



Assimilate Remobilization in Five Spring Grain Legumes Under Mediterranean Conditions

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Abstract

A comparative evaluation of grain legumes is essential for the effective planning of legume-based agricultural systems in a given environment. The goal of this work was to contrast the growth, translocation of assimilates, and grain yield of spring-planted common vetch (*Vicia sativa* L.), red pea (*Lathyrus cicera* L.), lentil (*Lens culinaris* Medik.), chickpea (*Cicer arietinum* L.), and field pea (*Pisum sativa* L.) under rainfed Mediterranean conditions. Two cultivars of each species were cultivated on a silty clay soil in northeastern Greece for 2 years (2014 and 2015) with contrasting rainfall patterns. Chickpea and field pea exhibited better early crop growth rate than any other legume. Species differences in assimilates availability prior to grain filling affected the remobilization of assimilates to seed, which increased by 45% for every kg ha⁻¹ rise in early dry matter accumulation. Dry matter translocation efficiency varied from 9 to 51% depending on species and year. Red pea was the best option in terms of seed yield, regardless of the seasonal rainfall. Chickpea in the drier year (2015) and field pea in the wetter year (2014) produced seed yields that were comparable to that of red pea. Lentil and common vetch were generally less productive species in terms of seed yield. Species seed yield was associated with their ability to accumulate biomass either before podding ($r=0.52$, $P<0.05$) or at maturity ($r=0.51$, $P<0.05$), but not with harvest index or translocation of dry matter. Findings provide new knowledge regarding growth attributes and reallocation of assimilate in five legume species grown simultaneously in the same environment, which has never been studied before. In addition, results highlight that selecting species with enhanced early or final biomass potential as well as adopting cultural practices that promote biomass accumulation in the growing season appear to be effective management strategies for improving seed yield of the tested grain legumes under Mediterranean conditions.

Keywords Dry matter remobilization · Crop growth rate · Seed yield

Introduction

European cropping systems are dominated by cereals, while the cultivation of grain legumes is restricted to less than 3% of the total arable land (Eurostat, 2019). This situation has raised several concerns regarding the lack of crop diversity (Plaza-Bonilla et al., 2017) and the increased dependence on chemical fertilizers (Sainju et al., 2012), which has been linked to serious environmental risks (Bouwman et al., 2013). Seed yields of grain legumes vary across species and European sub-regions, being generally more unstable compared with cereals grain yields (Cernay et al., 2015).

Aside from production uncertainty, European farmers are not encouraged to grow legumes in favorable environments and on high-quality soils; instead, they prefer to grow more profitable major crops in such situations than legumes (Cernay et al., 2015).

Legumes, when grown as part of a rotation scheme, contribute to the long-term environmental improvement because of their capacity to fix the atmospheric nitrogen, their beneficial effects on the following crop, as well as the services they provide to other agroecosystem components (Stagnari et al., 2017). Legume-wheat cropping systems, in particular, is an appealing choice for increasing soil nitrogen and organic carbon, as well as improving crop productivity, both in conventional and low-input cropping systems (Geng et al., 2023; Virk et al., 2022), regardless of whether the seeds of plants are harvested or not (Geng et al., 2023). Several factors, including growing season environmental

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conditions (Hungria & Vargas, 2000) and agronomic management strategies (Guinet et al., 2020), influence the extent of soil nutrient improvement achieved by legume cultivation. Furthermore, because grain legumes are used in animal feed, expanding their cultivation in Europe can reduce the dependency of livestock sector on imports of soybean (de Visser et al., 2014). Finally, grain legumes can also emerge as a group of crops that mitigate the threads of climate change, which arise by the increase of temperature and water scarcity (Dutta et al., 2022).

Seed yield of grain legumes is influenced by a wide range of physiological and biochemical functions taking place throughout the crop growth, as well as by crop management practices. In general, growth and productivity of crops depend on how effectively they convert solar energy into dry matter (DM), assuming that other resources are not limited (Sinclair & Muchow, 1999). In grain legumes, the supply of assimilate for the growing seed comes from two separate sources, i.e., the current assimilation and the remobilization of stored reserves. These sources can occur simultaneously and independently of one another, even though their significance relies on environmental factors and crop developmental stages (Turner et al., 2005). The accumulation and remobilization of DM, as well as seed yield are controlled by the association between source and sink (Zhang et al., 2020). The percentage of seed weight deriving from photosynthetic products during seed filling varies according to legume species and growing environment (Davies et al., 2000; Mohapatra et al., 2003; Turner et al., 2005). In European Mediterranean areas, the performance of several grain legumes, such as soybean and chickpea, in terms of seed yield is primarily associated with increases in plant DM following the onset of grain filling (Fotiadis et al., 2019; Koutroubas et al., 1998). Additionally, it has been observed that the supply of assimilates prior to the start of grain filling has less impact on variation in assimilate translocation in chickpea than dry matter translocation efficiency (DMTE) does (Fotiadis et al., 2017).

Proper sowing time is a crucial management decision in the cultivation of grain legumes. In terms of seed yield, autumn sowing performs better than spring one in several environments (López-Bellido et al., 2008; Neugschwandtner et al., 2013). Growing grain legumes in the winter rather than the spring has also been considered a promising option for adapting to future climate changes (Falconnier et al., 2020). However, in inland Mediterranean areas sowing of grain legumes is typically shifted from autumn to spring to avoid crop failure due to frost over the winter. Dry matter translocation to seeds is considered an adaptive response of plants to unfavorable conditions during the later stages of growth, such as terminal drought (Turner et al., 2005). Even though the reallocation of assimilates to seeds has been extensively studied in grain legumes, the majority of the

studies has centered on comparisons within species. In this context, great variation in pre-podding translocation of nitrogen and assimilates has been reported in several legumes, such as chickpea (Fotiadis et al., 2017), soybean (Gaspar et al., 2017), and lentil (Kurdali et al., 1997), depending on genotype and growing conditions. Additionally, agronomic practices, like intercropping with maize, can modulate DM translocation in peanut (Gao et al., 2022). Yet, there is a lack of understanding regarding the differences in growth attributes and reallocation of assimilates between legume species grown simultaneously in the same environment. Such information is necessary for the successful design of legume-supported agricultural systems across a range of various agro-ecological zones and management types (Virk et al., 2022). The goal of the current work was to compare how different spring grain legumes responded to seasonal environmental variations with respect to growth, assimilation translocation and partitioning, and grain yield under rainfed Mediterranean conditions. This knowledge can be used to improve spring legumes' adaptive response, implement appropriate agronomic practices in leguminous cultivation, and establish indirect selection criteria for seed yield.

Materials and Methods

Experimental Procedure

Common vetch (*Vicia sativa* L., cvs Pigasos and Tembi), red pea (*Lathyrus cicera* L., cvs Rodos and Argos), lentil (*Lens culinaris* Medik., cvs Thessalia and Samos), chickpea (*Cicer arietinum* L., cvs Andros and Kassos), and field pea (*Pisum sativum* L., cvs Vermio and Ithomi) were grown for two consecutive years (2014 and 2015) in field experiments at Democritus University of Thrace's farm in Orestiada (41°33'N, 26°31'E, 33 m elevation), Greece. The region, which is in northeastern Greece, has a Mediterranean climate with hot, dry summers and cool, rainy winters. The crops were rotated each year. The soil was silty clay with the following characteristics: pH (1:2 water) 6.68, organic matter 10.1 g kg⁻¹, electrical conductivity 0.04 S m⁻¹, total N 1.11 g kg⁻¹, NO₃-N 9.0 mg kg⁻¹, Olsen P 10.2 mg kg⁻¹, and available K 495.3 g kg⁻¹. Weather parameters (mean temperature and rainfall) during each experimental season, as well as the long-term (30 years) average are given in Table 1.

A trial with four replications was arranged in a randomized complete block design. Plots were 4 m wide (12 rows, 25 cm apart) and 3 m long. The sowing was done by hand on 17 March 2014 and 6 March 2015. Each year, 26 kg P ha⁻¹ (in the form of superphosphate) was applied prior to sowing. Following the emergence, the density of the seedlings were reduced to 40 plants per m² for common vetch, 60 plants per m² for red pea, 150 plants per m² for

Table 1 Mean air temperature and rainfall during the growing season in 2014, 2015, and 30-years average

Month	Mean air temperature (°C)			Rainfall (mm)		
	2014	2015	30-years average	2014	2015	30-years average
March	9.9	8.4	7.3	99.2	72.4	53.5
April	13.6	12.4	12.6	58.0	50.4	42.4
May	17.9	20.3	18.0	36.2	8.2	40.1
June	21.8	21.8	22.6	57.8	56.4	48.4
July	24.5	25.3	25.1	168.8	0.8	25.1
August	24.7	25.7	24.7	62.8	8.4	16.6

lentil, 50 plants per m² for chickpea, and 100 plants per m² for field pea. Weeds were controlled by hand weeding when necessary.

Samplings, Measurements, and Calculations

The time of the main growth stages [seedling emergence, beginning of seed filling (growth stage R5), and full maturity (growth stage R8)] were noted. At R5 and R8, plants from a row (1-m-long) were cut at the ground level in each plot and then split into distinct plant parts (i.e., leaf and stem, seeds, and pod walls). Samples of plants were weighted after being oven dried at 70 °C until constant weight. The total number of nodes (TNN) and the number of nodes under the first pod (NFP) at growth stage R5 were recorded on the main stems of 10 nearby plants randomly chosen by each plot. Crop growth rate (CGR) was determined by dividing the rise in DM across two samplings by the time (days) between these samplings. At growth stage R8, seed yield was determined by harvesting the six middle rows of each plot. The parameters related with translocation and partitioning of dry matter were calculated using the following equations (Koutroubas et al., 1998):

$$\begin{aligned} \text{Dry matter translocation (DMT, kg ha}^{-1}\text{)} \\ &= [\text{Dry matter of vegetative tissues at R5 (kg ha}^{-1}\text{)}] \\ &\quad - [\text{dry matter of vegetative tissues at R8 (kg ha}^{-1}\text{)}] \end{aligned}$$

$$\begin{aligned} \text{Dry matter translocation efficiency (DMTE, \%)} \\ &= \frac{\text{DMT (kg ha}^{-1}\text{)}}{\text{Dry matter of vegetative tissues at R5 (kg ha}^{-1}\text{)}} \times 100 \end{aligned}$$

$$\begin{aligned} \text{Harvest index (HI)} \\ &= \frac{\text{Seed dry matter at maturity (kg ha}^{-1}\text{)}}{\text{Total above ground dry matter at maturity (kg ha}^{-1}\text{)}} \end{aligned}$$

Statistical Analysis

Data were analyzed using the MSTAT-C (Michigan State University, East Lansing, MI) statistical software package. A year-combined ANOVA was used to analyze differences among species when averaged across all cultivars within each species. In addition, an over-years combined ANOVA was conducted separately for each species to compare cultivars within a particular species. Year, species, and cultivars as well as the interactions between them were regarded as fixed effects. Year was regarded as a variable with fixed effects, due to the considerable variation in precipitation between the research years. Means were compared with Fisher's protected least significant difference (LSD). Simple correlation analysis was used to evaluate relationships between traits.

Results

Weather Data and Plant Development

Growing season weather varied considerably between years (Table 1). The total amount of seasonal precipitation in 2014 (483 mm) was significantly higher than that in 2015 (197 mm), indicating a noticeable wetter growing season. Total seasonal precipitation in 2014 was 114% higher compared with that in 2015 and 13% below the long-term average (226 mm). When the grain filling of legumes took place (June and July), total rainfall was 227 mm in 2014 but only 57 mm in 2015. The average temperature of each growing season (18.7 °C in 2014 and 18.9 °C in 2015) was consistent between years. However, between March and April, when plants are first beginning to grow, the mean monthly temperature in 2014 was marginally higher than in 2015. On the other hand, starting with seed growth, the average monthly temperature in 2015 was a little bit higher than in 2014.

Regarding the timing of crop emergence, there were no differences between species in either year. Crop emergence was, on average, 10 days later in 2014 than in 2015 (35 DAS

Table 2 Number of nodes to first pod (NFP) and total number of nodes (TNN) at R5 as affected by legume species and year of the experimentation

Year/species	NFP	TNN
2014		
Common vetch	12 d	16 c
Red pea	9 f	17 c
Lentil	11 de	21 b
Chickpea	13 cd	26 a
Field pea	16 a	20 b
Mean	12 A	20 A
2015		
Common vetch	11 e	18 c
Red pea	8 f	17 c
Lentil	8 f	16 c
Chickpea	15 ab	24 a
Field pea	14 bc	20 b
Mean	11 B	19 B
Source of variation	df	Mean squares
Year (Y)	1	16.9*
Species (S)	4	62.7**
Y × S	4	7.5**

In each column, means followed by the same lowercase or uppercase letter are not significantly different at $P < 0.05$

*, ** Significant at $P < 0.05$ and $P < 0.01$, respectively

vs. 25 DAS, respectively). Common vetch, red pea, and field pea all started podding earlier in 2014 (75 DAS vs. 89 DAS for lentil and chickpea). For common vetch, red pea, lentil, and field pea, the total crop duration was 120 days, while for chickpea it was 141 days. The time needed to start podding and the length of the entire crop, which averaged 74 and 116 DAS, respectively, in 2015, were the same for all species.

Crop Growth and Dry Matter Accumulation

Except for lentil, which had higher values in 2014 than in 2015, species TNN was consistent between years (Table 2). In both years, chickpea displayed the highest TNN, followed by lentil and field pea in 2014 and field pea in 2015. Species performance varied across years in terms of NFP, but the response pattern was inconsistent. In 2014, red pea had the lowest and field pea had the highest NFP. In 2015, red pea and lentil had the lowest NFP, while chickpea had the highest.

Crop growth rate up to the beginning of seed growth was significantly higher in 2014 ($106 \text{ kg ha}^{-1} \text{ day}^{-1}$) than in 2015 ($55 \text{ kg ha}^{-1} \text{ day}^{-1}$). Early crop growth rates varied by species, with chickpea and field pea outperforming common vetch, red pea, and lentil (Fig. 1).

Year, species, and their interactions had a significant impact on accumulation of DM at both samplings (Table 3).

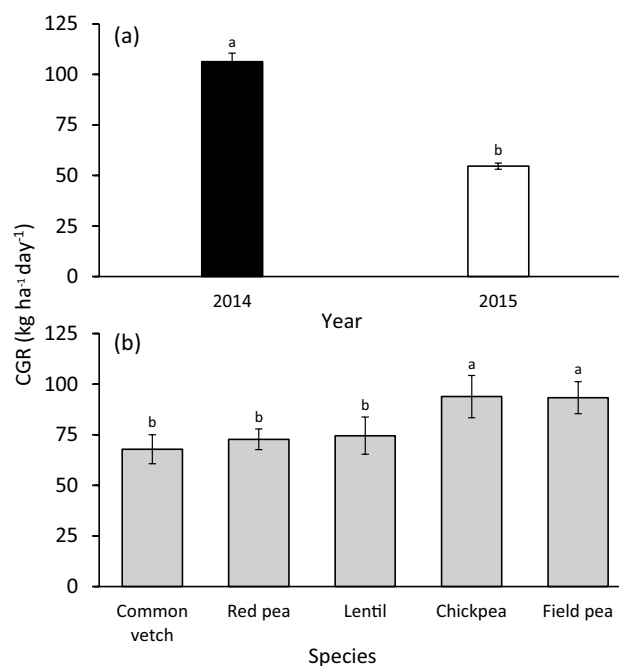


Fig. 1 Crop growth rate (CGR) up to the onset of seed growth as affected by **a** year of the experimentation and **b** legume species. Data for each year are means of five species and two cultivars for each species; data for each species are means of two cultivars and 2 years. Vertical bars represent the standard errors of the means. Bars with the same letter indicate means that are not significantly different at $P < 0.05$

On average, the total amount of DM accumulated up to the onset of seed growth was 45% lower in 2014 compared with that in 2015. This trend was consistent across species, but the percentage of decrease between years was above average for lentil (62%) and chickpea (55%), and below average for common vetch (40%), field pea (33%), and red pea (23%). Species variation in DM accumulation at R5 was more evident in 2014, where chickpea produced the highest early DM (6770 kg ha^{-1}). In 2015, field pea had the highest DM at R5 (3235 kg ha^{-1}), which was comparable to chickpea (3055 kg ha^{-1}) or red pea (2750 kg ha^{-1}). The picture for DM accumulation at maturity was similar to that observed at R5, showing a decline in 2015 compared to 2014, which averaged 31%. In both years, chickpea had the highest DM at maturity and common vetch had the lowest. Early and final DM accumulation were significantly correlated ($r = 0.77$, $P < 0.01$). Differences in early DM accumulation between cultivars within a particular species were observed for common vetch and lentil; however, these variations did not persist across years (Table 4). In particular, there were no differences between cultivars in 2015, but DM accumulation at R5 was significantly higher in common vetch cv. Pigasos and lentil cv. Thessalia compared to cvs Tempi and Samos, respectively.

Table 3 Dry matter accumulation at the beginning of seed growth (R5) and at maturity (R8) as affected by legume species and year of the experimentation

		Dry matter accumulation (kg ha ⁻¹)		
			R8	
Year/species	R5		Veg. parts	Total
<i>2014</i>				
Common vetch	3645 d		2543 bc	4746 b
Red pea	3575 d		2665 b	4974 b
Lentil	5670 b		2704 b	5158 b
Chickpea	6770 a		3967 a	6727 a
Field pea	4825 c		2603 bc	4753 b
Mean	4897 A		2896 A	5271 A
<i>2015</i>				
Common vetch	2185 f		1843 d	2880 e
Red pea	2750 ef		1936 d	3476 cd
Lentil	2160 f		1962 d	3067 de
Chickpea	3055 de		2674 b	4899 b
Field pea	3235 de		2211 cd	3744 c
Mean	2677 B		2125 B	3613 B
Source of vari- ation	df	Mean squares		
Year (Y)	1	49,284,000**	5,950,579**	27,516,174**
Species (S)	4	4,985,135**	1,687,274**	4,936,821**
Y × S	4	3,409,825**	211,663	352,862*

In each column, means followed by the same lowercase or uppercase letter are not significantly different at $P < 0.05$

*, ** Significant at $P < 0.05$ and $P < 0.01$, respectively

Dry Matter Translocation and Partitioning, and Seed Yield

Dry matter translocation from vegetative plant parts to seed between R5 and R8 was significantly higher in 2014 (2001 kg ha⁻¹) than in 2015 (1025 kg ha⁻¹) (Table 5). In 2014, lentil, chickpea, and field pea had similar DMT, which was significantly higher than that of common vetch and red pea. In 2015, there were no observable differences in DMT between species. Differences in DMT between cultivars within a particular species were observed for common vetch, red pea, and chickpea, but these differences were not always consistent across years (Table 4). In particular, DMT of red pea cv. Rodos was significantly higher than that of cv. Argos in both years. On the other hand, DMT was significantly higher in common vetch cv. Pigasos and in chickpea cv. Kassos in 2014 compared to cvs Tempi and Andros, respectively. However, this was not the case in 2015.

Dry matter translocation efficiency was significantly higher in 2014 (37%) compared with that in 2015 (20%) (Table 5). In 2014, lentil, field pea, and chickpea had similar DMTE that was significantly higher than that of common vetch and red pea. In 2015, field pea showed the highest DMTE, which was comparable to that of red pea but higher than that of common vetch, chickpea, and lentil. Dry matter translocation was positively correlated with DMTE (Fig. 2). Both DMT and DMTE were positively correlated with DM accumulation at R5 (Fig. 3).

Seed yield was significantly affected by year and species, as well as by the year × species interaction

Table 4 Dry matter accumulation (DMA) at the beginning of seed growth (R5) and dry matter translocation (DMT) of legume species as affected by cultivar and year of the experimentation

Species/cultivar	DMA at R5 (kg ha ⁻¹)			DMT (kg ha ⁻¹)		
	2014	2015	Mean	2014	2015	Mean
<i>Common vetch</i>						
Pigasos	4140 a	2200 c	3170 A	2118 a	409 b	1263 A
Tembi	3150 b	2170 c	2660 A	86 b	276 b	180 B
<i>Red pea</i>						
Rodos	3700 a	3000 ab	3350 A	1542 a	1199 a	1370 A
Argos	3450 a	2500 b	2975 A	279 b	429 b	354 B
<i>Lentil</i>						
Thessalia	6420 a	2170 c	4295 A	3414 a	193 b	1804 A
Samos	4920 b	2150 c	3535 A	2518 a	203 b	1361 A
<i>Chickpea</i>						
Kassos	7860 a	3070 b	5465 A	3996 a	294 b	2145 A
Andros	5680 a	3040 b	4360 A	1610 b	468 b	1039 A
<i>Field pea</i>						
Vermio	5010 a	3410 b	4210 A	2034 ab	969 c	1502 A
Ithomi	4640 a	3060 b	3850 A	2410 a	1079 c	1745 A

Within each species, cultivar means in a column followed by different uppercase letter are significantly different at $P < 0.05$

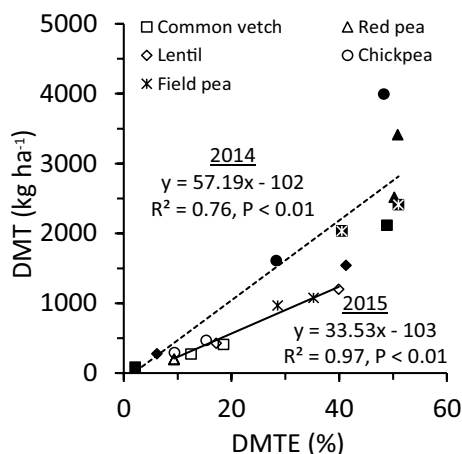
Within each species, means for a given trait followed by different lowercase letter are significantly different at $P < 0.05$

Table 5 Dry matter translocation (DMT), dry matter translocation efficiency (DMTE), seed yield (SY), and harvest index (HI) as affected by legume species and year of the experimentation

Year/species	DMT (kg ha ⁻¹)	DMTE (%)	SY (kg ha ⁻¹)	HI	
<i>2014</i>					
Common vetch	1102 b	26 bcde	1455 c	0.47 ab	
Red pea	911 bc	24 cde	2131 ab	0.47 ab	
Lentil	2966 a	51 a	1014 ef	0.48 a	
Chickpea	2803 a	39 ab	1915 b	0.41 c	
Field pea	2222 a	46 a	2196 a	0.46 ab	
Mean	2001 A	37 A	1742 A	0.46 A	
<i>2015</i>					
Common vetch	343 bc	16 def	924 f	0.36 d	
Red pea	814 bc	29 bcd	1498 c	0.43 bc	
Lentil	198 c	9 f	799 f	0.35 d	
Chickpea	381 bc	12 ef	1362 cd	0.45 abc	
Field pea	1025 bc	32 bc	1207 de	0.41 c	
Mean	552 B	20 B	1158 B	0.40 B	
Source of variation	df	Mean squares			
Year (Y)	1	20,984,419**	2,975**	3,414,064**	0.031**
Species (S)	4	1,583,749**	363*	1,189,266**	0.002
Y × S	4	2,527,212**	613**	153,232**	0.009**

In each column, means followed by the same lowercase or uppercase letter are not significantly different at $P < 0.05$

*, ** Significant at $P < 0.05$ and $P < 0.01$, respectively

**Fig. 2** Relationship between dry matter translocation efficiency (DMTE) and dry matter translocation (DMT) in 2014 (black symbols, solid line) and 2015 (open symbols, dashed line). Each relationship was based on means derived from five legume species (common vetch, red pea, lentil, chickpea, and field pea) and two cultivars for each species

(Table 5). In 2014, the average seed yield (1742 kg ha^{-1}) was much greater than it was in 2015 (1158 kg ha^{-1}). This pattern between years was common for all species, except for lentil that had similar seed yield in both years. In 2014, lentil produced the lowest seed yield, whereas field pea produced the highest seed yield, which was comparable to that of red pea. In 2015, chickpea showed the highest seed yield that was comparable with that of field pea and red pea, but higher than that of common vetch and lentil. Seed yield showed a positive correlation with early and final DM accumulation (Fig. 4). No correlation between seed yield and DMT or DMTE was observed ($r = 0.31$, $P > 0.05$ and $r = 0.29$, $P > 0.05$, respectively).

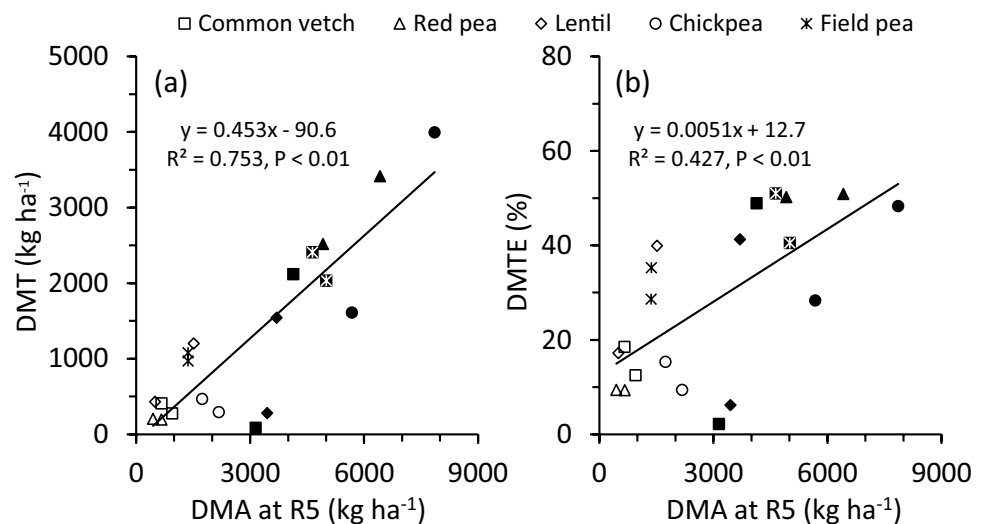
Harvest index remained constant between years in red pea and chickpea, while it increased in common vetch, lentil, and field pea in 2015 compared to 2014 (Table 5). No species differences in HI were observed in 2014, except for chickpea, which had the lowest value. In 2015, chickpea had the highest HI, which was comparable to those of red pea and field pea. Similar HI values were observed in common vetch and lentil, which were lower than those of the other species. No significant correlation between seed yield and HI existed ($r = 0.35$, $P > 0.05$).

Discussion

Early Crop Growth

Crop agronomic performance was influenced by legume species and year of experimentation, reflecting the variation in genotypic constitution of the species as well as the seasonal variation of the weather parameters. Most legumes produced large biomass, which was particularly noticeable the year with above-average rainfall, confirming their adaptation to the area even at spring sowing. Variation between species in accumulation of DM could be attributed to differences in intercepted photosynthetically active radiation (Estrada-Campuzano et al., 2012) along with the formation of green area (Thomson & Siddique, 1997), both of which influence grain legumes adaptation in Mediterranean conditions. Regardless of growing environment, chickpea ranked first in terms of final DM production, primarily owing to its rapid crop growth rate during the early stages. Vigorous early growth benefits crop in a variety of ways, including superior crop establishment (Huang et al., 2017), enhanced water use efficiency (Siddique et al., 2001), and weed competition (Damalas & Koutroubas, 2022). However, the advantages of rapid early growth in a given environment rely on the water availability, as rapid early growth may reduce soil water reserves throughout the reproductive establishment and filling period, particularly in late flowering environments

Fig. 3 Relationship (a) between dry matter accumulation (DMA) before the onset of grain filling (R5) and dry matter translocation (DMT), and (b) between DMA at R5 and dry matter translocation efficiency (DMTE). Each relationship was based on means derived from five legume species (common vetch, red pea, lentil, chickpea, and field pea), two cultivars for each species, and 2 years (2014, black symbols; 2015, open symbols)



(Turner et al., 2001). In the current study, chickpea and field pea showed better crop establishment, as evidenced by their higher early DM than the other legumes. This rapid growth during the early stages set the potential for a high final biomass production.

Assimilate Translocation

Early DM accumulation has been linked to the capacity of source to translocate photosynthetic products to developing sink (French & Turner, 1991; Koutroubas et al., 1998; Leport et al., 1999), enabling plants to continue providing assimilates to the grain even when current assimilate supply is limited (Wardlaw, 1990). Such a situation was supported by the present study, in which species-specific variation in parameters related with assimilate translocation to seeds followed that of biomass accumulation before the onset of seed filling. Actually, for every kilogram per hectare increase in DM accumulation up to the growth stage R5, DMT increased by 45% and DMTE increased by 0.51%. However, apart from the amount of the available carbohydrates for remobilization before seed filling begins, the reallocation of carbon from vegetative organs to the seed can be influenced also by the seed size (Koutroubas et al., 2021), as well as by the ability of the seed to incorporate the translocated carbon in the embryo or endosperm (Turner et al., 2001). In this context, plants that produced a high number of seeds were found to remobilize more DM than plants with a lower number of seeds (Davies et al., 2000). Such an association was not confirmed in the current study, suggesting that species differences in DMT and seed size were unrelated. It seems that differences in seed size were probably only able to account for the variation in DMT within species, but not between species, given that different species had different DMTE. Indeed, in the present study, DMTE varied greatly

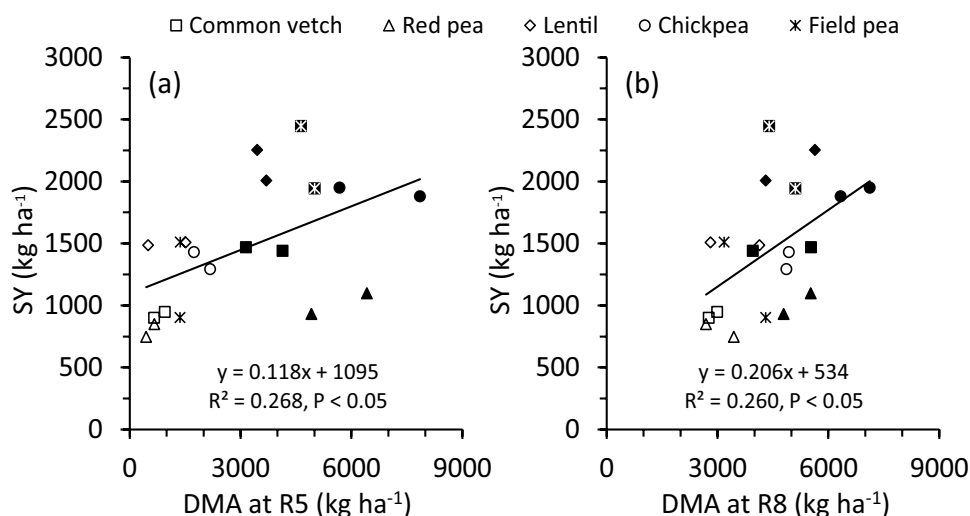
between species, ranging from 24% to 51% the favorable year and from 9% to 32% in the drier year. As the DMTE increased, so did the DMT, indicating that the efficiency of legumes to remobilize assimilates to seeds was a decisive parameter in determining the net amount of DMT.

Although the ability of grain legumes to remobilize stored assimilates may be an adaptation to rainless periods (Leport et al., 1999), photosynthetic products assimilated before podding may improve the availability of assimilates to the seed during the filling stage in both well-watered plants and plants experiencing water stress (Davies et al., 2000). In the current study, high legume yields in the favorable year appeared to be more reliant on assimilate translocation to seeds compared with low yields in the less favorable year. In addition, the drier year, species with large DMT (such as field pea, red pea, and chickpea) produced high seed yields, which highlights the importance of translocation in maintaining the supply of assimilates to the seeds under adverse conditions.

Seed Yield and Harvest Index

Species showed substantial variation in seed yield, but their ranking fluctuated throughout the years because of the year by species interaction. Actually, species accounted for nearly half (50.65%) of the overall seed yield variation, while the year of the experimentation contributed about one-third (36.35%) and the year by species interaction made a small contribution (6.53%). Regardless of the growing conditions, red pea produced a comparatively high seed yield. Additionally, chickpea in the drier growing season and field pea in the more favorable season both produced high seed yields, which were comparable to that of red pea. Finally, in terms of seed yield, lentil was ranked last and common vetch was ranked second from the end in both growing seasons.

Fig. 4 Relationship (a) between dry matter accumulation (DMA) before the onset of grain filling (R5) and seed yield (SY), and (b) between DMA at maturity (R8) and SY. Each relationship was based on means derived from five legume species (common vetch, red pea, lentil, chickpea, and field pea), two cultivars for each species, and 2 years (2014, black symbols; 2015, open symbols)



The superior seed yield of red pea agrees with previous studies showing that this crop has a substantial potential in Mediterranean environments with low annual rainfall (250–350 mm), owing to its resistance to water shortage and its suitability to poor soils (Hanbury et al., 2000). Furthermore, red pea had the highest individual seed weight (> 200 mg) among the legumes used in the present study, a yield component that probably contributed to its superior yield. On the other hand, lentil plants, as opposed to the other legumes, had a smaller and more determinate growth habit (Erskine & Goodrich, 1991), which led to a poor seed yield, in line with previous research in both subhumid (Ayaz et al., 2004) and Mediterranean environments (Siddique et al., 1999). Regarding the superiority of chickpea in the drier year, it was probably due to its deep roots that provide high level of drought resistance (Jacobsen et al., 2012). From this point of view, chickpea could be a good option in Mediterranean environments even as spring crop. Early planting was crucial for crop success in this case; depending on the growing season, March sowing yielded 48 to 80% greater seed yield than April sowing (Fotiadis et al., 2017). It has also been calculated that late spring sowing decreased the total seed number by 7–18.2 seeds per square meter per day of planting delay (Fotiadis et al., 2019). Concerning common vetch, a seed yield of approximately 160 kg ha⁻¹ has been reported under Mediterranean conditions (Siddique & Loss, 1996), a value comparable to that of the present study. Despite its poor seed yield, common vetch appears to be capable of producing a satisfactory silage yield, based on DM accumulation data, giving the crop an interesting alternative use.

Seed yield of legumes increased linearly with their capacity to accumulate biomass either before podding or at maturity. Therefore, selecting legume species with enhanced potential to produce biomass and improving management strategies favoring the accumulation of DM could boost

seed yield of the tested grain legumes. Actually, an increase in seed yield by 1 kg ha⁻¹ went along with an increase in vegetative DM of only 0.26 kg ha⁻¹, resulting in a gradual increase of HI. However, no significant correlation between seed yield and harvest index existed. It has been demonstrated that the cultivating environment influences the association of seed yield with DM accumulation and partitioning. While in subcontinental environments seed yield was associated with higher aboveground biomass, it was connected with greater harvest indices in Mediterranean environments (Annicchiarico, 2008).

Yearly and Cultivar Differences

Seed yield of grain legumes fluctuates largely between growing seasons, a fact that explains why farmers in Europe do not cultivate systematically these crops (Von Richthofen et al., 2006). In the current research, growth attributes and seed yield of grain legumes varied substantially between years because of the seasonal variations in environmental conditions, which are typical for Mediterranean environments. In general, grain legumes grew better and produced more seed yield in the year with high growing season rainfall. However, the reduction of seed yield due to the lack of rainfall varied by species, being above average (34%) for field pea (45%) and common vetch (36%), and below average for lentil (21%), chickpea (29%), and red pea (30%). In most studied traits, larger differences were observed between species than those within species. The cultivar differences in DMT for common vetch, red pea, and chickpea were noteworthy. From this point of view, the ability of some genotypes to remobilize more assimilates to growing seeds could be exploited for improving the overall crop adaptation. However, because in the current study each legume was represented by only two cultivars, additional research involving a large number of cultivars is necessary to examine

within-species variation and the potential for enhancing seed yield through breeding.

Conclusions

Data from the present research offer helpful evidence on the agronomic performance and assimilate remobilization in five spring grain legumes under Mediterranean conditions, whereas most previous studies have focused only on comparisons within single species. Therefore, the study improves our understanding of the differences in growth attributes and reallocation of assimilate between legume species grown simultaneously in the same environment, which has never been studied before. A broader understanding of how different legume species perform under specific conditions provides farmers with more tools for environmental and economic decision-making that could increase the adoption of more profitable production practices. Growth attributes and seed yield varied greatly by legume species and cultivation year, reflecting the differences in adaptation of species in the study area, as well as the fluctuations in seasonal patterns of rainfall. Early dry matter accumulation was critical in establishing the base for the final dry matter production. Between the evaluated species, red pea was the best option as a spring crop for cold Mediterranean areas in terms of seed yield, regardless of the seasonal pattern of rainfall. Furthermore, chickpea in the drier year and field pea in the wetter year appeared to be good options generating seed yields comparable to that of red pea. Less promising was the lentil and common vetch, which exhibited low seed yields in both years. Differences between species in seed yield appeared to be closely associated with biomass production rather than harvest index. Translocation of assimilates to seed was dependent on the availability of assimilates prior to grain filling. When rainfall was limited, species with greater dry matter translocation tended to produce higher seed yield. The ability of some genotypes to remobilize more assimilates to growing seeds could be exploited for improving the overall crop adaptation.

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Data Availability The data that support the findings of this study are available from the corresponding author, upon reasonable request, subject to restrictions and conditions.

Declarations

Conflict of Interest The authors declare no conflict of interest.

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