados en rasgos funcionales de especies y variedades de cereal para su cultivo en sistemas agroforestales.

ABSTRACT

Climate change effects, such as rising temperatures, heat waves and droughts, will become increasingly intense and frequent, especially in the Mediterranean area. These effects have already had a negative impact on food production, including cereals such as wheat and barley. This, together with a growing world population, will lead to an increase in the need of cropping lands and systems. However, due to the scarcity of new arable land, the increase in food production must be achieved through more intensified and, at the same time, more sustainable farming systems, known as "ecological intensification".

Agroforestry systems are among the ecological intensification approaches. These systems combine, in the same area, woody vegetation (trees or shrubs) with crop and/or animal production systems, resulting in a more efficient use of the available resources. The role of the agroforestry systems as a climate change adaptation mechanism (due to their resilience to extreme weather events) and mitigation strategy (due to carbon sequestration in soil and trees) has been recognized by different international institutions.

However, there are positive and negative interactions between the different strata in the agroforestry systems. That is why it is necessary to thoroughly know the species used and the relationships between them, in order to design the most appropriate combination and management practices to establish successful agroforestry systems.

One specific type of agroforestry system is the silvoarable one, in which trees and herbaceous crops combine the long-term benefits of trees with the annual income from crops. Trees are usually deciduous species for timber or fruit production, while the herbaceous crops are usually annual or horticultural crops, the most common being winter cereals such as wheat and barley. These crops are sown in autumn-winter and complete

most of their cycle during the dormant period of the deciduous trees, thus minimizing possible negative interactions.

Among the silvoarable systems, one of the most widespread in Europe is that composed of hybrid walnut (usually for the production of quality wood, *Juglans x intermedia*) with winter cereals, mostly wheat (*Triticum aestivum* L.). However, although numerous authors have studied the interaction of both strata regarding productive and root interactions, and found interesting results of walnut root plasticity, little or no research has been done to date on the adaptation of the cereal to the shade imposed by the tree.

Despite the fact that one of the fundamental assumptions of the agroforestry systems is the protection provided by the tree canopy against high temperatures, no attention has been paid to the simultaneous and possibly detrimental effect of shade on the availability of light for cereals, which in most cases causes a reduction in grain production in these systems. However, it is not clear yet whether the tree shade, contrary to the traditional belief, could have beneficial effects in areas of high light intensity, such as central Spain, under the hypothesis that the detrimental effects of shade increase with the latitude, and that under warm Mediterranean climate positive effects could surpass to negative ones of shade.

This thesis addresses the complex interactions between walnut trees and cereal in agroforestry systems, showing the negative effects and how to minimise them, while maximising the positive interactions. Furthermore, contrary to what happens with the availability of soil resources, the shade of the trees is difficult to manage in agroforestry systems without reducing the production of the trees, and this is why this work establishes the basis for the selection of cereal species and varieties based on their functional traits for cultivation under tree shade.

In the first chapter, the productive interactions between the walnut trees and cereals (wheat and barley) were explored in an agroforestry system in central Spain, during three consecutive climatological years, using cereal varieties widely commercialized in the area. This study revealed a changing effect of the trees on the cereal in terms of production depending on the climatic conditions of each year. Thus, in more favorable years for the cereal, with abundant spring rainfall, the trees had a detrimental effect on cereal production. However, in the least productive years, with low rainfall and heat waves, the trees had a protective effect on the crop, even increasing grain production and improving its quality compared to cereal

monoculture. The most innovative result of the experiment was the better adaptation of barley, previously barely used in agroforestry systems, than wheat, to the conditions imposed by tree alleys. On the other hand, the presence of the cereal decreased the diameter growth of the trees, revealing a strong competition for K between the two strata. Finally, the LER (*Land Equivalent Ratio*) of the system was higher than the unit in all years, showing the better efficiency in the use of available resources of the agroforestry system compared to the cereal monoculture and the walnut pure plantation.

In the second chapter, the isolated effect of shade on different varieties of wheat and barley was assessed under controlled conditions in an environment of high solar radiance, such as central Spain. This experiment revealed, for the first time, specific acclimations to shade in wheat and barley, even though they were traditionally selected for full light conditions. While barley showed high photosynthetic acclimation to shade (lower light saturation point and adaptive responses in fluorescence parameters), wheat developed a morphological adaptation (lower leaf mass per area in shaded flag leaves). Thus, both species increased their grain yield in shade compared to full light conditions, following different acclimation strategies. However, there were large differences between the varieties explored, which opened the way to selection programs for cereal varieties of interest for agroforestry systems.

In the third chapter, based also on the experiment of the second chapter, different plant traits of wheat and barley were assessed in shade conditions. Thus, phenological, morphological, physiological and biochemical adaptations to shade were thoroughly evaluated. The experiment showed different assemblages of trait changes in both species as response to the different shade levels studied. One of the most remarkable adaptations was the more advanced development of both cereal species in shade compared to full light conditions, which was related to an increase in grain yield. Regarding varieties, while all barley cultivars increased their grain yield in shade conditions, only wheat late cultivars managed to do the same, revealing the importance of cereal varietal selection for cultivation under shade in agroforestry systems.

In the fourth chapter, the best adapted cultivars to shade found in the previous chapter were selected for cultivation under walnut trees in a field trial with the aim to identify other effects, different to shade, of the trees on cereal crops. The experiment showed a buffering effect of the trees on the microclimatic conditions of the cereal, although it was not enough to avoid the decrease in grain production in the agroforestry system. This detrimental effect of the trees in cereal production was possibly due to the particularly very favorable climatological

conditions of the study year for open field cereals crops, which limited the potential benefits of the trees, as already observed in the first chapter. Nevertheless, trees had beneficial effect on cereal growing conditions, improving morphological and physiological traits compared to monoculture. In addition, although both strata revealed competition for N, trees increased the availability of P for the crop, improving the N/P ratio in the cereal. Finally, this study showed, for the first time, that the set of plant traits that finally determined grain yield was modified in the agroforestry system compared to monoculture, both in wheat and barley. This has implications for selection programs based on the adaptation of plant traits to the conditions imposed by agroforestry systems.

This Thesis has proved that wheat and barley production can increase in a silvoarable system that combines the hybrid walnut with a winter cereal under Mediterranean conditions. This increase is caused by both the improved microclimatic conditions and by changes in key functional traits in the cereal beneath the trees, especially in the case of barley. The overall yield of the system was always higher than the sum of yields of the sole tree plantation and cereals monoculture, highlighting the suitability of this system in the current context of climate change. However, the net balance of positive or negative interactions between the two strata depended to a large extent on the climatic conditions of the year and on the cereal varieties used. The latter have shown great variability in the acclimatation of their phenological, physiological, morphological and biochemical traits to shade, leading to increases or decreases in grain production. In addition, the trees influenced the productive dynamic of the cereal, affecting plant traits that ultimately determine grain yield. All this has highlighted the need for selection programs based on cereal plant traits of species and varieties for cultivation in agroforestry systems.

INTRODUCCIÓN GENERAL

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1. Población, cambio climático e intensificación ecológica

A lo largo de la segunda mitad del siglo XX la población mundial creció de forma paralela al aumento del rendimiento de los cultivos, posibilitado por la mejora de las técnicas agronómicas, el uso de fertilizantes, energías y pesticidas y la selección y la mejora genética (FAO, 1996). Estos avances, conocidos como la "revolución verde", permitieron multiplicar el rendimiento de los cultivos por unidad de suelo cultivado. Actualmente, se estima que la población mundial seguirá creciendo hasta alcanzar los 9 mil millones en 2050, experimentándose este aumento, prácticamente en su totalidad, en los países en desarrollo, lo que supondrá la necesidad de doblar, aproximadamente, la producción de alimentos. Sin embargo, lejos de poder aumentar la producción, ésta se ve amenazada hoy en día por dos problemas crecientes: el cambio climático y la escasez de nuevas tierras cultivables (Myers et al., 2017).

En lo referente al cambio climático, la temperatura global ha aumentado sin precedentes desde el comienzo de la era industrial, especialmente desde la década de los setenta (IPCC, 2015). El calentamiento global se ha puesto de manifiesto de un modo particularmente acentuado en el área mediterránea comparada con otras regiones, incrementándose la temperatura en 1,4 °C respecto a las últimas décadas del siglo XIX y aumentando la frecuencia e intensidad de eventos climatológicos extremos como las olas de calor y las sequías (Cramer et al., 2018). A nivel mundial, el cambio climático ya está amenazando la producción de alimentos, afectando de forma relevante en la zona sur-oeste mediterránea (España entre otros países) a dos de los diez cultivos más comunes en el mundo, el trigo, con una pérdida de producción del 16 %, y la cebada, con un descenso de un 9 % en su rendimiento (Ray et al., 2019).

Respecto a la escasez de tierras cultivables, ésta se ha acentuado en los últimos años, principalmente porque la mayor parte de la superficie susceptible de ser cultivada ya se encuentra en producción (Ausubel et al., 2013), lo que dificulta cumplir con los objetivos de alimentar a la creciente población. Por ello, en los países en desarrollo, el 80% del aumento de la producción debería proceder del aumento del rendimiento de los cultivos, mientras que sólo el 20% del incremento en la oferta de alimento debería proceder del aumento de tierras cultivables (FAO, 2009). Aun así, la solución para el aumento de producción de alimentos no debería buscarse a través del cultivo de las escasas nuevas tierras susceptibles de ser cultivadas, pues la mayoría ya quedan reducidas a los trópicos, que tienen alto valor natural en términos de carbono y biodiversidad, y deberían ser precisamente áreas de especial conservación en el escenario actual de cambio climático (Ramankutty et al., 2018).

Por otra parte, los monocultivos intensivos son más vulnerables que los sistemas diversificados, lo que ha impulsado el diseño de nuevos sistemas y la adopción de prácticas que protejan a los cultivos frente a las consecuencias de cambio climático, garantizando así la seguridad alimentaria (Lesk et al., 2016). En este contexto, la intensificación ecológica se plantea como una posible solución para el aumento de producción de alimentos, aumentando el rendimiento de los cultivos a través de un mejor uso de los recursos disponibles (Doré et al., 2011; Godfray et al., 2010). Una de las propuestas de intensificación ecológica que ha adquirido mayor relevancia en los últimos años han sido los sistemas agroforestales (Tittonell 2014), que combinan deliberadamente en una misma parcela arbolado y/o arbustos con producción agrícola/ganadera, generando interacciones en los estratos que pueden producir beneficios tanto ecológicos como económicos (Burgess et al., 2015). Un caso particular de este tipo de sistemas son los sistemas silvoagrícolas, que combinan árboles y cultivos en una misma parcela.

2. Sistemas agroforestales: características generales

Aunque los términos "agroforestal", "agroforestería" y "sistemas agroforestales" son relativamente recientes (Nair, 1983), las prácticas en las que se fundamentan no son en absoluto nuevas. Su estudio y desarrollo más extenso ha ocurrido en los países en vías de desarrollo, debido a sus economías de subsistencia (Nair y Graetz 2004), pero llevan miles de años practicándose en España y resto de países europeos (Eichhorn et al. 2006; Mosquera-Losada et al. 2012) y están ganando gran interés en los países más desarrollados por las múltiples ventajas ambientales que se les atribuye (Jose, 2009; Torralba et al., 2016).

Estos sistemas se basan en el aprovechamiento de los recursos de la forma más eficiente posible. Así, la combinación en una misma superficie, de un estrato arbóreo y/o herbáceo o arbustivo, origina una serie de interacciones de competencia o facilitación, que manejadas correctamente pueden aumentar la producción del sistema (Silva-Pando y Rozados 2002; Moreno 2005) y estabilizar la producción de pasto bajo arbolado en condiciones mediterráneas (Gea-Izquierdo et al. 2009; de Miguel et al. 2013).

Uno de los principales motivos de interés en este tipo de sistemas es que son reconocidos como un modelo de gestión sostenible y de adaptación al cambio climático, generando beneficios medioambientales tanto en superficie como en el suelo (Verchot et al. 2007; Schoeneberger et al. 2012): los árboles pueden amortiguar las temperaturas bajo el dosel en épocas calurosas en zonas mediterráneas (Moreno et al. 2007) y templadas (Kanzler et al. 2018), proporcionar refugio a los cultivos frente al viento y reducir la evaporación de la capa superficial del suelo (Brandle et al., 2004), contribuir a la disminución de la erosión hídrica y eólica de las parcelas agrícolas (Palma et al., 2007), reducir la pérdida de agua (Lasco et al., 2014) y nutrientes (Andrianarisoa et al. 2015; Cardinael et al. 2015) a través de la expansión de las raíces a capas más profundas, aumentar la captación de nutrientes atmosféricos (Sinclair et al., 2000), aportar materia orgánica mediante la caída al suelo de la hojarasca (Piatek y Alen 2000) e incrementar la biodiversidad en el medio (Moreno et al., 2016; Torralba et al., 2016), además de aportar beneficios paisajísticos y culturales (Dupraz y Liagre 2011).

Asimismo, estos sistemas son considerados como una de las prácticas agrícolas con mayor potencial para la mitigación del cambio climático (Lal 2004; Mosquera-Losada et al. 2018), pues se ha demostrado que los árboles pueden fijar y almacenar carbono durante largos períodos de tiempo, al contrario de lo que ocurre con los cultivos agrícolas, que lo liberan rápidamente a la atmósfera tras la cosecha (Mosquera-Losada et al., 2011). En los sistemas silvopastorales, la dinámica de secuestro de carbono en el suelo se ve influenciada, además de por la presencia del arbolado, por la prácticas de manejo, como por ejemplo, el laboreo (López-Díaz et al., 2017) o la carga ganadera existente (Ferreiro-Domínguez et al., 2016).

Por todo ello, el papel de los sistemas agroforestales como mecanismo de adaptación y mitigación del cambio climático se ha reconocido en los comités europeos *European Conference on Rural Development* (EU, 2016), *European Strategy for Climate Change* (EU, 2014) y *European Forestry Strategy* (EU, 2021), así como en el *International Panel on Climate Change* (Quinto Informe) (IPCC, 2015).

Sin embargo, a pesar de los beneficios ambientales y culturales, en los sistemas agroforestales también se producen interacciones negativas entre los estratos por los diferentes recursos: luz, agua y nutrientes (Jose et al., 2004). Estas interacciones pueden provocar la pérdida

de producción de los estratos, que, añadida a la mayor complejidad en la mecanización y en la gestión administrativa, provoca cierta reticencia entre la población y los agentes relacionados con el medio rural en la mayoría de los países europeos (Rolo et al., 2020).

El objetivo principal en el diseño de este tipo de sistemas es maximizar las interacciones positivas y minimizar las negativas. Para conseguirlo, es fundamental realizar, en primer lugar, una apropiada selección de especies, adecuadas para las condiciones presentes en el área de implantación del sistema agroforestal.

2.1. Sistemas agroforestales en el ámbito mediterráneo

En la zona mediterránea, los niveles de radiación solar son generalmente superiores a los requeridos por los cultivos, siendo las altas temperaturas y la sequía los principales factores limitantes para la fotosíntesis (Flexas et al., 2014). En este contexto, el arbolado puede ser especialmente beneficioso en términos de amortiguación de la radiación solar, las altas temperaturas y la sequía, haciendo de los sistemas agroforestales una apuesta especialmente interesante para el área mediterránea (Mosquera-Losada et al. 2012; Gonçalves et al. 2021).

El paradigma de este tipo de sistemas en el sureste de Europa es la dehesa en España o su equivalente, el montado portugués, que constituye el sistema agroforestal más importante de Europa, ocupando aproximadamente 4 millones de hectáreas en el suroeste de la península Ibérica (den Herder et al., 2017). Los humanos han moldeado este sistema adaptado a las condiciones edafoclimáticas del oeste Ibérico, con clima mediterráneo y suelos de baja fertilidad, compuesto fundamentalmente por arbolado disperso de encina (*Quercus ilex* L.) o alcornoque (*Quercus suber* L.), cultivos o pastos y arbustos, resultado de la diversificación de sus actividades: agricultura, ganadería y aprovechamientos forestales. En estas condiciones, los cultivos herbáceos son normalmente poco productivos, requiriendo de fertilización específica, dependiendo de la zona, para lograr una mayor producción y diversidad de especies (Santamaría et al., 2014). En este sistema, el arbolado de encina ha demostrado generar beneficios ambientales y productivos bajo la protección de su dosel (Moreno et al. 2007).

El caso de la dehesa y su éxito en la península Ibérica, establece un precedente para la instalación de otros tipos de sistemas agroforestales en la misma zona, con diferentes combinaciones de árboles y cultivos que puedan maximizar los beneficios para el agricultor, el medio ambiente y, por ende, la sociedad en su conjunto.

2.1.1.El cultivo de cereal en sistemas agroforestales mediterráneos

A pesar de que actualmente España es el cuarto país más productor de cereales de la Unión Europea (EUROSTAT, 2021), en 2020 importó 5,4 Mt de trigo blando y 1,4 Mt de cebada (Ministerio de Agricultura Pesca y Alimentación, 2021), principalmente para la producción de pienso animal. Este alto nivel de importaciones tiene una doble consecuencia: la primera, desde el punto de vista económico, para el sector agroganadero, y la segunda, desde una perspectiva medioambiental, por la utilización de combustibles fósiles para su transporte. Por ello, existe la necesidad de producir cereales de invierno en España, en concreto las especies de trigo y cebada, dos de los cereales tradicionalmente más cultivados en nuestro país y que están siendo objeto de investigación reciente para la mejora de su calidad nutricional para la población y el ganado, a través de procedimientos como la biofortificación (Rodrigo et al., 2013; Rodrigo et al., 2014).

Como ya se ha mencionado anteriormente, estos cereales afrontan en la actualidad una pérdida de producción debido a las consecuencias derivadas del cambio climático. Además, se ha demostrado que, en condiciones mediterráneas, el rendimiento y la calidad de los cereales disminuye con la excesiva intensidad lumínica y las altas temperaturas (ya sea en largos períodos con valores superiores a los óptimos o momentos puntuales de muy altas temperaturas), frecuentes en esta zona, llegando a provocar fotoinhibición (Jacobsen et al., 2012). Asimismo, el estrés térmico durante la fases previas a la floración (Slafer, 2003) y durante el llenado del grano (Brisson et al., 2010) provoca pérdidas de producción en el trigo. Por todo ello, en este contexto, el cultivo de cereales bajo arbolado en sistemas agroforestales puede suponer una protección para el cereal frente a los efectos más adversos del calentamiento global.

Sin embargo, se ha demostrado que una reducción de la intensidad lumínica, como la que puede ocasionar el arbolado en los sistemas agroforestales, puede afectar al cultivo de cereal en términos morfológicos, fisiológicos, productivos y cualitativos (Dong et al. 2015; Wang et al. 2015a). En concreto, algunos estudios han mostrado que la sombra del arbolado puede afectar negativamente al desarrollo de cereales como el trigo cuando se combinan en un sistema silvoagrícola en la zona mediterránea (Dufour et al. 2013). No obstante, otras investigaciones en zonas con clima templado (Kanzler et al. 2018) e incluso mediterráneo (Sudmeyer y Speijers 2007) identificaron efectos positivos del arbolado sobre determinados rasgos funcionales de algunos cultivos, lo que indica que el balance neto de interacciones positivas y negativas en los sistemas agroforestales varía en gran medida con las condiciones climáticas, la zona de estudio, las especies utilizadas y los rasgos funcionales considerados.

Hasta ahora, ningún estudio había arrojado luz sobre los posibles efectos de la sombra sobre cereales como el trigo y la cebada en una de las zonas mediterráneas con mayor intensidad lumínica, como es el centro peninsular español (https://solar gis.info/), siendo éste uno de los objetivos principales de la presente Tesis.

2.1.1.1. Selección de cereales para sistemas agroforestales mediterráneos

Además de reducir la intensidad lumínica, los árboles pueden afectar negativamente a los cultivos en los sistemas silvoagrícolas por la competencia por agua y nutrientes. No obstante, mientras que la competencia por estos recursos puede subsanarse con prácticas agronómicas y de gestión adecuadas (riegos, fertilización, etc.), la sombra producida por el arbolado apenas puede modificarse sin afectar negativamente en el crecimiento y producción del árbol (Dupraz y Liagre 2011), lo que obliga a que las especies escogidas para el cultivo deban adaptarse a la iluminación existente bajo el dosel arbóreo. En la actualidad, no existe una relación de variedades de cereal adaptadas a las condiciones de sombra impuestas en sistemas agroforestales mediterráneos (o la generada por paneles fotovoltaicos), por lo que son necesarios programas de selección de especies de cultivos y, en concreto, de variedades de cereales adaptadas a la sombra, de forma que se puedan maximizar las interacciones positivas y minimizar los efectos negativos con el estrato arbóreo en el sistema agroforestal.

En la selección para condiciones de sombra, la primera etapa es conocer si verdaderamente existe variabilidad suficiente entre las especies y variedades de cereal mediterráneas para poder iniciar una selección de las más adaptadas a las condiciones de menor intensidad lumínica, puesto que tradicionalmente han sido seleccionadas y cultivadas en condiciones de pleno sol (Vandeleur y Gill 2004).

Se ha demostrado que, en los programas de selección de especies para sistemas agrícolas complejos, como los agroforestales, una selección basada en rasgos funcionales (como los relacionados con los parámetros morfológicos y fisiológicos del cultivo) es más eficaz que la selección genotípica, ya que los rasgos funcionales de las plantas son factores clave para la comprensión de las relaciones entre el ecosistema y la vegetación existente (Hooper et al. 2005; de Bello et al. 2010). Algunos de los rasgos funcionales que resultan de mayor interés para la selección de cereales adaptados a sistemas agroforestales son: los componentes productivos, el estado nutricional, la fenología (Inurreta-Aguirre et al. 2018) y parámetros fisiológicos y morfológicos. Entre los parámetros morfológicos, además del área de las hojas o la altura de la planta, el más relevante es la masa foliar por área o *Leaf Mass Area* (*LMA*), que puede describir las adaptaciones de las plantas a las condiciones de sombra (Poorter et al. 2009). Respecto a los rasgos fisiológicos, parámetros fotosintéticos (como la fotosíntesis neta y el punto de saturación

de luz) y de fluorescencia, como el rendimiento del fotosistema II o *Quantum Yield* (Φ_{PSII}), el rendimiento no fotoquímico o *Non-Photochemical Quenching (NPQ)* y la tasa de transporte de electrones o *Electron Transport Rate* (*ETR*), han mostrado ser de gran utilidad en la evaluación de variedades de cereal para su adaptación a la sombra (Mu et al., 2010; Zheng et al., 2011).

Además, también han demostrado ser relevantes otros parámetros fisiológicos como el contenido relativo de agua o *Relative Water Content* (*RWC*), uno de los parámetros más relacionados con el estado hídrico de la planta (Hasanuzzaman et al., 2019), así como con los contenidos de los pigmentos clorofílicos y carotenoides en trigo (Keyvan, 2010) y cebada (Kaczmarek et al., 2017); el flujo de electrolitos, considerado como un indicador de daño en la membrana celular y, por tanto, un parámetro indirecto de estrés (Bajji et al., 2002; Bodner et al., 2015); el índice de vegetación normalizada o *Normalized Difference Vegetation Index* (*NDVI*) y el índice de reflectancia fotoquímica o *Photochemical Reflectance Index* (*PRI*), altamente relacionados con el contenido en clorofila (Gamon et al., 1992) y carotenoides (Sellers, 2007).

Esta selección basada en rasgos funcionales, se ha visto incrementada en los últimos años (Garnier y Navas 2012), en conjunto con el conocimiento de aspectos clave de la ecología de las comunidades (nichos ecológicos, relaciones de competencia y facilitación etc.) y de la ecofisiología (fenología, curvas de respuesta a la luz, localización de los recursos, etc.). Todos ellos son aspectos esenciales para el entendimiento de las relaciones del cultivo con los árboles en términos del funcionamiento del ecosistema (Brooker et al. 2014; Allan et al. 2015; Martin y Isaac 2015) y están siendo de gran utilidad en la búsqueda de especies y variedades de cultivo más adaptadas para los sistemas agroforestales (Wood et al., 2015).

Por otra parte, la mayoría de los estudios realizados en sistemas agroforestales con cereales se han enfocado en el trigo (Oelbermann et al. 2006; Inurreta-Aguirre et al. 2018; Sida et al. 2018; Yang et al. 2018), obviando cómo la sombra del arbolado puede afectar a la cebada, uno de los cultivos de cereal más relevantes en el ámbito mediterráneo, que se prioriza en numerosas ocasiones sobre otros cereales (López-Bellido, 1992) por su capacidad para adaptarse a un mayor rango de condiciones edafoclimáticas que el resto, debido a su rusticidad y resiliencia (Newton et al., 2011). No obstante, recientemente, algunos autores han señalado que la combinación de cebada con arbolado en un sistema silvoarable en las condiciones mediterráneas del norte peninsular puede incrementar el rendimiento económico del sistema, no ocurriendo así con el trigo (Blanc et al., 2019).

La cebada florece y termina su ciclo entre una semana y diez días antes que el trigo (Cossani et al. 2009), lo que le puede conferir ventajas por escapar de los usuales estreses terminales a finales de la primavera. Además, se ha demostrado que la cebada es capaz de adaptar su

respuesta fotosintética a condiciones de baja iluminación (Zivcak et al., 2014), lo que la convierte en una especie potencialmente adecuada para su cultivo bajo arbolado y que debe ser tenida en cuenta en el diseño de sistemas agroforestales mediterráneos.

2.1.2. El nogal para producir madera de calidad en sistemas agroforestales mediterráneos

El arbolado puede modificar las condiciones de crecimiento para el cultivo en los sistemas agroforestales en diversos aspectos. En primer lugar, la interceptación de la luz por los árboles depende de su edad, forma de la copa, distribución de las ramas, tamaño de las hojas, índice de área foliar, etc. En segundo lugar, la fenología del arbolado y presencia estacional de las hojas puede variar al considerar especies caducifolias o perennifolias. Por último, las operaciones de manejo del arbolado, como el control de la densidad de pies mediante clareos y claras, así como de la densidad de las ramas mediante las podas, pueden modificar las condiciones de crecimiento para el cultivo herbáceo. Por tanto, resulta evidente que el conocimiento de la arquitectura de las especies arbóreas implicadas, tanto aérea como radicular, así como de su fenología y su capacidad de competencia por los recursos, es de máxima importancia en la elección de las especies y sistemas más apropiados de manejo (Coello et al., 2015; Mosquera-Losada et al., 2009).

En la península Ibérica, son numerosas las especies arbóreas que se utilizan en sistemas agroforestales: encina, alcornoque, olivo, castaño, nogal, fresno, chopo… En esta Tesis, se ha seleccionado como especie arbórea el nogal, por ser España un país importador de su madera en la actualidad, que alcanza valores de entre 300 y 3000 €/m³ dependiendo de su calidad, para la fabricación de muebles. Por ello, existe un interés creciente en la producción de madera de calidad de esta especie en nuestro país, lo que ha provocado que proliferen numerosas plantaciones de nogal de carácter intensivo a lo largo de la geografía española.

El material vegetal más utilizado en España para la producción de madera de calidad de nogal está compuesto por distintas especies del género *Juglans*. Aunque se pueden emplear *J. nigra* L. y *J. regia* L., actualmente son más utilizados los híbridos entre especies de nogal negro (*J. nigra* L., *J. major* Torr. y *J. hindsii* Jeps., entre las más comunes) y nogal común (*J. regia* L.) (Aletá y Vilanova 2006). En concreto, la mayor parte del material vegetal utilizado está constituido por las progenies híbridas *Juglans x intermedia Ng23xRa* y *Juglans x intermedia Mj209xRa* (que es la utilizada en el presente estudio), cuyos turnos oscilan entre 25 y 30 años (Aletá y Vilanova 2011). Ambas presentan buenas características forestales y resistencia a agentes nocivos, facilitando su gestión (Coello et al., 2009).

Las primeras plantaciones de híbridos de nogal en Francia comenzaron en la década de los 70, mientras que en España lo hicieron más tarde, a finales de los 90, alcanzando en 2005 alrededor de 2500 ha. Los estudios de campo de la presente Tesis se han realizado en una plantación de nogal híbrido *Juglans x intermedia Mj209xRa,* propiedad de la empresa Bosques Naturales S.A., que cuenta con diversas plantaciones de madera de calidad en España.

Este híbrido, de origen francés, procede de la polinización de la variedad *Juglans major* Torr. Var. 209 (Mj209) con polen de *Juglans regia* L. (Ra). No se sabe con seguridad a qué especie pertenece el progenitor femenino (Mj209). Inicialmente se consideró *J. nigra*, posteriormente se clasificó como *J. major* y, en la actualidad, se cree que podría ser en sí mismo un híbrido con capacidad reproductora. Este híbrido, también conocido como *Juglans x intermedia*, destaca por su crecimiento elevado (debido a su vigor híbrido) y su escasa producción de fruto. También presenta una gran capacidad de adaptación a distintos tipos de suelos y a áreas cálidas de la península Ibérica. Su brotación es de tipo medio, posterior al 15 de abril (Aletá y Vilanova 2006).

Por otra parte, en este tipo de plantaciones con nogal híbrido, el crecimiento de plantas adventicias constituye un problema para la producción de madera. En este sentido, técnicas alternativas a los herbicidas han demostrado ser útiles en el control de dichas plantas (Coello et al., 2017) y deberían ser tenidas en cuenta en el diseño de sistemas agroforestales por su menor influencia en el cultivo intercalar.

2.2. Sistemas agroforestales de nogal y cereales

Uno de los principales inconvenientes de las plantaciones de nogal en régimen intensivo para madera de calidad son los elevados gastos iniciales y de mantenimiento, muy superiores a los escasos beneficios obtenidos durante los primeros años. El establecimiento de sistemas agroforestales en estas plantaciones permitiría compensar los altos gastos iniciales, así como los de las labores de control de la vegetación y poda. De esta forma, el cultivo bajo arbolado de especies herbáceas de gran demanda como los cereales, regularizaría los ingresos, al combinar los de corto plazo de la producción agrícola con los de largo plazo de la madera de calidad (Rigueiro-Rodríguez et al., 2008), para cuya producción, además, hay que anticiparse varias décadas a las necesidades del mercado (Mosquera-Losada et al., 2012).

Sin embargo, existe escasa información específica sobre la combinación de nogal con cereales de invierno y sus interacciones, siendo la mayoría referente al comportamiento de las raíces. Una de las características fundamentales a nivel radicular de los sistemas

agroforestales con cereales de invierno en los ambientes mediterráneos es que la absorción de agua y nutrientes por parte del cereal continúa tras la brotación de las especies arbóreas caducifolias como el nogal (Dufour et al. 2013). Al absorber el cereal buena aparte de los recursos de las capas superficiales del suelo, induce a los árboles a extender su sistema radicular a capas más profundas (Mulia y Dupraz 2006; Dupraz y Liagre 2011; Cardinael et al. 2015). De hecho, se ha demostrado que el nogal presenta suficiente plasticidad para extender sus raíces en una zona no ocupada por las raíces del cereal, tanto en combinación con trigo (Andrianarisoa et al., 2015) como con cebada (Link et al., 2015). Además, la combinación de nogal y trigo en sistema agroforestal modifica parámetros radiculares como la densidad de longitud de raíces (Cardinael et al., 2015), la longitud específica de raíces (Zhang et al. 2015), y también la capacidad de absorción de las mismas, pudiendo aumentar la velocidad de infiltración del agua en el sistema combinado respecto a los monocultivos de trigo y plantaciones puras de nogal (Wang et al., 2015b).

Respecto al microclima generado por el arbolado, estudios en sistemas agroforestales de árboles caducifolios y trigo, mostraron que el arbolado ayudaba a reducir la temperatura durante el día, elevándola durante la noche (Inurreta-Aguirre et al. 2018; Kanzler et al. 2018), lo que amortigua el rango de temperaturas experimentado por el cultivo y puede conferirle ventajas en el escenario actual de calentamiento global.

Sin embargo, la combinación de nogal y trigo en sistema agroforestal ha revelado algunos efectos negativas, como la reducción del N disponible para el cereal (Zhang et al. 2019b), desarrollo tardío del trigo en zona mediterránea con arbolado caducifolio (Inurreta-Aguirre et al. 2018) y perennifolio (Panozzo et al., 2020), y reducción de su crecimiento, índice de área foliar y producción (Dufour et al. 2013).

No obstante, se ha demostrado que los sistemas agroforestales de nogal con cereales de invierno como el trigo y la cebada incrementan el rendimiento global, a través del aumento del índice de relación equivalente del terreno *Land Equivalent Ratio* (*LER*) (Duan et al., 2017; Zhang et al., 2015). Este índice, que suele variar en zonas templadas entre 1,2 y 1,8 (Graves et al., 2007), es una estimación de la superficie necesaria, respecto a la hectárea, para producir la misma cantidad en un sistema agroforestal que en un sistema con el arbolado y el cultivo separados. De esta forma, un LER con valor 1,2 significa que 1 ha de sistema agroforestal produce lo mismo que 1,2 ha de un terreno con ambos estratos separados vegetales, lo que tiene implicaciones positivas tanto ecológicas como en términos de uso del suelo en el contexto actual de cambio global.

Por todo ello, es necesario profundizar en el conocimiento de las interacciones que se producen en los sistemas agroforestales de nogal en combinación con cereales de invierno (trigo y cebada) y la adaptación de éstos a la sombra generada por el arbolado en las condiciones mediterráneas del centro peninsular, donde los beneficios del arbolado podrían maximizarse debido a que la radiación solar y las temperaturas alcanzadas son, frecuentemente, superiores a otras regiones del mediterráneo mejor estudiadas, como es el sur de Francia (Dufour et al. 2013; Inurreta-Aguirre et al. 2018).

OBJETIVO GENERAL Y OBJETIVOS ESPECÍFICOS

El objetivo general de la Tesis es evaluar el potencial del cultivo de trigo (*Triticum aestivum* L.) y cebada (*Hordeum vulgare* L.) bajo arbolado en condiciones mediterráneas como propuesta de adaptación al cambio climático. A través de las variaciones de los rasgos funcionales de diferentes variedades de estas dos especies de cereal y de las interacciones que se producen con el arbolado, se pretende aportar información de interés para posibles programas de selección de variedades de cereal adaptadas a los sistemas agroforestales en un contexto de calentamiento global.

Los objetivos específicos de la Tesis son:

I: Valorar la producción de cereales de invierno (trigo y cebada) y madera de calidad (nogal) en un sistema agroforestal en años con condiciones climáticas contrastadas.

II: Evaluar, en condiciones controladas, la posible adaptación fotosintética y morfológica de diferentes variedades de trigo y cebada a la sombra.

III: Explorar, a través de los rasgos funcionales de las plantas, la importancia de la precocidad en las variedades de trigo y cebada en el rendimiento en grano en condiciones de sombra.

IV: Analizar el comportamiento en un sistema agroforestal de variedades de trigo y cebada preseleccionadas por su adaptación a la sombra, evaluando la influencia que ejerce el arbolado sobre los rasgos funcionales del cereal que determinan la producción de grano.

Para evaluar estos objetivos, se llevaron a cabo ensayos de campo (objetivos I y IV) e invernadero (II y III) y se realizaron las determinaciones "in situ" y de laboratorio necesarias. Cada objetivo se aborda en un capítulo diferente de la Tesis, relacionados desde el I al IV respectivamente.

MATERIALES Y MÉTODOS

En este apartado se pretende realizar una breve descripción de los materiales y métodos utilizados durante el desarrollo de la Tesis. Éstos se encuentran más extensamente detallados en cada uno de los capítulos de la Tesis (I-IV).

Zona de estudio

Los ensayos de campo correspondientes a los capítulos I y IV, que se realizaron desde el año 2013 hasta el año 2016 (capítulo I) y en el año 2017-2018 (capítulo IV), se llevaron ambos a cabo en una plantación del nogal híbrido situada en el centro-oeste de la península Ibérica. El clima en la zona de estudio es mediterráneo continental, con veranos secos y cálidos e inviernos fríos y lluviosos. La temperatura media anual es de 15,2°, siendo la media de las temperaturas máximas y mínimas 35° y 0,7° respectivamente. Las precipitaciones suelen tener lugar durante el invierno, mayoritariamente, siendo la media anual de 439 mm. La cantidad de radiación solar total anual es de 6406 MJ / m^2 · año. El suelo de la zona de estudio es un Fluvisol con textura limosa y ligeramente alcalino en la capa superficial de 30 cm (pH en agua de 7,4).

Por otra parte, los experimentos correspondientes a los capítulos II y III, que se realizaron en condiciones controladas, en estructuras abiertas de sombreo artificial, se llevaron a cabo en el Centro de Agricultura Ecológica y de Montaña del CICYTEX, en Plasencia (provincia de Cáceres) (40° 1' N, 6° 6' O). El clima es mediterráneo continental, siendo la temperatura media anual de 16° C y las medias de las temperaturas máximas y mínimas 34,3° C y 3 ° C respectivamente. La precipitación media anual es de 694 mm, concentrándose principalmente en invierno, siendo el verano la estación seca.

Material vegetal

Arbolado

El arbolado presente en los ensayos correspondientes a los capítulos I y IV se encontraba en una única plantación localizada en la finca "El Soto" (39° 50' 54'' N, 4° 28' 2'' O, ETRS89) dentro del término municipal de El Carpio de Tajo, en la provincia de Toledo (España), cedida parcialmente para el experimento por la empresa Bosques Naturales S.A. Los árboles constituían el clon denominado *Nat7* de la especie de nogal híbrido *Juglans intermedia Mj209xRa.* Este híbrido se caracteriza por un rápido crecimiento (resultado del vigor híbrido), baja producción de fruto (por estar especialmente destinado a la producción de madera de calidad) y buena adaptación a los suelos y condiciones climatológicas de la península Ibérica. La plantación presentaba, en el momento de la realización de los experimentos, una densidad de 333 pies/ha, con un espaciamiento de 6 m en las calles donde se sembró el cereal para los ensayos y 5 metros entre las filas de árboles. En el momento de inicio del experimento del capítulo I, los ejemplares tenían 9 años de edad, con una altura media de 10,5 m y un diámetro normal medio de 15,3 cm. En el capítulo IV, los árboles tenían 13 años, presentando una altura de 11,7 m y un diámetro normal medio de 18,5 cm.

Cereal: especies y variedades

En todos los ensayos se utilizaron como especies de cereales de invierno el trigo blando (*Triticum aestivum* L.), con una dosis de siembra de 220 kg/ha, y la cebada (*Hordeum vulgare* L.), con una dosis de siembra de 180 kg/ha. Las variedades de estas especies que se utilizaron para los ensayos fueron variedades ampliamente distribuidas en la zona mediterránea y especialmente en España.

En el capítulo I, las variedades de cebada utilizadas no habían sido previamente seleccionadas por su aptitud para el cultivo bajo sombra, sino que se escogieron de entre las disponibles en el mercado, estando ampliamente distribuidas en la zona de estudio por su probada adaptación a la sequía y las altas temperaturas, condiciones habituales en el área mediterránea. Las variedades de cebada utilizadas en este capítulo fueron Doña Pepa, Azara, Basic, Lukhas, Hispanic, Dulcinea y Meseta, mientras que las variedades de trigo fueron Kilopondio, Bologna, Ingenio, Sublim, Nogal, Borricelli e Idalgo. Las semillas fueron proporcionadas por las empresas suministradoras de las mismas para su utilización con fines de investigación.

Para los capítulos II y III, se escogieron nueve variedades de trigo y nueve variedades de cebada, abarcando tres categorías de precocidad de floración: muy temprana, temprana y media.

Cada categoría incluía tres variedades, de forma que se utilizaron nueve variedades en total de cada especie. Así, las variedades de trigo utilizadas fueron Nogal, Nudel y Tocayo (categoría de precocidad: muy temprana), Algoritmo, Paledor y Solehio (categoría de precocidad: temprana) y Toskani, Somontano y Nemo (categoría de precocidad: media). Respecto a la cebada, las variedades escogidas fueron Hispanic, Lavanda y Luzia (categoría de precocidad: muy temprana), Kalea, Lagalia y Carolina (categoría de precocidad: temprana) y Meseta, Ibaiona y Tocayo (categoría de precocidad: media). Las categorías de precocidad y las variedades que se incluyeron en cada una de ellas se establecieron en base a los datos de floración recogidos por las diferentes fincas colaboradoras del Grupo para la Evaluación de Nuevas Variedades de Cultivos Extensivos en España (GENVCE; http://www.genvce.org/). Las semillas fueron proporcionadas por el Instituto de Investigaciones Agrarias Finca "La Orden-Valdesequera" del Centro de Investigaciones Científicas y Tecnológicas de Extremadura (CICYTEX). Para simular la dosis de siembra en campo, se sembraron 10 semillas en cada maceta (13 x 13 x 17 cm), reduciéndose a cuatro plántulas una vez hubo emergido el coleóptilo del cereal.

Para el capítulo IV se seleccionaron aquellas variedades que mejor respondieron a la sombra artificial en los capítulos II y III, para su siembra bajo arbolado en la misma plantación de nogal que la mencionada en el capítulo I. Estas variedades fueron, en el caso del trigo, Nudel, Paledor y Solehio, y en la cebada, Lagalia, Carolina y Meseta. Las semillas del cereal fueron proporcionadas por las empresas suministradoras de las mismas para su uso en investigación en la presente Tesis.

Diseño experimental

En los capítulos I y IV, correspondientes a los ensayos de campo, se establecieron tres sistemas o tratamientos: arbolado con cultivo de cereal (agroforestal), cereal sin arbolado (monocultivo) y arbolado sin cultivo (forestal). En el capítulo I, en el sistema agroforestal, para cada variedad de cereal se establecieron seis parcelas de 80 m^2 (20 m de largo x 4 m de ancho), que incluían cinco árboles consecutivos en línea y calles de 4 m de ancho para el cultivo de cereal, permitiendo un margen de 1 m entre parcelas. En el sistema de monocultivo de cereal se establecieron seis parcelas de 4 m^2 (2 m x 2 m) por cada variedad, espaciadas 0.5 m entre ellas y situadas de forma aleatoria. El sistema forestal estaba formado por tres parcelas de arbolado sin cultivo, incluyendo 45 árboles por parcela. La situación de las parcelas varió a lo largo de los tres años de estudio, evitando posibles efectos acumulativos. Por otra parte, en el capítulo IV, para el sistema agroforestal se establecieron parcelas similares a las realizadas en el capítulo I. Para el monocultivo de cereal se diseñaron seis parcelas de 9 m^2 (3 x 3 m) para cada variedad de forma aleatoria, dejando 1 m de separación entre ellas. El sistema forestal se compuso de tres parcelas de 25 árboles en cada una de ellas.

Respecto a los capítulos II y III, correspondientes al mismo experimento realizado en condiciones controladas, se siguió un diseño *split-plot*. En primer lugar, para cada variedad de cereal se sembraron 18 macetas diferentes, que se dividieron al azar en tres grupos, de forma que a cada nivel de sombra correspondieron 6 macetas de la misma variedad. A continuación, todas las macetas que se asignaron de forma aleatoria a cada nivel de sombra se situaron en el mismo bloque/estructura de sombreo.

Condiciones de siembra

Fertilización

En el capítulo I, pocos días antes de la siembra del cereal (noviembre), en las parcelas de cereal, tanto en el tratamiento de monocultivo como en el sistema agroforestal, se aplicó un abono de fondo complejo NPK 8:12:12 a razón de 600 kg/ha con abonadora centrífuga, aportando las siguientes dosis: 48 kg/ha de N, 31 kg/ha de P y 60 kg/ha de K, que son las habituales en los monocultivos de cereal de la zona. Posteriormente, cuando el cereal estaba en fase de ahijado (febrero), se aplicó una cobertera con urea del 46 % en riqueza, a razón de 120 kg/ha, equivalente a una dosis de 55 kg/ha de N.

En el capítulo IV, debido a las deficiencias observadas en K en el sistema agroforestal en la misma plantación, se utilizó un abono de fondo complejo NPK 8:15:15 a razón de 300 kg/ha en las parcelas de cereal (tanto en monocultivo como en agroforestal), lo que proporcionó unas dosis de: 54 kg/ha de N, 47 kg/ha de P y 134 kg/ha de K. Como cobertera se utilizó urea al 46 % a razón de 100 kg/ha, aplicándose así una dosis de 46 kg/ha de N.

Durante la época estival, en los capítulos I y IV, se aplicó fertirrigación a los árboles, con unas dosis de 40 kg/ha de N, 17,5 kg/ha de P y 41,5 kg/ha de K.

En los capítulos II y III, se aplicó un abonado de fondo en las macetas de cereal con el abono complejo NPK 7:12:7, que proporcionó unas dosis equivalentes de 58 kg/ha de N, 44 kg/ha de P y 48 kg/ha de K. Como cobertera, se aplicó urea al 46 % hasta conseguir una dosis total de 200 kg/ha de N.

Sustrato, macetas y sombra artificial

En los capítulos II y III, las macetas utilizadas presentaban un volumen de 3 L (dimensiones de 13 x 13 x 17,4 cm). El sustrato consistió en una mezcla de turba, arena y perlita en la proporción de volumen 3:1:1. El pH de la turba era de 3,95, por lo que se corrigió con dolomita hasta alcanzar

valores del rango 5,3 – 6,5. La conductividad eléctrica de la mezcla final fue de 141-173 µs/cm y presentó un 38 % de capacidad de campo.

En estos mismos capítulos, se utilizaron mallas de sombreo para generar unos niveles de sombra artificial correspondientes a 0 %, 25 % y 50 % de sombra, en términos de reducción de la radiación fotosintéticamente activa (*PAR*, en inglés). Para el nivel de sombra 0 %, se utilizó una malla anti-pájaro para proporcionar condiciones similares de seguridad y ventilación que en el resto de los niveles de sombra. Así, se construyeron tres estructuras de invernadero cubiertas en toda su superficie por cada una de las mallas de sombreo, respectivamente. En cada estructura, la malla de sombreo se situó a una altura de 1,5 m medidos sobre la altura máxima esperada del cereal. El material de las mallas de sombreo fue polietileno de color verde, asemejándose a la sombra producida por el arbolado. La dimensión de las mallas y su porosidad (según la norma UNE 40606) fue respectivamente de 2,25 cm^2 y 90 % para la malla del 0 % de sombra, 0,0026 cm^2 y 43 % en la malla del 25 % de sombra y 0,0075 cm^2 y 36 % para la malla del 50 % de sombra. Los valores medios máximos de *PAR* alcanzados en los niveles de sombra 0 %, 25 % y 50 % fueron 1680, 1390 y 965 µmol/m$^2 \cdot$ s en la primavera, simulando niveles de radiación encontrados en las diferentes etapas de desarrollo foliar de árboles caducifolios presentes en sistemas agroforestales como el nogal. La instalación de las mallas de sombreo tuvo lugar al comienzo del espigado de los cereales, coincidiendo con la brotación del nogal en la zona de estudio y se mantuvieron hasta que los cereales alcanzaron la madurez.

Parámetros analizados

Cereal

Respecto a la fenología, producción y calidad nutritiva del cereal, se realizó un seguimiento fenológico del cereal según la escala de Zadoks et al. (1974) en todos los capítulos (I, II, III y IV), valorando también la producción de grano y sus diferentes componentes.

En cuanto a los parámetros fisiológicos del cereal, en el capítulo II se realizaron curvas de saturación de luz en términos de fotosíntesis, utilizando para ello el sistema de análisis de gas infrarrojo (LCpro +, ADC Bioscientific Ltd). En los capítulos II y III se analizaron los contenidos en clorofila y carotenoides a través de medición indirecta con *SPAD* (SPAD-502 Plus, Konica Minolta Holdings, Inc.). También se determinaron los parámetros de fluorescencia relativos al *Quantum Yield* (Φ_{PSII} o *Y*), *Electron Transport Rate* (*ETR*) y *Non-Photochemical Quenching* (*NPQ*) con fluorómetro de clorofila modulado (OS5p+,Opti-Sciences, Inc.). En el capítulo IV se valoraron el contenido relativo agua en hoja (*RWC*), según el método propuesto por Barrs y Weatherley (1962), y el daño en la

membrana celular de forma indirecta a través del flujo de electrolitos de acuerdo con la metodología propuesta por Bajji et al. (2002), además de los parámetros *NDVI* y *PRI*, ambos determinados con el espectómetro LabSpec-4 Hi-Res y su accesorio Plant Probe (ASD Inc., Malvern Panalytical Ltd.).

Con relación a los rasgos morfológicos del cereal, en los capítulos II, III y IV se analizaron la masa foliar por área (*LMA*) y el área foliar, utilizando para ello el software *ImageJ* (National Institute of Health, EEUU). Además de los parámetros morfológicos anteriores, en el capítulo IV también se determinó el índice de área foliar (*Leaf Area Index, LAI*) mediante ceptómetro (Accupar LP-80, Meter Group).

En cuanto a las determinaciones analíticas, en los capítulos I, III y IV se midió el contenido en N del grano para valorar su calidad nutricional mediante el método *Dumas* (ISO 16634-1:2008), incluyendo además en el capítulo III el contenido de P, mediante la técnica de análisis flujo segmentado (ISO15681-2:2003) y de K, mediante espectrometría de absorción atómica (ISO 9964-2:1993). En el capítulo III se analizaron también los contenidos de glucosa y almidón en hoja del cereal según el método propuesto por Oleksyn et al. (2000), así como los contenidos en N, P y K, siguiendo los protocolos descritos anteriormente. Por otra parte, en el capítulo IV, se analizaron los contenidos de N, P y K en las plantas de cereal, siguiendo la metodología antes descrita.

Arbolado

Los parámetros morfológicos, nutricionales y fisiológicos del arbolado se determinaron en los capítulos I y IV, pues fueron los correspondientes a los ensayos de campo. En ambos capítulos se midieron el diámetro normal y la altura de los árboles (con el hipsómetro Suunto PM-5/1520). Respecto a su estado nutricional, se valoraron los contenidos de N, P y K en hoja (de forma similar al cereal). Además de estos parámetros, en el capítulo IV se determinaron el índice de área foliar, de forma similar al medido en cereal y el estrés hídrico de los árboles mediante cámara de *Scholander* (Model 100 Pressure Chamber, PMS Instrument Company).

Clima y suelo

En los capítulos II y III las determinaciones de temperatura y humedad a la altura de la cubierta del cereal se realizaron con *dataloggers* registradores (PCE-H71N Data logger, PCE Instruments, Holding GmbH Inc). En el capítulo IV, la temperatura y la humedad relativa del aire a la altura del cultivo de cereal se determinó de forma análoga a la descrita para los capítulos II y III. Además, la radiación solar incidente se registró, en el capítulo IV, con *dataloggers* del modelo HOBO Pendant® Temperature/Light 64K Data Logger, Onset Computer Corporation.

Respecto a las determinaciones edafológicas, en los ensayos de los capítulos I y IV (correspondientes a los experimentos en campo) se realizaron análisis iniciales de suelo con parámetros como el pH, la textura, el contenido en materia orgánica, la capacidad de intercambio catiónico, y los contenidos totales de N, P disponible y cationes de cambio K, Ca, Mg, Na. Respecto a los análisis realizados en suelo para determinar posibles relaciones de competencia y facilitación entre los estratos arbóreo y herbáceo, en el capítulo I se realizaron dos extracciones en las muestras de suelos tomadas: una extracción con KCl 1 M, para evaluar los contenidos de amonio (NH_4^+) y nitrato (NO_3^-), según el método propuesto por Rayment y Lyons (2011), y otra extracción con Melich 1, para evaluar el contenido de P y K disponible, siguiendo la metodología expuesta por Sims (2000). Los análisis de los contenidos de amonio y nitrato se realizaron siguiendo el protocolo ISO 14256-2:2005, mientras que los contenidos de P y K se analizaron según los protocolos expuestos anteriormente. En el capítulo IV, para la determinación del N total mineral en las muestras de suelo, se realizó una extracción con KCl 1 M similar a la realizada en el capítulo I, siguiendo los mismos protocolos de análisis. Además, en el capítulo IV se instalaron resinas de intercambio iónico en la capa superficial del suelo (5-10 cm), a las que posteriormente se les realizó una extracción con HCl 0.5 M para analizar NH_4^+, NO_3^-, P y K, según los protocolos indicados previamente.

Análisis de datos

En lo referente a los métodos estadísticos, éstos se adaptaron a las características propias de cada experimento y capítulo, estando especificados de forma más detallada en cada uno de ellos.

Para analizar tanto las variables causantes de variación de los datos como las diferencias significativas entre grupos, se utilizaron modelos lineales generales (GLM), como en el capítulo I. Las comparaciones *post-hoc* de las medias se realizaron mediante el test LSD de *Fisher*. En el capítulo II, se ajustaron modelos generales aditivos (GAM) para evaluar las curvas de fotosíntesis neta y las curvas de los parámetros de fluorescencia del cereal. Además, se utilizaron modelos lineales mixtos (LMM) para evaluar la variación de los parámetros medidos en el cereal. En el capítulo III, los datos fueron sometidos a un análisis de componentes principales (PCA) con todos los parámetros medidos en el cereal y también se realizaron correlaciones de *Pearson* (coeficiente de correlación, *r*) para establecer posibles relaciones entre los parámetros medidos. Por último, en el capítulo IV se ajustaron modelos de ecuaciones estructurales (SEM) para evaluar las relaciones directas e indirectas entre los diferentes parámetros medidos.

El tratamiento estadístico de los datos se realizó con los software *Statistica* (StatSoft Inc., Maison-Alfort, France) y *R* (R Core Team, 2020), con los paquetes concretos que se especifican en cada capítulo.
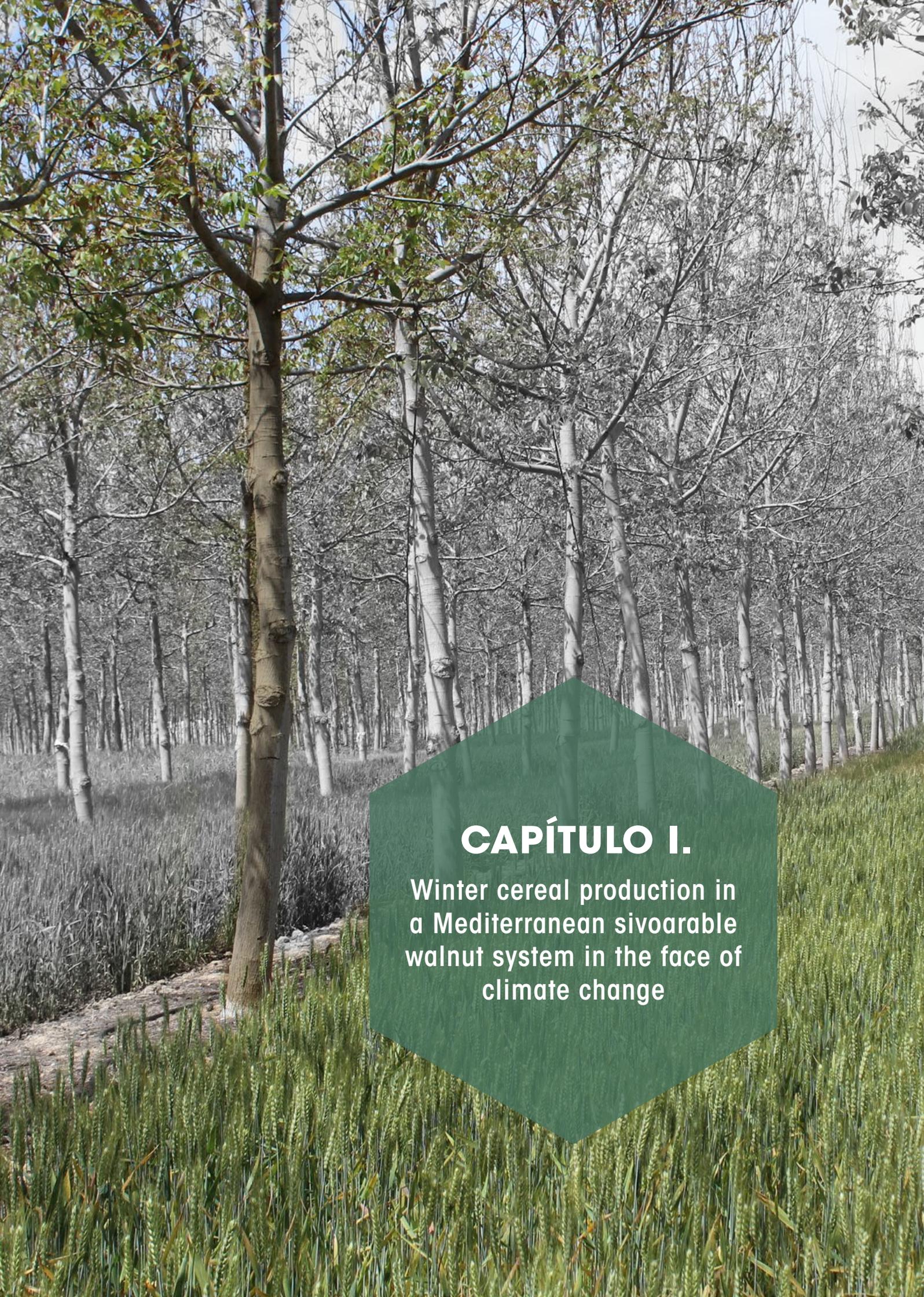
CAPÍTULO I.

Winter cereal production in a Mediterranean sivoarable walnut system in the face of climate change

CAPÍTULO I.

Winter cereal production in a Mediterranean silvoarable walnut system in the face of climate change

María Guadalupe Arenas-Corraliza, María Lourdes López-Díaz, Gerardo Moreno

INDEHESA Research Institute, University of Extremadura, Avenida Virgen del Puerto, 2. Plasencia, Cáceres 10600, Spain.

ABSTRACT

One of the foreseeable consequences of climate change is a reduction in crop yields. In recent years, agroforestry systems have been identified as a strategy for climate change mitigation and adaptation. In this study we assess the potential of a silvoarable system to protect crops against extreme climate events. We studied a 9-year-old hybrid walnut silvoarable system (*Juglans x intermedia Mj209xRa*) intercropped with cultivars of two winter cereals - wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) - for three consecutive years and compared it with monocrops and pure tree plantations. The parameters studied were grain and total biomass yield, harvest index, grain size and tree diameter increment. Plant phenology and soil and plant nutrients were also examined. Climate conditions and tree presence conditioned cereal yields, and the responses to silvoarable conditions differed among cereal species and cultivars. The silvoarable system with barley had higher production than monocrops in years with early heat events (yield increment of 55 % in the first year and 15 % in the second year). For wheat, no positive effect of trees in the silvoarable system was found, although grain quality improved significantly (2.56 % and 2.76 % N grain content in monocrops and silvoarable systems, respectively). Tree growth, measured as diameter at breast height increment, was lower in the silvoarable system (2.06 cm at the end of the study) than in the monospecific plantation (2.83 cm in the same period). The land equivalent ratio was always higher than 1 (1.34 to 2.08), showing that the silvoarable system was more productive than sole pure plantations and cereal monocrops.

Keywords: alley cropping, agroforestry, barley, silvoarable, wheat.

INTRODUCTION

World population growth in the second half of the 20th century required an increase in crop yield that was achieved by improved agronomic techniques and seeds. However, despite the need to double food production in the 21st century to feed the increasing human population, yields have stagnated in recent years (Tilman et al., 2002) as a result of climate change and recurrent extreme weather events such as heat waves and prolonged drought (Ray et al., 2012). In the coming years, global wheat yield is likely to decrease by 6 % for each degree-Celsius increment in mean temperature (Zhao et al., 2017). Any increase in arable land is expected to be insufficient to provide enough food for the rising human population this century (Alexandratos & Bruinsma, 2012), requiring the design of more productive and more sustainable systems. Many approaches have been suggested to achieve advances in ecological intensification, which aims to increase the yields of land through better use of its resources (Bommarco et al., 2013).

Agroforestry systems, defined as integrated land-use systems, are among these ecological intensification approaches (Tittonell, 2014). Agroforestry is the practice of deliberately integrating woody vegetation (trees or shrubs) with crop and/or animal production systems to benefit from the resulting ecological and economic interactions (Burgess et al., 2015). Many studies (e.g., Schoeneberger et al., 2012) have reported that trees help to regulate the climate beneath them by reducing temperature extremes, providing shelter from the wind and limiting soil surface evaporation. In Mediterranean areas, trees can stabilise grass production through the typical inter- and intra-annual rainfall variation (Gea-Izquierdo et al., 2009; Joffre & Rambal, 1993; Moreno, 2008). Woodland shade also limits water loss by crop transpiration, thus increasing the water use efficiency of the system, a key factor in adapting to climate change (Lasco et al., 2014). The role of integrated systems as a climate change adaptation mechanism has recently been recognised by the European Conference on Rural Development (EU, 2016), the European Strategy for Climate Change (EU, 2014), the European Forestry Strategy (EU, 2013) and the latest International Panel on Climate Change report (Fifth Report) (IPCC, 2015).

Silvoarable systems producing trees and crops are one of the possible combinations within agroforestry systems. The species used, wheat and walnut, are two of the most commonly studied species in temperate silvoarable systems (Wolz & DeLucia, 2018). Trees appear to have the ability to extend roots to deeper layers when there is competition in the shallower layer, which could help to ensure sufficient belowground resource acquisition (nutrients and water) and adequate growth rates (Andrianarisoa et al., 2015; Cardinael et al., 2015). Crop response to conditions imposed by trees under the Mediterranean climate and other water-limited regions remains uncertain (van der Werf et al., 2007). While some studies have identified plant traits

that could be beneficial in certain wheat cultivars to withstand partial shade caused by pollution in some areas (Li et al., 2010), interest has recently increased in studying how shade generated by trees affects wheat yield (Dufour et al., 2013; Mu et al., 2010). However, these studies have overlooked how barley, characterised by its drought tolerance (Xia et al., 2017), could respond differently from other cereals in silvoarable systems.

This study attempts to shed light on the production of winter cereals and timber trees in a silvoarable system in a Mediterranean area in years with contrasting climate conditions. In this area, high inter-annual rainfall variations and spring heat waves are becoming common, agreeing with foreseen future climate scenarios (Gerald & Tebaldi, 2004; Giorgi & Lionello, 2008; Trnka et al., 2014). We compared the productivity of different cultivars of barley and wheat cultivated in open fields and under 9-year-old hybrid walnuts. Our specific hypotheses were:

(i) *There is competition between crops and trees that negatively affects crop yield.* This hypothesis was assessed by comparing crop yield (and soil and plant nutrients) between silvoarable vs cereal monocrops in years with no specific climatic constraint.

(ii) *During spring heat waves, winter cereals could be more productive under trees.* Crop yield was compared between silvoarable and monocrops in years with spring heat waves.

(iii) *Crop yield under silvoarable conditions depends strongly on the crop species and cultivars.* Comparisons of phenology and crop yield among silvoarable and monocrops were performed for species and cultivars differing in precocity.

(iv) *Grain quality could differ between the silvoarable combination and monocrops.* Nutrient content of barley and wheat grains produced in monocrops and silvoarable plots were compared.

(v) *Tree growth diminishes in the silvoarable system.* Stem growth was compared between trees in silvoarable and forestry plots. Leaf nutrients were also compared.

Lastly, we evaluated the overall yields of the study systems by calculating the land equivalent ratio (R. Mead & Willey, 1980) over three years to determine whether the silvoarable system is more productive than forestry and monocrops in the face of climate change.

The experiment is part of the European project AGFORWARD, which aims to promote agroforestry systems in Europe through proposals for innovation and social recognition of their environmental services. This study helps to identify crops adapted to silvoarable systems under a Mediterranean climate.

MATERIAL AND METHODS

Study site

The experiment was conducted from 2013 to 2016 in a hybrid walnut plantation in central-western Spain (Toledo, Spain; coordinates ETRS89 39º 50' 54'' N 4º 28' 2'' W, 411 m a.s.l). The climate of the region is Mediterranean, with hot dry summers and cool rainy winters. Average annual temperature and rainfall are 15.2 °C and 439 mm, respectively. Drought usually occurs from June to September. The soil is Fluvisol, with a depth of more than 1.4 m. Initial soil analysis indicated a sandy loam texture with an acidic pH in the upper 20 cm (pH 6 in water) (Table A1), making the area suitable for cultivating the species used in the study.

The study was carried out in a 9-year-old (in 2013) hybrid walnut plantation, planted in former cereal fields at 6 m between-row and 5 m within-row spacing (333 trees ha^{-1}). Before 2013, the whole plantation had been treated with herbicides in tree rows and ploughed in alleys to keep it weed free. In the study period, canopy closure was almost complete and trees were pruned each year before and during the study. At the beginning of the experiment, mean tree height and diameter at breast height (DBH) were 10.5 m and 15.3 cm, respectively. Every summer (July-September), trees were irrigated at the same rate in the silvoarable and forestry systems using a drip irrigation system, with a total amount of 2000 m^3 ha^{-1} and water quality adequate for walnut irrigation (Table A2). The nutrient content applied to trees through irrigation in summer was 40 kg N ha^{-1}, 17.5 kg P ha^{-1} and 41.5 kg K ha^{-1}. The plantation was certified by the Forest Stewardship Council (FSC). The woodland was a clone of Nat7 of hybrid walnut *Juglans x intermedia Mj209xR*a, resulting from pollination of *Juglans major* Torr. *var. 209 (Mj209)* with *Juglans regia* L. *(Ra)*. This hybrid is known for its fast growth (hybrid vigour) and low fruit yield, and has considerable capacity to adapt to different soils and warm areas of the Iberian Peninsula. Walnut buds usually break after mid-April. A large adjoining area without trees that had previously been cultivated with winter cereals (wheat and barley) was used for the monocrop system.

Experimental layout

Three vegetation systems were compared: intercropping of cereals in walnut plantation alleys ("silvoarable"), cereals grown in open fields ("monocrops") and pure tree plantation without intercropping ("forestry"). Silvoarable and forestry plots were adjacent to each other, in the same walnut plantation area (Figure A1). Trees in the silvoarable and forestry plots had received similar management before the study and were similar in size. The systems were established at a distance from each other (Figure A1) because it was a private plantation that

did not allow a randomised block design. However, to ensure that soil conditions were similar between treatments, soil properties were evaluated and no apparent differences were detected for the more common parameters (Table A1).

For the silvoarable treatment, six plots measuring 120 m^2 (20 m long x 6 m wide, including 5 trees in each line and cropped alleys 4 m wide) were cultivated and located randomly per cultivar of cereal. Six 2x2 m plots were established per cereal variety without trees as a control for cereal production (monocrops), spaced 0.5 m apart (Figure A2). The forestry control comprised three plots of trees without cereals (45 trees per plot). The location of the plots varied across the three years. Cereal species were carefully sown by hand spreading in early November each year in the silvoarable and monocrop systems. Soil was prepared by harrowing in June and again a few days before sowing. All cereal plots were fertilised in November (just before sowing) with 48 kg ha^{-1} N, 31 kg ha^{-1} P and 60 kg ha^{-1} K and in February (cereal tillering) with 55 kg ha^{-1} N.

The winter cereal species were barley (*Hordeum vulgare* L.) and wheat (*Triticum aestivum* L.). The sowing rate was 180 kg ha^{-1} for barley and 220 kg ha^{-1} for wheat. The selected cultivars varied over the years depending on seed availability but were the same each year in the monocrop and silvoarable systems. Barley cultivars were Doña Pepa and Azara in 2013, Basic, Lukhas, Hispanic and Dulcinea in 2014 and Meseta and Hispanic in 2015. Wheat cultivars were Kilopondio and Bologna in 2013, Ingenio, Sublim and Nogal in 2014 and Ingenio, Nogal, Botticelli and Idalgo in 2015. All of these cultivars are commonly sown in Spain in Mediterranean areas because of their proven adaptation to drought and high temperatures.

Weather conditions

Climate data was obtained from Vegas de San Antonio weather station (coordinates ETRS 89 39º 57' 21'' N and 4º 42' 1'' W), 18 km from the plot but at the same altitude in a flat region. The annual precipitations (Figure A3) of the growing seasons studied (2013-2014, 2014-2015 and 2015-2016), at 387 mm, 284 mm and 302.2 mm, respectively, were lower than the 1999-2013 average (442 mm). Spring rainfall in the third year was almost triple that of the first year and twice that of the second year (Figure A3). Major differences also occurred in winter: in the first year, winter rainfall was almost 60 % of total rainfall (229 mm), whereas in the second and third years it was 15 % and 20 %, respectively (Figure A3). One notable occurrence was a long period with high temperatures in April and May in the first and second years, when flowering had already started in the cereals (Figure 1), but in the third year no heat waves occurred and temperatures were lower than in the previous years.
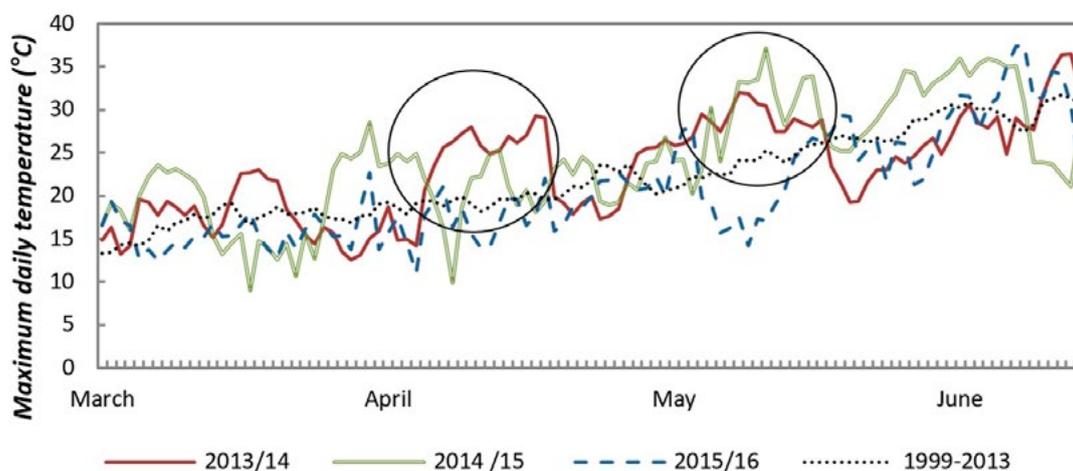
Figure 1. Maximum daily temperatures (° C) during 2013/14, 2014/15 and 2015/16 growing seasons and mean value for the period 1999-2013. Source: Based on data from *Vegas de San Antonio* weather station.

Field measurements and sampling

Cereal phenology was recorded in 16 plants per plot on three dates in 2016 (May 4, May 26, June 7) by Zadoks growth stages (Zadoks et al., 1974). Once cereal plants had matured, samples were harvested using hand clippers in June 2014, 2015 and 2016 at ground level in 50 x 50 cm squares, taking three samples per plot in the centre of the silvoarable system and two samples per plot in monocrops. Plants were dried at 60 °C to constant weight. The variables measured to determine cereal yield were total aerial biomass weight, total grain weight and weight of 1000 grains. The harvest index was calculated as the ratio between grain weight and total aerial biomass weight.

Tree DBH was measured using a diameter tape every year in the dormant period (January) in 180 trees in the silvoarable system (four central trees per plot) and 45 trees in the forestry system.

Tree leaves were sampled in July 2014, 2015 and 2016 after randomly selecting 12 trees in each treatment (forestry and silvoarable). In each tree, two shoots were cut in the middle of the crown in all directions (N, S, E, W) using telescopic shears. Terminal leaflets were collected from leaves in the middle of the shoot, stored in paper bags and dried at 60 °C to constant weight. In early June each year, during cereal ripening, five random soil samples at 20 cm depth were taken from each plot and dried at 60 °C to constant weight until analysis in the laboratory.

Chemical analyses

Plant samples were treated by acid digestion in Kjeldahl tubes in a Gerhardt Block-Digestion Unit, Model 20, for further determination of P and K content. Phosphorus content was analysed using the ISO 15681-2:2003 method with a Seal Analytical AA1 AutoAnalyzer. Potassium content was analysed using a Sherwood Flame Photometer, Model 410, following the ISO 9964-2:1993 method. Cereal grain and tree leaf N content was determined by combustion analysis using the Dumas method (ISO 16634-1:2008) in two replicated analyses per sample with an elemental analyser (DUMATHERM®, Gerhardt). The factor used to convert N content to protein in cereal grains was 5.83.

Soil samples were sieved to <2 mm and soil was extracted with 1 M KCl to analyse ammonium (NH_4^+) and nitrate (NO_3^-) content (Rayment & Lyons, 2011). Extractions were performed with Melich 1 (Sims, 2000) to determine available P and K. Ammonium content was analysed using the ISO 14256-2: 2005 method in an AutoAnalyzer (Seal Analytical, model AA1). Nitrate was analysed using the same method including a Cd column. Phosphorus and K were determined following the methods ISO 15681-2:2003 and ISO 9964-2:1993, respectively.

Data analysis

Land equivalent ratio was calculated for grain yield of barley and wheat following Mead & Willey (1980), using the allometric equation developed by López-Díaz et al. (2017) for *Juglans* species to calculate tree biomass.

Differences for mean values in the parameters grain and biomass yield, harvest index, and weight of 1000 grains were analysed by full-factorial ANOVAs, with three fixed factors (year, species and system) and cultivars as a random factor, nested in year and species (Table A3). Similarly, growth stages in 2016 were compared with one ANOVA per date, with species and system as fixed factors and cultivars as a random factor. Soil N, K and P were compared for the three systems (monocrop, silvoarable and forestry) by one-way ANOVAs. Differences between systems for N and K content in grains in 2016 were determined by ANOVAs, with system and species as fixed factors and cultivar as a random factor. Differences between systems in 2016 for stem diameter increment and N, P and K content in walnut leaf were determined by t-tests. Where ANOVA yielded statistically significant differences (p < 0.05), the least squares difference (LSD) test was used for subsequent pair-wise comparisons. All analyses were performed using STATISTICA software (StatSoft Inc., Maison-Alfort, France).

RESULTS

Cereal growth and yield

Grain yield differed between years, species and systems. In the first two years (2014 and 2015), barley grain yield increased in the silvoarable system (Figure 2). The increment was greater in the first year, at 50 % more than in monocrops (p = 0.008, Table 1), and less significant in the second year (p = 0.025), and was more pronounced in the second year in the Basic cultivar (p = 0.024, Table A4).

For wheat, the silvoarable system showed no significant differences in grain yields in the first year. In the second year, yields were significantly lower in silvoarable, with 2.07 Mg ha^{-1} compared to 3.9 Mg ha^{-1} in the monocrop system (p <0.001, Figure 2), especially in the Sublim and Nogal cultivars (p < 0.001, Table A4). In the third year, the silvoarable system produced significantly less grain in barley (p < 0.001) and wheat (p < 0.001) (Figure 2), showing significant differences for the Hispanic barley cultivar (p < 0.001) and the Ingenio, Botticelli, Nogal and Idalgo wheat cultivars (p <0.001, Table A4).
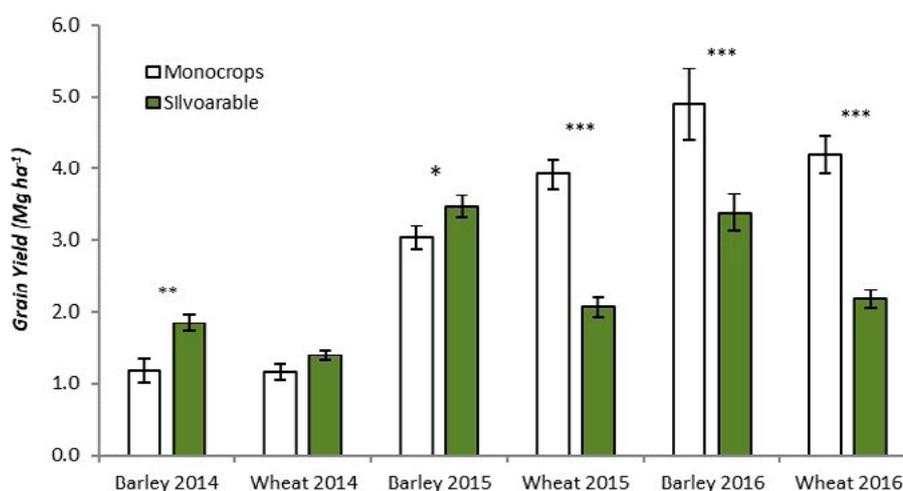
Figure 2. Grain yield (Mg ha^{-1} ± S.E.) in wheat and barley in the study years in monocrops and silvoarable systems. Significance level: * *p < 0.05; ** p < 0.01; *** p < 0.001.*

Plant biomass was greater in the silvoarable system in barley in the first and second years (p = 0.008 and p = 0.004, respectively, Table 1), especially for the Hispanic cultivar in the second year (p = 0.001, Table A4), but showed no difference for wheat. In the third year, when climate conditions were more favourable for cereal plants, monocrops had a higher

biomass yield in both species (p < 0.001, Table 1), in all cultivars (Ingenio, Botticelli, Nogal, Idalgo, Meseta and Hispanic, p < 0.001, Table A4). The harvest index in silvoarable system for barley was significantly lower in the second year (p = 0.01, Table 1), especially in the Hispanic (p < 0.001), Basic and Dulcinea (p = 0.03 and p = 0.02, respectively) cultivars (Table A4). The harvest index for wheat was also significantly lower in the silvoarable system in the second year (p < 0.001, Table 1), especially in the Ingenio (p = 0.02), Sublim and Nogal cultivars (p < 0.001), as shown in Table A4. Wheat grain size (weight of 1000 grains) was greater in monocrops than in the silvoarable system in the first year (p = 0.03, Table 1), especially in the Kilopondio cultivar (p = 0.004, Table A4). In contrast, barley grain size was significantly different between systems in the second year (p < 0.001), with a higher value in silvoarable (40.61 g) than in monocrops (31.11 g), especially in the Basic (p = 0.003), Lukhas (p = 0.017) and Hispanic (p = 0.043) cultivars, as shown in Table A4.

Table 1. Biomass yield (Mg ha^{-1} ± S.E.), harvest index and weight of 1000 grains (g ± *S.E.)* of wheat and barley in the study years in monocrops and silvoarable systems. Significance level (t-test): ** p < 0.05; ** p < 0.01; *** p < 0.001.*

Year	Species	Biomass yield (Mg ha^{-1})		Harvest index		Weight of 1000 grains (g)	
		Monocrops	Silvoarable	Monocrops	Silvoarable	Monocrops	Silvoarable
2014	Barley	6.32 ± 0.36	7.71 ± 0.27 **	0.19 ± 0.02	0.24 ± 0.01	29.78 ± 1.01	29.62 ± 0.64
	Wheat	8.23 ± 0.26	8.29 ± 0.29	0.14 ± 0.01	0.17 ± 0.01	24.82 ± 1.16	22.34 ± 0.66 *
2015	Barley	5.52 ± 0.22	6.72 ± 0.29 **	0.57 ± 0.03	0.52 ± 0.01*	31.11 ± 2.22	40.61 ± 0.75 ***
	Wheat	6.83 ± 0.16	7.18 ± 0.32	0.57 ± 0.03	0.28 ± 0.01 ***	26.25 ± 2.57	25.82 ± 0.99
2016	Barley	11.58 ± 0.87	7.94 ± 0.33 ***	0.42 ± 0.02	0.42 ± 0.03	26.30 ± 0.96	25.71 ± 0.91
	Wheat	17.10 ± 0.53	8.79 ± 0.40 ***	0.24 ± 0.01	0.25 ± 0.01	21.42 ± 0.80	20.57 ± 0.54

Crop phenology

Crop phenology was monitored from May 4 (just before walnut leafing) to June 7 (just after walnut leaf and cereal grain maturation). By tree leafing, crops had reached the stage of milk grain development (Zadoks growth stages 70-79), although barley was more advanced than wheat and its growth was faster in silvoarable than in monocrops (Figure 3). At more advanced growth, during stages 80-89 (dough development) and 90 (ripening), barley grain development was slightly slower in silvoarable than in monocrops. However, there was no difference between systems for wheat development during the milk and dough stages, although ripening was delayed in both wheat and barley in the silvoarable system.
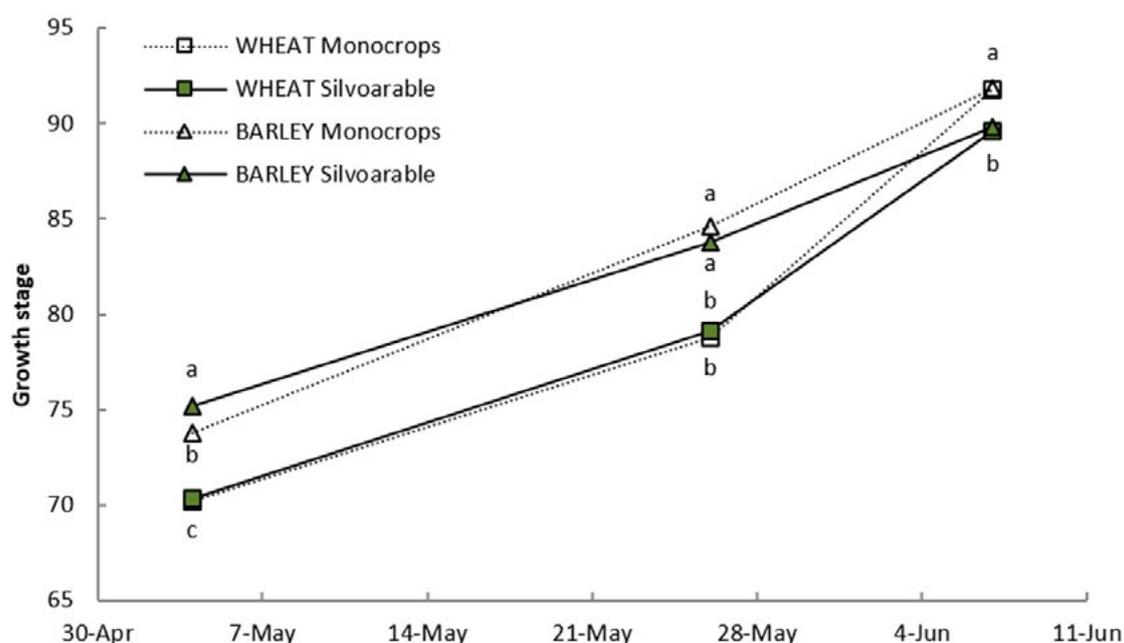
Figure 3. Growth stages according to Zadoks (1974) of wheat and barley in 2015-2016. Different letters indicate significant differences for the same period. Tree leafing occurred about the first fortnight of May.

Grain nutrient content

Wheat N and K content were significantly higher (p = 0.006 and p < 0.001, Figure 4). in silvoarable than in monocrops (6 % and 28 %, respectively). However, barley showed no significant difference in N or K and tended to be lower in N in silvoarable.
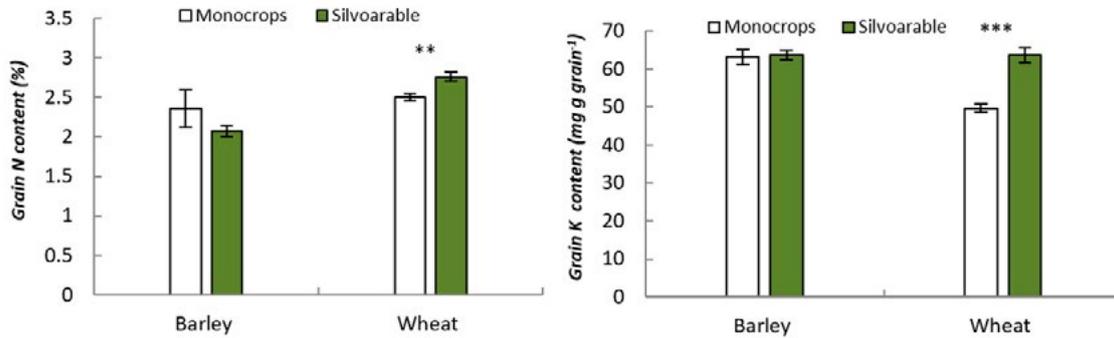
Figure 4. Grain N (% N ± S.E.) and K (mg g grain^{-1} ± S.E) content of barley and wheat in monocrops and silvoarable systems in 2016. Significance level (t-test): ** *p < 0.01; *** p < 0.001.*

Tree growth

Tree growth in terms of DBH was monitored in the study years. Trees in the forestry system grew faster than trees intercropped with cereal (Figure 5). The increment was 100 % greater in forestry than in silvoarable in the first year and 20 % greater in the second and third years.
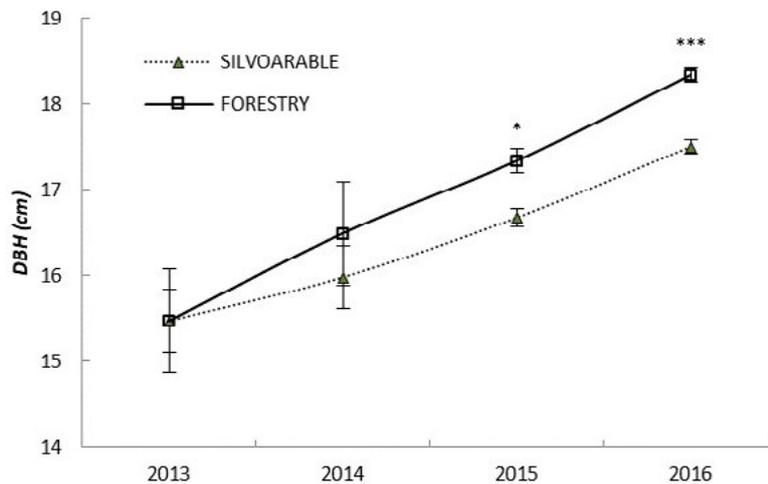
Figure 5. Means of *Diameter at Breast Height* (DBH) (cm ± S.E.) of *Juglans x intermedia Mj209xR*a in forestry and silvoarable systems in 2013, 2014, 2015 and 2016 study years. Significance level (t-test): * *p < 0.05; *** p < 0.001.*

Land equivalent ratio (LER)

Land equivalent ratio for both barley and wheat was > 1 in all years of study. The range was from 1.34 to 2.08 and LER was greater for barley every year (Table 2).

Table 2. Land equivalent ratio (LER) of wheat and barley in silvoarable combination with walnut in three study years. Parentheses contain the relative yields of crop grain and tree biomass, respectively.

Year	Tree age (years)	LER	
		Barley + Walnut	*Wheat + Walnut*
2014	10	2.08 (1.55 + 0.52)	1.72 (1.20 + 0.52)
2015	11	1.96 (1.15 + 0.81)	1.34 (0.53 + 0.81)
2016	12	1.55 (0.69 + 0.87)	1.39 (0.52 + 0.87)

Walnut leaf nutrient content

Walnut leaf N (mean value of 22.16 ± 0.51 mg g^{-1}) and P (mean value of 1.34 ± 0.11 mg g^{-1}) contents showed no significant differences between systems or years of study. In contrast, walnut leaf K content (Figure 6) was significantly lower ($p < 0.001$) in silvoarable (13.33 mg g^{-1} in 2015 and 19.15 mg g^{-1} in 2016) than in forestry.
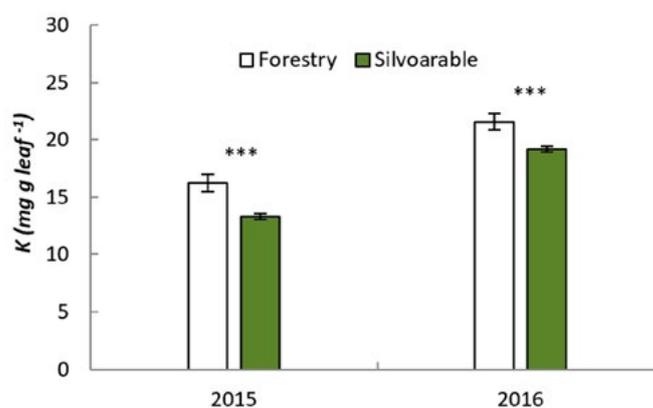
Figure 6. Walnut leaf K content (mg g leaf^{-1} ± S.E.) in wheat and barley in 2015 and 2016 in monocrops and silvoarable systems. Significance level (t-test): *** *p < 0.001.*

Soil resources

Soil K content values were higher in monocrops (172 ± 29 mg kg^{-1}), followed by forestry (146 ± 7 mg kg^{-1}) then silvoarable (132 ± 4 mg kg^{-1}), with a significant difference between monocrops and silvoarable (p=0.008). Differences in mineral N (mean value of 22.16 ± 0.51 mg g^{-1}) and available P (mean value of 1.62 mg g^{-1}) were not significant (data not shown).

DISCUSSION

Cereal yield is reduced by trees under a favourable climate for the crop

Cereal biomass and grain production are strongly related to water availability during plant development. Water stress during cereal tillering reduces the number of shoots (Passioura & Angus, 2010). However, most of the biomass grows in the first part of the vegetative cycle, especially during winter, when water deficit is less frequent. Thus grain yield is largely determined by the biomass assimilated in the last part of the cycle (Asseng & Savin, 2012), corresponding to late spring in our study area. A higher grain yield is therefore foreseeable in years with adequate rainfall in spring, as observed in 2015 and 2016. This is more important for grain formation than total annual precipitation.

In very favourable climate conditions for grain production, as in 2016, trees were detrimental to cereal plants, and grain yield was lower in silvoarable than in monocrops, as reported in previous studies of wheat combined with walnut (Dufour et al., 2013; He et al., 2012; Li et al., 2008), probably due to competition for resources such as light, water and nutrients between the two strata in agroforestry systems (Mead et al., 2010).

Water and nutrient absorption by winter cereals continues after leafing of deciduous trees in Mediterranean silvoarable systems (Dufour et al., 2013). The walnut root system can adapt to soil moisture conditions in silvoarable systems by absorbing more water in deeper layers. However, this cannot prevent competition in shallow layers, where most of the fine roots of the two strata are present, and therefore cereal yield is reduced (He et al., 2012; Zhang et al., 2015). The results showed K competition between the two strata, indicated by K content in the soil, walnut leaves and cereal grains. In cereals, K absorption takes place mainly during biomass production and peaks during flowering, when it starts to be transferred to the grain until ripening (Karlen et al., 1988). When walnuts started budburst in April (when wheat and barley were flowering), they began to consume K for their vegetative requirements. This competition for K seems to be essential to grain yield and nutritional value.

When climate conditions were favourable, biomass and grain yield of both cereals were lower in the silvoarable system due to light reduction and K (and presumably water) competition. Given our lack of a randomised block design, this result could be affected by initial soil differences between the silvoarable and monocrop plots. The change in crop yields in silvoarable, from higher to lower than monocrops under trees depending on the year (see next section) and species, indicates that differences in yields were more dependent on tree-crop interactions and species than on hidden differences in soil properties.

Trees protect crops against heat waves

Cereal biomass in both species and barley grain production were higher in the silvoarable system in the first two years, when heat waves occurred in April and May.

The climate in the Mediterranean area is characterised by considerable inter- and intra-annual differences in precipitation. Extreme weather events, such as spring heat waves and droughts, are increasingly more frequent and therefore a decline in grain yield is expected (Ray et al., 2012). High temperatures post-flowering (grain filling) and low water availability have traditionally been the most frequent causes of abiotic stress in winter cereals, causing reductions in yield (Sadras, 2007). In our study, grain yield values for the two unfavourable years were within the common Mediterranean range of 1-3 t ha^{-1} (Asseng & Savin, 2012).

Cereal production beneath trees could be an effective strategy to mitigate the effects of spring heat waves. Trees are known to have a buffer effect on maximum and minimum temperatures in Mediterranean environments (Gea-Izquierdo et al., 2009) and can reduce the desiccant effect of wind, even before leafing. They bring temperatures closer to the optimum in the first stages of the cereal cycle, when plants produce most of their dry matter between tillering and flowering, helping to keep cereal grain yields high. Moreover, translocation of available carbohydrates to grain is constrained above 25 ºC (Romero & German, 2001), which greatly reduces grain yields.

Cereal species and cultivars respond differently to silvoarable combination

Cereal yield in the silvoarable system is related to shade tolerance and the influence of trees at different developmental stages. Wheat is known to be a full-light plant, but in barley, the inclination angle of the leaves and foliage structure allow greater interception of solar radiation (Muurinen & Peltonen-Sainio, 2006). This decreases evapotranspiration and makes plants more

tolerant to drought in the ripening stage (Setter & Waters, 2003). As a result, barley has a greater yield under drought stress and is less sensitive than wheat to the possible negative effects of tree shading and soil water competition.

Grain filling in both cereal species is limited by their growth capacity rather than by metabolite accumulation and distribution (Acreche & Slafer, 2006). Stress before flowering can affect carpel growth by decreasing the size of the ovaries (which form the fruit pericarp), reducing potential grain weight regardless of conditions during grain filling (Calderini et al., 2001). Barley flowers and forms grains earlier than wheat (figure 3), which decreases the risk of harm from early heat waves and droughts at these critical stages. In dry Mediterranean conditions, barley is prioritised over other cereals (López-Bellido, 1992) because its precocity and rapid ripening have advantages in water use by avoiding the common terminal water stresses.

The silvoarable system slightly increased the speed of barley development until the stage of milk development and delayed the last stages of dough development in both cereals, thus delaying crop maturation. Therefore, in addition to being more premature and having a faster ripening and a shorter grain filling period than wheat (Cossani et al., 2009), barley was in a more advanced phase of grain filling when the walnut trees developed leaves and therefore suffered less water and nutrient competition from trees.

The silvoarable system was beneficial for the harvest index of barley in the first year, when the weather was less favourable, because this ratio is related to high efficiency in the use of resources by crops to increase grain yield (Kumudini et al., 2001). Barley grain yield also increased in the silvoarable system in the second year, indicating that trees are beneficial to barley under a wider range of climate conditions than for wheat. However, the cultivars of each species responded differently. In some cultivars the biomass was more affected and in others the impact was greater on grain number or size. This provides an opportunity to explore which plant traits are affected and favour or hamper productivity in silvoarable systems.

Grain quality improves in the silvoarable system

Barley and wheat grain size and weight are important for industrial applications. Grain filling depends partly on nitrogenous compounds, most of which are accumulated during preanthesis before moving into the grains in postanthesis (Bertheloot et al., 2008). Barley is more efficient

than wheat in translocating these compounds to the grain (Delogu et al., 1998), explaining the higher grain weight in barley than in wheat throughout the study period.

Barley tended to have a lower N content in silvoarable than in monocrops (protein content of 12.09 % and 13.75 %, respectively, although it should not exceed 12% for malting purposes). This was probably caused by environmental conditions during grain filling (e.g., high temperatures), traditionally considered a cause of malting quality variation (Henry, 1990). This situation could be buffered in the silvoarable system. In contrast, wheat grain N content was enhanced by tree presence and was 10 % higher in silvoarable than in monocrops, as reported by Dufour et al. (2013). High N content improves the quality of wheat for use as animal feed, pasta and flour for human intake.

Wheat grain K content was also significantly higher in silvoarable than in monocrops, which may be related to the synergistic relationship between N and K (Carvalho et al., 2016).

Tree growth is reduced by crops in silvoarable combination

Walnut water requirements are high, at more than 700 mm annual rainfall and as much as 1000-1200 mm in intensive plantations. The study area has an average annual rainfall of 437 mm and is irrigated in summer for normal tree development (60 l $tree^{-1}$ d^{-1}). Even with the same summer irrigation, walnut trees grew less in silvoarable than in forestry. Zhang et al. (2015) reported similar results in a walnut and wheat silvoarable system, mostly explained by competition for resources such as water. Water competition between the two strata begins in winter, because winter cereals consume a portion of the available soil water from winter precipitation. This competition continues from mid spring to early summer (cereal ripening), presumably causing lower available water content for trees in silvoarable than in forestry (Dupraz & Liagre, 2008).

Nitrogen and P levels in walnut leaves showed no difference between systems (forestry and silvoarable). Quantitatively, N is the most important nutrient in walnut. It is needed throughout the growth period because it is essential for tissue formation (Luna, 1990). Phosphorous interacts strongly with N and is especially important for root formation. Remarkably, no competition was observed, indicating that crop and walnut requirements for these two important nutrients are met by the same fertiliser.

However, a major difference was observed in walnut leaf K content between systems. The lower content in silvoarable could explain the greater DBH increment in trees in forestry than in

silvoarable, compared to the similar growth in trees in silvoarable and forestry before silvoarable management (Figure 5). Potassium is the second most important element (quantitatively) in walnut nutrition, because it favours carbohydrate synthesis (Luna, 1990). The considerable K competition between crops and trees should therefore be reduced to ensure adequate timber production.

Overall yield of silvoarable system in Mediterranean conditions

The silvoarable system presented LER > 1 for barley and wheat in all study years, indicating that the overall yield of the silvoarable system is more positive than the yield of sole cereal crops and trees.

The LER of the silvoarable system was higher than that reported by other authors for the combination of walnut and wheat (Duan et al., 2017; Graves et al., 2007; Zhang et al., 2015), which is partly explained by the climate constraints observed in two of the three years. Although tree effects on the crops varied between years, it was positive (especially for barley) in the years with extreme weather events such as high spring temperatures, which are expected to be more frequent in the coming years as a consequence of climate change in Mediterranean areas (Gerald & Tebaldi, 2004; Giorgi & Lionello, 2008; Trnka et al., 2014).

Using the RCP 4.5 climate change scenario generated with the climate model KNMI-RACMO22E (van Meijgaard et al., 2012) accessed through CliPick (Palma, 2017) for the study site, more than 57 % of the years from 2020 to 2050 will have maximum temperatures above 25 °C in the second fortnight of April, affecting barley anthesis and grain filling (Romero & German, 2001). Similarly, more than 80 % of these years will have such temperatures in the first fortnight of May, affecting wheat in the same way. Therefore, it seems evident that under the current climate change scenario in Mediterranean conditions, trees can increase winter cereal yields. Although this could cause a decrease in tree growth, silvoarable systems will increase their overall yield because the increase in grain crop production will outweigh the reduction in tree biomass, ensuring more productive and more efficient land use.

CONCLUSIONS

Combinations of winter cereals and late-bursting walnuts can increase grain yield and LER over monocrops and pure plantations under the current climate change scenario. In very productive years with no climate constraints, cereal yields were significantly reduced by competition with trees in the silvoarable system. In contrast, in years with dry/hot climate events in spring that constrained cereal maturation, tree sheltering acted as a safeguard. In this case yields were higher in silvoarable and the sheltering appeared to be more positive for barley, a more premature and drought resistant crop, than for wheat, although responses depended on the cultivar. Grain quality also improved in the silvoarable combination, especially for wheat.

Crops negatively affected tree growth in the silvoarable system. The competitive use of K among trees and cereal plants revealed in the study should be taken into account to design a specific fertilisation plan in silvoarable systems of winter cereals and walnut under Mediterranean conditions.

CAPÍTULO II.

Wheat and barley can increase grain yield in shade through acclimation of physiological and morphological traits in Mediterranean conditions

CAPÍTULO II.

Wheat and barley can increase grain yield in shade through acclimation of physiological and morphological traits in Mediterranean conditions

María Guadalupe Arenas-Corraliza, Víctor Rolo, María Lourdes López-Díaz, Gerardo Moreno

INDEHESA Research Institute, University of Extremadura, Avenida Virgen del Puerto, 2. Plasencia, Cáceres 10600, Spain.

ABSTRACT

Major cereal yields are expected to decline significantly in coming years due to the effects of climate change temperature rise. Agroforestry systems have been recognized as a useful land management strategy that could mitigate these effects through the shelter provided by trees, but it is unclear how shade affects cereal production. Most cereal species and cultivars have been selected for full light conditions, making it necessary to determine those able to acclimate to low irradiance environments and the traits that drive this acclimation. A greenhouse experiment was conducted in central Spain to assess the photosynthetic response, leaf morphology and grain yield of nine cultivars of winter wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) at three levels of photosynthetic active radiation (100%, 90% and 50%). Cultivars were selected according to three different precocity categories and were widely used in the studied area. The main objective was to assess whether the species and cultivars could acclimate to partial shade through physiological and morphological acclimations and thus increase their grain yield for cultivation in agroforestry systems. Both species increased grain yield by 19% in shade conditions. However, they used different acclimation strategies. Barley mostly performed a physiological acclimation, while wheat had a major morphological adjustment under shaded environment. Barley had lower dark respiration (42%), lower light compensation point (73%) and higher maximum quantum yield (48%) than wheat in full light conditions, revealing that it was a more shade-tolerant species than wheat. In addition, to acclimate to low irradiance conditions, barley showed a 21% reduction of the carotenoids/chlorophyll ratio in the lowest irradiance level compared to 100% light availability and adjusted the chlorophyll a/b ratio, photosystem II quantum efficiency, electron transport rate and non-photochemical quenching to shade conditions. On the other hand, wheat showed a 48% increase in single leaf area in the 50% irradiance level than in full light to maximize light capture. Our results showed that current commercialized wheat and barley cultivars had sufficient plasticity for adaptation to shade, supporting tree presence as a tool to reduce the negative effects of climate change.

INTRODUCTION

Global food production has risen as never before in the last 60 years due to agricultural expansion and intensification. However, it is increasingly questioned if global food production will meet future demands. Crop yields have stagnated in recent years, while human population continues to increase at the same rate. Climate change and scarcity of new arable land have been indicated as the main drivers of the widening gap between food production and demand (Myers et al., 2017). For major crops like barley and wheat, two of the world's four most important cereal crops, grain yield is expected to decrease 15-30% as a result of 2 °C warming forecast for 2040 (Moore & Lobell, 2014; Zhao et al., 2017). This makes it necessary to design more climate-resilient and sustainable systems.

Ecological intensification, where crop yield can increase through better use of resources, has been postulated as a possible solution (Doré et al., 2011; Godfray et al., 2010). Agroforestry systems are an example of this concept (Tittonell, 2014). Agroforestry has been recognized as a climate change adaptation tool, because trees help to regulate the climate beneath them by reducing extreme temperatures, providing wind shelter and reducing evaporation from the soil surface (Brandle et al., 2004; Schoeneberger et al., 2012). Integrating trees with crops (i.e., silvoarable agroforestry) has been shown to have a number of environmental benefits over conventional agriculture (Andrianarisoa et al., 2015; Lorenz & Lal, 2014), including a buffering effect on extreme temperatures (Kanzler et al., 2018). However, tree presence can affect negatively crop yields (Arenas-Corraliza et al., 2018; Yang et al., 2018) because of shading or competition for soil resources. Greater understanding is required of how low irradiation due to tree presence affects the functioning of major crops and, therefore, their yield, before silvoarable systems can be implemented as an ecological intensification strategy against foreseen climate change. It is uncertain how cereal cultivars will cope with tree shade in silvoarable systems, because most cultivars have traditionally been selected for full light conditions.

To overcome the lack of knowledge about how low irradiance conditions will affect current cultivars, selection programs are needed to identify shade-adapted cereal species and cultivars for cultivation in agroforestry systems, based on analysis of functional plant traits that determine crop yield. To our knowledge no research has been conducted on photosynthetic low irradiance acclimation of wheat and barley in Mediterranean conditions, where average annual irradiance is higher than in the rest of Europe (https://solargis.info/). In the Mediterranean area, irradiance levels are usually in excess of plant requirements, and the main photosynthetic constraints are temperature and drought (Flexas et al., 2014). Recent studies in the Mediterranean area, where

climate change consequences are expected to be more pronounced (IPCC, 2014), have shown a negative effect of tree presence on winter wheat grain yield (Dufour et al., 2013; Inurreta-Aguirre et al., 2018). However, there are mixed results when considering other areas with temperate (Kanzler et al., 2018) and Mediterranean climate (Sudmeyer & Speijers, 2007), so the effect of shade on wheat grain yield remains unclear. Less is known about how shade can affect barley in the Mediterranean area. Barley has been cultivated in a wider range than most other crop species (Newton et al., 2011) because it is a stress-tolerant crop. Furthermore, barley under low irradiance is able to change its photosynthetic performance in an acclimation process (Zivcak et al., 2014), making it a potential target for studies on agroforestry shaded environments in a global climate change context.

In addition to reducing available light, trees can negatively affect crops because of competition for soil resources (water and nutrients). Water and nutrient competition can be remedied by adoption of appropriate agronomic practices, but low irradiance cannot be modified and must be managed through selection programs for acclimated cultivars. In breeding programs for complex agrosystems (i.e., agroforestry systems), selection based on functional trait screening (e.g., physiology and morphology) could be more relevant than selection based on genotype screening, as functional plant traits are key factors in the understanding of ecosystem-vegetation functioning (Hooper et al., 2005). In the case of low irradiance acclimation, it is important to identify whether there is sufficient variability among crop species and within their cultivars that could help to identify shade-acclimated genotypes.

The aim of this research was to assess the extent of shade acclimations of winter wheat and barley and their cultivars. We determined if photosynthetic and morphological traits are involved in shade acclimation and influence grain yield. Our hypotheses were:

1. *Shade reduces the grain yield of wheat but not of barley, which is able to withstand low irradiance conditions.*

2. *Barley is able to photosynthetically and morphologically adapt to shaded environments, since it is known to be a more stress-tolerant crop than wheat.*

3. *Within the cultivars of each species, there is no enough variability for selection programs in physiological and morphological traits that could drive to an increase of grain yield in shade conditions.*

CAPÍTULO II. Wheat and barley can increase grain yield in shade through acclimation of physiological and morphological traits in Mediterranean conditions

CAPÍTULO II

MATERIAL AND METHODS

Plant material and experimental design

An open air greenhouse experiment was conducted at the Organic and Mountain Agriculture Research Center, Plasencia (40° 1'N, 6° 6'W), Spain, in the 2016-2017 growing season (November-June). The study comprised nine different cultivars of winter barley (*Hordeum vulgare* L.) and nine of winter wheat (*Triticum aestivum* L.). Cultivars were selected to span three categories of precocity (flowering dates): very early, early and medium. Each category included three cultivars of each species. Barley cultivars were named B1 to B9, representing the cultivars Hispanic, Lavanda and Luzia (very early), Kalea, Lagalia and Carolina (early) and Meseta, Ibaiona and Crescendo (medium). Wheat cultivars were named W1 to W9, representing the cultivars Nogal, Nudel and Tocayo (very early), Algoritmo, Paledor and Solehio (early) and Toskani, Somontano and Nemo (medium). Cultivar seeds were provided by CICYTEX (http://cicytex.juntaex.es/en/), which collaborates with the Group for the Evaluation of New Varieties for Extensive Crops in Spain (GENVCE: http://www.genvce.org/).

The experiment was a split design with irradiance as main block and cultivars as sub-block, with six replicate pots per cultivar of each species in each irradiance treatment (n=6 for cultivars and n=54 for species). Three irradiance levels were set for Photosynthetically Active Radiation (PAR): 100%, 90% and 50% by nets in different open greenhouse structures. The environmental conditions in each irradiance structure were recorded at the cereal canopy level (Table 1) by 2 dataloggers (PCE-H71N Data logger, PCE Instruments, Holding GmbH Inc., Hamburg, Germany). Nets were placed 1.5 m above plants to ensure sufficient ventilation. The material of the nets was green polyethylene. Mesh sizes were 2.25 cm^2, 0.0075 cm^2 and 0.0026 cm^2 for 100%, 90% and 50% nets respectively. The 100% irradiance coverage was set up to avoid bird damage and did not reduced PAR compared to full light conditions. The mean maximum PAR values achieved under the nets 100%, 90% and 50% were 1680, 1390 and 965 µmol m^{-2} s^{-1} respectively in spring and mimic shading levels potentially found in different stages in silvoarable systems with deciduous trees as walnut and poplar (Dufour et al., 2013). Each block was completely covered with nets from the start of booting (7 April 2017), coinciding with the leaf sprout of deciduous trees (common trees in silvoarable systems in the Mediterranean area), to maturity (15 June 2017). In each pot (13 x 13 x 17 cm), four seeds were sown in November 18th 2016. To avoid stem breakages, training rods and strings were installed around the plants before booting. The soil mixture comprised three parts black peat, one-part sand and one-part perlite, with soil water capacity 119% and pH 5.8. All pots were fertilized in November 2016 with 58 kg N ha^{-1}, 100 kg P$_2$O$_5$ ha^{-1} and 58 kg K$_2$O ha^{-1}. In February 2017, 200 kg N ha^{-1} was added to each pot with 46% urea. All pots were regularly

irrigated following the indications of a humidity probe to maintain soil water capacity above 50% and avoid soil water stress.

Table 1. Mean values of temperature, relative humidity and PAR in the different irradiance levels in the anthesis period (2017/04/23). Data represents means ± S.E. Different letters indicate significant differences between irradiance levels (*P < 0.05*).

Irradiance (%)	Temperature (°C)	Relative humidity (%)	PAR (µmol (photon) m^{-2} s^{-1})
100	22.40 ± 0.49	40.63 ± 0.25	1182.09 ± 48.39
90	23.67 ± 0.23	40.32 ± 0.025	897.95 ± 46.75
50	21.98 ± 0.41	41.13 ± 1.35	630.60 ± 35.73

Grain yield

When cereal plants reached ripening, all pots were harvested (June 14th 2017) using hand clippers. Plants were dried at 60 °C to constant weight. All grains of all spikes per pot were counted and weighed and grain yield was reported in g m^{-2}.

Photosynthesis parameters

Photosynthetic light response curves were measured during the flowering period in the middle part of the first leaf in wheat (known as the flag leaf, because it is the most important leaf for photosynthesis) and the second leaf in barley (the first leaf of this species is too small to measure). Measurements were made in one plant per pot of each species in the 100% irradiance treatment, when flowering was 50% complete in each cultivar. Curves were obtained using a portable infra-red gas analyzer (IRGA) (LCpro+, ADC Bioscientific Ltd., Hoddesdon, UK) set at 25°C, with a CO_2 concentration of 400 µl L^{-1} and a relative humidity of 65%. Leaves were first adapted to dark for 30 minutes, then exposed to increasing PAR intensities: 0, 176, 352, 616, 880, 1320 and 1584 µmol photons m^{-2} s^{-1} for 5 minutes, respectively. Net photosynthesis light-response curves were fitted according to the hyperbolic rectangular model, using the Solver function of Microsoft Excel 2013 (Lobo et al., 2013). Five parameters of the hyperbolic rectangular model were used to compare photosynthetic behavior between species: dark respiration (R_D); light compensation point (I_{comp}), defined at the PAR level where net photosynthesis is null; maximum net photosynthesis (PN_{max}); light saturation point beyond which there is no significant change in net photosynthesis (I_{max}); and maximum quantum yield (Φ), as the derivate of the curve in the range between I_{comp} and I = 200 µmol photons m^{-2} s^{-1}.

Chlorophyll fluorescence

Rapid-light response curves of variable chlorophyll fluorescence were measured after including the three irradiance treatments (100%, 90% and 50%), using a modulated chlorophyll fluorometer (OS5p+, Opti-Sciences, Inc., Hudson, USA). Leaves were first dark-adapted for 30 minutes and then exposed to increasing actinic light intensities: 120, 494, 1639, 2192 and 2557 μmol photons m^{-2} s^{-1} in 15 second intervals. Steady state fluorescence (Fs), maximum light-adapted fluorescence ($F'm$) and minimal fluorescence of the light-adapted state (Fo') were determined to calculate photosystem II (PSII) quantum efficiency (Φ_{PSII}) as:

$$(F'm - Fs)/(F'm)$$

Non-photochemical quenching (NPQ) was calculated by the expression:

$$(Fm - F'm)/(F'm)$$

Electron Transport Rate (ETR) was determined by:

$$(\Phi_{PSII}) \cdot PAR \cdot 0.84 \cdot 0.5$$

where PAR refers to photosynthetically active radiation, 0.84 to leaf absorption coefficient (Zivcak et al., 2013) and 0.5 to the equal distribution of absorbed light by PSI and PSII.

Photosynthetic pigments

For rapid assessment of photosynthetic pigment content with minimum damage to leaves, SPAD units were taken in three parts of one leaf per pot in each irradiance treatment using a SPAD meter (SPAD-502 Plus, Konica Minolta Holdings, Inc.). To calibrate SPAD readings, nine fresh leaves of each species (three per light treatment) were used to determine the photosynthetic pigments. Extraction was performed by grinding 100 mg fresh matter in 10 ml acetone 80% (v/v). the resulting mixture was stored in photoprotective tubes at 4°C and tubes were later centrifuged 15 minutes at 2500 rpm. The supernatant was stored in photoprotective tubes and analyzed later. The Chl a, Chl b, total Chl (a + b) and Carot (x + c) content were determined according to Lichtenthaler (Lichtenthaler, 1987) and correlated with SPAD units (Shah et al., 2017). We fitted linear regressions separately for each species to relate SPAD units and photosynthetic pigments. Linear regressions fitted the data well both for barley (R^2 = 0.893, 0.781, 0.881, 0.899 for each pigment respectively; $p < 0.001$) and wheat (R^2 = 0.965, 0.918, 0.980, 0.745 for each pigment respectively; $p < 0.001$).

Leaf mass area and single leaf area

Leaf mass area index was calculated as the ratio of leaf dry mass to leaf area, sampling one fresh leaf in each pot per cultivar. Fresh leaves were scanned and their area was calculated using *ImageJ* software (National Institute of Health, USA). These leaves were then dried at 60 °C to constant weight to obtain leaf dry mass.

Statistical analysis

Because net photosynthetic curves are nonlinear, we fitted a GAM model to assess the overall differences in net photosynthesis between species. To test whether the parameters of the hyperbolic rectangular model differed between species, we fitted linear mixed models, including species as a fixed effect and cultivar as a random effect. To fit rapid-light response curves of fluorescence parameters, we also used GAMs. Fluorescence parameter models were fitted separately for each species, including irradiance as a predictor. We fitted linear mixed models, including species and irradiance and their interaction as fixed effects and cultivar as a random effect to analyze the response of photosynthetic pigments, leaf mass area, leaf area and grain yield at varying light levels for each species. Self-defined contrast was used to assess pairwise comparison between irradiance levels within species. For all linear mixed models, we computed the marginal (R_m^2) and conditional (R_c^2) coefficient of determination to assess the amount of variance explained by the fixed effects and the entire model including random effects, respectively (Nakagawa & Schielzeth, 2013). To assess variability in cultivar response to light, we fitted linear regressions with grain yield, leaf mass area, total chlorophyll and non-photochemical quenching as response variables and light as a predictor for each cultivar separately. All analyses were performed using R version 3.5.3 (R Core Team, 2018). GAMs models were fit with "mgvc" (Wood, 2017), linear mixed models with "lme4" (Bates et al., 2015) pairwise comparisons were assessed with "multcomp" (Hothorn et al., 2008) and coefficients of determination were computed with "MuMIn" (Barton, 2019) R packages.

RESULTS

Grain yield

Grain yield increased significantly in reduced irradiance treatments in both barley and wheat (P < 0.001, R^2_m = 0.07, R^2_c = 0.24) (Table 2). Barley showed a 19% increase in grain yield in the 50% light availability level compared to 90% and 100% irradiance and wheat had a 19% higher grain yield at both 90% and 50% irradiance levels compared to full light.

Table 2. Grain yield, photosynthetic pigments and morphological parameters of barley and wheat for the irradiance levels studied. All chlorophyll samples were calculated from fresh material. Data represents means ± S.E. (n = 54). Different letters indicate significant differences between irradiance levels (*P < 0.05*). Chl a: chlorophyll a; Chl b: chlorophyll b; Carot: carotenoids; Chl a/b: ratio of chlorophyll a to chlorophyll b; Carot/Chl: ratio of carotenoids to total chlorophyll (a + b); LMA: leaf mass area; LA: single leaf area.

Species	Irradiance (%)	Grain yield (g m^{-2})	Chl a (mg g^{-1})	Chl b (mg g^{-1})	Carot (mg g^{-1})	Chl a/b	Carot/ Chl	LMA (mg cm^{-2})	LA (cm^{-2})
Barley	100	299.41± 10.22 **b**	1.13 ± 0.05 **b**	0.34 ± 0.01 **b**	0.37 ± 0.01 **b**	3.38 ± 0.01 **a**	0.28 ± 0.02 **a**	9.23 ± 0.22 **a**	2.30 ± 0.10
	90	304.65 ± 12.34 **b**	1.14 ± 0.05 **b**	0.34 ± 0.02 **b**	0.38 ± 0.01 **b**	3.38 ± 0.01 **a**	0.29 ± 0.02 **a**	8.13 ± 0.16 **ab**	2.30 ± 0.11
	50	355.84 ± 12.30 **a**	1.74 ± 0.05 **a**	0.52 ± 0.01 **a**	0.49 ± 0.01 **a**	3.34 ± 0.00 **b**	0.22 ± 0.00 **b**	7.87 ± 0.19 **b**	2.64 ± 0.12
Wheat	100	277.18 ± 11.27 **b**	1.47 ± 0.05 **b**	0.44 ± 0.01 **b**	0.44 ± 0.01 **b**	3.35 ± 0.00	0.24 ± 0.00	13.25 ± 0.48 **a**	3.81 ± 0.19 **c**
	90	322.54 ± 13.39 **a**	1.60 ± 0.04 **b**	0.48 ± 0.01 **b**	0.46 ± 0.01 **b**	3.35 ± 0.00	0.23 ± 0.00	10.01 ± 0.29 **b**	4.51 ± 0.18 **b**
	50	329.44 ± 11.50 **a**	2.01 ± 0.04 **a**	0.60 ± 0.01 **a**	0.54 ± 0.01 **a**	3.34 ± 0.00	0.21 ± 0.00	10.31 ± 0.26 **b**	5.65 ± 0.24 **a**

Physiological performance

Chlorophyll a and b increased at 50% irradiance compared to full light conditions in barley (54% and 53% respectively) and wheat (53% and 36% respectively) (Table 2), allowing plants to use the available light more efficiently. The Chl a/b ratio decreased a significant 1% at 50% irradiance in barley compared to full light conditions, while no acclimation was seen in wheat in this parameter. In addition, the Carot/Chl ratio decreased significantly in the 50% irradiance treatment in barley (21% less than in full light), and no shade effect was observed for wheat (Table 2).

Overall, wheat had lower net photosynthetic values than barley when considering the whole PAR gradient of the light response curve (GAM model, $R^2 = 0.75$, *P <0.001*). However, these differences were mainly observed at low PAR values (Figure 1). This agrees with the results of the hyperbolic rectangular mode fits, where there were significantly lower values of R_D, I_{comp} and I_{max} in barley than in wheat. The signifcantly lower I_{comp} in barley (9.6 ± 1.5 [μmol (photon) m^{-2} s^{-1}]) than in wheat (35.1 ± 6.6 [μmol (photon) m^{-2} s^{-1}]) (P < 0.022, $R_m^2 = 0.21$, $R_c^2 = 0.88$) was a result of the also significantly lower R_D in barley (0.46 ± 0.07 [μmol (CO_2) m^{-2} s^{-1}]) compared with wheat (0.79 ± 0.08 [μmol (CO_2) m^{-2} s^{-1}]) (P = 0.022, $R_m^2 = 0.17$, $R_c^2 = 0.57$), which was quickly balanced by lower rates of photosynthesis. In addition, the lower I_{max} in barley (1807.7 ± 41.2 μmol (photon) m^{-2} s^{-1}) allowed this species to maximize its net photosynthesis rate in relatively low light intensisties, while wheat continued to slightly raise its carbon assimilation to 1848.9 ± 60.8 μmol (photon) m^{-2} s^{-1}, showing a greater need for light to reach its highest photosynthetic activity (i.e. I_{max}). There was no difference in the maximum net photosynthesis between barley (18.3 ± 0.9) and wheat (17 ± 0.9). However, a strong difference was found in $\Phi_{(Icomp-I200)}$, which was 48% higher in barley (Figure 1) than in wheat (0.034 ± 0.002 and 0.023 ± 0.002) (P = 0.001, $R_m^2 = 0.28$, $R_c^2 = 0.52$), representing the initial slope of the light-response curve of net photosynthetic rate (i.e., the region limited by photochemical rather than biochemical reactions). Photosynthetic parameters showed a high variability among cultivars as indicated by the large differences between marginal (R_m^2) and conditional (R_c^2) coefficients of determination in all models.
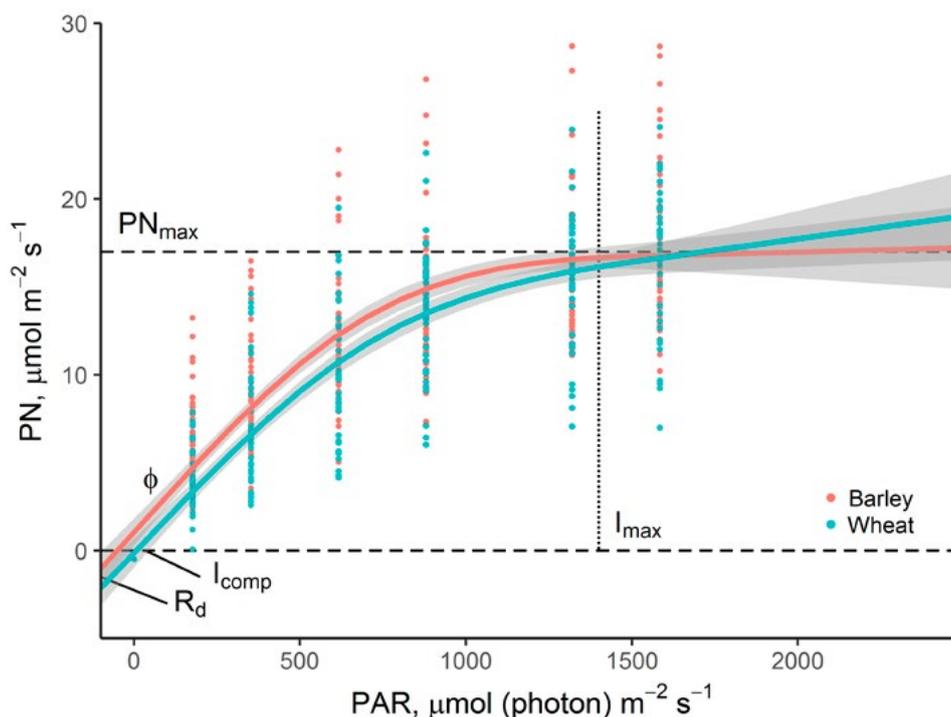
Figure 1. Net photosynthesis (PN) light-response curve (± 95% CI) and associated parameters of barley and wheat plants grown at 100% irradiance level (n=54). When CI are overlapped, there are no significant differences. R_D: dark respiration [μmol (CO_2) m^{-2} s^{-1}]; I_{comp}: light compensation point [μmol (photon) m^{-2} s^{-1}]; PN_{max}: maximum net photosynthesis [μmol m^{-2} s^{-1}]; I_{max}: light saturation point beyond which there is no significant increase in net photosynthesis [μmol (photon) m^{-2} s^{-1}]; $\Phi_{(Icomp-I200)}$: maximum quantum yield in the range between I_{comp} and I = 200 μmol (photon) m^{-2} s^{-1} [μmol (CO_2) μmol (photon)$^{-1}$]. Note that parameters values were calculated according to Lobo et al. (2013) (Lobo et al., 2013) and GAMs to assess the overall difference between species on the light-response curve and for visualization purposes.

Fluorescence parameters of the PSII (i.e., Φ_{PSII}, ETR and NPQ) responded differently to changing irradiances for wheat and barley (Figure 2). While no significant differences were detected for wheat, barley plants grown at 50% irradiance typically showed significant differences in Φ_{PSII}, ETR and NPQ than plants grown at 90% (P=0.011, P<0.001 and P=0.007, respectively) and 100% irradiance (P < 0.001, P < 0.001 and P = 0.019, respectively). Barley plants grown at 50% irradiance had higher Φ_{PSII} in low PAR values than those of plants grown at 90% and 100% irradiance. However, when exposed to high PAR intensities, barley grown at 50% irradiance showed lower $\Phi_{PSII,}$ (Figure 2-a) and ETR (Figure 2-b) and higher NPQ (Figure 2-c). Barley plants grown at 90% irradiance only showed significantly lower ETR values than plants grown at full light (P = 0.023).
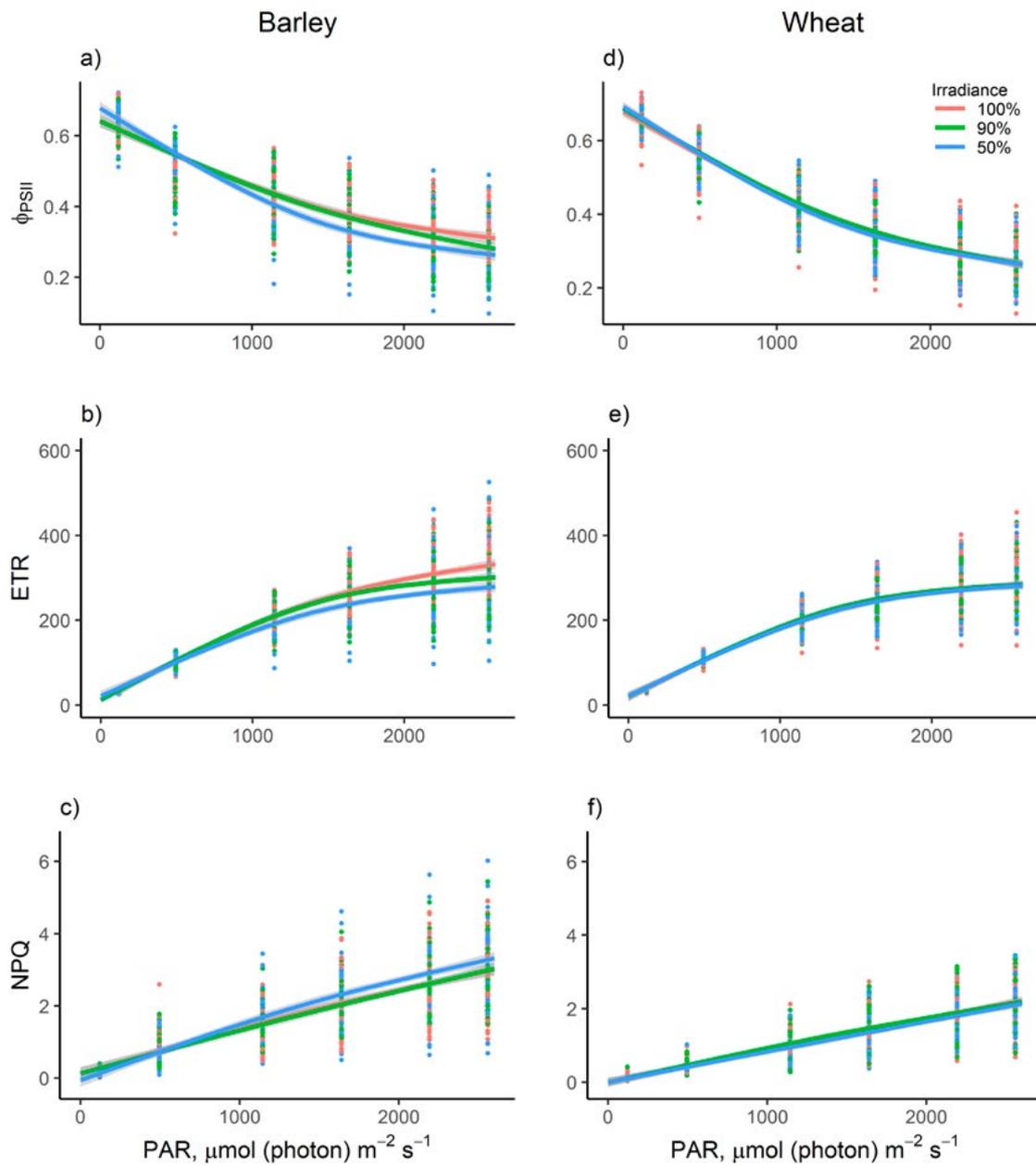
Figure 2. Rapid-light response curves (± 95% CI) of photosystem II quantum efficiency (Φ_{PSII}), electron transport rate (ETR) and non-photochemical quenching (NPQ) of barley (a, b and c) and wheat (d, e and f) grown in the irradiance conditions studied (100%, 90% and 50%) at different PAR intensities (n=54).

Morphological acclimation

A decrease in LMA in reduced irradiance treatments for both species barley and wheat compared to full light conditions was detected (maximum reductions of 15% in barley and 22% in wheat, LMA x species x irradiance, P < 0.001, R^2_m = 0.41, R^2_c = 0.41) (Table 2). In terms of single leaf surface (LA x species x irradiance, P < 0.001, R^2_m = 0.51, R^2_c = 0.65), for wheat, it was higher (48% and 18%) in the reduced irradiance levels of 90% and 50% respectively when compared to full light conditions (Table 2), in contrast with barley, which did not show this acclimation to shade. Marginal (R^2_m) and conditional (R^2_c) coefficients of determination showed similar values in both models, suggesting low variability of morphological parameters among cultivars.

Cultivars plasticity

Depending on the parameter consider, cultivar performances ranged from no acclimation to considerable changes in shade in both species. The tendency of increasing grain yield under low irradiance observed at species level (Table 2) was also confirmed in cultivars, because most barley grain increases were at 50% irradiance and those in wheat were at 90%, although grain yield increases depended on the cultivars and were significant only for cultivars B7 (barley) and W5 and W6 (wheat) (Figure 3). LMA showed higher variability in wheat than in barley (e.g 8.9% and 2.5% LMA coefficient of variation of wheat and barley, respectively), revealing that most wheat cultivars modify their LMA to adapt to different light environments (Figure 3). This was also observed at species level (Table 2). However, some wheat cultivars revealed no acclimation to shade (W5, W6 and W8) in this parameter, indicating that some cultivars were more able than others to modify this morphological trait. For Chl (a + b), even though almost all cultivars of both barley and wheat increased their content at low irradiance levels, agreeing with the results at species level (Table 2), wheat did not show a pattern as clear as barley. Barley cultivars had almost the same Chl (a + b) content in 100% and in 50% irradiance levels, while wheat cultivars showed more dispersion in Chl (a + b) values in each irradiance conditions. Furthermore, as observed in both barley and wheat species (Figure 2), barley cultivars revealed greater low-irradiance acclimation in NPQ than wheat, which showed no variation. Nevertheless, this adjustment was not as consistent in cultivars as at species level and was significant only in B2, B5 and B9 cultivars, while the others showed no acclimation. Wheat cultivars that had lower grain yield also had lower NPQ values, suggesting that non-photochemical quenching could be an interesting trait for cultivar selection. The precocity of the cultivars was not significant in any of the parameters studied.
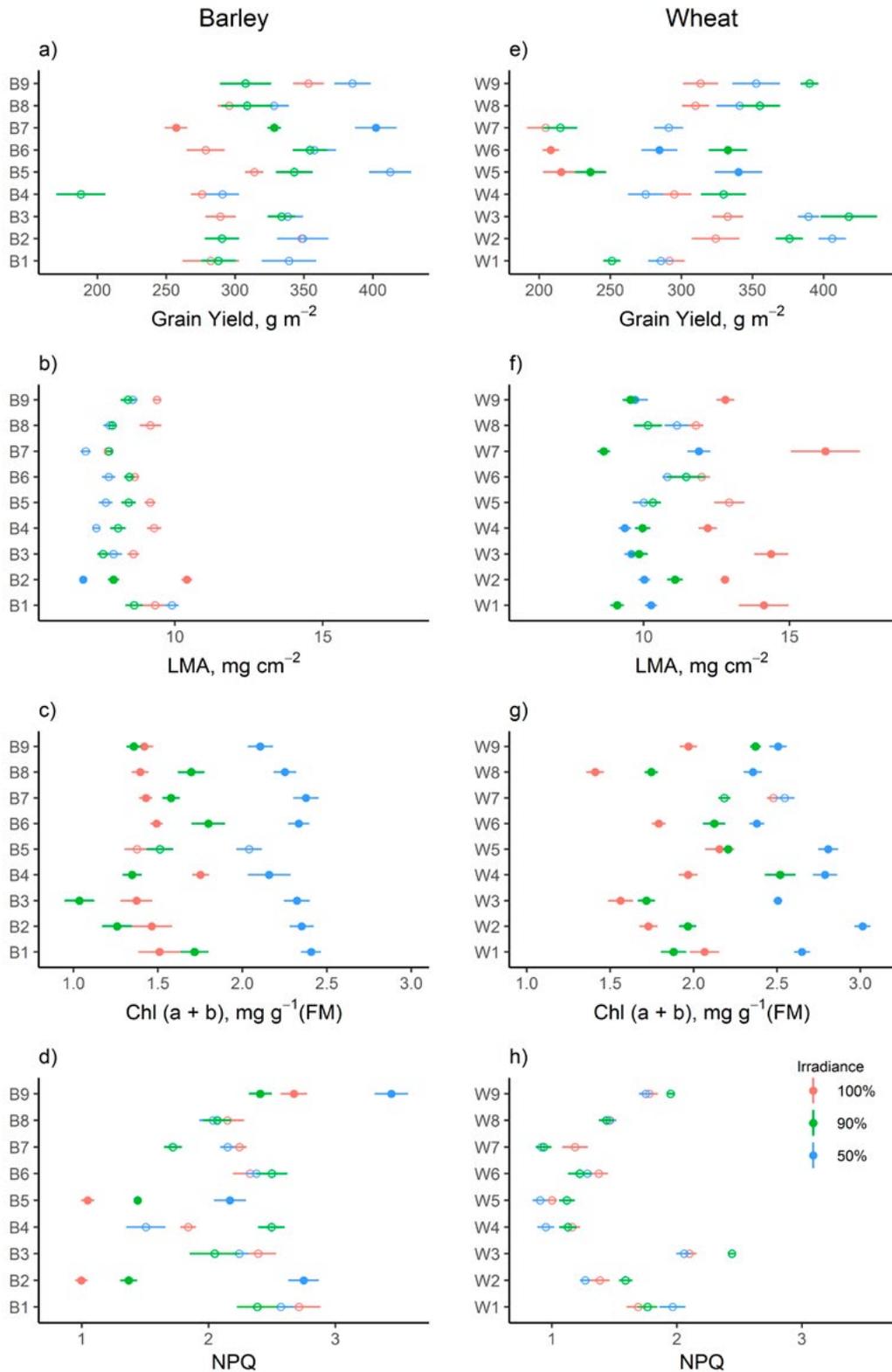
Figure 3. Grain yield and morphophysiological variables (± S.E.), including non-photochemical quenching (NPQ) at 1639 μmol photons m^{-2} s^{-1}, of the cultivars studied for each species at different levels of irradiance (100%, 90% and 50%) (n=6). Closed circles represent a significant effect of irradiance at *P < 0.05*.

DISCUSSION

Both wheat and barley increased grain yield in shade

In contrast to our expectation, both species increased grain yield in shade as compared to full light conditions. Although wheat increased grain yield with shade compared to full light, it reached the same grain yield at 90% irradiance treatment as in the 50% irradiance level. In fact, Xu et al. (2016) also reported that grain yield did not increase significantly below 90% light availability. Contrary to our results, decreases in grain yield under 70-80% irradiance treatments were found in 35% lower solar radiation conditions (Mu et al., 2010) than those in the Mediterranean (https://solargis.info/). However, barley increased grain yield significantly in the lowest irradiance level (i.e. 50% irradiance), according to the results reported under tree shade in a silvoarable system in the same Mediterranean conditions as our study (Arenas-Corraliza et al., 2018). All these results indicate that cereal species like barley and wheat grown in high irradiance conditions, such as those in the Mediterranean, can benefit from partial shade. Decreases in cereal production may be explained by lower solar radiation and/or competition for soil resources in agroforestry systems. Because this competition can be amended (with irrigation or fertilization) or avoided (deciduous trees that sprout when cereals have completed most of their nutrient uptake), agroforestry could be a sustainable land-use system to help meet future food demands in a climate change context.

Barley showed high physiological shade acclimation

The Chl a/b decrease at the lowest irradiance level in barley (50%) showed a typical vegetative response of acclimation to shade, as reported for other species (Marschall & Proctor, 2004). In this way, these plants are able to extend the wavelength useful range to a shorter wavelength, i.e., the blue fraction. However, wheat did not show any acclimation, in contrast with the results obtained by Dong et al. (2014) when studying different light intensities, which were always smaller than the PAR intensities of our study. In addition, the stronger decrease in the Carot/Chl ratio in the 50% irradiance level for barley agrees with the high capacity of acclimation to low light levels previously described for this species (de la Torre & Burkey, 1990). This suggests that barley plants in the full light treatment needed greater photoprotection than plants in the low light environment, in accordance with the photosynthethic parameters of shaded plants. This photoprotection process is partly performed by the carotenoids within the xantophyll cycle, which is known to be related to NPQ, to dissipate excess excitation energy as heat and thus avoid photodamage to PSII (Lu et al., 2001). This photoprotection process is also shown in the NPQ parameter in our study, which was found to be higher in barley grown under low irradiance when exposed to high light conditions, revealing that excessive light energy was dispersed

through non-photochemical reactions. However, no significant differences were found in wheat in the Carot/Chl ratio nor in the NPQ, even though some authors reported this acclimation for wheat cultivars (Zheng et al., 2011) in a region with lower solar irradiance intensity than the Mediterranean. Therefore, barley clorophyll pigments helped this species to acclimate to shade, in contrast with wheat, that did not show this adaptative response in our study.

The net photosynthetic light responses curves values for barley and wheat species in full light conditions (R_D, I_{comp} and I_{max}) indicated that barley leaves had a typical shade-leaf response (Lichtenthaler et al., 1981), whereas wheat leaves displayed charasteristic sun-leaf behavior. Furthermore, the higher $\Phi_{(Icomp-I200)}$ in barley compared with wheat showed greater photosynthethic efficiency to light capture and carbon fixation at low irradiance levels (Pang et al., 2018). All these parameters derived from the light responses curves indicate that barley has potentially better photosynthetic acclimation than wheat to shade conditions.

The fluorescence parameters studied showed that photochemical reactions at high PAR intensities were not as efficient in shaded plants as in full light plants, due to the higher ratio of closed PSII reaction centers caused by excessive incident light in the former. As a result, barley shade-acclimated plants, especially those at 50% irradiance, were less efficient than light-acclimated plants at transferring electrons through photochemical processes in high light availability. To alleviate light stress and avoid photodamage in the PSII antennae of these barley plants, chlorophyll excitation energy was dissipated as heat when exposed to excessive PAR intensities, as revealed by the significant NPQ increase. Therefore, the results obtained from the fluorescence parameters Φ_{PSII}, ETR and NPQ in barley indicate that this species developed an efficient shade acclimation strategy through changes in the photosynthetic apparatus, proving that this species is able to adapt its photosynthetic behavior to different light environments (Zivcak et al., 2014). For wheat, no acclimation was found in any of these parameters, in contrast with Zheng et al. (2011), who showed shade acclimation in terms of Φ_{PSII} and ETR in some wheat cultivars in a humid-subtropical climate. This could be due to the photosynthetic characteristics of wheat cultivars in each region. The light saturation point reported by Zheng et al. (2011) for wheat cultivars was approximately 1000 μmol (photon) m^{-2} s^{-1}, while in our study, they saturated by 1800 μmol (photon) m^{-2} s^{-1}. The lower saturation point in wheat cultivars could indicate a greater shade-tolerance that could drive low irradiance acclimation in photosynthetic parameters, in contrast the cultivars used in our region.

Wheat was morphologically better adapted than barley to low irradiance conditions through a major leaf area expansion

Leaf mass area (LMA) is an important plant trait that describes plant strategies to acclimate to varying environmental conditions (Castro-Díez et al., 2000; Poorter et al., 2009; Reich et al., 1992; Wright et al., 2006). In most species, LMA is negatively related to light availability. When light is not limiting, plants increase their biomass per leaf area in order to enhance photosynthesis, and conversely, more leaf area per biomass improves light interception unded shaded environments (Poorter et al., 2009). Our results show this adaptive response in barley and especially in wheat. Plants maximize light capture increasing single leaf surface, but in our study, no significant differences were found in leaf surface in barley between the irradiane treatments, in contrast with the results reported by Zivcak et al. (2014). On the other hand, wheat strongly increased its single leaf area in shade, in accordance with Li et al. (2010). This different response in the single leaf surface between species regarding low irradiance in our study, reveal that LMA decrease in barley in the reduced light conditions is mostly explained by reduced specific leaf biomass, while in wheat it is justified by larger leaf area. Although it is known that there is no phylogenetically constraint in barley to expand single leaf area (Gunn et al., 1999), wheat seems to have a greater morphological plasticity to expand leaf surface for increased light capture in reduced light environments in our study.

Cultivars showed highly different responses to low irradiance, with considerable variability in both barley and wheat

The cultivars responses to grain yield and to different morphophysiological parameters (LMA, Chl (a+b), and NPQ) showed that some barley and wheat cultivars had greater plasticity than others to adapt to lower irradiance conditions through a range of morphophysiological traits. However, our results showed that the amount of variability among cultivars was dependent on the trait considered. When considering the differences in the variability explained by mixed models with and without the cultivar (i.e. between the marginal and conditional coefficient of determination), we observed that the greatest differences were found in the parameters of the light response curve. On the other hand, for morphological parameters, such as LMA, or grain yield, the variability explained by cultivars was less important. These results suggests that selecting the appropriate trait can be an important step during the selection program. Overall, our result indicate that there could be sufficient variability in currently commercialized barley and wheat cultivars to start selection programs based on functional tratis that would help farmers to adopt agroforestry systems.

CONCLUSIONS

To the best of our knowledge, this is the first time that cultivars of winter wheat and barley have been studied and compared in physiological, morphological and production terms to determine whether they are shade-acclimated species with potential for use in agroforestry systems. Our results showed that both wheat and barley increased their grain yield under low irradiance conditions, using different acclimation strategies. Barley shows greater photosynthetic acclimation to shade than wheat, helping to improve physiological performance and therefore grain yield at reduced irradiance levels. Wheat undergoes a major morphological acclimation to reach a similar increase in grain yield. Cultivar responses to shade were considerably different in the parameters studied, with some showing high plasticity to shade acclimation and others showing no response. These results reveal that both barley and wheat species are suitable for growing under tree shade in high-radiance climates, highlighting the utility of cultivar selection programs to establish succesful agroforestry practices that could mitigate grain yield decreases caused by foreseeable temperature increases.

CAPÍTULO III.

Wheat and barley cultivars show plant traits acclimation and increase grain yield under simulated shade in Mediterranean conditions

CAPÍTULO III.

Wheat and barley cultivars show plant traits acclimation and increase grain yield under simulated shade in Mediterranean conditions

María Guadalupe Arenas-Corraliza, María Lourdes López-Díaz, Víctor Rolo, Gerardo Moreno

INDEHESA Research Institute, University of Extremadura, Avenida Virgen del Puerto, 2.
Plasencia, Cáceres 10600, Spain.

ABSTRACT

Agroforestry systems are reported as climate-resilient productive systems, but it is yet unclear how tree shade affects crops performance. The aim of this work was to assess how the phenology, plant traits and grain yield of wheat and barley were affected by shade. In an open greenhouse experiment, we cultivated in pots nine cultivars differing in precocity for each species, and imposed three artificial shading levels (S0 ~ 0%, S1 ~ 25 %, S2 ~ 50 %) at the start of cereal booting. Our results showed that shade speeded up first growth stages in both species, until the starting of milk development. Barley showed consistent phenological responses to the three irradiance levels among cultivars, but not wheat that showed larger phenological differences among cultivars at moderate shade. Deep shade prolonged the time needed for wheat grain ripening. Both species increased grain yield by 15-20% with shade, driven by shade-acclimations of plant traits that differed among species. For wheat, grain yield was determined by the assemblage of traits that contribute to yield, such as grain weight, precocity and non-photochemical quenching, while, for barley, SPAD value, precocity to reach phenological stages, grains per spike and plant height had the strongest influence. These traits varied widely among cultivars, and seem of interest to identify best suited cultivars for shading conditions of Mediterranean agroforestry systems.

Keywords*: agroforestry, light-stress, irradiance, precocity, phenology, photosynthesis.

INTRODUCTION

Global temperature has been increasing since the industrial period, especially since 1970s, when the rate of increase has no historical precedent (IPCC, 2014). As a result, effects associated to climate change, such as higher temperatures and extreme events, have negatively impacted crop yield, particularly, two of the top ten global crops, wheat (loss of 16.1 %) and barley (reduction of 8.7 %), in the south-western Mediterranean area (Ray et al., 2019). This crop yield reduction together with the scarcity of new arable land, make it difficult to meet the food demand of the increasing human population. In this context, the design of more climate-resilient agricultural systems becomes relevant to ensure food security.

Agroforestry systems have been reported as a climate-resilient practice (Schoeneberger et al., 2012). Monocrops have shown high vulnerability to climate change impacts, but intercrops can benefit of multiple cascading changes produced by trees at above- and belowground level (Schoeneberger et al., 2012; Verchot et al., 2007), as reducing temperature beneath canopy on warm days in the Mediterranean area (Moreno et al., 2007). However, the shade provided by trees is likely to have a negative impact on cereals performance (Inurreta-Aguirre et al., 2018; Shimoda & Sugikawa, 2019), partly because breeders have always selected cereal cultivars acclimated to full sun conditions (Vandeleur & Gill, 2004).

Reported shade effects due to the reduction of light intensity include changes in the morphology, physiology, biomass, grain yield, and quality of crops (Dong et al., 2015; Wang et al., 2015). For instance, in Mediterranean agroforestry systems, it has been found that deciduous tree shade negatively affected wheat (Dufour et al., 2013). However, evidence of tree shade effects on crops is mixed as positive effects have been also reported depending on the crop species (Arenas-Corraliza et al., 2018), or the characteristics of the studied trees, which define the shading period (gradual increase of shade in deciduous trees) and distribution (irregular incoming sunflecks). Under Mediterranean conditions, cereal yield and quality are usually negatively affected by high light and temperature that leads to photoinhibition and either long periods of above optimal temperatures or short periods of heat shock (Jacobsen et al., 2012). Under these circumstances, shade may alleviate the negative effects associated to high radiation or provide for temporal stability, resulting, in a positive net effect. Therefore, it is necessary to identify the best suited cereal species and cultivars for shaded conditions and that are able to maximize positive interactions with other components of agroforestry systems.

The aim of this study is to assess how shade affects the phenology and morpho-anatomical, physiological and biochemical traits of wheat and barley cultivars and how these changes ultimately

determine grain yield. To address this objective, an artificial shading experiment was carried out. Based on the same experiment, we previously found that both cereal species increased grain yield by aprox. 20 % in shade conditions through different acclimation strategies. While wheat shade acclimation was based on leaf adjustment (leaf area and leaf mass area), barley performed mostly a physiological adaptation (Arenas-Corraliza et al., 2019). The final objective of this study is to explore the role of cultivars precocity and search the best shade-responding wheat and barley cultivars to be used in Mediterranean agroforestry systems, based on a large range of functional traits indicative of crop yield. The hypothesis were:

1. Shade has an overall positive effect on wheat and barley grain yield, and we expect that earliest cultivars perform better under shading conditions than late cultivars, because they avoid in a greater extent deciduous tree shade.

2. Wheat and barley cultivars acclimate to shade by modifying different phenological, morphological, physiological and biochemical traits.

MATERIAL AND METHODS

Experimental design

Nine cultivars of wheat (*Triticum aestivum* L.) and nine of barley (*Hordeum vulgare* L.) widely used in the Mediterranean region were sown in an open greenhouse in the Organic and Mountain Agriculture Research Center at Plasencia, central Spain (40° 1'N, 6° 6'W), in the 2016-2017 growing season (November-June). The study site has a continental Mediterranean climate, the average mean annual temperatures is 16 °C, the average maximum temperature is 34.3 °C and average minimum temperature is 3 °C. The average annual rainfall is 694 mm, the summer season being especially dry. The cultivars covered three categories of precocity regarding flowering dates. For wheat, cultivars were named from W1 to W9, spanning precocity categories of very early, W1-W3 (Nogal, Nudel and Tocayo), early, W4-W6 (Algortimo, Paledor and Solehio) and medium, W7-W9 (Toskani, Somontano and Nemo). Cultivars named from B1 to B9 represented barley cultivars of the three precocity categories: very early, B1-B3 (Hispanic, Lavanda and Luzia), early, B4-B6 (Kalea, Lagalia and Carolina) and medium B7-B9 (Meseta, Ibaiona and Crescendo). These cultivars were provided by CICYTEX Research Center (http://cicytex.juntaex.es/en/), member of the Group for the Evaluation of New Varieties for Extensive Crops in Spain (http://www.genvce.org/).

The main treatment of the study was simulating three different shading levels, S0 (~0% of shade), S1 (~25% of shade) and S2 (~50% of shade), by installing three sets of green polyethylene nets in open greenhouse structures (see Appendix Table A1 for further details on abiotic conditions of each level). The mesh size and porosity (UNE 40606) of the nets were 2.25 cm² and 90%, 0.0026 cm² and 43%, and 0.0075 cm² and 36% for S0, S1 and S2 respectively. The S0 net did not reduce full light conditions and was installed to avoid bird damage in the cereal grain, and to avoid differences in ventilation with respect to the other two treatments. We used a split-plot design. First, the 18 pots cultivated for each cultivar were divided at random into three groups, 6 pots for each shading level. All pots (randomly) assigned to the same shading level were placed within the same block (structure). The replicates were n=6 for each cultivar and n=54 for each species. For each shading level, 2 dataloggers (PCE-H71N Data logger, PCE Instruments, Holding GmbH Inc., Hamburg, Germany) were placed at the cereal canopy to record temperature and humidity (Appendix Table 1). The daily curve of the Photosynthetic Active Radiation (PAR) of each shading level was measured on three days of the anthesis period (April 18th, 24th and 27th) with the PAR sensor of a portable infra-red gas analyzer (IRGA) (LCpro+, ADC Bioscientific Ltd., Hoddesdon, UK) (Appendix Table A1). To approach agroforestry conditions, shading nets were installed when leaf sprout of walnut trees took place in the region (around 7th of April,; day of the year 97 in 2017), coinciding with the start of booting in cereals (pre-anthesis period). Nets were placed 1.5 m above cereal canopy to make sure that there was enough ventilation for plant development and they were kept until harvest.

Ten seeds were sown in each pot (13 x 13 x 17 cm) the 18th November 2016, removing the excess of seedlings until retain only 4 seedlings per pot. Before booting, training rods and strings were installed around the plants to maintain the stems straight throughout the whole process of measurements. As substrate, a mixture with three parts of black peat, one part of sand and one part of perlite was used, being the water holding capacity 119% and the pH 5.8. To avoid water stress, soil moisture was regularly measured with a humidity probe (HH2 Moisture Meter, Delta-T Devices Ltd., Cambridge, UK) in all pots and irrigated when needed to keep soil water capacity above 50% of field capacity. Every pot was fertilized before sowing in November 2016 with a dose equivalent to 58 kg N ha⁻¹, 100 kg P_2O_5 ha⁻¹ and 58 kg K_2O ha⁻¹. During the cereal tillering (February 2017), urea 46% was applied in order to supply a dose equivalent to 200 kg N ha⁻¹ per pot.

Phenological growth stages

Cereal phenology was recorded weekly, from the setup of the net to the cereal maturity, according to the Zadoks scale (Zadoks et al., 1974). The following stages were monitored: stem elongation (Z.30-39; DS), booting (Z.40-49; DB), heading (Z.50-59; DH), flowering/anthesis (Z.60-69; DF), grain filling including milk development (Z.70-79; DM) and dough development (Z.80-89; DD) and ripening (Z.90; DR). In each pot, the stage present in 50% or more of the

plants was recorded. Based on the recorded phenological data, the days from seeding to each specific stages were estimated for wheat and barley in the different shading levels.

Physiological parameters

Chlorophyll content was un-destructively estimated with an SPAD meter (SPAD-502 Plus, Konica Minolta Holdings, Inc.). SPAD index is highly correlated with chlorophyll leaf content in wheat (Uddling et al., 2007) and barley (Arenas-Corraliza et al., 2019). Three different measurements were recorded at the anthesis period in a leaf of a randomly selected plant per pot. For this and the following parameters, we used flag leaf for wheat and the second leaf for barley.

Quantum Yield (Y), Electron Transport Rate (ETR) and Non-Photochemical Quenching (NPQ) values fixed at light saturation (2200 µmol photons m^{-2} s^{-1}) were obtained from cereal leaves in the anthesis period with a modulated chlorophyll fluorimeter (OS5p+, Opti-Sciences, Inc., Hudson, USA) using variable chlorophyll fluorescence rapid-light response curves (Coe & Lin, 2018). After adapting leaves to dark for 30 minutes, they were exposed in 15 second intervals to increasing actinic light intensities until reach 2200 µmol photons m^{-2} s^{-1}. The efficiency of Photosystem II is well featured by the Quantum Yield (Y) and the equivalent parameter Electron Transport Rate (ETR), which are correlated with photosynthetic rate. On the other side, the Non-Photochemical Quenching (NPQ) is indicative of the capacity of heat dissipation.

Morpho-anatomical traits and yield

Leaf area (LA) and Leaf Mass Area index (LMA), as the ratio of leaf dry mass to leaf area, were determined in the anthesis stage using same leaves used for SPAD measurements. Firstly, fresh leaves were scanned, subsequently their area was measured with the ImageJ software (National Institute of Health, USA). Then, leaves were dried at 60°C until constant weight to obtain dry mass.

Once cereal grains reached maturity (June 2017), the aerial parts of all plants were harvested in the same day and dried at 60°C until constant weight. Plant height of every plant was measured excluding the awns. Plant biomass, grains per spike and weight of 1000 grains were measured in the highest 4 tillers per pot. Finally, total number of spikes, total biomass and grain yield, along with the harvest index, as the ratio of grain yield to biomass yield, were measured per pot.

Biochemical determination

In the anthesis period, leaf glucose and starch content was measured in the same leaves used for SPAD readings (n=6). One additional leaf per pot was harvested to assess N content (n=6), and another

for P and K content (n = 6). Leaf glucose and starch was analyzed by spectrophotometry following the method proposed by Oleksyn et al. (2000). Leaf and grain N content was analyzed by combustion analysis using the Dumas method (ISO 16634-1:2008). Leaf P and K contents were determined by ICP-MS (ISO 17294-1:2004). P content in grain was determined by continuous flow analysis (ISO 15681-2:2003), and K was determined with by atomic absorption spectrometry (ISO 9964-2:1993).

Data analysis

To assess significant differences in phenology (Zadoks scale values) between the different precocity categories of wheat and barley, one-way ANOVAs were performed separately for each species, shading level and date of recording. Additionally, three-ways ANOVAs were run separately by species to compare the DOY (day of year) when different cultivars reached key Zadoks stages (DH, DF, DM, DD and DR) under different irradiance levels, with cultivars nested in precocity categories. When siginficant effects were found, Least squares difference test (LSD) for pair-wise comparisons were used.

General Linear Models (GLM) were performed per species (wheat and barley) to assess the effect of irradiance and cultivar on the following response variables: grain and biomass yield, harvest index, plant biomass, number of spikes, number of grains per spike, weigth of 1000 grains, plant height, leaf area, leaf mass area, SPAD value, ETR, NPQ, leaf glucose, starch, N, P and K content, and grain N, P and K content. The independent vairables used were: irradiance, precocity category, cultivar (nested in precocity) and their interacions with irradiannce.

A Principal Component Analysis (PCA) was done with all parameters recorded per species, to assess the relationships between grain yield and plant traits. Additionaly, correlations between grain yield and individual plant traits were assessed with Pearson correlation coefficient (r) for each species and shading level.

All the statistycal analysis was performed by STATISTICA software (StatSoft Inc., Maison-Alfort, France).

RESULTS

Influence of irradiance on phenology

At the time of the layout of shading treatment, plants were initiating the booting growth stages (Z.40-49). Very early wheat cultivars were significantly more advanced than early and medium cultivars, showing barley the same trend but less intense (Figure 1). Under full sunlight

(S0), differences among precocity categories tended to be maintained during the whole crop cycle, especially for wheat than for barley that showed higher differences during grain formation (Z.71-75) than in the rest of stages (Figure 1). Nevertheless, there were many differences in development stages among cultivars that did not respond to pre-defined precocity categories, especially in barley (Appendix Tables A2 and A3).
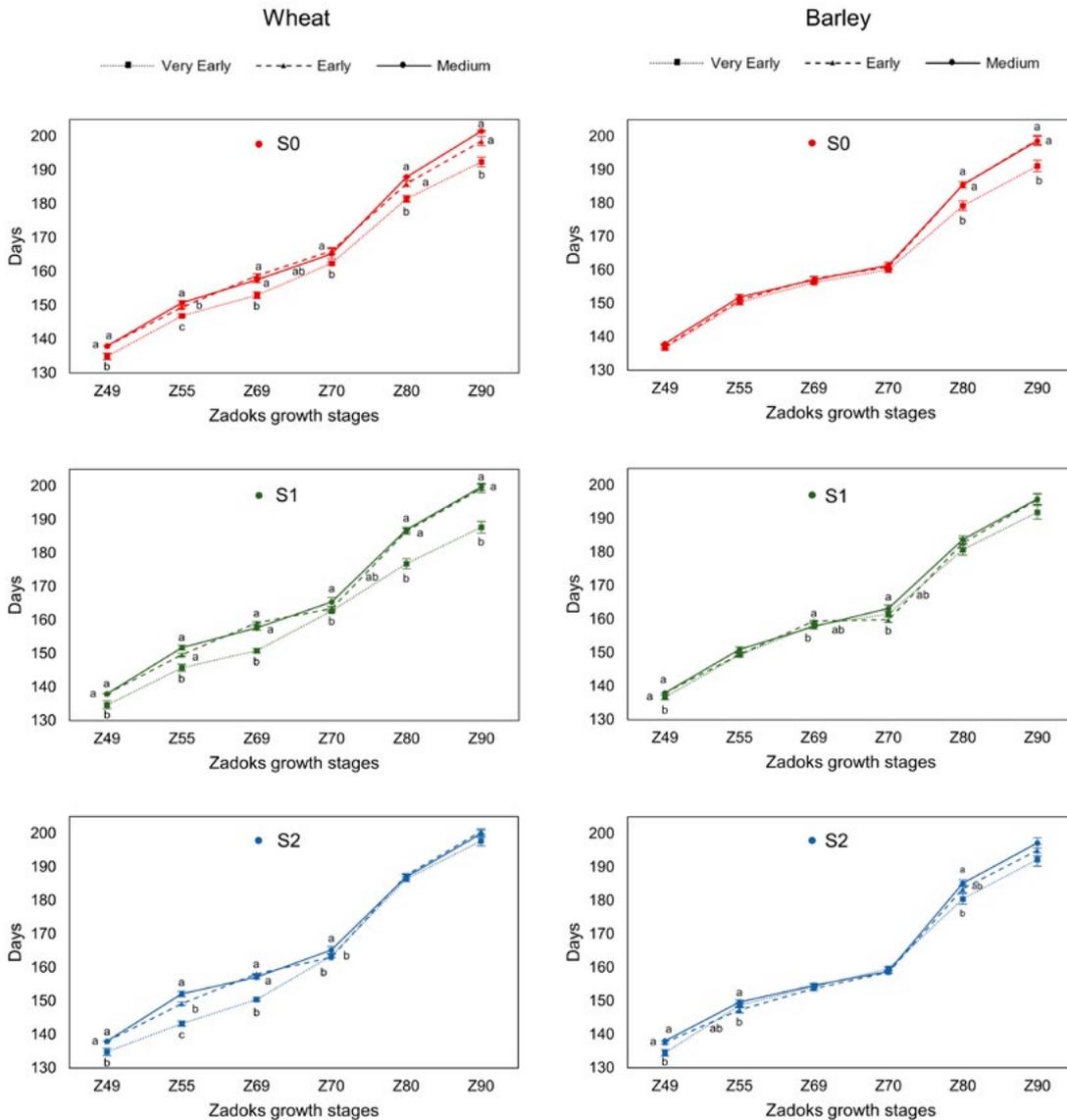
Figure 1. Days to reach key growth stages according to Zadoks et al. (1974) for wheat and barley in the different shading levels studied (S0, S1 and S2) from the beginning of the shading treatments. Data represents means ± S.E. (n=18). Different letters indicate significant differences between precocity categories (p < 0.05). The absence of letters indicates that significant differences were not detected between precocity categories.

Moderate shading (S1) tended to exacerbate differences between precocity categories in wheat (Figure 1), with very early cultivars reaching the anthesis and ripening stages (Z.83-89) earlier than early and medium cultivars. Dense shading (S2) also speeded up wheat plants until anthesis and highlighted differences among precocity groups, but these differences fade out in later stages. The already low differences among precocity groups of barley at early development fade out under S1 and S2. Time needed to reach particular growth stages differed also between species and irradiance level, although there were no significant differences in mean temperatures among irradiance levels (Appendix Table 1). For instance, barley significantly spent less time to reach DH and DF growth stages at S2 shading level compared to S1 and S0 levels (Table 1), while wheat did not show any difference. On the contratry, at later stages, wheat tended to reach DD and also DR earlier in the S0 and S1 shading levels compared to S2 treatment, while barley did not show any difference. The response of developmental stages to irradiance level varied greatly among cultivars, and again, these differences did not fit within the pre-defined precocity categories (Appendix Tables A2 and A3). Consequently, we redefined precocity categories based on the number of days needed by S0 plants of our experiment to reach the successive phenological stages. Henceforth, cultivars included in the new categories, by order of precocity, were: P1 (W1, W2, W3 and B1, B2, B7), P2 (W4, W8, W9 and B3, B6, B9) and P3 (W5, W6, W7 and B4, B5, B8).

Table 1. Days in which wheat and barley reached Zadoks key stages in the shading levels studied (S0, S1 and S2). Data represents means ± S.E. (n=54). Different letters indicate significant differences between shading levels in each species (p < 0.05). The absence of letters indicates that significant differences were not detected between shading levels for each species.

	Irradiance	Days to complete booting (pre-shading) Z49	Days to middle heading Z55 DH	Days to complete flowering Z69 DF	Days to start milk development Z70 DM	Days to start dough development Z80 DD	Days to start ripening Z90 DR
Wheat	S0	137 ± 0.4	149.1 ± 0.3	156.5 ± 0.6	164.6 ± 0.6	185.2 ± 0.6 **ab**	197.5 ± 0.8 **ab**
	S1	136.9 ± 0.4	149.1 ± 0.6	155.9 ± 0.6	163.9 ± 0.5	183.4 ± 0.9 **b**	195.6 ± 1.1 **b**
	S2	136.9 ± 0.4	148.2 ± 0.7	155.2 ± 0.5	163.9 ± 0.4	186.9 ± 0.4 **a**	199.4 ± 0.7 **a**
Barley	S0	137.3 ± 0.3	151.0 ± 0.4 **a**	156.9 ± 0.4 **b**	160.8 ± 0.5 **a**	183.4 ± 0.8	196.2 ± 0.9
	S1	137.6 ± 0.3	149.9 ± 0.4 **a**	158.5 ± 0.3 **a**	161.5 ± 0.5 **a**	182.4 ± 0.8	194.5 ± 1.0
	S2	136.7 ± 0.4	148.6 ± 0.4 **b**	154.2 ± 0.4 **c**	159.0 ± 0.3 **b**	183.1 ± 0.8	194.8 ± 1.0

Influence of irradiance on plant traits

Most of the plant traits varied significantly among cultivars and/or among precocity caterogies, with the exception of LMA in wheat and SPAD and grain P in barley. Also shade affected significant to most of the wheat and barley plant traits, with the exception of ETR and grain K in wheat, and grain N in barley. Nevertheless, the effects of irradiance depended on the cultivar and on the precocity for different traits in both species (Appendix Table A4).

Although biomass yield increased with shade in both wheat and barley, plant biomass only increased in wheat under shading conditions (Table 2). Plant height and leaf area increased significantly with shade in both species, especially in S2, and LMA decreased.

Table 2. Parameters studied in wheat and barley in the different shading levels (S0, S1 and S2). Data represents means ± S.E. (n=54). Different letters indicate significant differences between shading levels (p < 0.05) for each species. The absence of letters indicates that significant differences were not detected between shading levels for each species. All weight units were referred to dry matter.

Species	Irradiance	Grain yield (g pot^{-1})	Biomass yield (g pot^{-1})	Harvest Index	Plant biomass (g)	Number of spikes per pot	Grains per spike	Weight of 1000 grains (g)	Plant height (cm)	Leaf area (cm^{-2})
Wheat	S0	4.68 ± 0.19 **b**	13.81 ± 0.40 **b**	0.34 ± 0.01 **b**	2.21 ± 0.04 **b**	3.39 ± 0.26	28.24 ± 1.05	29.62 ± 0.79 **b**	54.05 ± 0.41 **b**	3.81 ± 0.19 **c**
	S1	5.45 ± 0.23 **a**	15.02 ± 0.40 **a**	0.37 ± 0.01 **ab**	2.45 ± 0.10 **a**	2.83 ± 0.27	28.77 ± 0.83	33.12 ± 0.86 **a**	55.03 ± 0.45 **b**	4.51 ± 0.18 **b**
	S2	5.57 ± 0.19 **a**	14.86 ± 0.40 **ab**	0.38 ± 0.01 **a**	2.29 ± 0.05 **ab**	3.15 ± 0.28	30.41 ± 1.01	30.49 ± 0.83 **b**	61.39 ± 0.47 **a**	5.65 ± 0.24 **a**
Barley	S0	5.06 ± 0.17 **b**	12.12 ± 0.38 **b**	0.42 ± 0.02	0.95 ± 0.04	11.13 ± 0.55	10.31 ± 0.41 **b**	41.71 ± 0.69 **a**	38.32 ± 0.38 **b**	2.30 ± 0.10 **b**
	S1	5.15 ± 0.21 **b**	13.40 ± 0.33 **a**	0.39 ± 0.02	0.95 ± 0.04	11.91 ± 0.56	9.53 ± 0.52 **b**	42.66 ± 0.74 **a**	39.75 ± 0.42 **b**	2.30 ± 0.11 **b**
	S2	6.01 ± 0.21 **a**	13.78 ± 0.38 **a**	0.43 ± 0.00	0.98 ± 0.04	12.02 ± 0.57	11.68 ± 0.46 **a**	38.63 ± 0.59 **b**	46.00 ± 0.46 **a**	2.64 ± 0.12 **a**

LMA: leaf mass area; ETR: electron transport rate and NPQ: non-photochemical quenching.

In relation to leaf biochemical parameters, glucose and N decreased with the intensity of shade in both species (Table 2). Leaf starch also decreased with shade, but differences among S1 and S2 shades were less evident. Besides, the responses to shade of these three parameters depended on irradiance, precocity and cultivars in both species ($p < 0.01$ for I, P and C) and on their interactions ($p < 0.001$ for I x P and I x C interactions). As levels of shade increased, starch decreased in earlier cultivars, but increased in late cultivars of wheat. For barley starch decreased in early and late cultivars and increased in intermedium ones. Glucose decreased in earlier cultivars of wheat and barley, and increased in late cultivars but only in some of them (e.g., W4 and B8). Leaf N decreased in late and intermedium cultivars and tended to increase in early cultivars of wheat, with the opposite for barley (Appendix Table A5 and A6). Leaf P and K increased significantly and steadily with shade intensity, and the response depended again on precocity and cultivars. For leaf P, mean values were higher in later cultivars in both species, but the response to shade was more intense in early cultivars, especially in barley. For K the response to shade was more intense in early cultivars of wheat and barley.

LMA (mg cm^{-2})	SPAD	ETR	NPQ	Glucose (mg g leaf $^{-1}$)	Starch (mg g leaf $^{-1}$)	N (mg g leaf $^{-1}$)	P (mg g leaf $^{-1}$)	K (mg g leaf $^{-1}$)	N (mg g grain $^{-1}$)	P (mg g grain $^{-1}$)	K (mg g grain $^{-1}$)
13.25 ± 0.48 a	34.54 ± 0.73 c	269.8 ± 5.82	1.92 ± 0.06 a	99.78 ± 7.13 a	4.47 ± 0.67 a	35.48 ± 1.89 a	1.59 ± 0.05 b	14.85 ± 0.53 b	26.71 ± 0.45 a	2.47 ± 0.08 a	12.61 ± 0.56
10.01 ± 0.29 b	36.56 ± 0.64 b	268.3 ± 4.76	1.93 ± 0.08 a	91.29 ± 3.80 b	2.47 ± 0.15 c	31.70 ± 1.30 b	1.62 ± 0.04 b	15.15 ± 0.53 b	25.20 ± 0.51 b	2.10 ± 0.08 b	11.53 ± 0.45
10.31 ± 0.26 b	42.73 ± 0.56 a	265.5 ± 6.24	1.83 ± 0.07 b	75.52 ± 4.50 c	3.25 ± 0.39 b	25.82 ± 1.10 c	2.05 ± 0.06 a	19.21 ± 0.59 a	25.07 ± 0.57 b	2.24 ± 0.06 b	11.65 ± 0.38
9.23 ± 0.22 a	29.54 ± 0.70 b	306.0 ± 7.3 a	2.65 ± 0.11 b	85.10 ± 4.23 a	13.51 ± 1.48 a	36.96 ± 1.27 a	1.48 ± 0.04 b	26.40 ± 0.70 c	23.70 ± 0.43	3.05 ± 0.12 a	21.38 ± 0.69 a
8.13 ± 0.16 b	29.65 ± 0.76 b	284.6 ± 7.0 b	2.67 ± 0.08 b	69.91 ± 5.04 b	9.58 ± 0.92 b	33.16 ± 1.67 b	1.54 ± 0.04 b	28.06 ± 0.75 b	23.32 ± 0.44	2.60 ± 0.08 b	20.16 ± 0.46 a
7.87 ± 0.19 b	38.64 ± 0.71 a	257.7 ± 7.4 c	2.98 ± 0.10 a	49.10 ± 2.06 c	10.42 ± 0.81 b	28.98 ± 0.81 c	1.75 ± 0.04 a	30.03 ± 0.70 a	22.72 ± 0.40	2.44 ± 0.06 b	19.00 ± 0.38 b

With regard to grain nutrient content, N, P and K contents differed among shading treatments in both wheat and barley (Table 2). Some barley cultivars showed a dilution effect with shade for grain P and K content (Appendix Table A4; p = 0.037 for P and p = 0.001 for K in I x C interactions); P content was lower in shaded environments for B2, B5, B7 and B9 cultivars, and K content decreased in B2, B5 and B6 cultivars. N dilution was more important in late cultivars in both species (Appendix Tables A5 and A6).

Concerning physiological parameters, the chlorophyll content (SPAD value) increased in the shading treatments in both wheat and barley (Table 2), although its response to shade in wheat varied among precocity categories (Appendix Table A4; p < 0.001 for I x P interaction). Chlorophyll content of earlier cultivars of wheat showed a higher response to shade (Appendix Table A5). Regarding fluorescence parameters (ETR and NPQ), ETR decreased significantly with shade in barley (Table 2), showing late cultivars a weaker response to shade. Shade also reduced significantly ETR in W1, W6 and W9 wheat cultivars, while the opposite was found for W2, W3 and W4 cultivars. Deep shade reduced significantly NPQ in wheat, but increased it in barley. In both cases, the effect of shade varied with precocity level and cultivars (Appendix Tables A5 and A6).

Influence of irradiance on grain yield

Shading treatments increased significantly grain yield for both wheat and barley, although each species showed a different pattern (Appendix Table A4). While for wheat, grain yield increased in S1 (16.36 %) and S2 (18.85 %) respect to full light (Figure 2; Table 2), barley grain yield increased only significantly in the S2 level compared to full light (18.85 %). There were significant differences among cultivars in both species, but precocity was only significant in wheat, and the effect of the irradiance was independent of precocity and cultivar in both species (p > 0.05 for I x P and I x C; Appendix Table A4 for statistical results and A5 and A6 for mean values). With relation to harvest index, wheat and barley showed a very different response. For wheat, shading treatments significantly increased the harvest index (Table 2), especially for W5 and W7 cultivars. In addition, the harvest index was highly influenced by irradiance, precocity and cultivars (and their interactions; I x P and I x C; p < 0.05; Appendix Table 4). On the contrary, for barley, shading levels did not show any effect on the harvest index and it varied only significantly between cultivars (p < 0.001; Appendix Table 4).

Differences among species also emerged at different yield components. The number of spikes per pot, grains per spike and grain weight varied significantly among cultivars and precocity categories in both species, with the exception of precocity for the number of wheat spikes. For

barley, the number of grains per spike increased significantly in the S2 shading level compared to S0 (13.28 %) and S1 (22.56 %), the response to shade being dependent of cultivars (p = 0.009 for I x C), with B4, B7 and B9 among the more sensitive to shade (Appendix Table A6). Grain weight was significantly higher in wheat in the S1 level in comparison with S0 and S2, and conversely, grain size decreased with shade in barley (Figure 2).
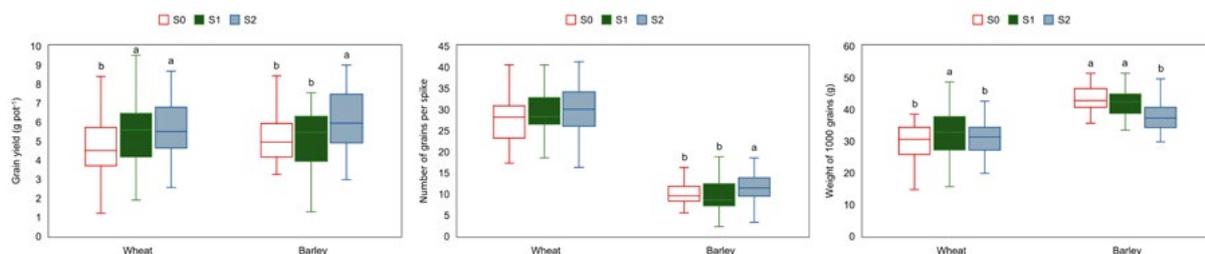
Figure 2. Boxplot of grain yield (g pot^{-1}), number of grains per spike and weight of 1000 grains (g) for wheat and barley (n=54) in the different shading levels studied (S0, S1 and S2). Different letters indicate significant differences between shading levels in each species (p < 0.05). The absence of letters indicates that significant differences were not detected between shading levels for each species. All weight units were referred to dry matter.

Determinants of grain yield

Pearson correlation coefficients showed that grain yield of wheat was positively correlated with biomass yield, plant biomass, number of grains per spike, weight of 1000 grains, leaf area, NPQ and precocity category (grain yield was higher in late cultivars) and to a lesser extent with K leaf content, and negatively correlated with P leaf content and grain N, P and K content. For barley, grain yield was positively correlated with SPAD value, and also with biomass yield, NPQ, plant height, number of grains per spike, leaf area, and negatively with DH, DF and DM, grain N, P and K content and to a lesser extent with LMA. Nevertheless, correlations varied accross shading levels (Table 3).

Table 3. Pearson correlation coefficient (r) between grain yield and the rest of parameters studied in the different shading levels (S0, S1 and S2) for wheat and barley (n = 54). Significance level: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Species	Grain Yield							
	Wheat				Barley			
Shade treatment	S0	S1	S2	All	S0	S1	S2	All
DH	-0.426 **	-0.490 ***	-0.223	**-0.359 ***	-0.345 *	-0.371 **	-0.274 *	**-0.376 ***
DF	-0.497 ***	-0.261	-0.327 *	**-0.369 ***	-0.265	-0.047	-0.409 **	**-0.338 ***
DM	-0.490 ***	-0.338 *	-0.193	**-0.363 ***	-0.278 *	-0.598 ***	-0.449 ***	**-0.477 ***
DD	-0.279 *	-0.280 *	-0.218	**-0.229 **	-0.376 **	-0.456 ***	-0.272 *	**-0.351 ***
DR	-0.129	-0.25	-0.25	**-0.193 ***	-0.337 *	-0.485 ***	-0.304 *	**-0.381 ***
Biomass yield	0.467 ***	0.365 **	0.607 ***	**0.483 ***	0.768 ***	0.621 ***	0.886 ***	**0.755 ***
Plant biomass	0.397 **	0.081	0.15	**0.184 ***	0.356 **	0.497 ***	0.529 ***	**0.459 ***
Number of spikes	0.209	0.032	0.202	0.111	0.266	-0.129	0.154	0.1
Number of grains per spike	0.441 ***	0.480 ***	0.218	**0.383 ***	0.510 ***	0.707 ***	0.644 ***	**0.653 ***
Weight of 1000 grains	0.569 ***	0.563 ***	0.525 ***	**0.555 ***	0.205	0.05	0.262	0.056
Plant height	-0.108	-0.181	-0.211	-0.046	0.358 **	0.317 *	0.487 ***	**0.469 ***
Leaf area	0.322 *	0.155	0.299 *	**0.318 ***	0.127	0.04	0.167	**0.161 ***
LMA	0.09	0.255	0.01	-0.015	0.382 **	0.218	0.129	0.149
SPAD	-0.156	0.129	0.344 *	**0.185 ***	0.288 *	0.228	0.153	**0.343 ***
ETR	-0.239	-0.165	0.103	-0.098	0.272 *	0.185	-0.04	0.024
NPQ	0.364 **	0.415 **	0.151	**0.292 ***	-0.195	-0.09	0.09	0.005
Leaf glucose	0.165	0.119	-0.157	0.000	0.112	0.114	-0.002	-0.050
Leaf starch	0.246	-0.502 ***	-0.128	-0.037	0.050	0.058	-0.082	-0.009
Leaf N	-0.372 **	0.042	0.008	**-0.201 ***	-0.332 *	0.120	0.035	-0.115
Leaf P	-0.416 **	-0.473 ***	-0.174	**-0.195 ***	-0.389 **	-0.030	0.052	0.013
Leaf K	0.036	0.127	0.254	**0.197 ***	-0.263	-0.193	0.017	-0.057
Grain N	-0.627 ***	-0.397 **	-0.665 ***	**-0.573 ***	-0.280	-0.112	-0.264	**-0.236 **
Grain P	-0.685 ***	-0.664 ***	-0.190	**-0.565 ***	-0.044	-0.522 ***	-0.462 ***	**-0.33 ***
Grain K	-0.508 ***	-0.291 *	-0.177	**-0.358 ***	-0.202	-0.190	-0.362 **	**-0.291 ***

DH: Days to middle heading (Z55); DF: to complete flowering (Z69); DM: to start milk development (Z70); DD: to start dough development (Z80); DR: to start ripening (Z90). LMA: leaf mass area; ETR: electron transport rate and NPQ: non-photochemical quenching.

Regarding the Principal Component Analysis (PCA), it separated quite well the assemblage of plant traits of barley plants growing under different shading levels, although surprisingly S2 located in an intermediate position between S0 and S1. The separation for wheat was less clear, and S0 took the intermediate position. These results show that the response to shade intensity was not so linear (Figure 3, right). By contrast, PCA did not reveal strong associations between grain yield and the rest of the plant traits studied, with the exception of SPAD in barley. For wheat, certain positive association was identified among grain yield and weight, precocity (higher grain yield with lower time needed to reach different stages) and NPQ; and negative association with ETR, grain N and P contents. For barley, besides SPAD, traits such as plant height, grain per spike, and leaf area were associated positively with grain yield, while days to reach phenological stages, grain K, P and N were negatilvey correlated.
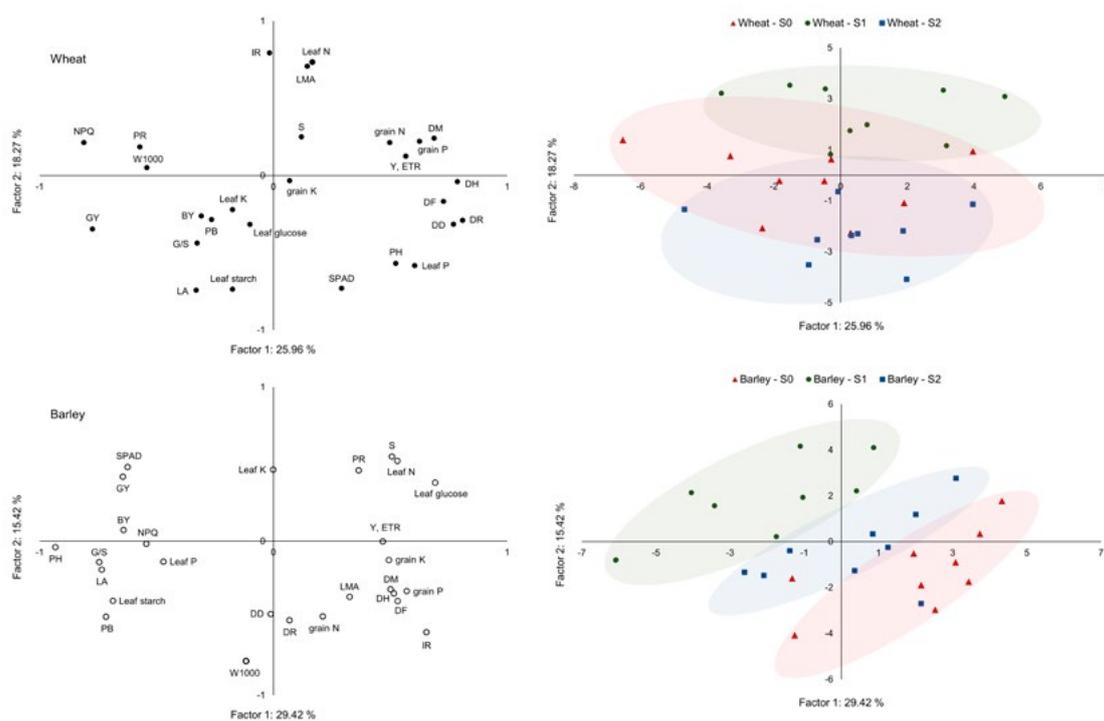
Figure 3. Components (left) and cultivars scores (right) of PCA analysis for wheat (top) and barley (bottom) in the different shading levels studied (S0, S1 and S2) of grain yield (GY), biomass yield (BY), plant biomass (PB), number of spikes (S), number of grains per spike (G/S), weight of 1000 grains (W1000), plant height (PH), spad index (SPAD), leaf area (LA), leaf mass area (LMA), quantum yield (Y), electron transport rate (ETR) non-photochemical quenching (NPQ), leaf glucose, leaf starch, leaf N, leaf P, leaf K, grain N, grain P, grain K, days to middle heading (DH), days to complete flowering (DF), days to start milk development (DM), days to start dough development (DD), days to ripening (DR), cereal precocity (PR) and irradiance (IR).

DISCUSSION

Phenological stages were advanced by shade in both species

Cultivars showed significant phenological differences when exposed to shade regardless of the predefined precocity category. Phenology of wheat and barley cultivars was mostly advanced by shade, inducing an earlier flowering with dense shade (50% of full sunlight) and grain development with moderate shade (75% of full sunlight) than in full sunlight. Contrary to our results, Dufour et al. (2013) did not found any shade modification in durum wheat phenology in different light environments (up to 42% and 60% artificial shading levels) and Inurreta-Aguirre et al. (2018) showed delays in flowering stages by agroforestry light reduction (33% reduction, on average). Nevertheless, both studies were carried out under Mediterranean climate in Southern France, where the average annual solar radiation (5446 MJ/m^2), being already enough for cereal development, is less intense than in our study site (6300 MJ/m^2) which is 14 % higher (https://solargis.info/). In these conditions, shade can play a more beneficial role for cereals in terms of advancing development by avoiding photoinhibition and the carbon cost of photoprotection (Jacobsen et al., 2012; Valladares & Pearcy, 1997). Inurreta-Aguirre et al. (2018) also found a delayed grain milk development in wheat with agroforestry shading, in agreement with our results.

Lack of light is an important driving force of leaf senescence, which is negatively associated with grain yield (Talukder et al., 2014). Xu et al. (2016) reported that mid and severe shading (67% and 35 % of full sunlight, respectively) advanced wheat leaf senescence. By contrast, slight post-anthesis shading can delay senescence because of the avoidance of light stress (Shimoda & Sugikawa 2019), resulting in an extended grain-filling period. Although we did not measure specifically leaf senescence, our data indicated rather the contrary, moderate shade produced a certain advancement of the last growth stages, which could be related to a slight uncontrolled temperature increase, while intense shade delayed it, especially in wheat. Besides, our results showed that lengthening the growing period (delayed growth stages) correlated negatively with grain yield. We observed that precocity was determinant for grain yield of both barley and wheat, in agreement with Moragues et al. (2006), who reported days from seeding to heading (DH) as the most important plant trait explaining variations in grain yield of Mediterranean wheat cultivars.

Our study highlights the importance of understanding the influence of precocity traits of cereals, such as days to flowering (DF), days to stat milk (DM) and dough development (DD) as well as days to reach the ripening stage (DR), because of its relationship with grain yield in warm Mediterranean conditions. The speed of development in cereals is determined by genes sensitive to photoperiod (Loss & Siddique, 1994). Efforts have been made in wheat and barley

to select those genes with less sensivity to photoperiod in order to advance development and reach anthesis earlier. These individuals could achieve greater grain yields because a decreased exposition to high temperatures and moisture stresses during grain filling (Fischer & Kohn, 1966; van Oosterom & Acevedo, 1992; Woodruff & Tonks, 1983). In this line, under Mediterranean conditions, other traits such as grain filling rate have been proved to be more important for grain weight than the duration of the grain filling period, what is seen as an adaptation to warm/ drought conditions of Mediterranean summer (Dias & Lidon, 2009). Reaching DF, DM, DD and DR stages earlier depends on light availability and temperature and represent major traits in the ultimate cereal performance. These features can be selected from the extensive availability of wheat and barley cultivars, in order to complete cereal cycle earlier, avoiding extreme climate events and high shading periods in agroforestry systems.

With regard to tree species, deciduous trees with a late budburst are commonly recommended to avoid high rates of shading to crops and limit undesired effects on cereal anthesis and therefore on grain yield. However, our results reveal that early budburst trees could be a good option in warm Mediterranean conditions.

Shade affected plant morphological traits with positive influence on grain yield

Shading conditions tended to increase crop biomass in both species (wheat and barley), which was finally linked to a greater grain yield. Studies conducted outside the Mediterranean area reported that slight pre-flowering shading (~20 %) maintained (Mu et al., 2010) or increased (Li et al., 2010) wheat biomass yield compared to full light conditions, while more intense shading led to biomass decreases, contrary to our study.

Crops can adjust their canopy to optimize light interception under shade (Li et al. 2010; Xu et al 2016). Indeed, our study revealed certain structural adjustments, such as an increased plant height and leaf area. The positive effect of shade on plant height, a common response to shade (Kutschera & Briggs, 2013; Wang et al 2015), was positively correlated with grain yield for barley. Similarly, shade positively affected leaf area, especially in wheat, improving light interception and grain yield, in accordance to Li et al. (2010). In this way, given the higher leaf area in S1 and S2 levels, wheat could have reached a similar light interception than plants grown in full light conditions (S0). The relationship between leaf area and grain yield was weaker in barley, whose leaves tend to be smaller than wheat. While flag leaf photosynthesis seems important for grain filling in wheat (Thorne, 1965), ear (spike and awns) photosynthesis does for barley (Biscoe et al., 1975; Ziegler-Jöns, 1989), but this was not measured in our study. Further studies should assess the effects of shading on ears, especially in Mediterranean conditions, where the shading of spikes and awns could reduce to a larger extent grain yield than shading flag leaf (Merah & Monneveux, 2015).

Leaf mass area has been traditionally used to describe acclimation strategies to different environmental conditions such as shade and can vary greatly within the same species (Poorter et al., 2009; Wright et al., 2006). In our study, leaf mass area was significantly lower (thinner leaves) in shaded conditions compared with full light in both species. This is explained by the need of shaded plants to develop bigger leaves to intercept light (Witkowski & Lamont, 1991; Wang et al 2015).

Shade affected biochemical plant traits with variable influence on grain yield

Leaf biochemical contents were equally affected by shading in barley and wheat, although with large differences among cultivars. Shade usually reduce the accumulation of non-structural carbohydrate in leaves due to a reduced photosynthetic rate (Judel & Mengel, 1982). We found that both glucose and starch were reduced with shade, and that the reduction was more intense with dense shading, but not for all cultivars. Xu et al. (2013) reported lower values of soluble sugars during the whole grain filling phase in the flag leaves of shaded plants (50% and 90% of shading) with respect to full-sunlight plants in two wheat cultivars. However, low-intensity shading plants (22% of shading) tended to accumulate more soluble sugar than control plants, especially in shade-tolerant cultivars (Xu et al. 2013). In our case, the reduction in non-structural carbohydrates was more intense for barley than for wheat, more intense with dense shading than with moderate shading, and less intense for latest cultivars. Indeed, moderate shading (25%) favored the accumulation of glucose and starch in leaves of late cultivars of wheat.

Reduction in glucose and starch could explain why shaded plants had also less N leaf content that plants grown at full light. N is optimized at plant level and its uptake by roots depends on availability of carbohydrates exported from leaves, what in turns depend on light absorption and carbon assimilation (Dreccer, et al., 2000a; Omondi et al., 2019; Rideout & Raper, 1994). Contrary to N, leaf P and K leaf content was higher in the shaded treatments for both wheat and barley, showing that shading conditions benefited their assimilation.

Concerning grain nutrient content, there was a general dilution of N, P and K grain content in both species, supported by the increased grain yield with shade and the negative correlation between nutrients content and grain yield. Although the dilution effect of N (and therefore, grain protein content) in wheat have been also shown in other artificial shading experiments (Artru et al., 2017; Shimoda & Sugikawa, 2019), other authors have reported an increase in protein content with artificial shade (Dufour et al., 2013). However, shading conditions did not significantly reduce grain N content in barley, indicating that barley could be an interesting species for cultivation under trees to produce quality feeds. With regard to P, as well as probably K grain content,

previous works have suggested that current low values could have been a consequence of cereal breeding programs that aimed to increase grain yield and therefore dilute nutrient grain content (Murphy et al., 2008; Wang et al., 2017).

Shade affected physiological plant traits with variable influence on grain yield

Photosynthetic attributes are pivotal for the response of plant productivity to shading and some of our results suggest different adaptive mechanisms among species and cultivars.

Despite the reduction of the leaf N content, chlorophyll content (SPAD values) increased with shade in accordance with other shading studies on cereal crops (Li et al., 2010; Xu et al., 2013; Zheng et al., 2011; Wang et al 2015). Shade-adapted species typically have high leaf chlorophyll content compared with light plants, a trait that maximizes light capture (Valladares & Niinemets, 2008; Zhen & van Iersel, 2017), and commonly acclimation to shade results on greater leaf chlorophyll/Nitrogen ratio (Evans, 1996). In our case, this compensatory acclimation was more evident in earliest cultivars of barley and intermedium cultivars in both species, but not sufficient to avoid a reduction of non-structural carbohydrates with shading. Nevertheless, late wheat cultivars, with the high SPAD values, responded positively to moderate shading in terms of leaf glucose and starch contents. By contrast, earliest cultivars of barley and wheat, with low SPAD values, suffered the greatest reductions of glucose and starch with moderate shading.

Acclimation to shade triggers changes such as lowering ETR and upregulating NPQ. Shade-adapted plants usually display lower values of ETR when exposed to high light with respect to those adapted to full sun. Besides, plants adapted to shade show a prominent increase of NPQ in high light conditions (Zhen & van Iersel, 2017).

Since both barley and wheat are typical annual crops adapted to sunny habitats (usually grown as monocrops in full light), no acclimation response to shade was expected. Indeed, the photochemical apparatus of wheat remained insensitive to shading, but barley displayed a typical pattern of acclimation to shade, such as decreasing ETR and increasing NPQ (Kurasová et al., 2000; Zivcak et al., 2014).

In contrast to the likely acclimation response of barley, we only detected a significant correlation among grain yield and NPQ values in wheat. Working with rice cultivars, Wang et al. (2015) found that shading decreased the electron transport rate (ETR) which resulted in a reduced grain yield. Thus, photosynthetic acclimation to shade displayed by plants, such as reducing ETR or increasing NPQ, does not necessarily translate to a grain yield increase. Improvements in light-harvesting and -use capability under shading might be important characteristics for plant

breeders to select shade-tolerant varieties, but further research is needed to ascertain how these plant traits ultimately affect grain yield.

Shade increased grain yield relates to different traits in wheat and barley

The effect of shade on grain yield is still controversial. Most authors have reported wheat grain yield decreases under artificial shading in non-Mediterranean conditions (Dong et al., 2014; Mu et al., 2010; Shimoda & Sugikawa, 2019) and under artificial (Dufour et al., 2013) and natural shading in Mediterranean environments (Dufour et al., 2013; Inurreta-Aguirre et al., 2018). By contrast, some studies have also found wheat grain production increments when light availability was slightly reduced (10-15% of shading) (Li et al., 2010; Xu et al., 2016). Nevertheless, there are few evidences in Mediterranean conditions for wheat and barley (Arenas-Corraliza et al., 2018), where there is an excess of light for most cultivars.

Our results support the hypothesis that shade has a positive effect on wheat and barley grain yield in our study site, where irradiance is higher than in previous studies done in other Mediterranean areas. In our conditions, light saturation and photoinhibition are common in plants exposed to direct sunlight (Jacobsen et al., 2012; Long & Humphries, 1994). Therefore, shade had an important effect on reducing the risk of photosynthetic damage and thus, the carbon cost of photoprotection (Valladares & Pearcy, 1997).

With regard to the harvest index, although it increased significantly with shade for wheat, it did not reveal any shade effect for barley, remaining, therefore, its response to shade in Mediterranean conditions still unclear (Dufour et al., 2013; Inurreta-Aguirre et al., 2018).

Concerning the number of spikes, since shading nets were set out in the pre-anthesis period (start of booting stage), when spikes number were already established, it could not have been possibly affected by shade. However, shading did have significant effects on other components. The interactions between number of grains per spike and weight of grains depend strongly on the environment in wheat (García del Moral et al., 2003) and barley (Rasmusson & Cannell, 1970), so it can probably vary in different shading conditions. Additionally, our study revealed that it also depends on the species.

With regard to grains per spike, there are controversial results in the literature. Xu et al. (2016) found that the number of grains per spike in wheat increased with a slight post-anthesis shading, but others reported a decrease with a post-anthesis shade (Shimoda & Sugikawa, 2019). As to the response to pre-anthesis shading levels, Li et al. (2010) did not find differences, while other authors reported decreases (Acreche et al., 2009; Dufour et al., 2013; Inurreta-Aguirre et al., 2018; Wang et al., 2003). For the weight of grains, there are also contradictory

outcomes. Some studies confirmed that wheat grain weight was not affected or increased under shading conditions initiated either before (Dong et al., 2015; Inurreta-Aguirre et al., 2018; Li et al., 2010) or after anthesis (Xu et al., 2016), while other authors reported a negative effect of pre-anthesis (Dufour et al., 2013) and post-anthesis shading (Chen et al., 2013; Dong et al., 2014).

The weight of grain depends on the supply of stored assimilates previously and gained during the grain filling stage. Therefore, it can be directly affected by shade at any time (Gebbing et al., 1999; Wang et al., 2003; Yang & Zhang, 2006) or indirectly by altering traits and processes, included leaf senescence (Xu et al. 2016). As commented above, shading speeded up successive growth stages, but ripening was only significantly advanced in wheat with moderated shading (S1), maybe due to a slight temperature increase, in agreement with the higher weight of 1000 grains respect to S0 and S2. These results could explain the positive correlation among the weight of wheat grains and grain yield. As grain filling depends on previously accumulated assimilates, a higher plant development before the onset of shading, as happened in earliest cultivars, could result in less changes at later developmental stages. However, when shade affects plants that are at early stages of development, as it was the case of late cultivars, they can compensate for the lack of radiation by adjusting certain features during the middle and later stages, and therefore increasing grain yield.

CONCLUSIONS

This study revealed, for the first time, that wheat and barley increased grain yield under shading conditions through phenological, morphological, physiological and biochemical acclimations. Shade altered significantly the phenology of wheat and barley cultivars, mostly shortening the time needed to reach successive phenological stages, what in turns affected positively to grain yield. Moreover, grain yield was determined by the assemblage of different plant traits, which changed with shading depending on species and cultivars. The most significant positive traits for wheat grain yield included grain weight, precocity (higher grain yield with lower time needed to reach diffetrent stages), and NPQ. For barley, SPAD value and lower days to reach phenological stages (i.e. higher precocity), and, to a lesser extent, grains per spike and plant height were positively related to grain yield. Regarding cereal precocity, all barley cultivars showed a general grain yield increase with shade, but in wheat, only late cultivars positively stood out from the others. Breeding programs based on the studied plant traits are needed to identify the most suited cultivars, which is the next step to develop successful agroforestry systems. Nevertheless, further research is needed to assess the response of shade-adapted cultivars in actual agroforestry conditions, where the progressive and irregular pattern of shading interplays with other tree-crops interactions.
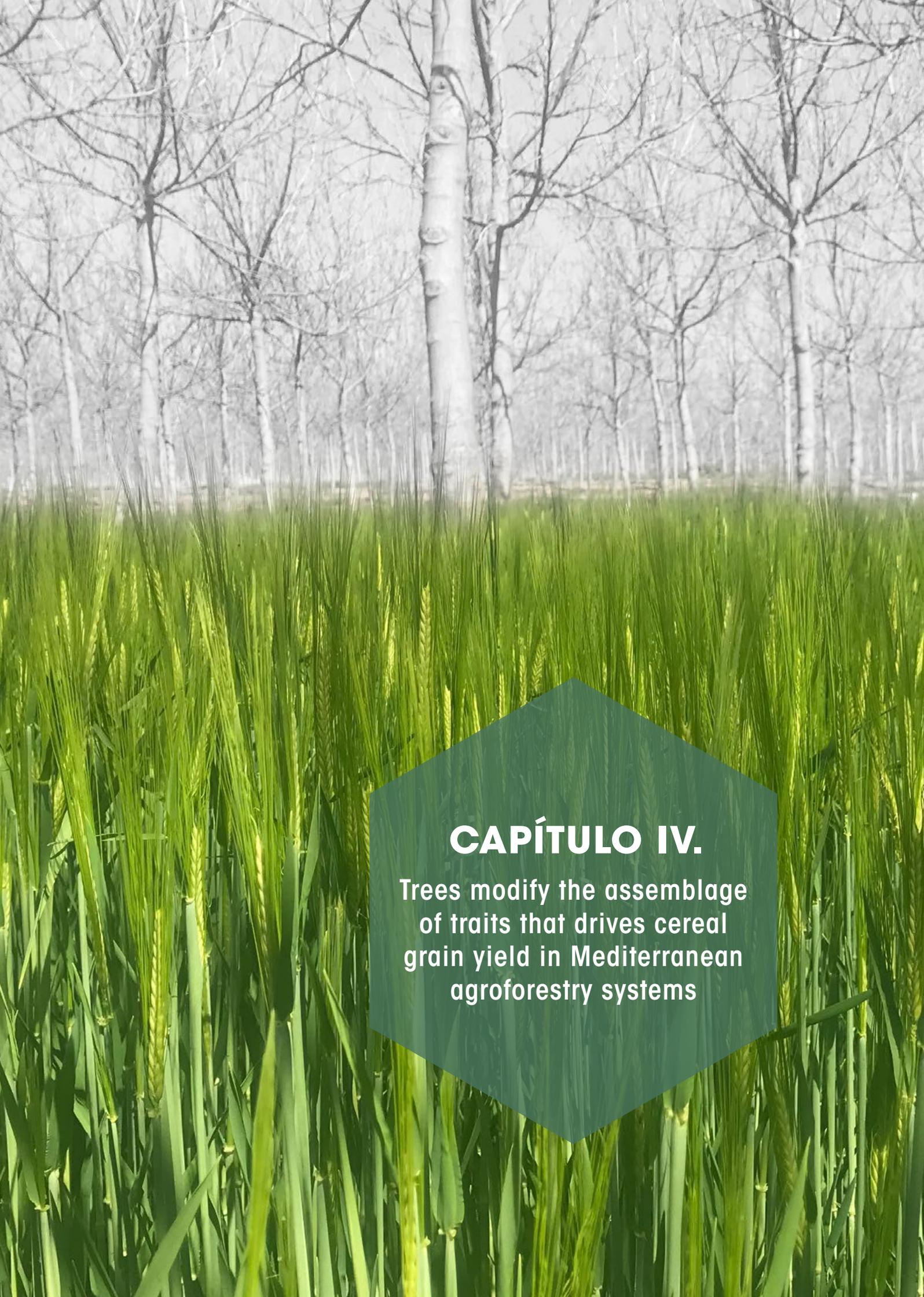
CAPÍTULO IV.

Trees modify the assemblage of traits that drives cereal grain yield in Mediterranean agroforestry systems

CAPÍTULO IV.

Trees modify the assemblage of traits that drives cereal grain yield in Mediterranean agroforestry systems

María Guadalupe Arenas-Corraliza, María Lourdes López-Díaz, Víctor Rolo, Yonatan Cáceres, Gerardo Moreno

INDEHESA Research Institute, University of Extremadura, Avenida Virgen del Puerto, 2. Plasencia, Cáceres 10600, Spain.

ABSTRACT

Climate change effects on crops will pose a major threat to the food supply worldwide. Agroforestry has been proposed as an effective approach to minimize its effects. However, to design sustainable and productive agroforestry systems, net responses of trees and crops need to be clarified, particularly in regions where competitive will outweigh facilitative interactions. The study of plant traits has become a useful approach to select best-adapted plants for specific conditions. In this experiment, we assess the response of walnut trees (*Juglans x intermedia Mj209xRa*) and shade-adapted cultivars of winter wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.), growing in an agroforestry system (AF), as compared to cereal monocrops (MC) and pure tree plantation (FO). Agroforestry reduced the light intercepted by crops by 58 %, buffered extreme temperatures on the crop canopy and increased air relative humidity, advancing plant development for wheat and barley. Major effects on crops were observed after walnut budburst. The presence of trees increased the relative water content (RWC), Photochemical Reflectance Index (PRI) and P content of both wheat and barley leaves, increased Normalized Difference Vegetation Index (NDVI) of barley leaves, and reduced leaf mass area (LMA) in wheat and cell membrane damage in both species. Among the negative effects, the agroforestry combination reduced plant growth, leaf area (LA), leaf area index (LAI) and grain yield in both wheat and barley, showing competition for N in the case of barley. Cereal plants did not affect tree growth, although competition for soil nutrients but not water was observed in tree leaves. Plant traits related to grain yield differed among agroforestry and open conditions in both species, showing for the first time that the selection of cereal cultivars could be based on these traits, along with the shade tolerance, to establish successful agroforestry systems.

Keywords: alley-cropping, silvoarable, cereal, shade-stress, phenology, plant traits.

INTRODUCTION

In the last decades, the rate of climate warming has been more intense in the Mediterranean basin than in other regions. The current mean temperature in this area has already increased by 1.4 ºC as compared to the last decades of the nineteenth century, with extreme events such as heatwaves and droughts becoming more frequent and intense (Cramer et al., 2018). On the global scale, climate change is a major threat to food production, with an estimated 6 % decrease for each ºC of further warming (Asseng, 2014). In addition, by 2050 it is estimated that the global population will reach 9 billion, which will almost double the food demand (FAO, 2009). Given that the cropland expansion has stagnated in recent years (Ausubel et al., 2013), in part because most arable land is already cultivated, meeting global food demands is an increasing global concern. Established intensive crops are more vulnerable than diversified systems, which has spurred the adoption of practices that may protect them against a changing climate (Lesk et al., 2016). Agroforestry has been proposed as a sustainable and climate resilient agriculture management, through the integration of trees and/or shrubs into crop/animal production, provides benefits at both aboveground and belowground components. Agroforestry has been shown to increase C sequestration, soil protection and wildlife habitat, to reduce greenhouse gases emissions and fertilization lixiviation and smooth extreme weather events for crops (Schoeneberger et al., 2012). The ameliorated microclimatic conditions provided by agroforestry, such as milder radiation and lower temperature and dryness, make it especially suitable for the southern areas of Europe (Mosquera-Losada et al., 2012).

Given the intense solar irradiance common in Mediterranean areas during spring, tree shade could protect plants against detrimental effects of excessive light such as photoinhibition (Jacobsen et al., 2012), but the protective effect may depend on cereal species and cultivars (Arenas-Corraliza et al., 2020). In a previous study of the same walnut-cereal agroforestry system combination, we found mixed positive and negative responses of crops, in part due to a cereal species and cultivars specific response (Arenas-Corraliza et al., 2018). Moreover, under similar climatological conditions, artificial shading was beneficial for most of the cereal cultivars in terms of grain yield (Arenas-Corraliza et al. 2019). However, negative effects of shade on cereals has been also reported in this region (Dufour et al., 2013; Inurreta-Aguirre et al., 2018), but they have been partly attributed to the traditional cereal selection for full light conditions (Vandeleur & Gill, 2004). This suggests that the net balance of positive/negative interactions in agroforestry systems strongly depends on the climate, the site and the plant trait considered.

The use of a trait-based approach has been increasingly adopted to understand plant functioning and interactions in agroecosystems (Garnier & Navas, 2012). Trait-based approaches along with key concepts from community ecology – namely niche differentiation, facilitation, competition – and ecophysiology such as phenology, light response curve and resource allocation, are of great interest to understand the relations between crops and trees in term of yield or other ecosystem functions (Allan et al., 2015; Brooker et al., 2014; Martin & Isaac, 2015) and are becoming very useful in the search of crop species and cultivars that perform better under agroforestry conditions (Arenas-Corraliza et al., 2020; Wood et al., 2015). For instance, by studying the phenology of cereals and trees, the importance of the precocity of the cereals respect to tree budburst may be assessed. Morphological traits such as leaf area (LA), leaf area index (LAI) and, in particular, leaf mass area (LMA) can be used to describe environmental acclimations to shading environments (Poorter et al., 2009). Regarding physiological parameters, the relative water content (RWC) has been suggested as one of the most relevant indicator of plant water status (Keyvan, 2010; Hasanuzzaman et al., 2019), and is envisaged as one of the main traits in cereal breeding programs for Mediterranean conditions. Furthermore, RWC is directly linked to chlorophyll and carotenoids content in wheat (Keyvan, 2010) and barley (Kaczmarek et al., 2017). In relation with drought stress, electrolyte leakage (EL) is considered as a promising early indicator of cell membrane injury (Bajji et al., 2002; Bodner et al., 2015). Progress in plant functioning researhc has benefited from the recent advances in remote and proximal sensing (Tattaris et al., 2016). For instance, Normalized Difference Vegetation Index (NDVI) and Photochemical Reflectance Index (PRI) are highly related to the chlorophyll content (Gamon et al., 1992) and the carotenoid pigments (Sellers, 2007). Finally, the nutritional status of the cereal plants and trees can provide information on the net balance of tree-crops interactions.

The aim of this study was to assess how the assemblage of plant traits is altered by the presence of trees in agroforestry combinations and to what extent grain yield is mediated by modifications of cereal plant traits (Fig. 1). The ultimate objective was to explore how different functional traits could contribute to the breeding programs to select more suitable cereal cultivars for agroforestry cropping conditions.

Figure 1. Cereal (wheat and barley species) cultivation in agroforestry system (left) and monocrops conditions (right) in the south-Mediterranean area (central Spain).

Based on the previous studies mentioned, our hypotheses were:

1. Trees modifies crop microclimate, buffering excessive light availability and extreme temperatures common in the Mediterranean area.

2. The agroforestry conditions help cereal plants to improve their water status through a less stressful environment and to increase nutrient availability by soil nutrient mobilization.

3. Cereal morphological, physiological and phenological traits are altered by the presence of trees, which ultimately affects grain yield. Barley can benefit more from being in combination with trees than wheat, as shown in previous studies.

4. Tree growth can be reduced in the agroforestry system because of cereal competition for soil resources.

MATERIAL AND METHODS

Study site

The experiment was carried out during the 2017-2018 growing season (November-June) in a hybrid walnut plantation located in Toledo province in central-western Spain (39°50'N. 4°28'W, 411 m a.s.l.). The climate is Continental Mediterranean, the average mean annual temperature is 15.2°C, and the averages of maximum and minimum temperatures are 35°C and 0.7°C respectively. The total solar radiation is 6406 MJ m^{-2} year^{-1}. The rainfall mostly occurs in the winter season, being the annual average 439 mm. During the experiment, spring rainfall was well above the long-term average (Fig. A1). The soil of the study site is a Fluvisol with a silt loam texture and a slightly alkaline pH in the upper 30 cm layer (pH 7.4 in water) (Table A1).

Previous to the hybrid walnut plantation, the land had been used for cereal crops. In 2004, part of the land (45 ha) was planted with the clone Nat7 of hybrid walnut *Juglans x intermedia Mj209xRa*, resulting from *Juglans major Torr. var. 209* with *Juglans regia L.* Trees were placed 6 m between-row and 5 m within-row spacing (density of 333 trees ha^{-1}). During the summer, trees were irrigated with a drip irrigation system at a rate of 2000 m^3 ha^{-1} that also applied a fertilization of 40 kg N ha^{-1}, 17.5 kg P ha^{-1} and 41.5 kg K ha^{-1}. Previous to our experiment, tree rows were treated with herbicides and alleys were ploughed to control weeds. At the moment of the experiment (autumn 2017), the hybrid walnuts were 13 years old and tree height and diameter at breast height (DBH) means and standard errors were 11.7 ± 0.08 m and 18.5 ± 0.09 cm, respectively, being the canopy closure almost complete.

Experimental design

The experimental design included the following systems: cereals intercropped with trees (Agroforestry, AF), cereals grown in open field (Monocrops, MC) and tree plantation without cereals (Forestry, FO). Monocrops were located in the unplanted area of the farm, next to the walnut plantation. Three shade-adapted cultivars of two cereal species, wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.), were selected through a previously carried out artificial shading experiment in which the response of cultivars widely used in the region to shade was studied (Arenas-Corraliza et al., 2019). Wheat cultivars were Nudel (W1), (Paledor) (W2) and Solehio (W3) and barley cultivars Lagalia (B1), Carolina (B2) and Meseta (B3).

For the AF system, six replications/plots of 80 m^2 (20 m long x 4 m wide, spaced 1 m apart and including 4 trees in each plot) were cultivated for each wheat and barley cultivar in the alleys.

To study the effect of cereal species and cultivars on trees, replications were paired, so target trees had the same cultivar at both sides (alleys). Thus, for each cultivar, AF included 6 cultivated plots grouped in three blocks, and 12 trees grouped in three lines. For the MC system, six replications/plots of 9 m² (3 m long x 3 m wide, spaced 1 m apart) for each cultivar were randomly assigned in the area without trees. The FO system was placed next to the AF, (spaced 5 trees in the row from the AF) and comprised 3 plots of 25 trees in each plot.

The sowing was done by hand spreading on 13th November 2017, when soil humidity was adequate for seeding. The sowing rate was 180 kg ha^{-1} for barley and 220 kg ha^{-1} for wheat. Before sowing, all cereal plots were fertilized with 54 kg ha^{-1} N, 47 kg ha^{-1} P and 134 kg ha^{-1} K. On March 7th, in coincidence with cereal tillering, 46 kg ha^{-1} N was applied as urea 46 %.

Microclimatic conditions

To record the microclimatic effect of the trees in the crop, solar radiation, air temperature and relative humidity were registered from walnut budburst (cereal at booting/anthesis stage) to cereal ripening in both AF and MC systems. Data were recorded every hour using a climatological data logger (PCE-H71N, PCE Instruments, Holding GmbH Inc., Hamburg, 106 Germany) as well as a solar radiation data logger (UA-002-64 HOBO Pendant temp/light, Onset Computer Corporation, Bourne, Massachusetts 02532, USA). Sensors were installed on 8 March at 1.5 m above the ground (cereal canopy level), placed randomly in the AF (five points) and MC (two points) systems, avoiding the borders. Hand-made shields were used to protect temperature and relative humidity sensors of direct solar radiation and rainfall. Since walnut budburst took place by 28 April, microclimatic data was separated in two periods: before (from 8 March to 27 April) and after tree budburst (28 April to 21 June).

Plant and soil measurements

Phenology stage was assessed for cereals, according to the Zadoks scale (Zadoks et al., 1974). Measurements started on 16 April, before walnut budburst (by 28 April). At that time, barley plants were between stem elongation (Z.30-39) and booting (Z.40-49) stages and some wheat plants had reached heading stage (Z.50-59). From this moment on, cereal phenology was recorded once a week approx., covering the stages of flowering/anthesis (Z.60-69), grain milk (Z.70-79) and dough (Z.80-89) development, and ripening (Z.90). Phenology was measured in five tillers per plot in the AF and in three tillers per plot in the MC. Tillers were randomly selected over the plot, avoiding the borders (as done in the rest of measurements). Dry matter of the same tillers was measured to assess the evolution of plant biomass during the same period.

Cereal leaf Area Index (LAI) was measured before (23 April) and after (16 May) the walnut budburst (28 April), with a ceptometer (Accupar LP-80, Meter Group, 81379 Munich, Germany) placed at one third of the cereal total height and in four different points in each plot. In the same dates, morphological traits: Leaf Area (LA, cm^2) and Leaf Mass Area (LMA; g cm^{-2}) were measured in five different flag leaves of wheat and second leaves of barley (since barley flag leaf do not allow measurements) randomly selected in each plot.

The same leaves were used to measure physiological traits such as Relative Water Content (RWC) according to Barrs and Weatherley (1962). On 16 May, two vegetation indexes, NDVI and PRI, were measured at leaf level as proxies of chlorophyll content and the carotenoid pigments, respectively. Measurements were performed with the LabSpec-4 Hi-Res spectrometer and the Plant Probe accessory (ASD Inc., Malvern Panalytical Ltd., WR14-1XZ Malvern, United Kingdom), in six cereal flag leaves (second leaves in barley) in each plot. In addition, on 22 May, cell membrane damage in cereal leaves was indirectly evaluated by the electrolyte leakage, as a stress indicator, following the protocol proposed by Bajji et al. (2002). Lastly, on cereal tillers harvested in the same day (22 May), N, P and K content were analyzed. N content was analyzed by the Dumas method (ISO 16634-1:2008), P by continuous segmented flow analysis (ISO15681-2:2003) and K by atomic absorption spectrometry (ISO 9964-2:1993).

Once cereals reached the ripening stage (18 July), three samples per plot were harvested in 50 x 50 cm squares using hand clippers. Samples were dried until constant weight and total aerial biomass, number of spikes, number of grains per spike, weight of 1000 grains and grain N content (Dumas method) were measured.

Concerning trees, DBH and height was measured with a diameter tape and a clinometer, respectively, in the dormant period (February) of two consecutive years (one growing season, with cereal intercrop). Walnut LAI was measured periodically from 23 April, before budburst, until crop harvesting. On 4 July, when walnut leaves were already fully expanded, one shoot located in the middle of the crown of 6 trees (two central trees of each block) were sampled using telescopic shears. All leaves of the shoot were later dried at 60°C until constant weight, and N, P and K were determined following the same methods than for cereal plants. On 25 July and 21 August, tree water stress was assessed at predawn and midday by measuring leaf water potential with a *Scholander Chamber* (Model 100 Pressure Chamber, PMS Instrument Company, 97322 Oregon, USA) in one random leaf of a shoot in the middle of the crown in 6 trees per cultivar (two central trees of each block).

Ion exchange resins were installed in the topsoil layer (5-10 cm) of the center of each plot from 23 April to 28 June, and then extracted with HCl 0.5M to analyze mineral N (nitrate and

ammonium), phosphate and potassium. Additionally, soil samples up to 30 cm were taken on 25 April to determine the mineral N after the extraction with a KCl 1M solution. Continuous segmented flow analysis was used to determine nitrate and ammonium (ISO 14256-2:2005(en) and phosphate (ISO15681-2:2003). K was determined by atomic absorption spectrometry (ISO 9964-2:1993).

Data analysis

One-way ANOVAs were used to compare soil nutrients (N, P and K in soil and resin extracts) of wheat and barley intercrops (AF-Wheat, AF-Barley), monocrop (MC) and pure tree plantation (FO). Daily curves of light availability, air temperature and air relative humidity in AF and MC were compared by mean of one-way ANOVAs, performed every hour.

Crop phenology (Zadoks stages) and plant biomass of AF and MC were also compared by one-way ANOVAs done for each species in each sampling date. All cultivars of each species were grouped after checking the lack of differences among them. Concerning the morphological, physiological and nutritional traits of cereal plants (LAI, LA, LMA, NDVI, PRI, RWC, Electrolyte leakage, and N, P and K content) and yield parameters (biomass, number of spikes, number of grains per spike, weight of 1000 grains, grain yield and grain nitrogen content), general linear models (GLM) were performed including system, species and cultivar (nested in species), and their interactions as independent variables. For parameters measured in different dates, separate GLMs were performed by date.

Concerning tree parameters, to compare stem diameter increment and N, P and K leaf content among trees intercropped with wheat and barley (AF-Wheat, AF-Barley, respectively) and trees in plantation (FO), we used one-way ANOVAs. For tree leaf water potential, two-way ANOVAs were used including time (predawn vs midday) as a second factor.

When significant effects were found, least square difference test (LSD) was done for pair-wise comparisons. ANOVAs were performed by Statistica software (StatSoft Inc., Maison-Alfort, France).

Structural equation models (SEM) were fit for each wheat and barley species in monocrops and agroforestry conditions separately to assess direct and indirect relationships betweem plant traits and grain yield. Parameters were grouped for each category, phenological (phenology before and after walnut budburst), morphological (LMA, LAI and LA after walnut budburst), physiological (RWC, NDVI, PRI, electrolyte leakage after the walnut budburst) nutritional (plant N, P and K content, ratio N/P after the walnut budburst) and productive (biomass yield, number

of spikes, number of grains per spike, weight of 1000 grains, grain yield and N grain content), and all plausible interactions with biological sense were tested in a stepwise procedure to obtain the most parsimonious SEM model. Biomass and phenology before and after walnut budburst were calculated as the average value resulting from the two dates of measurement before and after walnut budburst separately. Shipley's test of d-separation was used to assess the fit of each model and was accepter when the χ2-test of Fisher's C statistic was higher than p = 0.05. These analyses were performed using piecewiseSEM package (Lefcheck, 2016) in R, version 4.0.2. (R Core Team, 2020).

RESULTS

Tree influence on microclimate

After leaf budburst, tree presence reduced the radiation received by cereal plants (mean light reduction of 58.26 %), especially near midday (Fig. 2). Before tree budburst, the pattern was similar but less marked. After leaf budburst, trees also buffered air temperature and relative humidity beneath them, notably decreasing the temperature during the day (mean temperature difference -3.25 °C) and slightly increasing it during the night (mean temperature difference of +1.77 °C). The pattern was the opposite for relative humidity, with +8.48 % during the day and -7.25 % during the night. On very hot days, the maximum temperature decreased beneath the trees up to 13.97 °C. After the walnut budburst (28 April to 21 June), light, air temperature, and relative humidity were remarkably buffered in the AF system in comparison with the period before tree budburst (Fig. A2). After walnut budburst, both the AF and the MC systems exceeded 25°C from 7 to 18 h on average, being the mean value 29.50 °C and 25.73 °C in MC and AF, respectively.
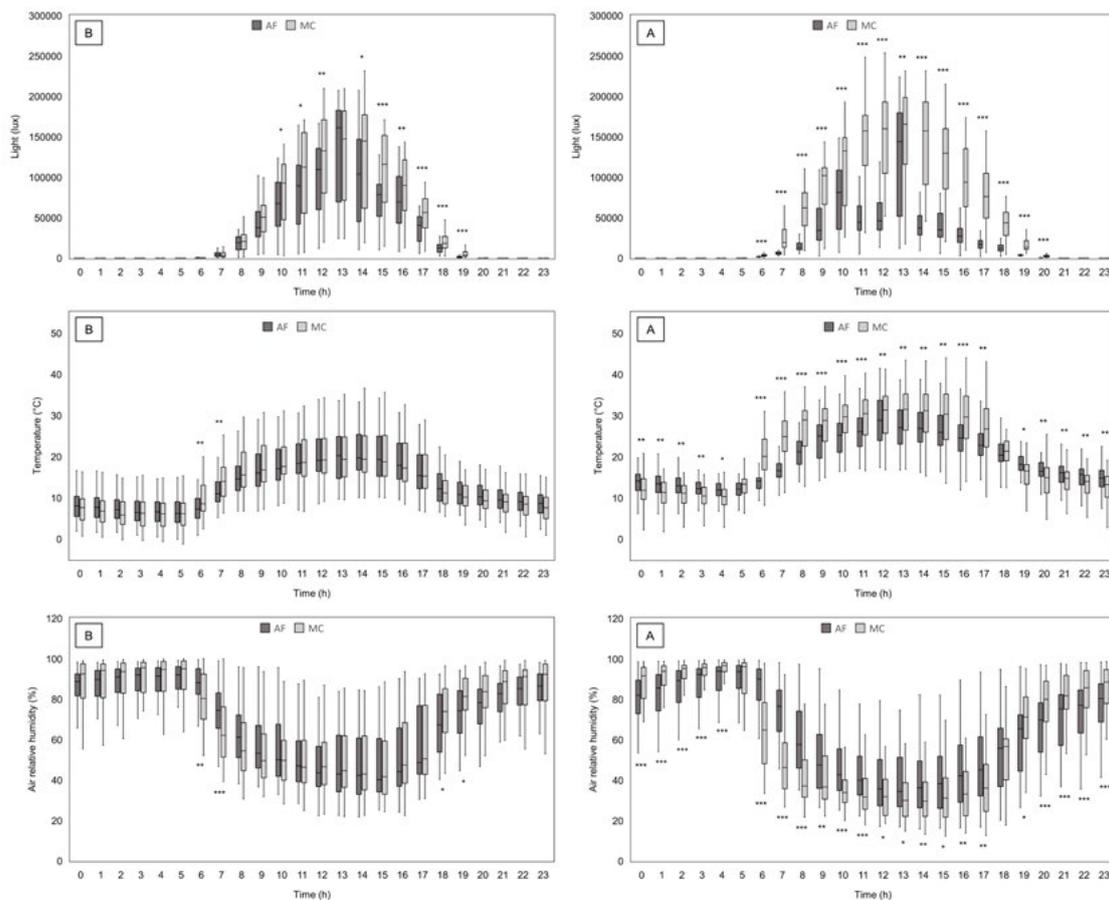
Figure 2. Boxplot of light (lux), temperature (°C) and air relative humidity (%) in the Agroforestry (AF) and Monocrops (MC) systems in the before (B) and after (A) tree budburst continuous periods. Significance level: * p < 0.05; ** p < 0.001; *** p < 0.001.

Soil nutrient availability

Soil analysis before walnut budburst and when cereal species were during booting and anthesis stages, revealed a lower mineral N in the AF compared with the MC, with intermediate values for the FO system (Table A2). After budburst, ion exchange resins showed that, on average, there were no differences in the availability of mineral N or K among systems, but a significantly higher P availability in AF and FO systems than in MC. When considering cereal plots, barley mineral N was significantly lower in AF than in MC, both in soil sample (pre-anthesis period) and ion exchange resins (grain filling period), while no difference was found for wheat (Table A2).

Cereal development

By early April, before tree budburst, wheat and barley were around the booting stage (Z.40) in the MC system, being in the AF system significantly more advanced (p<0.001), especially in barley, which had already reached the inflorescence emergence stage (Z.50) (Fig. 3). Differences were maintained, even increased (for wheat) until 2-3 weeks after the walnut budburst (28 April, 4 and 16 May). From this moment on, differences started to fade out, and when walnut leaf expansion ended (by early June), the difference had almost disappeared. At that time, wheat was at the stages of late milk (Z.77-79) and barley in the last stages (soft dough; around Z.85) in both systems. Grain ripening was reached at the same dates in both systems (wheat ending its cycle later than barley).
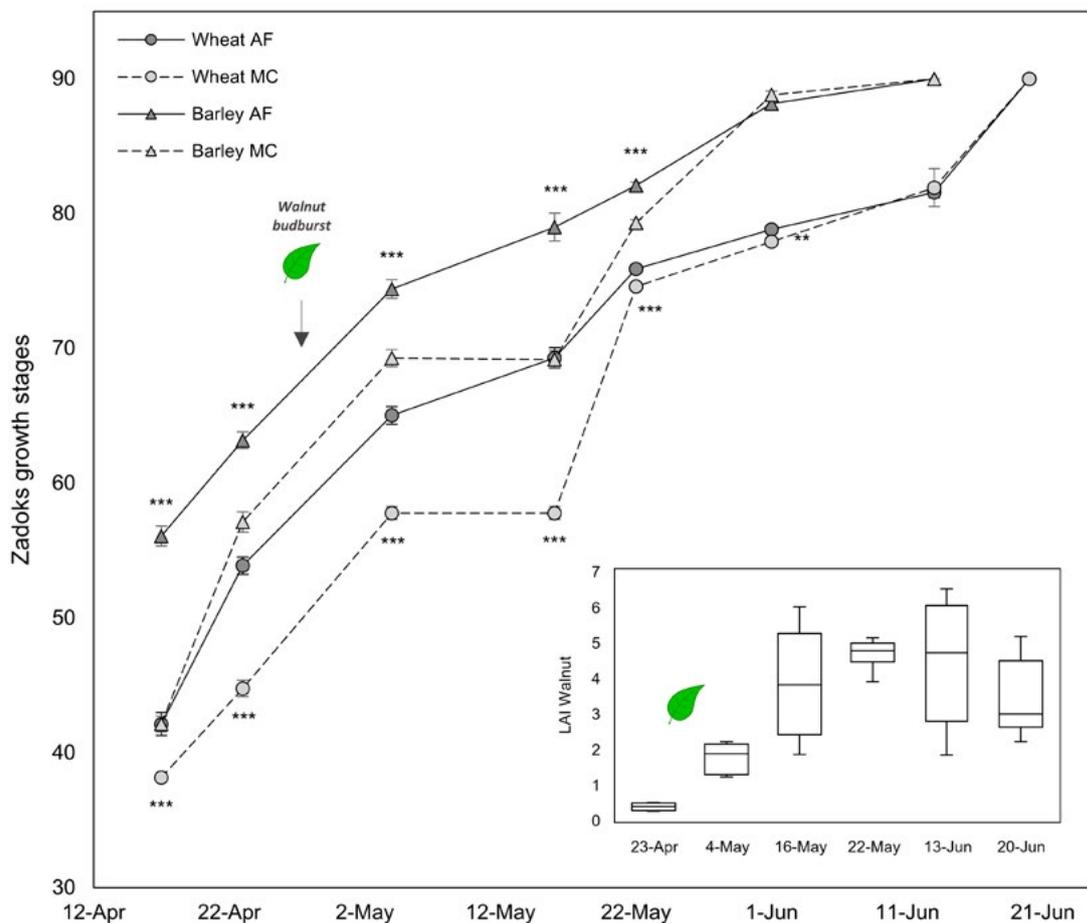
Figure 3. Zadoks growth stages (± S.E.) of wheat and barley at different sample dates in the Agroforestry (AF) and Monocrops (MC) systems studied. Walnut LAI index of the tree leaf development is shown in the boxplot of the right-bottom corner. Significance level: ** p < 0.01; *** p < 0.001.

Regarding cereal plant biomass, the results showed three stages. Firstly, during the spring until mid-April, before walnut budburst, plant biomass was significantly higher in the AF system compared to the MC, specially in wheat (Fig. A3). Secondly, from mid-April to mid-May, which is the walnut sprout beginning, plant biomass tended to be similar in both systems. Thirdly, from mid-May on, when walnut leaves are fully expanded, cereal plant biomass was reduced in the AF system compared to the MC, particularly in wheat, but showing barely the same trend.

Morphological, physiological and nutritional traits of cereal plants

The influence of trees on cereals was dependent on the trait considered for each species (Fig. 4 and A4) and cultivars (Table A3). LMA significantly decreased for wheat in AF compared to MC system after the walnut budburst. Similarly, all wheat cultivars revealed a significant LMA decrease in AF compared to MC system, while none of barley cultivars showed any difference between systems. LAI was consistently lower in AF as compared to MC system (p<0.001), before and after the walnut budburst, in both wheat and barley species, ant at cultivar level. LA was significantly lower in the AF compared to the MC system, before and after the walnut budburst, for both wheat (p< 0.05) and barley (p<0.001), being the reduction especially remarkable for barley cultivars before walnut sprout.
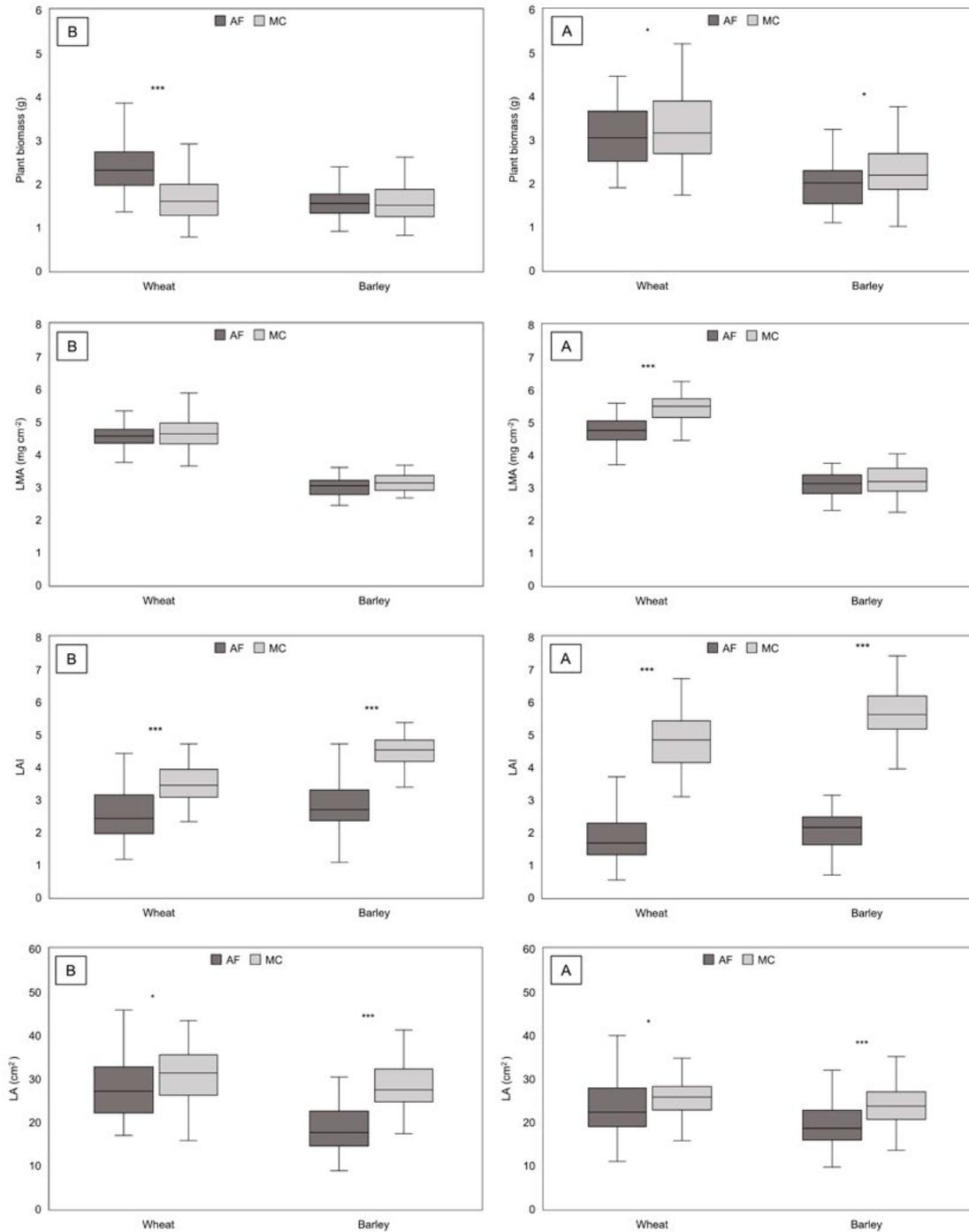
Figure 4. Boxplot of the cereal morphological traits plant biomass, Leaf Mass Area (LMA), Leaf Area Index (LAI) and Leaf Area (LA) , of wheat and barley in the Agroforestry (AF) and Monocrops (MC) systems in two sample dates: before (B) and after (A) tree budburst. For all parameters the date before was April 23rd and the date after was always May 16th, except from the plant biomass which was May 22nd for being more representative of the cereal biomass after tree budburst. Significance level: * p < 0.05; *** p < 0.001.

The AF system significantly increased cereal RWC compared to the MC system (Table A3). For wheat, it increased from 55% to 62% and for barley, from 39% to 54% in the MC and the AF system respectively. However, while all barley cultivars (B1, B2 and B3) revealed a significant increase of RWC in the AF system, none of wheat cultivars showed any significant difference. Concerning cell membrane damage, the AF system significantly decreased ($p<0.001$) electrolyte leakage for both wheat and barley. This trend was also confirmed for all cultivars, especially for W2, B1 and B3. With regard to vegetation indexes, NDVI values were significantly higher ($p < 0.001$) in the AF system compared to the MC system for barley, showing cultivars W1 and B3 the highest response. PRI values reveled greater differences between the AF and the MC systems in both cereal species ($p<0.001$) than NDVI, being significantly higher in the AF system in most cultivars (W1, W3, B1 and B3).

Plant N content was higher in the MC system compared with AF, both for wheat and barley ($p<0.01$), particularly for cultivars W3 and B2 (Table A3). Conversely, P content showed the opposite trend, being significantly higher ($p<0.001$) in the AF system for both cereal species, which was also confirmed in all cultivars. As a result, N/P ratios were much higher in the MC system than in the AF system, for wheat and barley species and cultivars ($P < 0.001$). No differences were found in K content between the systems in wheat and barley, although W3 and B1 cultivars revealed a slightly lower content in AF.

Cereal yield

In general, the AF system reduced cereal yield compare to full light conditions (Table 1). The AF system decreased cereal biomass and grain yield compared to MC in all wheat and barley cultivars ($p<0.001$), being the B3 barley cultivar less negatively affected by the trees than the others ($p=0.02$). With regard to the yield components, in general, the numer of spikes of wheat was not affected by trees (although the W1 cultivar had a 19% lower number of spikes in the AF than in MC). However, the numer of spikes of barley was affected by trees, being significantly lower in the AF system than in the MC ($p<0.001$), especially the B1 and B2 cultivars (14% and 33% reduction, respectively). There was a remarkable decrease of the number of grains per spike in the AF system in all wheat cultivars ($p<0.001$), being less evident for barley, showing only the B3 cultivar a significant reduction, ($p=0.02$). Similarly, the weight of 1000 grains was significantly lower for wheat in the AF system compared to MC (20% lower), which was also revealed for all wheat cultivars. No difference in grain weight between systems was found for barley , although B1 and B2 cultivars showed a significant decrease in the AF system (9 % decrease on average). In relation to wheat grain N content, although it was not significantly affected by trees at species level, there was a slight increase in the AF system for the W1 cultivar ($p=0.03$). On the contrary,

barley showed a significant 13% decrease of grain N content in the AF system compared to MC, which was also revealed by B1 and B3 cultivars (p<0.001).

Table 1. Yield parameters (biomass and grain yield, number of spikes, number of grains per spike and weight of 1000 grains and grain N content) of wheat and barley species and cultivars (W1, W2 and W3 for wheat) and (B1, B2 and B3 for barley) in the Agroforestry (AF) and the Monocrops (MC) systems studied. Data represents means ± S.E. Significante level: * p < 0.05; *** p < 0.001.

		System	Biomass yield (Mg ha⁻¹)	Grain yield (Mg ha⁻¹)	Number of spikes (spikes m⁻²)	Number of grains per spike	Weight of 1000 grains (g)	% grain N
Wheat	W1	AF	12.9 ± 0.6 ***	4.2 ± 0.3 ***	667.3 ± 26.7 *	29.3 ± 0.9 ***	20.9 ± 0.83 *	2.9 ± 0.1 *
		MC	21.2 ± 0.8	6.8 ± 0.3	825.9 ± 24.3	34.2 ± 1.1	24.1 ± 0.6	2.7 ± 0.1
	W2	AF	11.7 ± 0.3 ***	3.7 ± 0.3 ***	613.6 ± 47.6	26.8 ± 1.2 ***	22.7 ± 0.9 ***	2.6 ± 0.1
		MC	19.3 ± 1.0	6.3 ± 0.4	568.7 ± 27.2	39.5 ± 1.2	28.1 ± 1.0	2.5 ± 0.1
	W3	AF	11.6 ± 0.4 ***	3.5 ± 0.3 ***	504.9 ± 33.7	27.3 ± 1.4 ***	25.9 ± 1.2 ***	2.6 ± 0.1
		MC	21.2 ± 1.0	6.7 ± 0.5	616.9 ± 34.8	33.0 ± 0.8	33.9 ± 1.2	2.5 ± 0.0
	Mean	AF	12.1 ± 0.3 ***	3.8 ± 0.2 ***	595.6 ± 23.2	27.8 ± 0.7 ***	23.1 ± 0.6 ***	2.7 ± 0.1
		MC	20.5 ± 0.6	6.6 ± 0.2	667.5 ± 22.6	35.6 ± 0.7	28.8 ± 0.8	2.6 ± 0.0
Barley	B1	AF	14.0 ± 0.7 ***	5.7 ± 0.4 ***	885.1 ± 54.4 *	20.7 ± 0.5	31.5 ± 0.9 *	2.1 ± 0.1 ***
		MC	22.2 ± 1.3	7.8 ± 0.5	1034.8 ± 65.0	22.0 ± 0.5	34.7 ± 1.1	2.4 ± 0.0
	B2	AF	14.7 ± 0.5 ***	4.9 ± 0.3 ***	684.7 ± 22.1 ***	20.9 ± 0.5	34.5 ± 1.2 *	2.2 ± 0.1
		MC	24.7 ± 1.0	8.3 ± 0.7	1014.1 ± 59.3	21.5 ± 0.5	37.5 ± 1.4	2.4 ± 0.0
	B3	AF	14.1 ± 0.7 ***	5.9 ± 0.4 *	1048.8 ± 22.1	18.8 ± 0.6 *	29.8 ± 0.9	2.1 ± 0.1 ***
		MC	23.4 ± 1.0	7.3 ± 0.6	1148.0 ± 79.7	21.6 ± 0.6	28.7 ± 1.2	2.4 ± 0.0
	Mean	AF	14.3 ± 0.3 ***	5.5 ± 0.2 ***	869.6 ± 33.9 ***	20.2 ± 0.3 *	32.0 ± 0.6	2.1 ± 0.0 ***
		MC	23.4 ± 0.7	7.8 ± 0.4	1067.7 ± 40.1	21.7 ± 0.3	33.5 ± 0.9	2.4 ± 0.0

Relationship between plant traits and cereal yield

The parameters retained in the SEM varied among species and systems (Fig. 5), showing a better fit and explained more grain yield variability in MC than AF models.

For wheat in the agroforestry system, the model explained 66 % and 22 % of grain yield and N grain content respectively. Grain yield related positively with the number of spikes and the grain weight, and to a lesser extent with plant K content and grain N content. Biomass before tree budburst related negatively with the number of spikes, and positively with grain weight but the relationship was marginally significant. LAI and biomass after tree budburst showed an indirect positive effect on grain yield via grain weight. Finally, N grain content, which was negative affected by biomass after tree budburst, related negatively with grain weight and positively with grain yield.

The model was also robust for wheat cultivated in the open field (P=0.800), explaining 74 % of the variability in grain yield, which was mostly determined again by the number of spikes and the grain weight. Nevertheless, the assemblage of variable retained varied respect to the agroforestry conditions. Here plant P instead K related positively with gran yield. Phenology and stress (electrolyte leakage) were important for the number of spikes. Contrary to agroforestry, the relationship between grain yield and N grain content became negative.

Concerning barley in the agroforestry system, the model explained 81 % of the variability of grain yield, which was again highly correlated with the number of spikes and the grain weight. The number of spikes was positively affected by PRI and phenology before tree budburst, and negatively by NDVI. The grain weight was positively affected by plant P content and negatively affected plant K content and PRI. Although marginally, LAI related negatively with both the number of spikes and grain weight. The most noticeable variations in the open field model were the positive effect of LAI on grain yield and the biomass on grain weight, and the negative effect of phenology on grain weight.
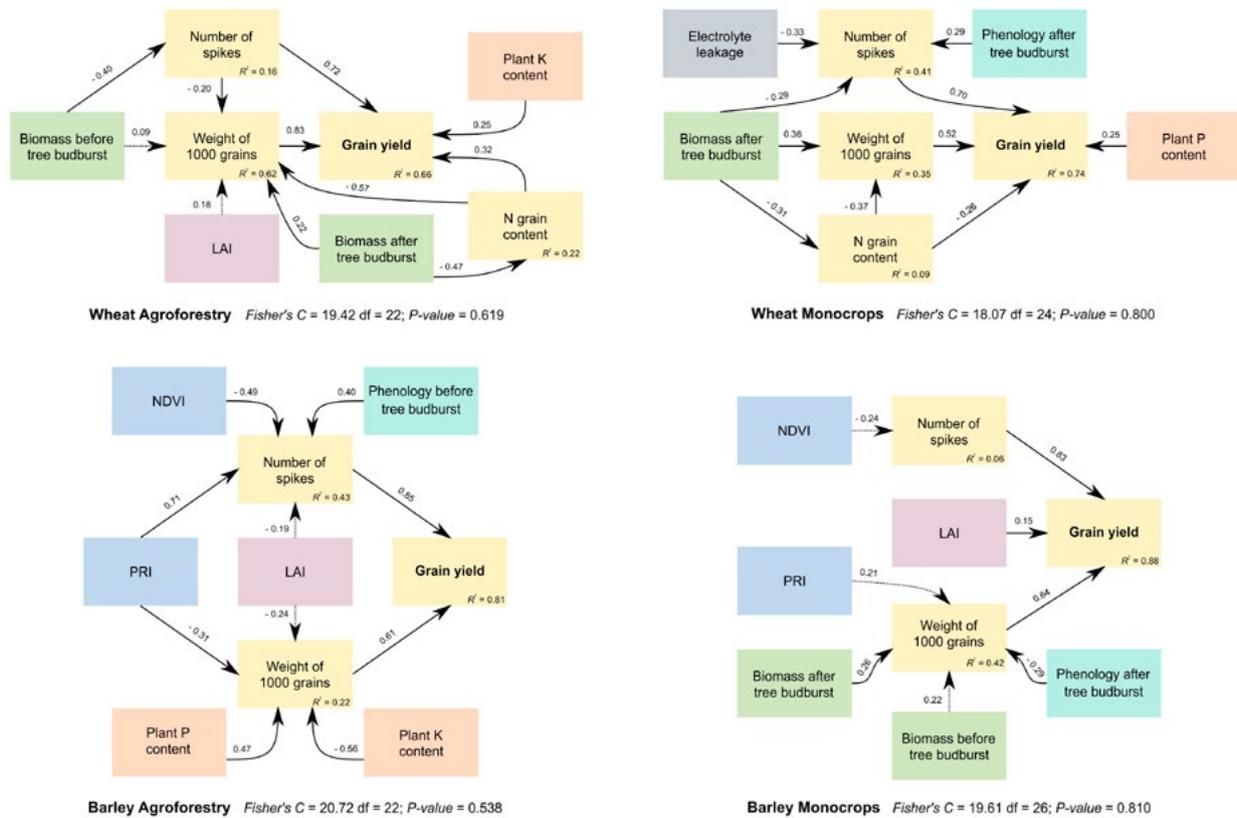
Figure 5. Different SEM done for each wheat and barley species in the Agroforestry and Monocrops systems showing the direct and indirect impacts of morphological (LA, biomass before and after walnut budburst), physiological (NDVI, PRI, electrolyte leakage), phenological (phenology before and after walnut budburst), and nutritional parameters (plant N, P and K content) on yield components (biomass yield, number of spikes, number of grains per spike, weight of 1000 grains, grain yield and N grain content). Only significant paths are shown, apart from dotted lines that show marginally significant effects (0.05 < p-value < 0.10). The headed arrows showed the direction of causality. Numbers besides the lines are standardized path coefficients.

Tree growth and performance

The cereal crop did not affect significantly tree growth (diameter increment; Table 2) as compared to the pure tree plantation. However, AF significantly reduced N, P and K tree leaf contents compared to the FO system (Table 2). N content was approx. 10% lower in AF than in FO for both cereal species. The decrease of P content was especially remarkable in AF-barley (22% lower), while the decrease of K was more evident in AF-wheat (21% lower) in comparison to pure tree plantation.

Table 2. Tree parameters of diameter growth ad N, P and K leaf content. Data represents means ± S.E. Different letters indicate significant differences between systems.

System	Diameter growth (cm)	mg N g leaf^{-1}	mg P g leaf^{-1}	mg K g leaf^{-1}
AF –Wheat	1.0 ± 0.1	28.0 ± 0.4 **b**	1.6 ± 0.0 **b**	18.7 ± 0.5 **c**
AF- Barley	1.1 ± 0.1	27.5 ± 0.4 **b**	1.4 ± 0.0 **c**	20.0 ± 0.3 **b**
FO	1.2 ± 0.1	30.8 ± 1.3 **a**	1.8 ± 0.0 **a**	23.8 ± 0.2 **a**

Concerning tree leaf water potential, on July (one month after cereal harvest), trees in the AF system, both with wheat and barley, revealed a more negative leaf water potential than in the FO system at midday (Table 3). One month later (August), trees in the AF system, both with wheat and barley, showed a less negative leaf water potential than the FO system, both at predawn and at midday.

Table 3. Tree leaf water potential (bar ± S.E.) of trees intercropped with wheat (AF – Wheat) and barley (AF – Barley) and in the sole forestry plantation (FO) at difference hours in the day in two different dates. Different letters indicate significant differences between systems.

Date		Hour	Leaf water potential (bar)		
			AF - Wheat	AF - Barley	FO
25-Jul	Sunrise	06:00 – 07:00	- 5.4 ± 0.3	- 5.3 ± 0.2	- 4.4 ± 0.3
		07:00 – 08:00	- 5.3 ± 0.1	- 4.7 ± 0.1	- 5.8 ± 0.3
	Midday	12:00 – 13:00	- 14.9 ± 0.5 **a**	- 15.5 ± 0.61 **a**	- 11.7 ± 0.6 **b**
		13:00 – 14:00	- 14.6 ± 0.4 **a**	- 14.3 ± 0.4 **a**	- 12.1 ± 0.3 **b**
21-Aug	Sunrise	07:00 – 08:00	- 6.0 ± 0.4 **ab**	- 5.9 ± 0.3 **b**	- 7.4 ± 0.3 **a**
		08:00 – 09:00	- 6.1 ± 0.4 **b**	- 5.1 ± 0.5 **b**	- 8.2 ± 0.2 **a**
	Midday	11:00 – 12:00	- 14.0 ± 0.6	- 13.6 ± 0.9	- 13.0 ± 0.4
		12:00 – 13:00	- 12.2 ± 0.9 **b**	- 12.6 ± 1.3 **b**	- 16.1 ± 0.3 **a**

DISCUSSION

Trees smoothed the microclimate experienced by crops

Trees affect the microclimate beneath them, reducing extreme weather conditions experienced by understory plants in agroforestry systems (Karvatte et al., 2020), which can benefit physiological processes of crop plants. Trees buffered the daily variation in air relative humidity beneath them, increasing it during the day and decreasing it during the night, compared to open conditions, in accordance with Lin (2007). Trees also decreased air temperature during the day and increased it during the night, as shown in previous studies in Mediterranean conditions in similar agroforestry systems (Inurreta-Aguirre et al., 2018; Serrano et al., 2017). The buffering effect was approximately two times more intense in our site than that reported in Serrano et al. (2017) and Inurreta-Aguirre et al. (2018), and in line with results reported for Iberian dehesa trees in CW Spain (Moreno et al., 2007). The differences in solar irradiance (https://solargis.info/) and temperature range among studies may drive the different buffering potential of trees among studies. This accords with Kanzler et al. (2018), whose study revealed that the higher the air temperature, the stronger the buffer effect of trees.

It is known that the milder microclimatic conditions under trees could reduce the water demand of crops in agroforestry systems compared to the open fields during the spring-summer period in Mediterranean conditions (Dupraz & Liagre, 2011), which could limit crop transpiration and increase water use efficiency. Furthermore, the presence of trees reduces wind speed and soil evaporation in the agroforestry systems compared to the open conditions, which can lead to a higher soil water content available for the crops in the tree alleys (Lin, 2007; Quinkenstein et al., 2009). This has been also reported for Mediterranean silvopastoral systems, such as Iberian dehesas (Joffre & Rambal, 1993), and it is viewed of remarkable interest to face the climatic change scenario foreseen for Mediterranean region (Vicente-Serrano et al., 2014).

Nevertheless, the improved microclimatic conditions and reduced transpiration rate in the agroforestry systems may not neccesarilly translate into an increased crop yield, as is the case of our study. Even when crop yield was increased, Kanzler et al. (2018) could not find a direct relationship between climatological conditions beneath the trees and wheat grain yield in the agroforestry system. Indeed, trees can compete with crops for the available water. In alley cropping systems, as the study case, while some authors show that competitive use of water exceeded the microclimatic improvement and ultimately reduced crop yield (Jose et al., 2000), others show rather the contrary and trees and crops do not compete for water. The lack of competition results

from exploring different soil layers (spatial complementarity) because of the reduction of the crop root length in the proximity of the tree row (Livesley et al., 2000) and/or the deeper rooting profile of intercropped trees, as showed by Mulia and Dupraz (2006) and Cardinael et al. (2015) in other Mediterranean walnut plantations intercropped with cereal. Although we did not measure rooting profiles, López-Díaz et al. (2017) did not found this spatial complementarity in other walnut-based agroforestry system of CW Spain.

A complementary use of resources can aslo occur in time which can also reduce the competition for water among trees and crops (van Noordwijk et al., 2015). In our case, the development of crop plants was very advanced when tree leaves sprouted, even more in AF than in MC plants. This together with the fact that AF and MC crop plants reached maturity and dried at the same time, seem to point out that trees barely reduced water availability for crop plants. This was confirmed by the better leaf water status of cereal plants cultivated in AF, with higher values of RWC and PRI in AF than in MC plants, even though cereals in the agroforestry system were phenologically more advanced and leaf senescence could be greater. Other studies have also reported higher water use efficiency (WUE) in cereals intercropping systems in limited-water areas, such as maize-apple tree agroforestry system (Liu et al., 2020), and wheat-maize combination (Yang et al., 2011).

Trees altered nutrient availability for crops

Both, soil samples taken before cereal anthesis and walnut budburst, and ion exchange resins installed from flowering until grain ripening revealed that mineral N was lower in AF than in MC and FO, indicating some level of competition among trees and crop plants for soil nitrogen. Indeed, leaf N concentration was up to 20% lower in wheat and barley plants cultivated in AF compared to plants cultivated in MC, in line with results reported by Zhang et al. (2019) in a similar agroforestry system with wheat. This was not confirmed by NDVI values, with higher values in AF plants (significant for barley). High values of NDVI at leaf level is frequently associated with high values on N content (Cabrera-Bosquet et al., 2011), although this can saturate above NDVI > 0.7 for most common crops (White et al., 2019). Moreover, the positive relationship between N and NDVI stands well for biomass N content but can become negative for leaf N concentration (Yang et al., 2017).

Contrary to N, the agroforestry system facilitated wheat and barley access to P, as revealed by the higher soil P content in AF and FO compared to MC, and by the crop leaf P concentration, which was up to 40% higher in wheat and barley plants cultivated in AF. Trees can enable

P mobilization in the soil (Moreno et al., 2007; Radersma & Grierson, 2004), which allowed AF-wheat and AF-barley to maintain N/P ratios close to common values in wheat straw (N/P ratio < 25; Takahashi & Anwar, 2007), in contrast to MC-wheat and MC-barley that had much higher N/P ratios, indicating a strong deficit in P. High N/P ratios are linked to greater biomass production (Güsewell, 2004), as revealed in our study, but also to a lower WUE, compared to more equilibrated N/P ratios (El-Madany et al., 2021). Besides more favourable RWC and PRI values for intercropped cereal plants of our study, as commented above, the results of electrolyte leakage showed that intercropped plants grew in lower stressful conditions, with lower electrolyte leakage. At the moment of electrolyte leakage determination in the cereals, wheat and barley were in a more advanced phenological stage in the AF system than in the MC conditions. This reveals that the lower electrolyte leakage, and therefore the lower cell membrane damage found in the AF system, was not a consequence of leaf senescence, but more favourable growing conditions.

Thus, although agroforestry systems could reduce crop yield compare to open fields as showed here, they could help crops to cope with dry periods (Arenas-Corraliza et al. 2018), which positive effect could only become apparent with climate change. Moreover, agroforestry could help cope with the increased vegetation N/P ratios that result of the increased atmospheric N depositions caused by industrial and farming activity (Gruber & Galloway, 2008).

Trees affected the form and timing of cereal growth patterns

Trees accelerated the development of barley and wheat plants in their first stages, before walnut budburst, although once tree leaves unfolded, the advantage vanished and both AF- and MC-cereal plants that reach grain maturation at the same time. This is in accordance with previous results in the same agroforestry system (Arenas-Corraliza et al., 2018) and with artificial shading (Arenas-Corraliza et al., 2020). Other authors working in Northen Mediterranean region found a delayed wheat development through the whole cereal growth cycle under agroforestry systems with deciduous (Inurreta-Aguirre et al., 2018) and evergreen trees (Panozzo et al., 2020). Advancing winter wheat and barley development can be especially advantageous to escape from the heat waves and droughts that usually take place in the late spring and early summer in the Mediterranean region (Dettori et al., 2017; van Oosterom & Acevedo, 1992), and also to minimise the likely negative effect of the dense shading after tree budburst.

Regarding plant growth, there were three separated stages. First, before walnut budburst (until mid-April), trees increased plant biomass of barley and wheat. Since this phase took place

mostly during winter conditions and when trees are devoid of leaves, cereal may have benefited from reduced competition and buffered low temperatures. Later, when walnut sprout took place, that is middle spring (first half of May or earlier for barley), differences faded out and plant biomass was equal in both AF and MC, probably because the environmental conditions were still beneficial for both strata and trees had not a noticeable competitive effect yet. Lastly, when tree leaves were fully displayed (from middle May on), the cereal growth slowed down in the AF and also the LAI compared to MC plants, in line with results reported by Dufour et al. (2013) and Zhang et al. (2019a), showing a negative effect because of the tree shading or competition for soil nutrients.

At the walnut budburst, barley was in a more advanced stage (grain filling) than wheat (flowering), because of its more precocious cycle. Consequently, the detrimental effect of trees on the development of cereal plants observed once tree leaves were fully displayed was stronger for wheat. The reduction of wheat plant biomass beneath trees was in agreement with Li et al. (2008) and Yang et al. (2018), who found that wheat aerial biomass was negatively affected by tree shade in agroforestry conditions, although those authors found a much stronger reduction on plant growth than in our study.

Interestingly, before tree budburst, leaf area and LAI of both wheat and barley were already lower in AF than in MC despite differences in plant biomass were minimal, indicating that plants responded even to the slight shading produced by stems and leafless branches. This reveals that cereal plants allocate a higher share of resources to stems in AF than in MC, as reported for a similar Mediterranean wheat-olive trees agroforestry system (Panozzo et al., 2020). Differences among barley and wheat were also shown by LMA values. In our experiment, AF reduced significantly LMA of wheat, revealing a morphological acclimation of wheat to shade, while barley was not affected, in accordance with previous studies with artificial shading (Arenas-Corraliza et al. 2019, 2020). The higher response of LMA in wheat could be related to a strategy to avoid leaf dehydratation in MC, as RWC was less affected in wheat than in barley, suggesting a higher susceptibility but also plasticity of wheat to a foreseen increment in temperatures.

Trees affect cereal yield and their components

Since the cereal cultivars used for this study were previously selected for shading environments (Arenas-Corraliza et al., 2020), we expected that they could better acclimate to agroforestry conditions and even increase yield beneath trees. However, the agroforestry

system reduced grain yield for both wheat and barley compared to the full light conditions, what was also found in a more open agroforestry system in the Mediterranean area (Dufour et al., 2013).

Grain yield in MC was 6.6±0.2 and 7.8±0.4 Mg ha^{-1} for barley and wheat, respectively, quite above the mean south Mediterranean values of 2.9 and 3.3 Mg ha^{-1} for barley and wheat respectively (averaged for the last two decades; FAO, 2021). This is explained by the very favourable climate conditons of spring in 2018 when rainfall was above the normal average precipitation for the season in the area. In a previous research in the same agroforestry experimental site with non-shade-adapted cultivars, we found that differences between AF and MC for wheat and barley grain yield depended on the spring climate, being AF more favourable only in low productive years with warm and dry springs, especially for barley (Arenas-Corraliza et al., 2018). Kuemmel (2003) and Sida et al. (2018) argued that cereal plants benefit more from trees during dry years because of the hydraulic lift of trees and the reduced atmospheric water demand. Additionally, Inurreta-Aguirre et al. (2018) also reported that the water pumping capacity of trees can benefit crop plants in a Mediterranean agroforestry system. AF reduced grain yield more severely in wheat than in barley, which was associated with a different set of traits in the two cereal species. As showed by SEM models, barley grain yield reduction was dominated by a lower number of spikes, whereas in wheat was dominated by the reduction in the number of grains per spike and grain weight.

In barley, the number of spikes and to a lesser extent the grain weight, were directly linked to grain yield in both AF and MC. It is well known that the number of spikes is the main yield component affecting grain yield in two-row barley (Prado et al., 2017), in accordance with our study. This is due to its early vigour and therefore higher LAI and tillering capacity than wheat at the beginning of the cycle. SEM models showed a positive relationship among the phenology and the number of spikes for AF crop, but not for MC, indicating the importance of precocity for the selection of cultivar for agroforesrty crops.

On the other hand, Prystupa et al. (2003) demonstrated that higher N availability increases cereal tillering and therefore the number of spikes. Since barley grown in AF had lower LAI values and also lower N soil content even before walnut budburst compared to MC, it can be concluded that the AF conditions negatively affected spikes determination because of a N competition issue, which call for fertilization plans adapted to agroforestry conditions. Nevertheless, this deserves further studies as NDVI (proxy of chlorophyl content) showed a negative relationship with the number of spikes of barley plants, while the relationship of PRI (proxy of carotenoid content) and the number of spikes was positive.

Regarding the grain weight, the positive relationship with P suggests a possible benefit of tree presence because of their capacitiy to mobilise soil P. This relationship was not selected by the SEM model for barley growing in open fields. Indeed, the quite different assemblage of variables that explained the two main components of the grain yield of barley growing in AF and MC (this also applies to wheat) supports the idea that plant traits of most interest for the selection of cultivars are quite context-dependent and the ones used for MC are not valid for AF.

In wheat, the grain yield was also directly linked to the number of spikes and the grain weight. Our results suggest that low values of plant biomass before walnut budburst may be related to an increased number of spikes in AF system. This is in accordance with a trade-off in the allocation of photosynthates in the steam and spikes during early plant elongation (Álvaro et al., 2008). This effect was also observed in MC, although with plant biomass after tree budburst. Besides, the precocity of wheat cultivars was linked to an increased number of spikes in MC, probably by scaping from the early hot spring events (Dettori et al., 2017), especially intense in open conditions. The stressful conditions of MC were also revealed in the higher electrolyte leakage, that was linked to a lower number of spikes, ultimately affecting grain yield. Lower grain weight in the AF may be related to the delayed cycle of wheat as compared to barley, which will result in wheat being less developed than barley when walnut budburst takes place. As a result, wheat could be more vulnerable to tree competition and late spring weather events during grain formation . Plant K and P affected the grain yield of AF and MC, respectively. The much lower soil P availability in MC than in AF could point to limiting role of P for wheat in MC. However the different roles of K among AF and MC for wheat, and to a lesser extent in barley, remain unexplained and claim for further studies given the frequently neglected importance of this nutrient for plant growth (Sardans & Peñuelas, 2015).

With regard to grain quality, wheat slightly increased its N grain content in the agroforestry system, contrary to barley, which significantly decreased the N grain content beneath the trees, in accordance with previous results in the same agroforestry system with different cultivars (Arenas-Corraliza et al., 2018). The neutral (Dufour et al., 2013) or even positive impact on wheat protein content have also been reported in other Mediterranean agroforestry systems (Panozzo et al., 2020) and is typically linked to a decrease in the grain yield in open conditions (Lollato et al., 2019). However, in our study, the grain N increment found in AF for wheat was associated with a grain yield increase, showing a different grain N-grain yield dynamic than in MC. On the other hand, the dynamics of wheat plant biomass after tree budburst negatively affected grain N content in both systems, revealing that the N invested in biomass production was not efficiently translocated to

the grains. For barley, less is known about how trees affect protein content and our study did not reveal any key relationships. Nevertheless, the grain N reduction found in barley in AF is of great interest for malting industry, since trees could help to reduce the usually excessive grain protein content, which is a current issue for the main malting barley producers (Le Bail & Meynard, 2003; O'Donovan et al., 2011).

Tree growth is barely affected by intercrops

Tree production was not significantly affected by cereal crops in AF in terms of diameter growth. However, walnut leaves revealed a slight competitive effect with crops for N, P and K in AF.

With regard to the tree water access in the agroforestry system, deciduous trees as walnuts have shown great plasticity when growing in combination with wheat in alley cropping systems (Andrianarisoa et al., 2015). They can develop deeper roots in AF than in plantations, being able to resist the summer drought by exploring deeper soil layers unavailable for cereals root systems (Cardinael et al., 2015). This agrees with our study where trees were significantly more hydrated at the end of the summer as compared to the pure plantation, even though the slight competition for water with cereals was revealed in the middle of the summer (when cereals were already harvested). This suggests that walnuts had better access to the water stored in deeper soil layers due to a greater root exploration, avoiding water stress in the driest period.

CONCLUSIONS

Walnuts trees can provide a mild microclimate to cereals that grow in Mediterranean agroforestry system, buffering high light availability and temperatures. However, they can affect crop yields as compared to open fields. Nevertheless, trees still benefit cereal performance, advancing phenology, reducing cereal stress, and improving physiological traits. The agroforestry conditions enhanced P availability for cereals but may compete for N, particularly for barley. This effect should be considered to adopt practices that minimize possible deficits. Our study showed for the first time how plant traits that affected grain yield highly differed between agroforestry and open conditions. The future cereal selection programs to cultivate under agroforestry combinations should be based not only on shade tolerance but also on the assemblage of plant traits that ultimately define grain yield in agroforestry systems. Beyond crop yield, knowledge of the links between functional plant traits and soil structural stability, nutrient dynamic and carbon sequestration is essential for the development of agroforestry.

DISCUSIÓN GENERAL

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Esta Tesis ha demostrado que la combinación de cereales y arbolado de nogal en sistemas agroforestales en el área mediterránea es posible, e incluso beneficiosa en algunos aspectos, en el escenario actual de calentamiento global. En este apartado se discuten los resultados más relevantes obtenidos en los diferentes capítulos de la Tesis.

El primer estudio del sistema agroforestal de nogal con cereal durante tres años mostró el potencial de estas especies para el cultivo intercalar, reflejando algunas limitaciones por parte del cereal. Esto provocó la realización de un segundo experimento, en condiciones controladas, para valorar específicamente la respuesta a la sombra de distintas variedades trigo y cebada y poder realizar una selección de aquellas más adaptadas a las condiciones de radiación reducida. Este ensayo señaló, por primera vez, que ambas especies de cereal, al contrario de la creencia tradicional, pueden incrementar su producción en ambientes de sombra, como la producida en un sistema agroforestal en el área mediterránea de estudio. Por último, utilizando las variedades que mejor se adaptaron a la sombra en el ensayo de condiciones controladas, se realizó un tercer experimento, en el mismo sistema agroforestal que el primero. Éste reveló interacciones positivas entre ambos estratos (nogal y cereal) que reflejaban un menor grado de estrés tanto en cultivo como en arbolado en el sistema agroforestal, convirtiéndolo en un modelo de gestión de adaptación al cambio climático para la producción de alimentos y madera de calidad en condiciones mediterráneas de alta disponibilidad lumínica.

Efecto del arbolado en las condiciones edafoclimáticas del cultivo

Se ha demostrado que el arbolado en los sistemas agroforestales puede amortiguar los eventos climatológicos extremos perjudiciales para el cultivo (Karvatte et al., 2020). Esto está en concordancia con los resultados obtenidos en los ensayos de campo (capítulo I y especialmente

capítulo IV), que evidenciaron que los árboles, a partir de la primavera, amortiguaron la temperatura del aire para el cereal, especialmente en los episodios de olas de calor. Es conocido que las temperaturas puntuales superiores a los 25°C durante las etapas de pre y post floración afectan negativamente a la translocación de carbohidratos hacia el grano y reducen en gran medida la producción (Romero y German 2001). De esta forma, el arbolado tuvo un papel protector sobre el cereal frente a las altas temperaturas, consideradas como una de las principales formas de estrés abiótico durante la floración y formación del grano en cereales de invierno, causantes de la reducción de la producción (Sadras, 2007).

Esta amortiguación de las temperaturas por el arbolado durante la primavera (disminuyéndolas durante el día y aumentándolas durante la noche respecto a los cultivos abiertos), estuvo en concordancia con lo obtenido por Inurreta-Aguirre et al. (2018) y Serrano et al. (2017) en sistemas similares en condiciones mediterráneas. Sin embargo, la amortiguación de las temperaturas por el arbolado fue casi dos veces mayor en nuestro estudio que en los citados anteriormente, probablemente por la mayor radiación solar y el mayor rango de temperaturas experimentado en la zona de estudio, lo que intensifica el efecto moderador del árbol (Kanzler et al. 2018).

No obstante, no existen evidencias directas entre la mejora de las condiciones climáticas para el cereal en el sistema agroforestal y la producción de grano (Kanzler et al. 2018). Es posible que esta protección del arbolado quede, en ocasiones, enmascarada e incluso superada por la competencia entre los estratos por los recursos disponibles. Se ha demostrado que en los sistemas silvoarables mediterráneos con árboles caducifolios, tras la brotación de éstos, los cereales de invierno, debido a su ciclo, siguen consumiendo agua y nutrientes (Dupraz y Liagre 2011; Dufour et al. 2013), estableciéndose relaciones de competencia con el arbolado. En este sentido, algunos autores señalan la competencia por agua como una de las principales interacciones negativas que puede disminuir la producción del cultivo (Jose et al., 2000). Por el contrario, otros autores han demostrado que esta competencia se puede evitar debido a la plasticidad radicular de algunas especies arbóreas caducifolias, como el nogal, para explorar capas más profundas del suelo en sistemas agroforestales intercalares (Mulia y Dupraz 2006; Cardinael et al. 2015). Sin embargo, esto no evita que se genere competencia por los recursos en las capas más superficiales, donde se encuentra la mayor parte de las raíces de ambos estratos, pudiendo reducirse el rendimiento del cereal en el sistema agroforestal (He et al., 2012; Zhang et al., 2015).

En el presente estudio, no se encontraron evidencias de falta de recursos hídricos para el cultivo en el sistema agroforestal, sino al contrario, de acuerdo con lo obtenido por otros autores en zonas áridas (Liu et al., 2020; Yang et al., 2011). El hecho de que, en el capítulo IV, ambas especies de cereal tuvieran un desarrollo avanzado en el sistema agroforestal cuando brotó el nogal (más que en el monocultivo de cereal) unido a que en ambos sistemas ambas especies alcanzaron la madurez

prácticamente al mismo tiempo, indica que el arbolado apenas redujo la disponibilidad de agua para el cultivo. La falta de competencia por agua se evidenció también en el mejor estado hídrico del cereal en el sistema agroforestal en el mismo ensayo, revelado por sus mayores valores de *RWC* y *PRI* y menor flujo de electrolitos, incluso cuando las plantas de cereal estaban fenológicamente más avanzadas bajo arbolado que a plena luz y sería esperable una mayor senescencia.

Respecto a la disponibilidad de nutrientes, el estudio del capítulo IV mostró un menor contenido de N, tanto a nivel de suelo como foliar en el cereal, en concordancia con lo obtenido en un sistema agroforestal similar con trigo por Zhang et al. (2019b). Por el contrario, hubo una mayor disponibilidad de P para el cereal en el sistema agroforestal, revelado también tanto a nivel de suelo como en la hoja del cultivo, probablemente por la movilización de P en el suelo realizada por el arbolado (Radersma y Grierson 2004; Moreno et al. 2007).

Alteración de la fenología y el crecimiento del cereal en el cultivo agroforestal

Respecto a la fenología del cereal, los dos niveles de sombra instalados en el ensayo de condiciones controladas (capítulos II y III) aceleraron el crecimiento y floración del trigo y la cebada, hasta la fase de grano lechoso, en comparación con las condiciones de plena luz. El patrón fenológico observado en el ensayo controlado se confirmó en los ensayos de campo, donde la presencia del arbolado también aceleró, en general, la fenología del cereal en el sistema agroforestal. Esto fue observado tanto en el capítulo I (con variedades de cereal no preseleccionadas) como en el IV (con variedades de cereal preseleccionadas por su adaptación a la sombra). En el capítulo IV, el arbolado aceleró la fenología de ambas especies de cereal, trigo y cebada, hasta las últimas etapas cercanas a la maduración. La coincidencia de resultados en los ensayos de campo y el ensayo en condiciones controlada pone de manifiesto que el adelanto de la fenología del cereal se debe muy probablemente a la sombra ejercida por el arbolado.

Otras investigaciones en sistemas agroforestales mediterráneos de árboles caducifolios no mostraron ningún efecto de la sombra sobre la fenología del trigo (Dufour et al., 2013) o incluso un retraso en la floración de éste (Inurreta-Aguirre et al., 2018). No obstante, estos estudios se realizaron en las condiciones mediterráneas existentes en el sur de Francia, donde la radiación solar media anual (5,466 MJ/m^2), aun siendo suficiente para el desarrollo del cereal, es menos intensa que en la zona del presente estudio (6,300 MJ/m^2), que es un 14 % mayor (https://solargis. info/). Este retraso en el desarrollo del cereal también se ha observado en sistemas agroforestales basados en árboles perennifolios (Panozzo et al., 2020). En cambio, en las condiciones del centro Ibérico, con mayor radiación, la sombra puede ejercer un papel protector más beneficioso para los cereales, evitando la fotoinhibición y la inversión de recursos en la fotoprotección que

necesitarían para protegerse de la intensa radiación solar (Valladares y Pearcy 1997; Jacobsen et al. 2012), posibilitando, de esta forma, un desarrollo más adelantado.

A pesar del aparente beneficio de la sombra en las condiciones de nuestros ensayos, esto fue más evidente en los estadíos tempranos del cereal que en los tardíos. A partir de la fase de grano lechoso, la sombra más intensa retrasó la maduración del grano en el trigo, de acuerdo con los resultados encontrados por Inurreta-Aguirre et al. (2018). Igualmente, aunque antes de la brotación de los árboles, éstos produjeron un aumento de la biomasa de las plantas de cebada y especialmente de trigo (capítulo IV), a partir de su brotación, los árboles tuvieron un efecto perjudicial para la biomasa de la planta de ambas especies de cereal, probablemente por la mayor sombra ejercida y la competencia por nutrientes. Este efecto fue especialmente perjudicial para el trigo, de acuerdo con lo obtenido por otros autores (Li et al., 2008; Yang et al., 2018) y menos negativo para la cebada, explicado posiblemente por su ciclo más precoz que el trigo, que provocó que se encontrara en un estado fenológico más adelantado en el momento de la brotación del nogal.

Además, cabe destacar que la respuesta fenológica a la sombra en condiciones controladas fue consistente en las diferentes variedades de cebada, pero presentó amplias diferencias en el caso de las variedades de trigo. Por otra parte, en el ensayo de condiciones controladas, se observó que los ciclos de crecimiento más cortos y avanzados de trigo y cebada, se correlacionaban con mayores producciones de grano. Esto subraya la importancia de avanzar estados fenológicos clave para incrementar la producción de grano en condiciones mediterráneas, de acuerdo con lo revelado por Moragues et al. (2006). Puesto que estos rasgos fenológicos pueden seleccionarse dentro de la extensa disponibilidad de variedades de trigo y cebada, escoger aquellas con la fenología más adelantada permitiría escapar a las condiciones de sombra intensa impuestas por los sistemas agroforestales de arbolado caducifolio al final del ciclo del cereal. Además, avanzar la fenología también permitiría evitar los eventos climatológicos extremos de finales de primavera e inicios de verano, como ya se ha intentado en la selección tradicional de estos cultivos para el área mediterránea (Fischer y Kohn 1966; Woodruff y Tonks 1983; van Oosterom y Acevedo 1992), entre los que se encuentran las olas de calor y las sequías, que se prevé que sean cada vez más frecuentes en el área mediterránea en el contexto actual de calentamiento global (Dettori et al., 2017).

Alteración de los rasgos funcionales del cereal en condiciones de sombra

En el ensayo experimental de cereal en condiciones controladas correspondiente a los capítulos II y III, se evaluó la respuesta de distintos rasgos funcionales (fenológicos, morfológicos, fisiológicos y bioquímicos) a las condiciones de sombra artificial en diferentes variedades de trigo

y cebada ampliamente comercializadas en España. Los resultados mostraron una clara separación entre los conjuntos de rasgos funcionales de las plantas desarrolladas en los diferentes niveles de sombra, siendo esta separación mucho más evidente para la cebada que para el trigo. Además, no se estableció una gradación entre la agrupación de estos rasgos y los distintos niveles de sombra, revelando la falta de linealidad de la respuesta general a las condiciones de sombra de los diferentes rasgos funcionales de trigo y cebada.

En este experimento, se descubrió por primera vez que, para su adaptación a la sombra, la cebada y el trigo siguieron diferentes estrategias. Por una parte, la cebada presentó una fuerte aclimatación fotosintética, confirmando que esta especie tiene una elevada capacidad para adaptarse a diferentes ambientes lumínicos (Zivcak et al. 2014). Esta adaptación a la sombra quedó patente, por un lado, por sus ratios más reducidas de clorofila a/b y carotenoides/clorofila en los niveles de menor intensidad lumínica, típicas en las adaptaciones vegetativas a la sombra en esta y otras especies (de la Torre y Burkey 1990; Marschall y Proctor 2004). Por otro lado, las curvas de fotosíntesis neta mostraron que la cebada tenía una respuesta a la luz característica de las especies adaptadas a la sombra, con un punto de saturación de luz inferior al del trigo, que mostró un comportamiento típico de las especies de luz (Lichtenthaler et al., 1981).

Además, la exposición a altos niveles de *PAR* de la cebada cultivada en los tratamientos de sombra, reveló mayores niveles de *NPQ* que en la cebada cultivada a plena luz, mostrando que las plantas cultivadas en sombra se habían adaptado a las condiciones de poca iluminación y disipaban el exceso de energía y el posible daño fotosintético al fotosistema II al exponerse a una radiación *PAR* elevada, a través de mayores reacciones no-fotoquímicas (*NPQ*) de fotoprotección (Lu et al., 2001). De igual forma, los parámetros de fluorescencia relativos al rendimiento fotosintético (ϕ_{PSII} , *ETR*) mostraron que las plantas de cebada que habían crecido en los tratamientos de sombra eran menos eficientes en las reacciones fotoquímicas que las plantas cultivadas a plena luz cuando se las exponía a altas intensidades de *PAR*, mostrando, de nuevo, una adaptación de su sistema fotosintético a condiciones de sombra. Sin embargo, el trigo no reveló ninguna de las adaptaciones fotosintéticas descritas para la cebada, en contraste con lo obtenido en algunas variedades por otros autores en diferentes condiciones climáticas a las del presente estudio (Zheng et al. 2011; Dong et al. 2014). Esta divergencia respecto a los resultados de la literatura científica posiblemente se explique por el mayor punto de saturación de luz de las variedades utilizadas en el área mediterránea, lo que presumiblemente determina un menor potencial para desarrollar adaptaciones fotosintéticas a la sombra.

En el mismo experimento, a pesar de la disminución del contenido de N en hojas, la sombra incrementó el contenido de clorofila (valores *SPAD*) en ambas especies de cereal, de

acuerdo con lo obtenido por otros autores en cultivos de cereal (Li et al., 2010; Wang et al., 2015a; Xu et al., 2013; Zheng et al., 2011). El aumento de la ratio clorofila/N en las hojas (Evans, 1996) es una respuesta típica de las especies adaptadas a la sombra, lo que permite maximizar la intercepción de luz (Valladares y Niinemets 2008; Zhen y van Iersel 2017). Pese a las adaptaciones fisiológicas observadas en la cebada, los resultados no han permitido desvelar una relación directa entre estas adaptaciones y los niveles de producción de grano de la cebada, pero curiosamente sí para el trigo.

En cuanto a la adaptación de los rasgos morfológicos, es conocido que los cultivos pueden adaptar su estructura aérea para optimizar la interceptación de luz en condiciones de sombra (Li et al., 2010; Xu et al., 2016). De hecho, en este experimento, la sombra aumentó la altura de las plantas y el área foliar tanto en trigo como en cebada, respuestas típicas de los cultivos en condiciones de sombra (Dong et al., 2015; Kutschera y Briggs, 2013; Li et al., 2010), correlacionándose ambas positivamente con la producción de grano. El trigo, en términos morfológicos, desarrolló una mayor adaptación a la sombra que la cebada, mostrando valores inferiores de *LMA* (Poorter et al., 2009; Wright et al., 2006) y superiores de área foliar (Li et al., 2010) en los niveles de sombra, en comparación con el tratamiento de plena luz. Estas diferencias se acrecentaron tras la brotación del arbolado. Resulta interesante que, pese al ligero aumento de biomasa en las plantas de cereal bajo el arbolado, antes de la brotación, al mismo tiempo se produjo una disminución del área foliar y del *LAI* de ambas especies, indicando que estas especies son sensibles y responden, incluso, a la sombra ejercida por el tronco y las ramas de los árboles antes de la brotación.

Respecto al contenido de nutrientes en hoja, en primer lugar, la sombra redujo los contenidos de glucosa y almidón en las hojas de cebada y de trigo, de acuerdo con lo obtenido por Xu et al. (2013). Esta reducción en el contenido de carbohidratos fue más intensa en la cebada que el trigo, más acentuada en el nivel de sombra más intensa y menos relevante para las variedades menos precoces. De igual modo, la sombra redujo el contenido de N en hoja en ambas especies de cereal, lo que pudo explicarse también por la reducción de carbohidratos (Rideout y Raper 1994; Dreccer et al. 2000b; Omondi et al. 2019). Al contrario que el N, los contenidos de P y K en hoja fueron mayores en las plantas de los tratamientos de sombra respecto a plena luz en ambas especies, mostrando que las condiciones reducidas de iluminación pueden beneficiar su asimilación. Además, hubo un efecto general de dilución en el contenido de N, P y K en grano en trigo y cebada, apoyado por el aumento de producción de grano en sombra y la correlación negativa entre el contenido de estos nutrientes y el rendimiento en grano, de acuerdo con lo reportado para el N en grano en otros ensayos de sombra artificial (Artru et al. 2017; Shimoda y Sugikawa 2019).

La producción de cereal bajo arbolado: balance de efectos facilitadores y competitivos

Puesto que el trigo y la cebada son cultivos anuales típicamente adaptados a condiciones de plena luz, podría ser difícil esperar incrementos de producción de las variedades actuales de cereal en las condiciones de sombra y competencia impuestas por el arbolado en sistemas agroforestales.

Actualmente, el efecto de la sombra sobre la producción de grano continúa siendo dispar según el tipo de sombra y las condiciones climáticas en las que se valore su efecto (Dong et al., 2014; Dufour et al., 2013; Inurreta-Aguirre et al., 2018; Mu et al., 2010; Shimoda y Sugikawa, 2019). En el momento de la realización de esta Tesis, no existían evidencias del efecto aislado de la sombra en las condiciones mediterráneas del centro peninsular español, donde la disponibilidad de luz es superior al resto de ambientes estudiados y podría ejercer un efecto beneficioso sobre el cultivo de cereal. Por ello, en este trabajo se realizaron tanto ensayos en condiciones controladas con sombra artificial, como en campo en sistema agroforestal, permitiendo esclarecer el efecto de la sombra en la producción de los cereales en este tipo de sistemas.

Al contrario que los experimentos realizados hasta la fecha, en el ensayo de condiciones controladas, la sombra artificial, en sus dos niveles (leve y más severo), aumentó la producción de grano respecto a plena luz (15-20 % más) en ambas especies de cereal, trigo y cebada, posibilitado por la adaptación de un conjunto de rasgos funcionales, como se ha comentado con anterioridad. Hasta el momento, otros estudios únicamente habían mostrado un aumento de producción de grano en trigo en sombra leve (Xu et al. 2016) e incluso disminuciones de producción al aumentar la intensidad de ésta (Mu et al., 2010), aunque éstos se llevaron a cabo en áreas climáticas diferentes a la mediterránea. Este aumento de producción de ambas especies de cereal en los niveles de sombra artificial, demostró que tanto trigo como cebada podrían beneficiarse de las condiciones de sombra generadas por el arbolado en sistema agroforestal en las condiciones de estudio de alta luminosidad presentes en la zona mediterránea del centro peninsular español.

En cuanto a los componentes del rendimiento, en condiciones controladas, la cebada aumentó el número de granos por espiga en el nivel de sombra más intensa, lo que se compensó más tarde con un menor peso de grano, finalmente aumentando la producción con la sombra en todas sus variedades. Por otro lado, el trigo no presentó diferencias significativas en el número de granos por espiga en los distintos niveles de sombra, aunque aumentó el peso del grano en la sombra moderada, lo que se correlacionó positivamente con la producción final de grano, mostrando un efecto de dilución en el contenido en N. Además, las variedades más tardías de trigo fueron las que aumentaron significativamente su producción en sombra.

Esos resultados pusieron de manifiesto que la reducción de la producción de cereal en sistemas agroforestales con árboles caducifolios que se había observado hasta la fecha en otros estudios en la zona mediterránea francesa (Dufour et al., 2013; Inurreta-Aguirre et al., 2018), se debería, en parte, a un efecto perjudicial de la sombra del arbolado debido a una menor disponibilidad lumínica en esa área en comparación con la alta intensidad solar del centro peninsular español (https:// solargis.info/), aunque también, podría deberse, en parte, a la competencia por los recursos del suelo (agua y nutrientes) generados en el propio sistema agroforestal.

En este sentido, los ensayos de campo en sistema agroforestal realizados en el marco de la Tesis, tanto con variedades no pre-seleccionadas para la sombra (capítulo I) como con aquellas previamente seleccionadas para condiciones de menor iluminación (capítulo IV), arrojaron luz sobre las relaciones de competencia y facilitación generadas entre ambos estratos Estos experimentos mostraron un efecto mayoritariamente negativo del arbolado sobre la producción de cereal, aunque el efecto positivo/negativo del arbolado sobre el cereal dependía en gran medida de las condiciones climatológicas del año, las especies y las variedades de cereal utilizadas.

Así, el ensayo en el sistema agroforestal durante varios años agrícolas consecutivos (capítulo I), mostró que los años que tuvieron una cantidad adecuada de precipitaciones en primavera, presentaron, en general, una mayor producción de cereal, tanto en el sistema agroforestal como en el monocultivo. Es conocido que el rendimiento del grano está determinado fundamentalmente por la biomasa asimilada en la última parte del ciclo del cereal (Asseng y Savin 2012), que en la zona de estudio corresponde a la primavera tardía. Por esta razón, la abundancia de precipitaciones favoreció la producción de grano y limitó el potencial facilitador del arbolado, reduciéndose la producción de grano, especialmente en trigo, en el sistema agroforestal, como demostraron estudios anteriores en un sistema silvoagrícola similar de nogal y trigo (Dufour et al., 2013; He et al., 2012; Li et al., 2008). Por el contrario, los años con eventos climatológicos extremos como olas de calor en primavera (perjudiciales para la translocación de carbohidratos hacia el grano, como se ha comentado anteriormente), el arbolado ejerció un papel protector sobre el cereal. De esta forma, el arbolado incluso aumentó la producción de grano de cebada, al contrario que el trigo, tradicionalmente considerado como una especie de plena luz. Esta ventaja sobre la cebada se debe posiblemente a una combinación de características favorables que debe ser tenida en cuenta, junto con las características y rasgos funcionales de cada variedad, para seleccionar las especies y variedades más adaptadas a este tipo de sistemas.

Por otra parte, en el experimento de sistema agroforestal con las variedades preseleccionadas para la sombra de trigo y cebada (capítulo IV), se esperaba que éstas, aumentaran o, al menos, no disminuyeran su producción de grano en el sistema agroforestal, por su probada capacidad

de adaptación a la sombra. Sin embargo, el arbolado redujo la producción de grano de todas las variedades de ambas especies de cereal en comparación con las condiciones de monocultivo. Esto pudo estar debido a que el año de estudio presentó unas condiciones climatológicas muy favorables para el cereal, con abundantes precipitaciones primaverales, lo que lo convirtió en un año muy productivo respecto a la media de los últimos años (aproximadamente tres veces más). Como ya se demostró en el capítulo I, el sistema agroforestal resulta especialmente beneficioso en los años poco productivos con primaveras calurosas y secas, en concordancia con los expuesto por Kuemmel (2003), resultando, por el contrario, perjudicial en los años más favorables y productivos para el cereal. Además, corroborando también resultados anteriores, el sistema agroforestal redujo en mayor medida la producción de grano en trigo en comparación con la cebada.

La disminución en el sistema agroforestal de la producción de grano en las variedades adaptadas a la sombra (ensayo de campo del capítulo IV), hace pensar en la importancia que podría tener la competencia entre el árbol y el cereal por los recursos edáficos. Sin embargo, en ese mismo ensayo el arbolado mejoró el estado hídrico del cereal, como revelaron los mayores valores de *RWC* y *PRI* y los valores inferiores de flujo de electrolitos en hoja de trigo y cebada en el sistema agroforestal en comparación con el monocultivo de ambas especies de cereal. Estos resultados apuntan a la posibilidad de explicar la disminución de la producción de grano en el sistema agroforestales por la competencia por nutrientes del suelo. De hecho, las hojas de trigo y cebada revelaron una competencia por N con el árbol en el sistema agroforestal.

No obstante, ambas especies de cereal mostraron un mayor contenido en P en hoja, posiblemente porque el arbolado movilizó las reservas del suelo en este elemento, como se ha comentado con anterioridad, dando lugar a una menor ratio N/P en el sistema agroforestal en comparación con el monocultivo de cereal de ambas especies. Esto permitió que el sistema agroforestal mantuviera unas ratios de N/P cercanas a los valores comunes (ratio N/P < 25; Takahashi y Anwar 2007), en contraste con las elevadas ratios que presentó el cereal del monocultivo, mostrando un fuerte déficit de P. De esta forma, el sistema agroforestal se presenta como un modelo de gestión con potencial para amortiguar las elevadas ratios de N/P habituales en los sistemas de cultivo actuales como consecuencia de las deposiciones atmosféricas de N procedentes de la actividad industrial (Gruber y Galloway 2008).

Por otra parte, el arbolado mejoró la calidad de grano de trigo, presentando un mayor contenido en N (y por tanto, en proteína) en el sistema silvoagrícola en ambos experimentos en campo (capítulos I y IV), de acuerdo con los resultados obtenidos por otros autores en sistemas similares condiciones mediterráneas (Dufour et al., 2013; Panozzo et al., 2020). Esto contrasta con lo ocurrido para la cebada, que redujo su contenido de N también en ambos experimentos. Curiosamente, esta reducción del N en el grano de cebada resulta de gran interés, pues los niveles elevados suponen un problema de

actualidad para la industria maltera (Le Bail y Meynard 2003; O'Donovan et al. 2011), frente al cual los sistemas agroforestales pueden representar una posible estrategia de solución.

Programas de selección de variedades de cereal para los sistemas agroforestales

Los sistemas agroforestales presentan una compleja red de interacciones, que, en ocasiones, resultan perjudiciales para el cultivo. Sin embargo, mientras que la competencia por los recursos podría compensarse (con planes de riego y fertilización adecuados) o incluso evitarse (a través de la selección de árboles caducifolios y cereales cuyas máximas necesidades no coincidieran en el tiempo), las condiciones de sombra establecidas por el arbolado obligan a realizar programas de selección de especies y variedades adaptadas para el cultivo bajo los árboles.

Las especies de cereal, trigo y cebada, si bien se cultivan ampliamente en el clima mediterráneo, no son escogidas por igual para los sistemas agroforestales. Entre las dos, ha sido el trigo la especie que se ha cultivado mayoritariamente en los sistemas silvoagrícolas similares al del presente estudio (Dufour et al. 2013; Inurreta-Aguirre et al. 2018). Sin embargo, la cebada presenta un conjunto de características que la hacen más adecuada para su cultivo en sistema agroforestal en comparación con el trigo. En primer lugar, su mayor precocidad la permite estar más avanzada en su desarrollo en comparación con el trigo cuando comienza la brotación de los árboles caducifolios, incluso madurando más rápido que éste (Cossani et al., 2009), evitando así en mayor medida el posible efecto negativo de la sombra y la competencia por agua y nutrientes. En segundo lugar, el ángulo de disposición de las hojas de la cebada y la estructura de su follaje permiten una mayor intercepción de la luz solar (Muurinen y Peltonen-Sainio 2006) y disminuyen la evapotranspiración (Setter y Waters 2003). Estas características ya conocidas, junto con los resultados aportados por este estudio, convierten a la cebada en una especie más adecuada que el trigo para la combinación con arbolado caducifolio en sistemas agroforestales mediterráneos.

Además, no todas las variedades de trigo y de cebada presentan el mismo comportamiento que a nivel de especie, como se observó en el primer ensayo de campo en sistema agroforestal (capítulo I), estando algunas más afectadas que otras por la presencia del arbolado en cuanto a la producción de biomasa o el tamaño de los granos. Esta circunstancia remarcó la importancia de la selección varietal para el cultivo en sistemas agroforestales y abrió la posibilidad de realizar una selección de variedades de trigo y cebada para este tipo de sistemas. Por ello, en los capítulos II y III se realizó una selección de entre una amplia gama de variedades, en función de sus diferentes adaptaciones al entorno de iluminación reducida en condiciones controladas. Este experimento de selección confirmó la sospecha del primer capítulo, mostrando la gran variabilidad existente entre variedades de la misma especie en la adaptación a la sombra de sus parámetros fenológicos, morfológicos, bioquímicos,

fisiológicos y productivos. Así, este ensayo permitió escoger aquellas variedades que presentaron un mejor comportamiento general y aumentaron su producción bajo sombra en condiciones de clima mediterráneo, para, posteriormente, cultivar dichas variedades en campo en un sistema agroforestal mediterráneo, comprobando su aptitud para este tipo de sistemas (capítulo IV).

Los rasgos funcionales como determinantes de la producción del cereal

La amplia variabilidad de respuesta que mostraron las diferentes variedades de trigo y cebada ensayadas en los distintos experimentos de este trabajo revela la importancia de realizar una selección de las mismas para el cultivo en sistemas agroforestales mediterráneos. Esta selección, inicialmente basada en su respuesta a la sombra, podría ajustarse en base a distintos rasgos funcionales relacionados directamente con la producción de grano en este tipo de sistemas. Esta selección afectará al balance final de las interacciones entre los estratos y de ella dependerá, en última instancia, el éxito del sistema.

Los resultados de los diferentes ensayos mostraron que algunas variedades de trigo y cebada mostraron mayor plasticidad que otras en la adaptación a la sombra, dependiendo ésta, en gran medida, del rasgo fisiológico o morfológico considerado y revelando la importancia de la selección varietal para este tipo de sistemas. Los rasgos funcionales que tuvieron una mayor influencia en la producción de grano variaron entre las especies de cereal y las condiciones de cada experimento.

Por una parte, en el ensayo en condiciones controladas para el cereal (capítulos II y III), a nivel de especie, los rasgos que más contribuyeron al aumento de producción fueron el peso del grano, la precocidad y el *NPQ*, mientras que, para la cebada, fueron el *SPAD*, la precocidad, el número de granos por espiga y la altura de la planta.

Por otra parte, en el ensayo de sistema agroforestal con variedades preseleccionadas por su adaptación a la sombra (capítulo IV), la reducción de la producción de grano bajo arbolado se asoció, en el caso de la cebada, con un menor número de espigas, mientras que, en el trigo, estuvo determinada por un menor número de granos por espiga y peso de los granos. A su vez, estos parámetros estuvieron influenciados por diferentes rasgos funcionales (precocidad, *LAI*, *NDVI*, *PRI*, biomasa de la planta, contenido de P y K en la planta...) que variaron en las dos especies de cereal y también entre los sistemas agroforestal y monocultivo. Esto reveló que el arbolado era capaz de modificar los rasgos que determinan la producción de grano en ambas especies de cereal en comparación con el monocultivo, lo que resulta de gran relevancia en la selección de especies y variedades de cereal basada en rasgos funcionales para sistemas agroforestales.

DISCUSIÓN

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El crecimiento del nogal: evidencias de la competencia por los recursos edáficos

En lo referente al crecimiento del arbolado en diámetro, éste se vio mermado en el sistema agroforestal respecto a la plantación pura en el ensayo inicial (capítulo I, arbolado de 9 años de edad), en concordancia con sistemas similares con trigo y nogal, explicado por la competencia de recursos hídricos y nutricionales entre ambos estratos (Zhang et al., 2015). Sin embargo, éste no se vio afectado por el cultivo de cereal en el ensayo posterior en el mismo sistema agroforestal (capítulo IV), cuando el arbolado había alcanzado la edad de 13 años. No obstante, en ambos ensayos, el sistema reveló una fuerte competencia por nutrientes: en el primer caso por K y en el segundo también por N y P, aunque éste último no provocó un menor crecimiento en diámetro, probablemente debido a su edad más avanzada.

Por otra parte, aunque ambos estratos compitieron ligeramente por el agua durante el desarrollo del cereal (al final del ciclo de crecimiento del cereal el suelo estaba ligeramente más seco en el sistema agroforestal que en el monocultivo), pasada la cosecha de éste, el estado hídrico del arbolado mejoró en el sistema agroforestal a finales de verano, en comparación con la plantación pura. Esto sugiere que el nogal en combinación con el cereal desarrolló un sistema radicular más profundo que le permitió el acceso al agua presente en capas más profundas del suelo, evitando así, en mayor medida que en la plantación pura, el estrés hídrico común en la época de sequía estival. Estos resultados confirman lo obtenido por Andrianarisoa et al. (2015) y Cardinael et al. (2015) respecto a la gran plasticidad radicular del nogal en combinación con los cereales y su potencial en sistemas agroforestales.

Por tanto, el diseño de futuros sistemas agroforestales similares en condiciones mediterráneas, debe tener en cuenta la competencia por macronutrientes esenciales y atenuarla en la medida de lo posible con un plan de fertilización adecuado, especialmente en los primeros años, así como la disponibilidad de agua para el arbolado, intentando garantizar una menor competencia y por tanto una mayor producción de ambos estratos del sistema.

Los sistemas agroforestales para los retos del siglo XXI

Como se ha señalado antes, la producción de cereal llegó a ser más elevada en el sistema agroforestal que en el cultivo abierto en años climatológicamente más desfavorables. Dado que los años desfavorables para el cultivo del cereal, especialmente aquellos con eventos cálidos tempranos y/o sequías primaverales con probabilidad serán cada más frecuente, los sistemas agroforestales ofrecen mayor estabilidad interanual y seguridad alimentaria frente al cambio

climático que los cultivos abiertos (Hernández-Morcillo et al., 2018; Mosquera-Losada et al., 2018; Raj et al., 2020). Este eventual beneficio de los sistemas agroforestales será mayor aún si se utilizan las variedades mejor adaptadas a la sombra y se manejan adecuadamente los posibles déficit de agua y nutrientes que pudiera producir la competencia del arbolado.

En ambos ensayos de campo, en todos los años estudiados, el sistema agroforestal de arbolado de nogal con cereal de invierno presentó un *LER* mayor que la plantación pura de nogal y el monocultivo de cereal por separado para ambas especies (trigo y especialmente cebada), que incluso superó el reportado por otros autores en sistemas silvoagrícolas similares con trigo y nogal (Duan et al., 2017; Graves et al., 2007; Zhang et al., 2015). Esto evidencia que, el sistema agroforestal, a pesar de la posible reducción de la producción de cereal y de madera en comparación a sus monocultivos, presenta una mayor relación equivalente de territorio, es decir, un uso más eficiente de la tierra y mayor productividad global.

Estos resultados ponen de manifiesto el gran potencial de este tipo de sistemas en el contexto global de escasez de alimentos y aumento de la población, representando un modelo de gestión sostenible y de mitigación y adaptación al cambio climático, que se prevé especialmente acentuado en el área mediterránea en las próximas décadas.

Además, la expansión en los últimos años de las centrales fotovoltaicas en Europa ha abierto la posibilidad producir energía renovable al mismo tiempo que alimentos en estas superficies, dedicadas anteriormente, en su mayoría, a la agricultura. Al igual que ocurre en los sistemas agroforestales, la combinación en un mismo terreno de paneles fotovoltaicos con cultivos permite un mayor aprovechamiento de la superficie, recibiendo el nombre de "agrivoltaicas". Este tipo de sistemas ha sido objeto de investigación reciente (Dupraz et al., 2011; Weselek et al., 2019), señalando la oportunidad que suponen en el contexto global de cambio climático y reseñando algunas de las limitaciones que conllevan, como la sombra generada por los paneles fotovoltaicos. Es en este sentido donde, precisamente, la selección de variedades de cereal adaptadas a la sombra artificial en las condiciones mediterráneas del centro peninsular es de gran utilidad para garantizar el éxito de este tipo de sistemas en España, uno de los países de la Unión Europea que más superficie agrícola ha convertido en los últimos años para la producción de energía solar.

CONCLUSIONES
GENERALES

CONCLUSIONES GENERALES

I. El arbolado en el sistema agroforestal amortiguó las altas temperaturas durante la primavera, protegiendo al cereal en las etapas de floración y formación de grano. Además, lejos de competir por el agua disponible, mejoró el estado hídrico del cereal en comparación con el monocultivo. Sin embargo, aunque el contenido de P aumentó en el sistema agroforestal, tanto en suelo como en el cereal, con el N ocurrió lo contrario, mostrando un efecto competitivo.

II. La sombra, tanto artificial como la del arbolado, aceleró el crecimiento de trigo y cebada hasta la fase de grano lechoso. No obstante, existió gran diversidad de respuesta entre las variedades, especialmente en el trigo. Los ciclos de crecimiento más avanzados en ambas especies se correlacionaron con mayores producciones de grano.

III. El conjunto de rasgos funcionales del cereal separó claramente las plantas crecidas en los diferentes niveles de sombra artificial, siendo más evidente para la cebada que para el trigo. La cebada presentó una fuerte aclimatación fotosintética a la sombra, que, sin embargo, no estuvo directamente relacionada con su aumento de producción de grano en sombra. El trigo, por su parte, desarrolló una mayor adaptación morfológica. La sombra redujo los contenidos de glucosa y almidón en las hojas del cereal, atenuándose en las variedades menos precoces.

IV. Contrariamente a estudios anteriores, la sombra aumentó la producción de cebada (en todas sus variedades) y trigo (especialmente en las variedades tardías) respecto al cultivo a plena luz en el experimento en condiciones controladas. No obstante, en el sistema agroforestal, el efecto neto del arbolado dependió de las condiciones climatológicas de cada año y de las variedades utilizadas. Se demostró que el sistema agroforestal fue beneficioso en los años poco favorables para el cereal (escasez de precipitaciones y primaveras calurosas), resultando perjudicial en los años más productivos. No obstante, el arbolado mejoró siempre la calidad (contenido de nutrientes) de grano del cereal.

V. Las condiciones de sombra impuestas en los sistemas agroforestales obligan a realizar una selección previa del cultivo intercalar. El ensayo realizado en condiciones controladas para conocer la respuesta a la sombra de las diferentes especies y variedades de cereal, ha demostrado que la cebada es una especie más adecuada que el trigo para cultivarse en ambientes de luminosidad reducida. Además, se ha puesto de manifiesto que ambas especies presentan gran diversidad entre sus variedades respecto las adaptaciones a la sombra de los diferentes rasgos funcionales. Esto evidencia la necesidad de programas de selección de especies y variedades para su cultivo en condiciones de sombra.

VI. Este estudio reveló que los rasgos funcionales determinantes de la producción de grano variaron entre las especies de cereal y las condiciones de cada experimento. En el sistema agroforestal, el arbolado modificó dichos rasgos en ambas especies en comparación con el monocultivo, revelando la importancia de la selección de especies y variedades basada en los rasgos funcionales que determinan la producción de grano en sistemas agroforestales.

VII. El cereal influyó de manera distinta en el crecimiento del arbolado en los diferentes ensayos, disminuyéndolo cuando el arbolado era más joven y no afectándolo posteriormente, aunque siempre revelando una fuerte competencia por nutrientes. No obstante, la presencia del cereal mejoró el estado hídrico del arbolado a finales de verano, evitando así el estrés hídrico común en esta época.

VIII. El sistema agroforestal presentó un *LER* (producción equivalente de la tierra) mayor que la plantación pura de nogal y el monocultivo de cereal en todos los ensayos de campo realizados y para ambas especies de cereal (especialmente en la cebada), revelando un uso más eficiente de los recursos disponibles y una mayor productividad global. Esto pone de manifiesto el potencial de este tipo de sistemas en el escenario global de escasez de alimentos y cambio climático, que se prevé especialmente acentuado en el área mediterránea en las próximas décadas.

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APÉNDICES

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APÉNDICE CAPÍTULO I

Table A1. Soil properties of the three systems studied: silvoarable, monocrops, and forestry.

System	pH	OM(1)	CEC(2)	K(2)	Ca(2)	Mg(2)	Na(2)	P(3)
Silvoarable	6.0	1.1	15.7	0.36	9.8	3.4	1.2	30.2
Monocrop	6.1	1.0	15.2	0.41	9.5	3.9	0.7	38.6
Forestry	6.0	1.1	15.2	0.37	9.7	3.7	0.7	28.6

OM: Organic matter. CEC: Cation Exchange Capacity. Units: 1 [%]; 2 [meq/100gr]; 3 [mg/kg]

Table A2. Chemical analysis of tree irrigation water from the *Tajo* river. Data obtained from *Cebolla* Station from *Confederación Hidrográfica del Tajo*, 11 km from the study site.

Parameter	Content
pH	7.8
Conductivity (μS/cm)	1720
BOD (mg O_2/l)	2.3
QOD (Cr_2O_7) (mg O_2/l)	25.0
Nitrates (mg NO_3/l)	8
Nitrites (mg NO_2/l)	0.260
Ammonium (mg NH_4/l)	0.12
Total N (mg N/l)	3.8
Total P (mg P/l)	0.53
Phosphates (mg PO_4/l)	1.1
Sulphates (mg SO_4/l)	550
Chlorides (mg Cl/l)	200
Fluorides (mg F/l)	0.37
Calcium (mg Ca/l)	170
Magnesium (mg Mg/l)	55
Sodium (mg Na/l)	160
Potassium (mg K/l)	9

Table A3. Univariate tests of significance for grain and biomass yield (Mg ha^{-1}), harvest index and weight of 1000 grains (g).

	Degrees of freedom	Grain yield (Mg ha-1)		Biomass yield (Mg ha-1)		Harvest index		Weight of 1000 grains (g)	
		F	p	F	p	F	p	F	p
Intercept	1	401.5535	0.000000	3109.080	0.000000	543.6843	0.000000	868.7856	0.000000
Year	2	21.8340	0.000147	80.165	0.000000	41.0904	0.000008	3.7802	0.056949
System	1	10.9640	0.006655	55.124	0.000007	1.4953	0.246494	2.6974	0.120859
Species	1	3.9555	0.071727	30.621	0.000142	17.8527	0.001370	14.5144	0.002693
Year*System	2	9.1954	0.004475	98.638	0.000000	5.4986	0.022086	8.1967	0.009620
Year*Species	2	0.4709	0.636479	5.091	0.027110	1.1017	0.366314	0.3746	0.696155
System*Species	1	7.2753	0.020166	26.133	0.000223	2.8272	0.120237	12.7025	0.002455
Year*System*Species	2	2.2736	0.149025	7.988	0.007090	2.1493	0.162893	4.7977	0.038545
Cultivar(Year*Species)	11	2.1462	0.110518	2.212	0.101866	1.2160	0.375716	11.1710	0.000187
System*Cultivar(Year*Species)	11	3.4317	0.000145	0.941	0.500786	5.9803	0.000000	0.8476	0.592520

Table A4. Grain and biomass yield (Mg ha⁻¹± S.E.), harvest index and weight of 1000 grains (g ± S.E.) of cultivars tested in wheat and barley in the study years in monocrops (MON) and Silvoarable (SA). Significance level (t-test): *p < 0.05; ** p < 0.01; *** p < 0.001.*

Year	Species	Cultivars	Cycle	Grain yield (Mg ha-1)		Biomass yield (Mg ha-1)		Harvest index		Weight of 1000 grains (g)	
				MON	SA	MON	SA	MON	SA	MON	SA
2014	Barley	Azara	Early-Very Early	1.09 ±0.11	1.77 ±0.18	6.14 ±0.49	7.60 ±0.37	0.19 ±0.03	0.23 ±0.02	26.46 ±0.66	26.55 ±0.76
		Doña Pepa	Early-Very Early	1.30 ±0.30	1.94 ±0.15	6.50 ±0.57	7.83 ±0.41	0.19 ±0.03	0.24 ±0.01	33.11 ±1.06	32.69 ±0.52
	Wheat	Kilopondio	Medium-Early	1.20 ±0.19	1.33 ±0.08	7.92 ±0.29	8.43 ±0.39	0.15 ±0,02	0.16 ±0,01	29.19 ±0.80	24.56 ±1.01 **
		Bologna	Medium-Early	1.13 ±0.12	1.46 ±0.12	8.53 ±0.43	8.14 ±0.44	0.13 ±0.01	0.18 ±0.01	20.46 ±0.54	20.13 ±0.56
		Basic	Very Early	2.29 ±0.37	3.22 ±0.27 *	5.35 ±0.36	6.12 ±0.50	0.43 ±0,07	0.53 ±0,01 *	30.66 ±1.16	42.95 ±1.29 **
	Barley	Lukhas	Early	3.31 ±0.43	3.91 ±0.44	7.38 ±0.58	7.57 ±0.78	0.46 ±0.07	0.50 ±0.02	25.00 ±0.97	35.00 ±1.65*
		Hispanic	Very Early	3.24 ±0.22	3.68 ±0.25	4.79 ±0.12	7.24 ±0.53 **	0.68 ±0.05	0.51 ±0.01 ***	34.70 ±1.34	43.21 ±1.19*
2015	Wheat	Dulcinea	Medium	3.19 ±0.28	3.08 ±0.17	5.25 ±0.25	5.96 ±0.39	0.62 ±0.06	0.52 ±0.01 *	34.07 ±1.26	41.28 ±0.78
		Ingenio	Medium-Early	2.58 ±0.26	2.06 ±0.25	6.19 ±0.16	6.97 ±0.67	0.41 ±0.04	0.29 ±0.02 *	30.38 ±0.87	30.17 ±1.50
		Sublim	Medium	5.25 ±0.20	2.36 ±0.26 ***	7.55 ±0.25	7.70 ±0.55	0.71 ±0.03	0.30 ±0.02 ***	30.06 ±1.24	26.30 ±1.89
	Barley	Nogal	Medium-Early	2.94 ±0.21	1.81 ±0.17 ***	6.27 ±0.20	6.90 ±0.45	0.48 ±0.04	0.26 ±0.02 ***	18.48 ±0.64	21.31 ±0.77
		Meseta	Medium-Early	5.13 ±0.72	4.17 ±0.33	11.94 ±1.07	8.37 ±0.50 ***	0.42 ±0.03	0.50 ±0.03	25.77 ±0.91	25.85 ±1.26
		Hispanic	Very Early	4.67 ±0.77	2.60 ±0.19 ***	11.23 ±1.48	7.51 ±0.42 ***	0.41 ±0.02	0.35 ±0.02	26.83 ±1.78	25.57 ±1.39
2016	Wheat	Ingenio	Medium-Early	3.67 ±0.56	1.96 ±0.19 ***	17.52 ±1.20	8.80 ±0.90 ***	0.21 ±0.02	0.23 ±0.02	23.45 ±1.36	20.57 ±0.69
		Botticelli	Medium-Early	4.05 ±0.42	2.03 ±0.27 ***	15.4 ±1.07	8.92 ±0.81 ***	0.26 ±0.02	0.22 ±0.02	20.73 ±1.69	21.00 ±1.36
		Nogal	Medium-Early	4.20 ±0.31	2.54 ±0.26 ***	17.17 ±0.84	8.78 ±0.72 ***	0.24 ±0.01	0.29 ±0.01	18.94 ±1.30	20.57 ±0.69
		Idalgo	Very Early	4.85 ±0.70	2.21 ±0.31 ***	18.29 ±1.00	8.67 ±0.85 ***	0.27 ±0.04	0.25 ±0.02	22.56 ±1.69	20.84 ±1.26
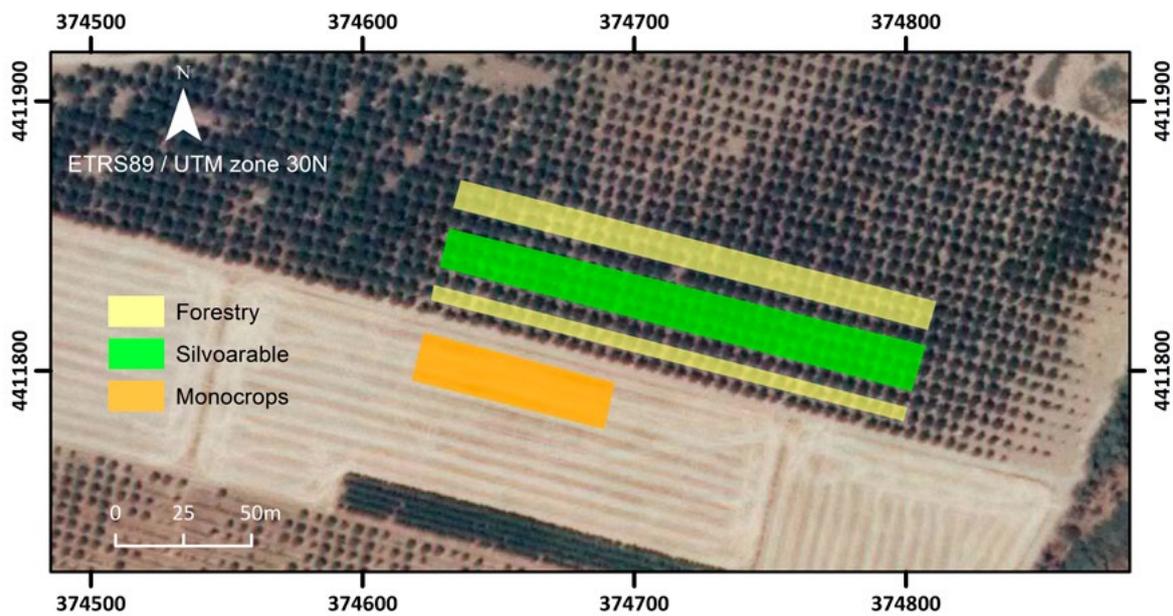
Figure A1. Plot arrangement of the different treatments in the study site.

Figure A2. Silvoarable system plot (left) and cereal monocrops (right).
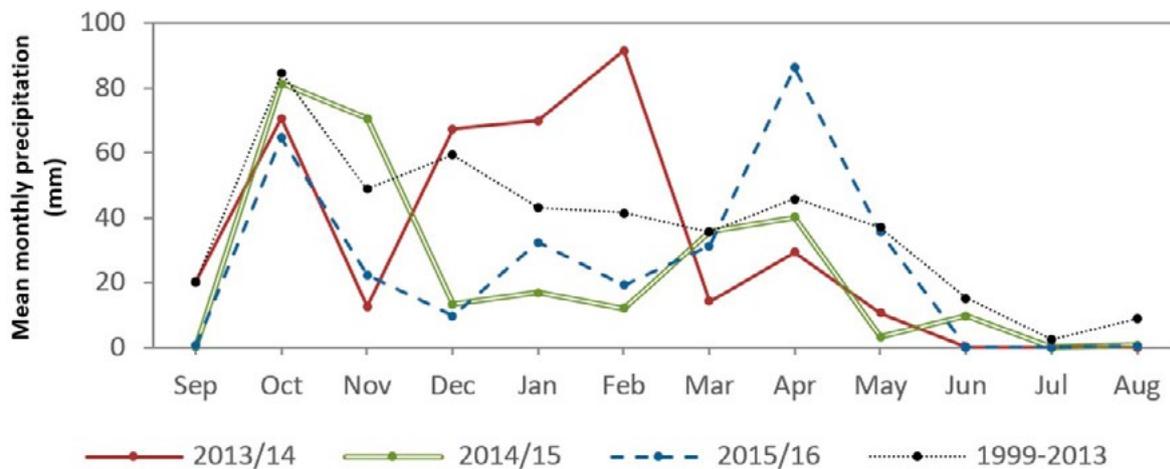
Figure A3. Mean monthly precipitation (mm) during 2013/14, 2014/15 and 2015/16 growing seasons and average value for the period 1999-2013. Source: Based on data from *Vegas de San Antonio* weather station.

APÉNDICE CAPÍTULO III

Table A1. Greenhouse parameters (PAR, temperature and relative humidity) in the shading levels studied (S0, S1 and S2) in the anthesis period. Data represents means ± S.E. No significant differences were found in mean values among irradiance treatments.

Irradiance	Mean PAR (μmol photons m^{-2} s^{-1})	Mean temperature (°C)	Mean relative humidity (%)
S0	1182.09 ± 48.39	22.40 ± 0.49	40.63 ± 3.74
S1	897.95 ± 46.75	23.67 ± 0.23	40.32 ± 3.88
S2	630.60 ± 35.73	21.98 ± 0.41	41.13 ± 3.54

Table A2. Zadoks stages reached by the wheat cultivars studied in the different shading levels (S0, S1 and S2). Data represents means ± S.E. (n=6). Different letters indicate significant differences between cultivars in each irradiance level (p < 0.05).

Species	Irradiance	Precocity	Cultivar (code)	Days to complete booting Z49 (pre-shading)
Wheat	S0	Very Early	W1 Nogal	138.0 ± 0.0 **a**
			W2 Nudel	136.7 ± 1.3 **b**
			W3 Tocayo	130.0 ± 0.0 **c**
		Early	W4 Algoritmo	138.0 ± 0.0 **a**
			W5 Paledor	138.0 ± 0.0 **a**
			W6 Solehio	138.0 ± 0.0 **a**
		Medium	W7 Toskani	138.0 ± 0.0 **a**
			W8 Somontano	138.0 ± 0.0 **a**
			W9 Nemo	138.0 ± 0.0 **a**
	S1	Very Early	W1 Nogal	138.0 ± 0.0 **a**
			W2 Nudel	138.0 ± 0.0 **a**
			W3 Tocayo	128.0 ± 1.0 **b**
		Early	W4 Algoritmo	138.0 ± 0.0 **a**
			W5 Paledor	138.0 ± 0.0 **a**
			W6 Solehio	138.0 ± 0.0 **a**
		Medium	W7 Toskani	138.0 ± 0.0 **a**
			W8 Somontano	138.0 ± 0.0 **a**
			W9 Nemo	138.0 ± 0.0 **a**
	S2	Very Early	W1 Nogal	138.0 ± 0.0 **a**
			W2 Nudel	138.0 ± 0.0 **a**
			W3 Tocayo	128.5 ± 0.8 **b**
		Early	W4 Algoritmo	138.0 ± 0.0 **a**
			W5 Paledor	138.0 ± 0.0 **a**
			W6 Solehio	138.0 ± 0.0 **a**
		Medium	W7 Toskani	138.0 ± 0.0 **a**
			W8 Somontano	138.0 ± 0.0 **a**
			W9 Nemo	138.0 ± 0.0 **a**

Days to middle heading Z55 DH	Days to complete flowering Z69 DF	Days to start milk development Z70 DM	Days to start dough development Z80 DD	Days to start ripening Z90 DR
148.3 ± 0.3 **cd**	154.3 ± 2.0 **bcd**	163.0 ± 0.0 **cd**	183.5 ± 2.0 **bc**	195.2 ± 3.1 **bc**
147.5 ± 0.5 **d**	154.0 ± 1.8 **cd**	163.0 ± 0.0 **cd**	180.5 ± 1.5 **c**	191.0 ± 2.2 **b**
145.0 ± 0.0 **e**	150.8 ± 0.8 **d**	1613 ± 1.05 **d**	180.5 ± 1.5 **c**	191.2 ± 2.2 **c**
148.3 ± 0.3 **cd**	157.7 ± 1.6 **abc**	163.0 ± 0.0 **cd**	183.5 ± 2.0 **bc**	195.3 ± 3.0 **bc**
149.7 ± 0.3 **bc**	160.7 ± 0.8 **a**	166.2 ± 2.0 **bc**	186.5 ± 1.5 **ab**	199.3 ± 2.3 **ab**
150.3 ± 0.3 **ab**	158.0 ± 0.0 **ab**	169.7 ± 1.3 **ab**	188.0 ± 0.0 **a**	201.0 ± 0.4 **a**
152.0 ± 0.0 **a**	159.7 ± 1.0 **a**	172.3 ± 2.5 **a**	188.0 ± 0.0 **a**	201.7 ± 0.3 **a**
148.7 ± 0.6 **bc**	157.5 ± 1.1 **abc**	160.5 ± 1.1 **d**	188.0 ± 0.0 **a**	201.4 ± 0.6 **a**
150.7 ± 1.6 **ab**	155.7 ± 1.8 **bc**	163.0 ± 0.0 **cd**	188.0 ± 0.0 **a**	201.3 ± 0.4 **a**
148.0 ± 0.0 **b**	150.0 ± 0.0 **e**	162.2 ± 0.8 **b**	181.3 ± 2.2 **bc**	192.7 ± 3.0 **bc**
148.0 ± 0.0 **b**	150.0 ± 0.0 **e**	163.0 ± 0.0 **b**	176.8 ± 2.7 **cd**	188.3 ± 3.1 **cd**
141.3 ± 2.3 **c**	152.7 ± 1.7 **d**	163.0 ± 0.0 **b**	172.3 ± 1.3 **d**	182.2 ± 1.2 **d**
148.7 ± 0.4 **b**	158.7 ± 0.4 **ab**	163.0 ± 0.0 **b**	188.0 ± 0.0 **a**	201.3 ± 0.4 **a**
151.0 ± 1.0 **ab**	160.5 ± 0.5 **a**	164.6 ± 1.6 **b**	186.5 ± 1.5 **a**	199.7 ± 2.3 **a**
149.3 ± 0.4 **b**	158.3 ± 0.3 **ab**	163.0 ± 0.0 **b**	185.0 ± 1.9 **ab**	197.0 ± 2.9 **ab**
154.0 ± 1.3 **a**	158.0 ± 0.0 **b**	169.7 ± 3.2 **a**	188.0 ± 0.0 **a**	201.1 ± 0.6 **a**
151.0 ± 1.0 **ab**	159.7 ± 0.3 **ab**	164.3 ± 1.3 **b**	186.5 ± 1.5 **a**	199.0 ± 2.3 **a**
150.3 ± 1.2 **b**	155.3 ± 1.7 **c**	162.2 ± 0.8 **b**	186.5 ± 1.5 **a**	199.4 ± 2.1 **a**
144.0 ± 1.0 **e**	151.3 ± 1.3 **c**	164.3 ± 1.3 **b**	188.0 ± 0.0 **a**	201.7 ± 0.3 **a**
146.0 ± 0.0 **de**	150.0 ± 0.0 **c**	163.0 ± 0.0 **b**	188.0 ± 0.0 **a**	201.3 ± 0.4 **a**
139.7 ± 1.1 **f**	150.0 ± 0.0 **c**	163.0 ± 0.0 **b**	183.0 ± 1.0 **c**	190.3 ± 2.3 **c**
148.0 ± 0.0 **cd**	158.0 ± 0.0 **a**	163.0 ± 0.0 **b**	188.0 ± 0.0 **a**	201.3 ± 0.4 **a**
150.3 ± 1.2 **b**	158.3 ± 0.3 **a**	163.0 ± 0.0 **b**	186.5 ± 1.5 **ab**	199.0 ± 2.3 **ab**
149.3 ± 0.4 **bc**	158.0 ± 0.0 **a**	163.0 ± 0.0 **b**	188.0 ± 0.0 **a**	201.3 ± 0.4 **a**
156.0 ± 0.0 **a**	158.0 ± 0.0 **a**	168.3 ± 2.7 **a**	188.0 ± 0.0 **a**	201.1 ± 0.7 **a**
150.7 ± 1.1 **b**	158.0 ± 0.0 **a**	163.0 ± 0.0 **b**	188.0 ± 0.0 **a**	201.5 ± 0.4 **a**
149.7 ± 0.8 **bc**	155.3 ± 1.7 **b**	164.3 ± 1.3 **b**	185.0 ± 1.9 **bc**	197.0 ± 2.9 **b**

Table A3. Zadoks stages reached by the barley cultivars studied in the different shading levels (S0, S1 and S2). Data represents means ± S.E. (n=6). Different letters indicate significant differences between cultivars in each irradiance level (p < 0.05).

Species	Irradiance	Precocity	Cultivar (code)	Days to complete booting Z49 (pre-shading)
Barley	S0	Very Early	B1 Hispanic	134.0 ± 1.8 **b**
			B2 Lavanda	138.0 ± 0.0 **a**
			B3 Luzia	138.0 ± 0.0 **a**
		Early	B4 Kalea	136.7 ± 1.3 **a**
			B5 Lagalia	138.0 ± 0.0 **a**
			B6 Carolina	136.7 ± 1.3 **a**
		Medium	B7 Meseta	138.0 ± 0.0 **a**
			B8 Ibaiona	138.0 ± 0.0 **a**
			B9 Crescendo	138.0 ± 0.0 **a**
	S1	Very Early	B1 Hispanic	135.3 ± 1.7 **b**
			B2 Lavanda	138.0 ± 0.0 **a**
			B3 Luzia	136.7 ± 1.3 **ab**
		Early	B4 Kalea	138.0 ± 0.0 **a**
			B5 Lagalia	138.0 ± 0.0 **a**
			B6 Carolina	138.0 ± 0.0 **a**
		Medium	B7 Meseta	138.0 ± 0.0 **a**
			B8 Ibaiona	138.0 ± 0.0 **a**
			B9 Crescendo	138.0 ± 0.0 **a**
	S2	Very Early	B1 Hispanic	131.3 ± 1.3 **c**
			B2 Lavanda	138.0 ± 0.0 **a**
			B3 Luzia	134.0 ± 1.8 **b**
		Early	B4 Kalea	136.7 ± 1.3 **a**
			B5 Lagalia	138.0 ± 0.0 **a**
			B6 Carolina	138.0 ± 0.0 **a**
		Medium	B7 Meseta	138.0 ± 0.0 **a**
			B8 Ibaiona	138.0 ± 0.0 **a**
			B9 Crescendo	138.0 ± 0.0 **a**

Days to middle heading Z55 DH	Days to complete flowering Z69 DF	Days to start milk development Z70 DM	Days to start dough development Z80 DD	Days to start ripening Z90 DR
150.3 ± 2.3 **abc**	156.8 ± 1.3 **ab**	161.0 ± 2.2 **ab**	176.7 ± 3.6 **c**	189.2 ± 4.2 **c**
150.3 ± 0.3 **abc**	155.0 ± 0.0 **b**	158.0 ± 0.0 **b**	180.5 ± 1.5 **bc**	191.2 ± 2.2 **c**
150.3 ± 0.3 **abc**	157.0 ± 0.6 **ab**	161.3 ± 1.1 **ab**	180.5 ± 1.5 **bc**	193.0 ± 2.5 **bc**
150.0 ± 0.7 **bc**	156.8 ± 0.9 **ab**	160.5 ± 1.2 **ab**	186.5 ± 1.5 **a**	201.7 ± 0.3 **a**
153.7 ± 1.4 **a**	156.8 ± 0.9 **ab**	161.3 ± 1.1 **ab**	186.5 ± 1.5 **a**	199.7 ± 2.9 **ab**
149.2 ± 1.1 **c**	158.5 ± 1.8 **a**	161.0 ± 2.2 **ab**	183.5 ± 2.04 **ab**	195.5 ± 2.9 **abc**
152.8 ± 1.4 **ab**	158.2 ± 1.5 **ab**	162.7 ± 1.9 **a**	185.0 ± 1.9 **ab**	199.3 ± 2.3 **ab**
153.7 ± 1.4 **a**	158.0 ± 1.6 **ab**	161.8 ± 2.1 **ab**	188.0 ± 0.0 **a**	201.3 ± 0.4 **a**
149.3 ± 0.4 **bc**	155.2 ± 1.2 **ab**	159.7 ± 1.1 **ab**	183.5 ± 2.0 **ab**	195.3 ± 3.0 **abc**
148.7 ± 1.8 **b**	158.7 ± 0.4 **ab**	162.7 ± 1.9 **ab**	182.2 ± 2.9 **abc**	193.8 ± 3.8 **abc**
149.3 ± 0.4 **ab**	156.7 ± 1.3 **b**	162.2 ± 0.8 **ab**	180.7 ± 2.6 **bc**	191.5 ± 3.5 **bc**
150.0 ± 0.52 **ab**	159.3 ± 0.4 **ab**	159.7 ± 1.1 **bc**	179.3 ± 3.1 **c**	190.3 ± 3.9 **c**
150.0 ± 0.7 **ab**	158.7 ± 0.4 **ab**	162.7 ± 1.9 **ab**	188.0 ± 0.0 **a**	201.3 ± 0.4 **a**
149.7 ± 0.3 **ab**	160.0 ± 0.0 **a**	158.0 ± 0.0 **c**	177.8 ± 2.1 **c**	190.5 ± 2.3 **c**
148.7 ± 0.4 **b**	159.7 ± 0.3 **a**	158.8 ± 0.8 **bc**	182.2 ± 2.7 **abc**	195.2 ± 3.1 **abc**
150.0 ± 0.0 **ab**	158.3 ± 0.3 **ab**	162.2 ± 0.8 **ab**	181.3 ± 2.2 **bc**	192.8 ± 2.9 **bc**
151.0 ± 0.7 **ab**	156.7 ± 1.3 **b**	165.7 ± 1.7 **a**	186.5 ± 1.5 **ab**	199.8 ± 2.2 **ab**
151.8 ± 2.3 **a**	158.5 ± 2.0 **ab**	161.8 ± 2.1 **abc**	183.5 ± 2.0 **abc**	195.0 ± 3.1 **abc**
149.0 ± 0.4 **a**	153.8 ± 1.3 **ab**	158.8 ± 0.8 **ab**	178.0 ± 3.4 **b**	189.2 ± 4.2 **b**
149.0 ± 0.7 **a**	154.8 ± 1.6 **ab**	160.5 ± 1.1 **a**	181.5 ± 2.2 **ab**	192.7 ± 3.0 **ab**
148.0 ± 1.9 **ab**	154.3 ± 1.5 **ab**	159.7 ± 1.1 **ab**	182.0 ± 2.7 **ab**	195.0 ± 3.1 **ab**
148.0 ± 0.5 **ab**	154.7 ± 1.1 **ab**	158.8 ± 0.8 **ab**	185.0 ± 1.9 **a**	197.3 ± 3.0 **ab**
149.3 ± 1.9 **a**	154.7 ± 1.1 **ab**	158.8 ± 0.8 **ab**	182.0 ± 1.9 **ab**	192.7 ± 3.0 **ab**
144.7 ± 1.8 **b**	151.7 ± 1.1 **b**	158.0 ± 0.0 **b**	183.5 ± 2.0 **ab**	195.0 ± 3.1 **ab**
150.3 ± 1.3 **a**	154.7 ± 1.1 **ab**	158.8 ± 0.8 **ab**	183.5 ± 2.0 **ab**	195.0 ± 3.1 **ab**
149.0 ± 0.7 **a**	155.2 ± 1.2 **a**	159.7 ± 1.1 **ab**	187.0 ± 1.2 **a**	199.7 ± 2.3 **a**
149.7 ± 0.8 **a**	154.2 ± 0.8 **ab**	158.0 ± 0.0 **b**	185.0 ± 1.90 **a**	197.0 ± 2.9 **ab**

Table A4. P-values of the influence factors: irradiance, precocity and cultivar and their respective interacions with irradiance. Data are presented separately by species for all the parameters studied: grain yield, biomass yield, harvest index, plant biomass, number of spikes, number of grains per spike, weight of 1000 grains, plant height, leaf area, leaf mass area (LMA), SPAD value, electron transport rate (ETR), non-photochemical quenching (NPQ), leaf glucose, starch, N, P and K and grain N, P and K. Irradiance (n=54), precocity (n=18), and cultivar (n=6).

Species	Factors	Degrees of freedom	Grain yield	Biomass yield	Harvest Index	Plant biomass	Number of spikes	Grains per spike	Weight of 1000 grains	Plant height
Wheat	Irradiance	2	**0.000**	0.059	**0.038**	**0.026**	0.326	0.173	**0.002**	**0.000**
	Precocity	2	**0.000**	0.668	**0.000**	0.854	0.411	**0.000**	**0.029**	**0.000**
	Cultivar	6	**0.000**	**0.037**	**0.034**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
	I x P	4	0.136	0.485	**0.044**	0.769	0.837	0.359	0.109	0.546
	I x C	12	0.273	0.315	**0.043**	0.261	0.702	0.349	0.152	0.105
Barley	Irradiance	2	**0.000**	**0.002**	0.106	0.670	0.166	**0.000**	**0.000**	**0.000**
	Precocity	2	0.249	**0.189**	0.173	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
	Cultivar	6	**0.014**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
	I x P	4	0.816	0.533	0.716	0.510	0.912	0.478	0.900	0.735
	I x C	12	0.328	0.296	0.498	0.197	0.131	**0.009**	0.167	0.709

Leaf area	LMA	SPAD	ETR	NPQ	Leaf gluco-se	Leaf starch	Leaf N	Leaf P	Leaf K	Grain N	Grain P	Grain K
0.000	**0.000**	**0.000**	0.583	**0.040**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.007**	**0.000**	0.166
0.000	0.392	**0.031**	**0.000**	**0.000**	**0.002**	**0.000**	**0.000**	**0.000**	**0.004**	**0.000**	**0.000**	**0.158**
0.000	0.993	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.217	**0.001**
0.705	0.376	**0.000**	0.700	**0.049**	**0.000**	**0.000**	**0.000**	0.190	**0.000**	**0.009**	0.094	0.114
0288	0.275	0.129	**0.000**	0.065	**0.000**	**0.000**	**0.000**	**0.003**	**0.000**	0.698	0.230	0.600
0.012	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.247	**0.000**	**0.003**
0.000	0.958	0.566	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.011**	**0.000**	0.423	0.910	0.075
0.000	**0.019**	0.372	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.004**	0.153	**0.000**
0.427	0.835	0.721	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.018**	**0.016**	0.365	0.342	0.563
0.102	0.230	0.564	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.054	0.085	0.784	**0.037**	**0.001**

Table A5. Parameters studied in wheat cultivars of the precocity categories calculated (P1, P2 and P3) in the different shading levels (S0, S1 and S2). Data represents means ± S.E. (n=6). LMA: leaf mass area; ETR: electron transport rate and NPQ: non-photochemical quenching. All weight units were referred to dry matter.

Species	Precocity measured	Cultivar (code)	Irradiance	Grain yield (g pot⁻¹)	Biomass yield (g pot⁻¹)	Harvest Index	Plant biomass (g)	Number of spikes per pot	Grains per spike	Weight of 1000 grains (g)	Plant height (cm)
Wheat	P1	Nogal W1	S0	4.93 ± 0.45	11.43 ± 0.91	0.43 ± 0.01	2.28 ± 0.16	2.00 ± 0.58	29.96 ± 0.95	32.76 ± 2.17	54.43 ± 1.63
			S1	4.24 ± 0.25	16.20 ± 3.22	0.30 ± 0.04	3.10 ± 0.72	1.50 ± 0.50	31.42 ± 1.80	26.69 ± 0.95	54.04 ± 2.12
			S2	4.83 ± 0.37	12.73 ± 1.19	0.39 ± 0.03	2.24 ± 0.08	2.00 ± 1.06	32.25 ± 2.25	30.00 ± 2.20	60.25 ± 2.48
		Nudel W2	S0	5.48 ± 0.70	15.26 ± 1.11	0.35 ± 0.02	2.23 ± 0.06	2.40 ± 0.87	33.46 ± 6.4	28.97 ± 3.17	53.20 ± 0.78
			S1	6.35 ± 0.40	15.74 ± 1.27	0.41 ± 0.02	2.31 ± 0.06	3.17 ± 0.70	27.25 ± 1.34	36.31 ± 1.90	52.27 ± 0.86
			S2	6.86 ± 0.40	16.52 ± 0.70	0.42 ± 0.02	2.34 ± 0.09	4.00 ± 0.52	29.63 ± 2.12	33.56 ± 1.27	57.74 ± 1.67
		Tocayo W3	S0	5.62 ± 0.45	14.50 ± 1.23	0.39 ± 0.02	2.065 ± 0.08	3.83 ± 0.79	27.67 ± 0.94	31.04 ± 0.78	49.83 ± 1.31
			S1	7.06 ± 0.82	15.83 ± 1.10	0.44 ± 0.03	2.27 ± 0.09	3.67 ± 0.71	27.96 ± 1.15	37.66 ± 2.66	49.46 ± 1.04
			S2	6.58 ± 0.31	15.35 ± 0.63	0.43 ± 0.01	2.23 ± 0.10	3.33 ± 0.56	27.42 ± 1.50	36.09 ± 2.18	58.75 ± 1.43
	P2	Algoritmo W4	S0	4.98 ± 0.50	13.86 ± 0.72	0.36 ± 0.04	2.35 ± 0.13	2.00 ± 0.52	34.83 ± 1.45	27.73 ± 1.47	54.45 ± 2.37
			S1	5.57 ± 0.65	12.99 ± 0.76	0.42 ± 0.04	2.41 ± 0.21	1.33 ± 0.42	34.88 ± 2.53	31.84 ± 2.23	55.10 ± 2.21
			S2	4.65 ± 0.52	12.72 ± 0.50	0.37 ± 0.04	2.28 ± 0.23	1.67 ± 0.49	32.96 ± 3.09	26.53 ± 2.58	64.65 ± 1.73
		Somontano W8	S0	5.24 ± 0.40	13.92 ± 0.50	0.38 ± 0.03	1.99 ± 0.08	4.00 ± 0.73	27.00 ± 1.15	31.04 ± 2.19	48.00 ± 1.07
			S1	6.00 ± 0.58	15.86 ± 1.58	0.38 ± 0.02	2.14 ± 0.11	4.00 ± 0.73	27.00 ± 0.52	30.96 ± 1.08	51.71 ± 1.90
			S2	5.76 ± 0.68	15.30 ± 1.15	0.37 ± 0.03	2.09 ± 0.10	4.17 ± 0.54	27.75 ± 1.76	28.13 ± 1.36	55.65 ± 1.33
		Nemo W9	S0	5.30 ± 0.51	13.39 ± 0.80	0.39 ± 0.02	2.33 ± 0.17	3.00 ± 0.84	31.00 ± 2.19	31.41 ± 2.14	53.07 ± 2.06
			S1	6.59 ± 0.26	15.98 ± 0.83	0.42 ± 0.02	2.66 ± 0.10	2.50 ± 0.56	33.54 ± 1.58	34.09 ± 1.13	53.42 ± 1.11
			S2	5.96 ± 0.69	15.26 ± 0.91	0.38 ± 0.03	2.36 ± 0.15	3.00 ± 0.58	37.33 ± 5.23	27.89 ± 3.29	60.70 ± 1.70

Leaf area (cm^{-2})	LMA (mg cm^{-2})	SPAD	ETR	NPQ	Glucose (mg g leaf^{-1})	Starch (mg g leaf^{-1})	N (mg g leaf^{-1})	P (mg g leaf^{-1})	K (mg g leaf^{-1})	N (mg g grain^{-1})	P (mg g grain^{-1})	K (mg g grain^{-1})
2.91 ± 0.40	14.12 ± 2.10	36.40 ± 2.49	290.85 ± 3.80	2.18 ± 0.02	68.10 ± 3.62	6.49 ± 0.35	34.27 ± 1.82	1.71 ± 0.09	11.74 ± 0.63	27.56 ± 0.65	2.04 ± 0.12	7.72 ± 0.65
3.89 ± 0.21	9.10 ± 0.58	34.27 ± 2.15	240.95 ± 14.23	2.25 ± 0.07	67.50 ± 3.59	4.22 ± 0.22	41.23 ± 2.19	1.83 ± 0.10	13.03 ± 0.69	27.61 ± 1.04	2.50 ± 0.10	12.03 ± 0.71
5.59 ± 0.24	10.26 ± 0.50	43.12 ± 1.37	259.45 ± 9.71	2.41 ± 0.11	54.50 ± 2.90	5.19 ± 0.28	38.38 ± 2.04	2.09 ± 0.11	17.67 ± 0.94	27.15 ± 1.00	2.35 ± 0.11	9.42 ± 1.25
4.07 ± 0.50	12.79 ± 0.38	32.53 ± 1.51	304.80 ± 15.19	1.83 ± 0.11	71.50 ± 3.81	16.81 ± 0.89	13.00 ± 0.69	1.24 ± 0.07	13.25 ± 0.71	22.72 ± 0.84	2.24 ± 0.24	12.84 ± 1.51
4.49 ± 0.50	11.08 ± 0.66	35.25 ± 1.44	298.02 ± 13.38	2.05 ± 0.12	109.80 ± 5.84	2.63 ± 0.14	39.29 ± 2.09	1.31 ± 0.07	14.64 ± 0.78	22.43 ± 1.19	1.99 ± 0.19	14.75 ± 1.40
6.12 ± 0.53	10.03 ± 0.50	47.28 ± 1.37	335.77 ± 2.64	1.69 ± 0.07	63.60 ± 3.39	4.45 ± 0.24	26.02 ± 1.38	1.67 ± 0.09	21.53 ± 1.1**5**	20.63 ± 1.01	2.46 ± 0.24	13.76 ± 0.37
4.19 ± 0.68	14.38 ± 1.44	30.62 ± 2.13	206.67 ± 8.12	2.70 ± 0.03	215.90 ± 11.49	2.41 ± 0.13	30.56 ± 1.63	1.14 ± 0.06	17.75 ± 0.95	24.48 ± 0.80	2.29 ± 0.18	12.48 ± 1.21
5.08 ± 0.63	9.85 ± 0.74	32.40 ± 1.43	235.64 ± 2.04	2.97 ± 0.03	105.70 ± 5.62	2.10 ± 0.11	36.63 ± 1.95	1.20 ± 0.06	20.13 ± 1.07	2.41 ± 1.00	1.81 ± 0.16	9.71 ± 0.60
6.31 ± 0.55	9.59 ± 0.60	41.45 ± 0.76	193.03 ± 3.71	2.60 ± 0.06	80.00 ± 4.26	2.22 ± 0.12	33.95 ± 1.81	1.51 ± 0.08	24.68 ± 1.31	2.31 ± 0.61	2.06 ± 0.15	10.06 ± 0.28
5.83 ± 0.56	12.20 ± 0.78	35.27 ± 1.58	207.68 ± 11.54	1.50 ± 0.14	85.00 ± 4.52	7.03 ± 0.37	34.37 ± 1.83	1.54 ± 0.08	12.53 ± 0.67	30.61 ± 1.14	2.39 ± 0.25	13.93 ± 1.81
5.24 ± 0.58	9.97 ± 0.64	41.62 ± 2.60	269.11 ± 5.05	1.51 ± 0.12	95.70 ± 5.09	2.26 ± 0.12	18.92 ± 1.00	1.86 ± 0.10	12.76 ± 0.68	25.07 ± 0.50	2.31 ± 0.41	12.37 ± 2.41
7.00 ± 1.00	9.36 ± 0.53	44.70 ± 2.07	248.46 ± 3.41	1.30 ± 0.11	153.40 ± 8.17	1.52 ± 0.08	18.13 ± 0.97	2.28 ± 0.12	14.07 ± 0.75	30.52 ± 1.84	2.00 ± 0.13	13.48 ± 0.98
3.56 ± 0.38	11.80 ± 0.61	28.87 ± 1.50	269.57 ± 9.08	1.89 ± 0.06	49.30 ± 2.62	1.32 ± 0.07	35.65 ± 1.89	1.87 ± 0.10	22.98 ± 1.2**2**	25.49 ± 0.80	2.41 ± 0.15	12.46 ± 1.28
3.67 ± 0.51	10.15 ± 1.18	32.73 ± 1.13	249.14 ± 8.55	1.81 ± 0.11	61.00 ± 3.25	1.30 ± 0.07	38.70 ± 2.06	1.68 ± 0.09	18.26 ± 0.97	23.88 ± 0.72	1.66 ± 0.15	11.22 ± 0.95
5.16 ± 0.61	11.15 ± 1.03	39.73 ± 1.54	251.10 ± 7.74	1.93 ± 0.10	50.40 ± 2.68	1.42 ± 0.08	19.76 ± 1.05	2.15 ± 0.11	23.88 ± 1.27	24.26 ± 1.29	2.06 ± 0.13	11.62 ± 1.35
4.22 ± 0.47	12.80 ± 0.74	35.30 ± 1.45	279.55 ± 11.66	2.33 ± 0.13	157.80 ± 8.40	0.87 ± 0.05	35.48 ± 1.89	1.36 ± 0.07	12.49 ± 0.66	23.71 ± 1.12	2.26 ± 0.19	13.79 ± 2.08
6.26 ± 0.35	9.55 ± 0.63	39.92 ± 0.91	245.02 ± 3.67	2.43 ± 0.02	99.28 ± 20.33	0.79 ± 0.04	29.38 ± 1.56	1.46 ± 0.08	14.51 ± 0.77	21.20 ± 0.64	1.77 ± 0.09	11.32 ± 1.03
5.86 ± 0.84	9.71 ± 1.08	41.47 ± 1.4**7**	246.44 ± 12.65	2.27 ± 0.05	65.60 ± 3.49	0.82 ± 0.04	21.17 ± 1.13	1.95 ± 0.10	15.45 ± 0.82	23.50 ± 1.10	1.84 ± 0.12	13.13 ± 0.99

Species	Precocity measured	Cultivar (code)	Irradiance	Grain yield (g pot^{-1})	Biomass yield (g pot^{-1})	Harvest Index	Plant biomass (g)	Number of spikes per pot	Grains per spike	Weight of 1000 grains (g)	Plant height (cm)
Wheat	P3	Paledor W5	S0	3.64 ± 0.53	13.47 ± 0.96	0.27 ± 0.04	2.41 ± 0.14	3.25 ± 0.48	28.33 ± 2.28	25.52 ± 2.00	62.20 ± 1.74
			S1	3.99 ± 0.46	13.51 ± 1.04	0.29 ± 0.02	2.40 ± 0.16	2.17 ± 0.31	28.29 ± 2.06	27.52 ± 2.46	60.89 ± 0.93
			S2	5.75 ± 0.69	14.66 ± 1.10	0.39 ± 0.02	2.37 ± 0.16	1.83 ± 0.31	34.29 ± 2.32	28.23 ± 1.89	68.73 ± 0.84
		Solehio W6	S0	3.52 ± 0.24	12.09 ± 0.87	0.29 ± 0.02	2.19 ± 0.15	2.00 ± 0.32	20.67 ± 1.06	33.01 ± 2.26	54.55 ± 0.85
			S1	5.62 ± 0.56	15.09 ± 0.51	0.37 ± 0.03	2.93 ± 0.09	1.50 ± 0.67	28.96 ± 2.09	41.28 ± 1.99	60.14 ± 1.31
			S2	4.81 ± 0.52	15.63 ± 1.17	0.32 ± 0.04	2.67 ± 0.28	2.67 ± 1.28	24.54 ± 3.08	37.00 ± 1.92	58.97 ± 1.77
		Toskani W7	S0	3.46 ± 0.55	16.38 ± 1.63	0.21 ± 0.02	2.01 ± 0.07	4.33 ± 0.56	21.29 ± 2.48	25.10 ± 3.14	56.76 ± 1.58
			S1	3.63 ± 0.50	13.97 ± 0.41	0.26 ± 0.04	1.85 ± 0.10	5.67 ± 0.76	19.67 ± 3.18	31.72 ± 2.39	58.25 ± 1.89
			S2	4.92 ± 0.43	15.59 ± 1.20	0.32 ± 0.02	2.03 ± 0.13	5.67 ± 0.56	27.54 ± 2.18	26.94 ± 1.51	67.06 ± 1.85

Leaf area (cm^{-2})	LMA (mg cm^{-2})	SPAD	ETR	NPQ	Glucose (mg g leaf^{-1})	Starch (mg g leaf^{-1})	N (mg g leaf^{-1})	P (mg g leaf^{-1})	K (mg g leaf^{-1})	N (mg g grain^{-1})	P (mg g grain^{-1})	K (mg g grain^{-1})
3.95 ± 0.55	12.94 ± 1.28	37.43 ± 2.46	273.15 ± 1.36	1.43 ± 0.07	68.40 ± 3.64	0.66 ± 0.04	66.18 ± 3.52	1.90 ± 0.10	13.89 ± 0.74	29.31 ± 0.93	2.89 ± 0.35	15.17 ± 2.66
4.40 ± 0.61	10.32 ± 0.66	38.02 ± 0.79	266.97 ± 8.55	1.45 ± 0.12	61.30 ± 3.26	4.06 ± 0.22	38.92 ± 2.07	1.74 ± 0.09	9.60 ± 0.51	29.02 ± 1.75	2.53 ± 0.18	12.80 ± 1.49
6.60 ± 0.51	10.01 ± 0.94	44.92 ± 1.70	290.99 ± 12.44	1.22 ± 0.07	62.00 ± 3.30	1.17 ± 0.06	19.89 ± 1.06	2.73 ± 0.15	15.38 ± 0.82	24.82 ± 1.35	2.62 ± 0.18	11.18 ± 1.41
2.80 ± 0.29	11.99 ± 0.69	33.25 ± 1.17	271.81 ± 4.15	1.83 ± 0.13	99.10 ± 5.28	1.6 ± 0.09	39.74 ± 2.12	1.87 ± 0.10	12.87 ± 0.69	28.41 ± 0.93	2.82 ± 0.17	12.85 ± 1.23
3.61 ± 0.40	11.47 ± 1.59	37.07 ± 1.89	282.74 ± 11.29	1.66 ± 0.22	117.00 ± 6.23	2.23 ± 0.12	21.36 ± 1.14	1.69 ± 0.09 **b**	13.51 ± 0.72	27.20 ± 2.45	1.95 ± 0.19	10.70 ± 1.10
4.59 ± 0.61	10.82 ± 0.41	40.00 ± 1.27	244.93 ± 8.86	1.80 ± 0.05	100.00 ± 5.32	2.21 ± 0.12	28.26 ± 1.50	1.98 ± 0.11	20.38 ± 1.09	27.06 ± 2.07	2.48 ± 0.15	12.43 ± 1.24
2.71 ± 0.35	16.24 ± 2.90	41.15 ± 1.09	324.17 ± 5.52	1.58 ± 0.05	82.90 ± 4.41	3.04 ± 0.16	30.04 ± 1.60	1.72 ± 0.09	16.13 ± 0.86	28.07 ± 0.83	2.93 ± 0.13	12.21 ± 1.14
3.92 ± 0.18	8.64 ± 0.53	37.77 ± 1.00	327.21 ± 1.96	1.27 ± 0.04	104.30 ± 5.55	2.62 ± 0.14	20.84 ± 1.11	1.78 ± 0.09	19.93 ± 1.06	26.17 ± 0.78	2.40 ± 0.20	8.84 ± 0.65
3.62 ± 0.36	11.90 ± 0.98	41.92 ± 1.65	319.54 ± 10.93	1.23 ± 0.05	50.20 ± 2.67	10.29 ± 0.55	26.82 ± 1.43	2.09 ± 0.11	19.88 ± 1.06	24.55 ± 1.79	2.31 ± 0.19	9.62 ± 0.84

Table A6. Parameters studied in barley cultivars of the precocity categories calculated (P1, P2 and P3) in the different shading levels (S0, S1 and S2). Data represents means ± S.E. (n=6). LMA: leaf mass area; ETR: electron transport rate and NPQ: non-photochemical quenching. All weight units were referred to dry matter.

Species	Precocity measured	Cultivar (Code)	Irradiance	Grain yield (g pot^{-1})	Biomass yield (g pot^{-1})	Harvest Index	Plant biomass (g)	Number of spikes per pot	Grains per spike	Weight of 1000 grains (g)	Plant height (cm)
Barley	P1	Hispanic B1	S0	4.77 ± 0.85	13.40 ± 1.38	0.34 ± 0.04	0.81 ± 0.09	15.17 ± 1.70	7.79 ± 0.88	44.12 ± 2.18	35.12 ± 1.65
			S1	4.87 ± 0.53	14.54 ± 0.42	0.33 ± 0.03	0.72 ± 0.03	16.83 ± 0.60	7.11 ± 0.37	43.47 ± 1.86	36.31 ± 1.22
			S2	5.73 ± 0.82	14.61 ± 1.33	0.38 ± 0.02	0.84 ± 0.90	15.33 ± 1.99	8.92 ± 1.05	39.86 ± 1.18	41.11 ± 1.37
		Lavanda B2	S0	5.89 ± 0.67	12.63 ± 1.14	0.46 ± 0.02	0.76 ± 0.07	15.33 ± 0.84	9.63 ± 0.86	37.49 ± 1.91	36.14 ± 0.91
			S1	4.91 ± 0.52	12.73 ± 0.48	0.39 ± 0.05	0.70 ± 0.04	13.67 ± 0.80	8.67 ± 0.42	35.45 ± 4.45	35.32 ± 0.98
			S2	5.90 ± 0.77	12.58 ± 1.34	0.46 ± 0.02	0.72 ± 0.08	13.00 ± 0.82	10.67 ± 1.52	34.86 ± 1.23	43.40 ± 1.79
		Meseta B7	S0	4.35 ± 0.34	8.92 ± 1.19	0.55 ± 0.10	0.83 ± 0.03	8.50 ± 0.50	10.33 ± 0.65	35.98 ± 0.96	36.03 ± 1.30
			S1	5.55 ± 0.20	11.21 ± 1.45	0.58 ± 0.13	0.90 ± 0.06	9.33 ± 0.76	10.58 ± 1.14	41.13 ± 0.90	37.49 ± 1.93
			S2	6.80 ± 0.63	14.70 ± 1.67	0.47 ± 0.01	1.01 ± 0.06	12.33 ± 1.71	14.13 ± 0.78	35.09 ± 1.55	46.55 ± 2.11
	P2	Luzia B3	S0	4.89 ± 0.46	10.53 ± 1.70	0.58 ± 0.16	0.71 ± 0.01	13.83 ± 1.54	8.08 ± 0.31	41.80 ± 2.55	33.37 ± 0.40
			S1	5.64 ± 0.41	13.99 ± 0.86	0.40 ± 0.01	0.69 ± 0.02	16.33 ± 1.99	7.46 ± 0.50	40.18 ± 1.39	34.37 ± 0.14
			S2	5.71 ± 0.47	12.49 ± 0.70	0.45 ± 0.01	0.65 ± 0.05	17.17 ± 0.87	8.59 ± 0.78	37.25 ± 0.97	42.02 ± 1.74
		Carolina B6	S0	4.71 ± 0.57	11.88 ± 0.78	0.39 ± 0.01	1.42 ± 0.13	5.83 ± 0.54	14.00 ± 1.17	46.92 ± 2.25	45.27 ± 1.84
			S1	5.99 ± 0.52	14.45 ± 0.83	0.41 ± 0.02	1.55 ± 0.09	6.50 ± 0.67	16.08 ± 0.79	45.98 ± 1.08	45.09 ± 0.95
			S2	6.04 ± 0.65	13.37 ± 1.04	0.45 ± 0.02	1.34 ± 0.09	5.33 ± 0.21	13.83 ± 1.46	43.67 ± 1.27	52.63 ± 3.13
		Crescendo B9	S0	5.97 ± 0.47	14.69 ± 0.81	0.40 ± 0.02	1.34 ± 0.05	8.33 ± 0.71	15.08 ± 0.66	41.08 ± 0.66	47.31 ± 0.97
			S1	5.20 ± 0.77	14.90 ± 0.66	0.34 ± 0.04	1.15 ± 0.09	8.67 ± 0.49	10.04 ± 1.98	45.07 ± 1.18	49.59 ± 1.67
			S2	6.51 ± 0.55	16.10 ± 0.81	0.40 ± 0.03	1.39 ± 0.10	9.83 ± 0.70	15.25 ± 1.10	39.78 ± 1.14	52.35 ± 1.99

Leaf area (cm⁻²)	LMA (mg cm⁻²)	SPAD	ETR	NPQ	Glucose (mg g leaf⁻¹)	Starch (mg g leaf⁻¹)	N (mg g leaf⁻¹)	P (mg g leaf⁻¹)	K (mg g leaf⁻¹)	N (mg g grain⁻¹)	P (mg g grain⁻¹)	K (mg g grain⁻¹)
2.26 ± 0.38	9.34 ± 1.75	30.02 ± 3.53	249.90 ± 16.66	3.38 ± 0.20	62.70 ± 3.34	22.59 ± 1.20	33.70 ± 1.80	1.30 ± 0.07	23.33 ± 1.24	24.91 ± 0.72	2.89 ± 0.14	19.32 ± 0.96
2.15 ± 0.37	8.62 ± 0.73	32.40 ± 2.31	249.10 ± 3.25	3.06 ± 0.13	47.60 ± 2.53	10.83 ± 2.26	27.96 ± 1.49	1.25 ± 0.07	25.10 ± 1.34	24.51 ± 0.74	2.80 ± 0.21	23.17 ± 1.63
1.74 ± 0.22	9.90 ± 0.56	40.32 ± 1.68	231.10 ± 3.22	3.19 ± 0.14	63.30 ± 3.37	16.09 ± 0.86	19.73 ± 1.05	1.45 ± 0.08	30.06 ± 1.60	24.96 ± 2.55	2.56 ± 0.17	20.71 ± 0.75
1.86 ± 0.21	10.41 ± 0.45	29.48 ±3.40 **b**	388.62 ± 4.54	1.35 ± 0.06	120.70 ± 6.42	27.90 ± 1.49	32.35 ± 1.72	1.25 ± 0.07	30.37 ± 1.62	21.50 ± 0.22	3.65 ± 0.71	23.74 ± 0.73
1.96 ± 0.29	7.93 ± 0.46	27.13 ± 2.48	352.09 ± 8.53	1.80 ± 0.06	121.70 ± 6.48	21.09 ± 4.39	18.56 ± 0.99	1.33 ± 0.07	31.82 ± 1.69	21.51 ± 0.68	2.32 ± 0.17	18.92 ± 1.63
2.33 ± 0.15	6.90 ± 0.32	39.68 ± 2.01	237.24 ± 16.89	3.50 ± 0.22	44.40 ± 2.36	22.27 ± 1.19	31.83 ± 1.69	1.59 ± 0.08	37.68 ± 2.01	20.81 ± 1.09	2.41 ± 0.24	17.72 ± 1.01
2.11 ± 0.22	7.74 ± 0.33	29.08 ± 1.12	289.56 ± 10.90	2.78 ± 0.10	49.70 ± 2.65	12.46 ± 0.66	49.15 ± 2.62	1.72 ± 0.09	33.56 ± 1.79	24.77 ± 0.60	3.04 ± 0.08	18.21 ± 0.69
2.31 ± 0.26	7.78 ± 0.23	30.80 ± 1.46	320.45 ± 8.66	2.22 ± 0.09	39.60 ± 2.11	11.37 ± 0.61	42.50 ± 2.23	1.78 ± 0.09	35.40 ± 1.88	24.38 ± 0.62	2.56 ± 0.13	18.58 ± 0.70
3.06 ± 0.39	6.98 ± 0.42	39.97 ± 2.12	277.28 ± 11.33	2.70 ± 0.11	35.30 ± 1.88	8.77 ± 0.47	33.02 ± 1.76	2.14 ± 0.11	33.79 ± 1.80	23.20 ± 0.78	1.98 ± 0.16	15.54 ± 1.74
2.08 ± 0.18	8.60 ± 0.48	28.45 ± 2.65	283.32 ± 14.20	3.17 ± 0.19	75.60 ± 4.02	4.45 ± 0.24	49.10 ± 2.61	1.41 ± 0.07	22.64 ± 1.21	21.33 ± 1.10	2.99 ± 0.14	23.58 ± 1.60
2.27 ± 0.14	7.58 ± 0.47	24.57 ± 2.46	278.60 ± 15.60	2.66 ± 0.27	55.20 ± 2.94	2.67 ± 0.14	56.83 ± 3.02	1.24 ± 0.07	22.96 ± 1.22	24.25 ± 2.03	2.77 ± 0.18	21.63 ± 1.04
1.77 ± 0.26	7.93 ± 0.71	39.35 ± 2.15	231.03 ± 9.70	2.85 ± 0.10	45.80 ± 2.44	8.39 ± 0.45	27.04 ± 1.44	1.75 ± 0.09	29.72 ± 1.58	22.19 ± 0.79	2.75 ± 0.10	20.49 ± 0.95
2.60 ± 0.22	8.65 ± 0.33	29.82 ± 1.03	278.01 ± 9.22	3.07 ± 0.20	110.20 ± 5.87	0.83 ± 0.04	43.46 ± 2.31	1.87 ± 0.10	24.52 ± 1.31	24.51 ± 0.78	2.91 ± 0.11	22.39 ± 1.19
2.26 ± 0.28	8.46 ± 0.41	33.33 ± 2.79	255.21 ± 8.48	3.35 ± 0.09	69.91 ± 3.72	10.44 ± 0.56	28.22 ± 1.50	1.71 ± 0.09	21.77 ± 1.59	24.46 ± 1.55	2.76 ± 0.10	19.23 ± 1.11
3.26 ± 0.22	7.76 ± 0.56	39.48 ± 1.78	269.02 ± 9.65	2.93 ± 0.04	38.80 ± 2.07	9.36 ± 0.50	22.73 ± 1.21	2.04 ± 0.11	25.76 ± 1.37	23.30 ± 1.24	2.79 ± 0.14	17.41 ± 0.65
3.47 ± 0.26	9.40 ± 0.36	28.98 ± 1.44	287.03 ± 8.34	3.38 ± 0.20	101.50 ± 5.40	5.88 ± 0.31	37.40 ± 2.00	1.28 ± 0.07	22.58 ± 1.20	21.55 ± 0.54	3.19 ± 0.82	16.62 ± 0.98
3.57 ± 0.37	8.41 ± 0.58	28.27 ± 1.24	223.17 ± 11.34	3.01 ± 0.09	57.82 ± 3.08	10.21 ± 2.14	23.02 ± 1.23	1.39 ± 0.07	24.91 ± 1.33	21.22 ± 1.22	2.08 ± 0.16	18.01 ± 0.92
3.46 ± 0.23	8.58 ± 0.42	36.87 ± 2.08	174.84 ± 13.08	4.18 ± 0.26	42.60 ± 2.27	1.69 ± 0.09	29.27 ± 1.56	1.51 ± 0.08	27.03 ± 1.44	22.47 ± 0.91	2.30 ± 0.12	18.33 ± 0.50

Species	Precocity measured	Cultivar (Code)	Irradiance	Grain yield (g pot^{-1})	Biomass yield (g pot^{-1})	Harvest Index	Plant biomass (g)	Number of spikes per pot	Grains per spike	Weight of 1000 grains (g)	Plant height (cm)
Barley	P3	Kalea B4	S0	4.67 ± 0.34	11.74 ± 0.47	0.40 ± 0.02	0.82 ± 0.06	11.67 ± 1.09	8.71 ± 0.93	41.89 ± 1.33	36.23 ± 1.28
			S1	3.18 ± 0.73	11.67 ± 1.03	0.26 ± 0.04	0.76 ± 0.07	13.83 ± 0.65	5.42 ± 1.16	45.82 ± 1.34	36.44 ± 0.62
			S2	4.91 ± 0.50	12.13 ± 0.65	0.40 ± 0.03	0.81 ± 0.06	12.33 ± 0.88	10.63 ± 0.67	35.31 ± 0.55	43.61 ± 1.09
		Lagalia B5	S0	5.31 ± 0.27	13.44 ± 0.52	0.39 ± 0.01	1.11 ± 0.06	8.50 ± 0.62	10.75 ± 0.42	44.29 ± 1.48	38.84 ± 1.35
			S1	5.79 ± 0.55	13.85 ± 0.76	0.42 ± 0.03	1.23 ± 0.08	8.50 ± 0.56	11.67 ± 1.18	44.06 ± 1.51	43.14 ± 0.89
			S2	6.97 ± 0.63	15.29 ± 1.01	0.45 ± 0.02	1.18 ± 0.09	10.33 ± 1.09	12.80 ± 1.06	42.76 ± 0.82	47.85 ± 2.31
		Ibaiona B8	S0	5.00 ± 0.34	11.84 ± 0.47	0.42 ± 0.02	0.74 ± 0.07	13.00 ± 0.97	8.42 ± 0.52	41.79 ± 1.45	36.61 ± 0.75
			S1	5.22 ± 0.76	13.23 ± 1.18	0.38 ± 0.03	0.89 ± 0.08	13.50 ± 0.76	8.75 ± 1.02	42.77 ± 1.24	40.04 ± 0.85
			S2	5.55 ± 0.44	12.77 ± 0.74	0.43 ± 0.02	0.86 ± 0.09	12.50 ± 1.38	10.33 ± 1.11	39.09 ± 2.56	44.54 ± 2.57

| Leaf area (cm^{-2})	LMA (mg cm^{-2})	SPAD	ETR	NPQ	Glucose (mg g leaf^{-1})	Starch (mg g leaf^{-1})	N (mg g leaf^{-1})	P (mg g leaf^{-1})	K (mg g leaf^{-1})	N (mg g grain^{-1})	P (mg g grain^{-1})	K (mg g grain^{-1})
2.27 ± 0.19	9.30 ± 0.59	32.80 ± 1.42	321.48 ± 6.05	2.41 ± 0.05	63.20 ± 3.36	13.46 ± 0.72	31.96 ± 1.70	1.34 ± 0.07	23.42 ± 1.25	24.34 ± 0.68	2.75 ± 0.16	18.71 ± 1.36
2.19 ± 0.26	8.08 ± 0.63	28.15 ± 1.61	239.28 ± 6.87	3.23 ± 0.12	41.20 ± 2.19	5.21 ± 0.28	25.23 ± 1.34	1.50 ± 0.08	28.76 ± 1.53	25.40 ± 2.15	3.49 ± 0.29	16.61 ± 0.83
2.52 ± 0.07	7.35 ± 0.29	37.47 ± 3.58	347.29 ± 24.33	1.88 ± 0.27	32.60 ± 1.74	12.10 ± 0.64	31.42 ± 1.67	1.59 ± 0.08	26.99 ± 1.44	22.84 ± 0.79	2.60 ± 0.12	20.05 ± 0.76
2.08 ± 0.20	9.17 ± 0.45	28.48 ± 2.06	386.59 ± 5.42	1.49 ± 0.07	129.50 ± 6.89	31.59 ± 1.68	30.82 ± 1.64	1.79 ± 0.10	31.15 ± 1.66	25.28 ± 2.69	2.95 ± 0.15	23.93 ± 1.19
2.16 ± 0.20	8.44 ± 0.59	30.03 ± 2.19	358.93 ± 6.01	1.95 ± 0.01	145.20 ± 7.73	11.34 ± 0.60	33.56 ± 1.79	1.75 ± 0.10	30.93 ± 1.65	21.75 ± 0.86	2.40 ± 0.18	22.42 ± 1.96
3.22 ± 0.54	7.67 ± 0.57	36.10 ± 2.15	282.07 ± 10.12	2.80 ± 0.19	68.00 ± 3.62	11.63 ± 0.62	35.51 ± 1.89	1.88 ± 0.10	31.44 ± 1.67	22.32 ± 0.87	2.14 ± 0.10	18.95 ± 0.60
1.98 ± 0.44	9.17 ± 0.89	28.70 ± 1.38	269.29 ± 15.42	2.80 ± 0.25	52.80 ± 2.81	2.39 ± 0.13	24.72 ± 1.32	1.35 ± 0.07	26.06 ± 1.39	25.08 ± 1.59	3.04 ± 0.15	20.83 ± 1.44
1.79 ± 0.22	7.89 ± 0.30	32.17 ± 2.23	284.23 ± 10.36	2.74 ± 0.16	51.00 ± 2.71	3.11 ± 0.17	42.61 ± 2.27	1.90 ± 0.10	30.92 ± 1.65	22.40 ± 0.49	2.25 ± 0.17	20.86 ± 0.74
2.43 ± 0.28	7.80 ± 0.53	38.53 ± 1.88	269.72 ± 14.46	2.81 ± 0.16	71.10 ± 3.78	3.48 ± 0.19	30.27 ± 1.61	1.80 ± 0.10	27.74 ± 1.48	22.40 ± 0.89	2.45 ± 0.11	21.79 ± 0.68

APÉNDICE CAPÍTULO IV
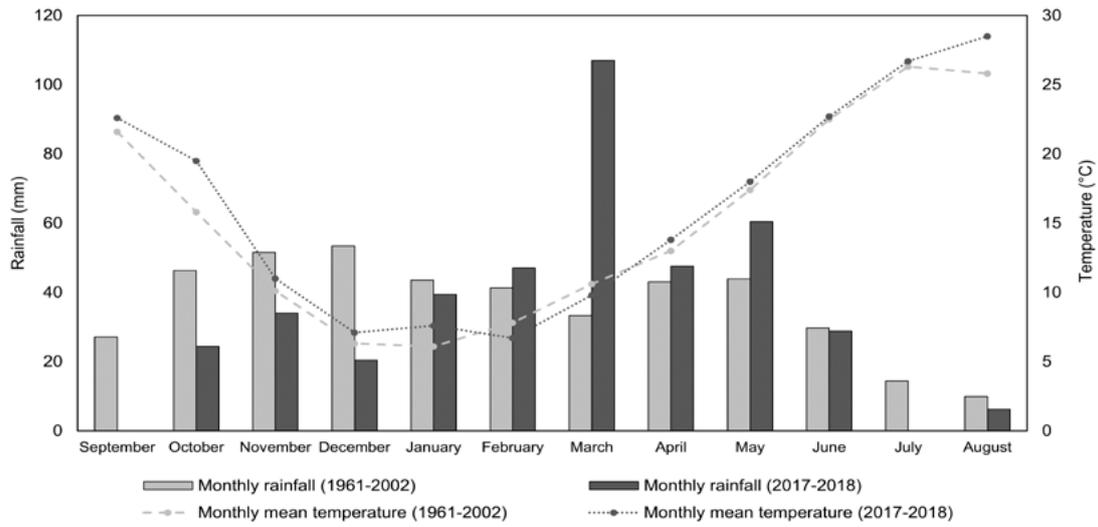
Figure A1. Thermo-pluviometric diagram of "El Carpio de Tajo" meteorological station between 1961 and 2002. The monthly rainfall and mean temperature for the agricultural year of the study (2017-2018) are shown.

Table A1. Initial soil analysis of the study site. Data represents means ± S.E.

						Soil parameters				
% C	% N	Ca (mEq 100 g soil^{-1})	Mg (mEq 100 g soil^{-1})	Na (mEq 100 g soil^{-1})	K (mEq 100 g soil^{-1})	P Olsen (mg kg soil^{-1})	Sand (%)	Clay (%)	Silt (%)	pH
1.10 ± 0.32	0.06 ± 0.00	29.04 ± 9.71	6.02 ± 0.51	0.23 ± 0.03	1.58 ± 0.05	11.68 ± 2.08	24.26 ± 2.84	4.30 ± 0.26	71.44 ± 2.81	7.39 ± 0.22

Table A2. Soil analysis (cereal pre-anthesis period, before walnut budburst) and ion exchange resins (cereal grain filling and ripening period, after walnut budburst) of total mineral N, P and K in the Agroforestry (AF), Monocrops (MC) and Forestry (FO) systems. Data represents means ± S.E. Different letters indicate significant differences between systems. Significance level: ** $p < 0.01$; *** $p < 0.001$.

|		Soil analysis (before walnut budburst)	Ion exchange resins (after walnut budburst)		
		mg total mineral N kg soil^{-1}	ppm total mineral N 85 cm^{-2}	ppm P 85 cm^{-2}	ppm K 85 cm^{-2}
Wheat	AF	2.2 ± 0.4	6.5 ± 1.2	11.7 ± 0.8 ***	55.1 ± 4.0
	MC	3.1 ± 0.8	3.1 ± 0.4	1.6 ± 0.2	67.0 ± 5.4
Barley	AF	1.9 ± 0.6 **	10.5 ± 1.2 ***	11.9 ± 0.8 ***	73.1 ± 6.4
	MC	5.3 ± 1.2	19.2 ± 2.7	1.6 ± 0.1	76.9 ± 6.2
AF	**Mean**	2.0 ± 0.4 **b**	8.5 ± 0.9	11.8 ± 0.6 **a**	64.1 ± 3.9
MC	**Mean**	4.2 ± 0.7 **a**	11.1 ± 1.9	1.6 ± 0.1 **b**	71.9 ± 4.1
FO	**Mean**	3.2 ± 0.6 **ab**	16.9 ± 4.7	10.8 ± 0.9 **a**	59.1 ± 5.4
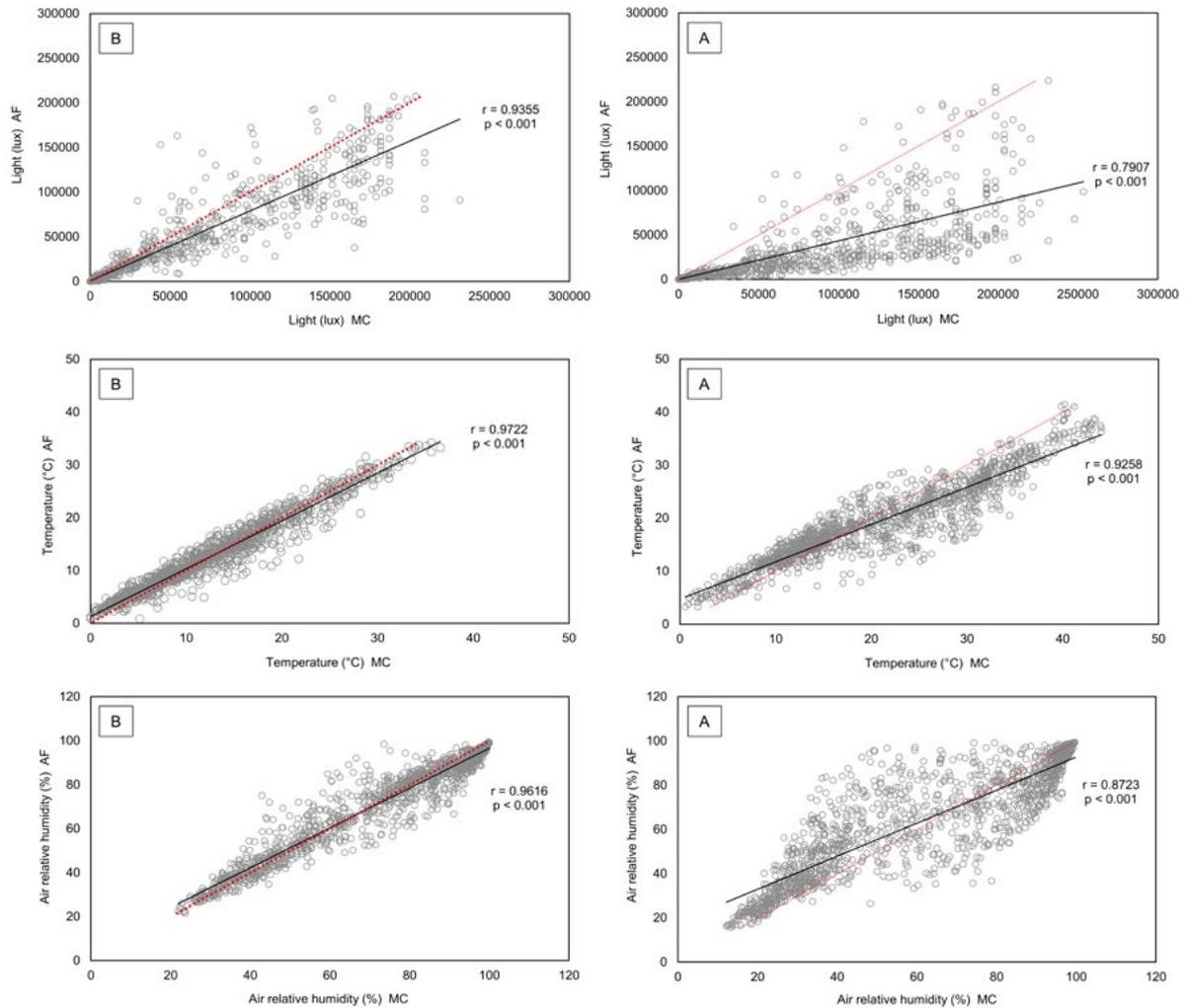
Figure A2. Scatterplots of light (lux), temperature (°C) and air relative humidity (%) in the Agroforestry (AF) and Monocrops (MC) systems before (B) and after (A) tree budburst continuous periods. Red-dotted lines represented the 1:1 line. Black lines show the linear regression in each parameter for both systems with the Pearson's correlation coefficient (r) and its significance (p-value).
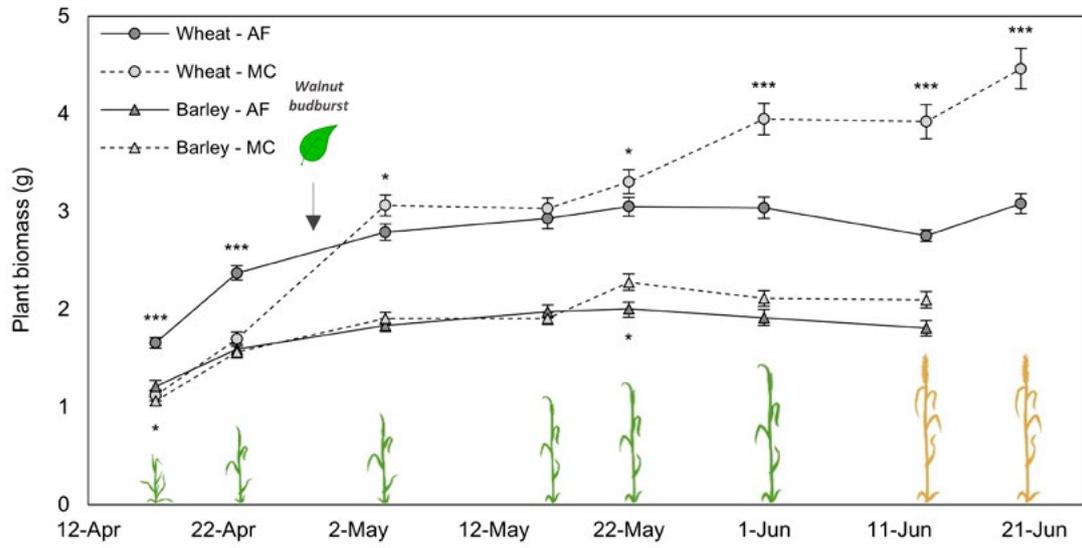
Figure A3. Evolution of plant biomass (g ± S.E.) of wheat and barley in the Agroforestry (AF) and Monocrops (MC) systems. Significance level: * p < 0.05; ** p < 0.001.
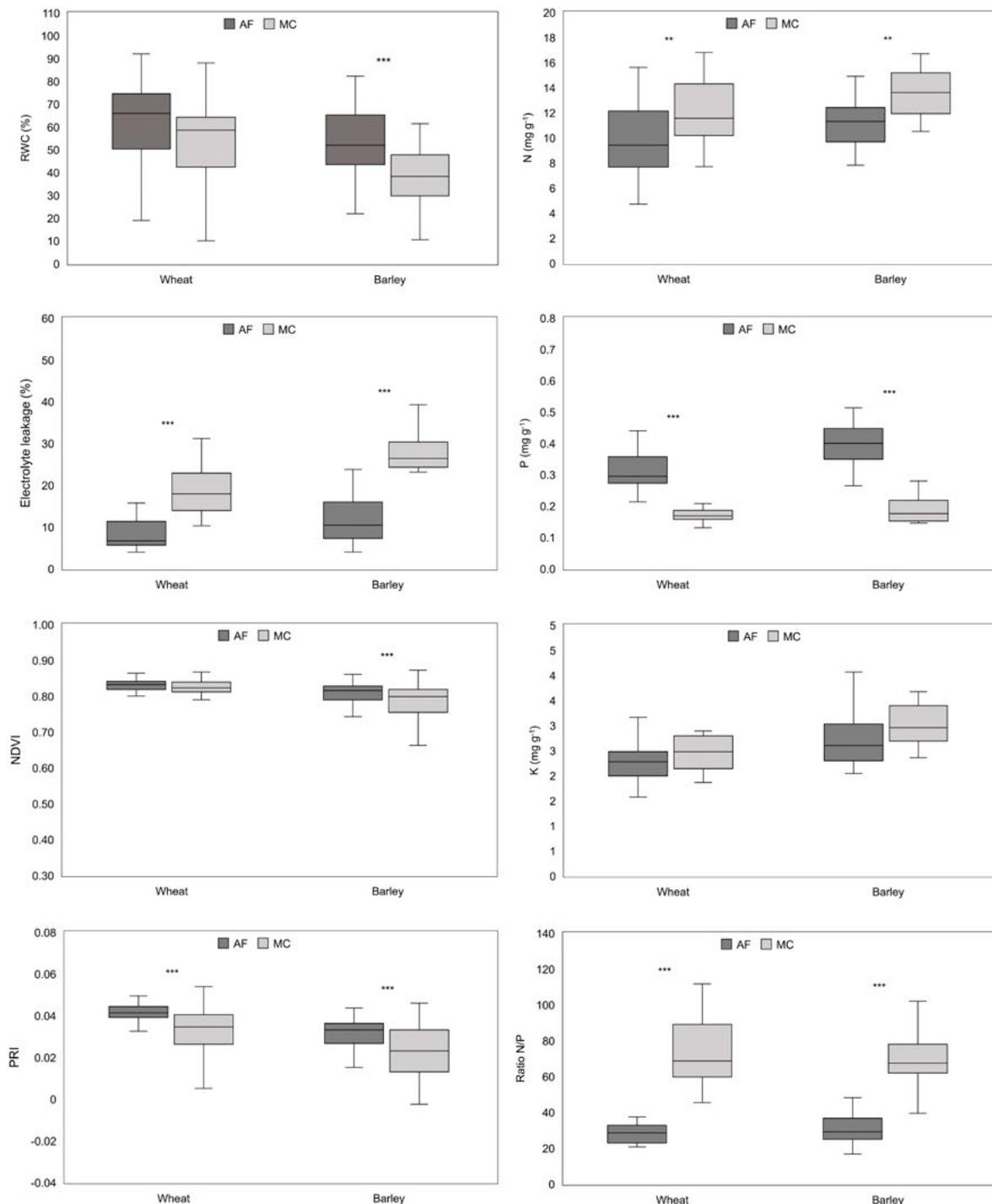
Figure A4. Boxplot of Relative Water Content (RWC), Electrolyte leakage, Normalized Difference Vegetation Index (NDVI), Physiological Reflectance Index (PRI), N, P and K leaf content of wheat and barley in the Agroforestry (AF) and Monocrops (MC) systems studied after walnut budburst. Significance level: * p < 0.05; ** p < 0.001; *** p < 0.001.

Table A3. Relative Water Content (RWC), Leaf Mass Area (LMA) and Leaf Area Index (LAI) of the cultivars studied of wheat (W1, W2 and W3) and barley (B1, B2 and B3) in the Agroforestry (AF) and Monocrops (MC) conditions before (B) and after (A) walnut budburst. Data represents means ± S.E. Pair-wise c omparisons were done for the different systems in the same date and cultivar. Significance level: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

| | | Wheat | | | | | |
| | | W1 | | W2 | | W3 | |
		AF	MC	AF	MC	AF	MC
LMA (mg cm^{-2})	23-Apr (B)	4.8 ± 0.1	5.0 ± 0.1	4.5 ± 0.1	4.5 ± 0.1	4.4 ± 0.1	4.5 ± 0.1
	16-May (A)	5.0 ± 0.1 **	5.5 ± 0.1	4.7 ± 0.1 ***	5.5 ± 0.1	4.5 ± 0.1 ***	5.3 ± 0.1
LAI	23-Apr (B)	2.8 ± 0.1 ***	3.6 ± 0.1	2.5 ± 0.2 *	3.0 ± 0.1	2.3 ± 0.2 ***	3.8 ± 0.1
	16-May (A)	2.4 ± 0.3 ***	5.0 ± 0.2	1.4 ± 0.1 ***	4.9 ± 0.2	2.1 ± 0.3 ***	4.4 ± 0.2
LA (cm^2)	23-Apr (B)	25.6 ± 1.6	26.13 ± 1.3	27.0 ± 1.45 *	32.0 ± 1.1	31.9 ± 1.6	34.4 ± 1.3
	16-May (A)	22.7 ± 1.5	23.0 ± 0.9	23.6 ± 1.7	26.7 ± 1.2	24.4 ± 1.9 *	29.4 ± 1.7
RWC (%)	23-Apr (B)	80.1 ± 1.8	79.6 ± 1.9	80.4 ± 3.6	79.6 ± 1.9	77.7 ± 3.2	73.9 ± 5.9
	16-May (A)	58.8 ± 3.0	51.9 ± 2.8	64.3 ± 4.2	57.0 ± 4.4	62.3 ± 4.3	55.6 ± 4.0
Electrolyte leakage (%)	22-May	7.7 ± 1.7 *	15.5 ± 1.7	7.1 ± 1.5 ***	20.3 ± 3.0	11.2 ± 2.4 *	20.6 ± 2.3
NDVI	15-May	0.82 ± 0.0 ***	0.78 ± 0.01	0.83 ± 0.00	0.84 ± 0.00	0.83 ± 0.00	0.83 ± 0.00
PRI	15-May	0.04 ± 0.00 ***	0.03 ± 0.00	0.04 ± 0.00	0.04 ± 0.00	0.04 ± 0.00 ***	0.03 ± 0.00
N (mg g^{-1})	22-May	11.2 ± 1.0	10.0 ± 0.7	9.9 ± 1.6	12.2 ± 0.9	8.0 ± 0.7 ***	14.2 ± 0.9
P (mg g^{-1})	22-May	0.31 ± 0.02 ***	0.18 ± 0.02	0.33 ± 0.03 ***	0.21 ± 0.04	0.29 ± 0.02 ***	0.16 ± 0.01
K (mg g^{-1})	22-May	2.5 ± 0.2	2.5 ± 0.1	2.3 ± 0.2	2.2 ± 0.1	2.1 ± 0.2 *	2.6 ± 0.1

Barley					
B1		B2		B3	
AF	MC	AF	MC	AF	MC
3.0 ± 0.1	3.1 ± 0.0	3.1 ± 0.1	3.2 ± 0.0	3.0 ± 0.1	3.1 ± 0.1
3.0 ± 0.2	3.2 ± 0.1	3.3 ± 0.1	3.3 ± 0.1	3.1 ± 0.1	3.1 ± 0.1
3.4 ± 0.3 ***	4.5 ± 0.1	2.8 ± 0.2 ***	4.4 ± 0.1	2.6 ± 0.2 ***	4.5 ± 0.1
2.2 ± 0.2 ***	5.6 ± 0.2	2.0 ± 0.1 ***	5.7 ± 0.2	1.9 ± 0.1 ***	5.6 ± 0.1
19.0 ± 1.14 ***	28.2 ± 1.2	22.2 ± 1.4 ***	31.0 ± 1.3	14.4 ± 0.7 ***	25.3 ± 1.5
19.7 ± 1.1 *	23.2 ± 1.3	23.3 ± 1.5	26.0 ± 1.1	16.6 ± 1.2 **	22.1 ± 1.3
83.3 ± 3.5	81.0 ± 1.9	83.1 ± 3.4	83.2 ± 0.8	79.4 ± 2.1	81.0 ± 1.7
49.2 ± 3.7 *	37.4 ± 2.2	61.9 ± 1.8 ***	40.7 ± 3.1	53.3 ± 3.1 **	37.4 ± 3.1
9.2 ± 2.0 ***	28.7 ± 2.7	14.4 ± 3.1 *	24.8 ± 4.0	10.9 ± 1.9 ***	29.8 ± 4.4
0.81 ± 0.01	0.80 ± 0.01	0.79 ± 0.01	0.78 ± 0.02	0.80 ± 0.01 ***	0.71 ± 0.02
0.03 ± 0.00 ***	0.02 ± 0.00	0.03 ± 0.00	0.03 ± 0.00	0.04 ± 0.00 ***	0.02 ± 0.00
11.2 ± 0.9	13.5 ± 0.7	11.6 ± 0.9 *	14.5 ± 0.8	10.8 ± 0.5	12.7 ± 0.9
0.34 ± 0.02 ***	0.18 ± 0.02	0.48 ± 0.04 ***	0.19 ± 0.02	0.38 ± 0.03 ***	0.19 ± 0.01
2.4 ± 0.1 *	3.0 ± 0.1	3.2 ± 0.2	3.3 ± 0.1	2.6 ± 0.2	2.7 ± 0.1