

Radiation-use efficiency and dry matter partitioning of a young olive (*Olea europaea*) orchard

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Summary Radiation-use efficiency (RUE) relates biomass production to the photosynthetically active radiation (PAR) intercepted by a plant or crop. We determined RUE and biomass partitioning coefficients of young olive (*Olea europaea* L.) trees for use in a general growth model.

In 1995, 1-year-old olive trees var. 'Picual' were planted at a density of either 0.5 or 2.0 trees m⁻² near Córdoba, Spain, at a site providing favorable growth conditions. During the experiment (1995–1997), both PAR interception by the canopy and plant area index (PAI) were measured with radiation sensors. Regular harvests were performed to determine leaf area and biomass accumulation in roots, wood (stem, branches and trunk) and leaves. Leaf, wood and root biomass partitioning coefficients were calculated. The leaf area partitioning coefficients were also estimated. Dry matter production was linearly related to cumulative intercepted PAR. Seasonal RUE, calculated as the slope of the regression of aboveground biomass and cumulative intercepted PAR, was 1.35 g (MJ PAR)⁻¹. Radiation-use efficiency appeared to respond to environmental conditions, but was independent of planting density and PAI. The young olive trees allocated 0.26 of their total biomass to roots. Partitioning of aboveground dry matter was 0.60 to wood and 0.37 to leaves. As competition increased, dry matter partitioning to wood increased to 0.70.

Keywords: biomass production, crop modeling, PAR, partitioning coefficient, plant area index.

Introduction

Dry matter production of vegetation growing under non-limiting conditions of water and nutrients may be modeled as a function of the time-integration of daily incident photosynthetically active radiation (PAR), the fraction of this radiation intercepted by the canopy and radiation-use efficiency (RUE). Radiation-use efficiency is defined as the ratio of dry matter produced per unit of radiant energy used in its production (Monteith 1977). Because efficiency should be dimensionless, Russell et al. (1989) suggested the term dry matter: radiation quotient; however, RUE is considered a useful tool for simulating growth of woody species (Bartelink et al. 1997).

Linearity between biomass and accumulated intercepted radiation has been demonstrated for several herbaceous crops

(e.g., beans, Fasheun and Dennett 1982; soybean, Unsworth et al. 1984; lettuce, Hand et al. 1985) and for a few tree species (e.g., willow, Cannell et al. 1987; mesquite and juniper, Kiniry 1998). Linder (1985) reported a mean RUE of 0.9 g (MJ shortwave)⁻¹ (approximately 1.8 g (MJ PAR)⁻¹) for a set of evergreen canopies. Values of RUE for tree species are generally smaller than those for C₃ herbaceous species (Kiniry et al. 1989), because of the high energy cost of woody biomass and the respiration of supporting organs.

Radiation-use efficiency is dependent on light (Connor and Sadras 1992, Villalobos et al. 1992), temperature (McMurtrie and Wang 1993), vapor pressure deficit (Stockle and Kiniry 1990, Landsberg and Hingston 1996) and factors inherent to plant species. For example, RUE increases with increasing rate of leaf photosynthesis (Sinclair and Horie 1989). Likewise, RUE should decrease with increasing leaf age, respiration (Russell et al. 1989), and with the higher energy costs of some plant constituents (Trapani et al. 1992).

Mariscal et al. (1996) developed a model to calculate the PAR intercepted by olive orchards. We used this model to calculate intercepted PAR, so that we could estimate dry matter production from RUE. Dry matter distribution is usually characterized by means of partitioning coefficients (e.g., the ratio of organ growth rate to plant growth rate). However, few data on dry matter distribution are available for olive trees. An analysis of partitioning for olive trees is also needed to define the relationship for our general growth model.

Despite the importance of olive groves in the Mediterranean basin, the response of olive trees to radiation has rarely been studied either at the leaf (Proietti et al. 1988, Angelopoulos et al. 1996) or the tree level (Tombsi and Standardi 1977, Tombsi and Cartechini 1986), and no work has been done at the canopy level. The objectives of this study were to determine the RUE of olive stands (seasonal values and time course) and to obtain biomass partitioning coefficients for olive trees grown at different densities.

Materials and methods

The field experiment

The experiment was performed at the Agricultural Research Center of Córdoba, Spain (37°52' N, 4°49' W) from 1995 to

1997. The soil is a sandy-loam of alluvial origin, classified as Typic Xerofluvent. Global radiation was measured with an automatic weather station located 700 m from the experimental site.

On March 1, 1995, 849 1-year-old olive (*Olea europaea* L. var. 'Picual') trees were planted at two densities: 0.5 (D1) or 2.0 (D2) trees m^{-2} in a random-block design with four replications. The planting densities were chosen to obtain a large range in leaf area index (LAI). Each plot consisted of 10 rows with 10 trees per row. In each plot, 12 labeled trees were cut during the experimental period. The selected trees were located in the following positions: (3, 3); (3, 6); (3, 9); (4, 3); (4, 6); (4, 9); (7, 3); (7, 6); (7, 9); (8, 3); (8, 6); (8, 9), where the coordinates indicate the position in rows and row number. Sprinkler irrigation was applied weekly when necessary. Weeds, mostly nutgrass (*Cyperus rotundus*), were controlled by hand. Nitrogen fertilizer and pesticides were applied following recommended rates for the area.

Measuring trunk diameter, tree height and plant area index

Trunk diameter 10 cm aboveground and height of the labeled trees were measured monthly. Plant area index (PAI) was estimated with a plant canopy analyzer (PCA, LAI-2000, Li-Cor, Inc., Lincoln, NE) every other week. Above- and below-canopy measurements of diffuse radiation were taken under completely overcast conditions, which is required for the best performance of the PCA (Welles and Norman 1991). In each plot, below-canopy PCA measurements were taken in five fixed positions diagonally distributed in the square area delimited by four trees. A first data set was obtained by orienting the PCA in the row direction. A second data set was obtained by orienting the PCA in the opposite direction. Mean PAI and the fraction of diffuse radiation intercepted by the canopy (Q_{dif}) were obtained from these data. Values of Q_{dif} were used to compute the PAR intercepted by the olive trees.

Radiation interception

The fraction of diffuse radiation intercepted by the canopy was measured every other week with the PCA as described for the PAI measurements. The Q_{dif} versus time relationships were fit with equations of the type:

$$Q_{dif} = a + \frac{b}{1 + \exp^{-(t-c)/d}}, \quad (1)$$

where t is time (day of the year since January 1, 1995) and a , b , c and d are estimated parameters (Table 1). A fit was performed for each density and growing season to obtain estimates of the fraction of incident PAR intercepted by the trees under overcast sky conditions (Q_{dif}') for every day during 1995, 1996 and 1997.

The daily fraction of incident PAR intercepted by the trees under clear sky conditions (Q_d) was measured once a month. In each plot, radiation interception was calculated as the difference between incident radiation above the canopy (I_{oi}) and radiation transmitted to the soil (I_t). The transmitted radiation, at a given solar position, was determined with a 1.0×0.01 m

linear quantum sensor (Decagon, Delta-T Devices, Pullman, WA). In D2 (0.7 m between rows), measurements were taken with the sensor located at 14 fixed positions below the four central trees of each plot, displacing the sensor parallel to itself at a regular spacing of 0.05 m. For each measurement, the sensor was oriented at an angle to the row to locate the extremes of the 1-m sensor in two adjacent rows. In D1 (1.4 m between rows), 28 fixed positions were marked, and the sensor was moved in 0.1 m increments. A first set of measurements was obtained from the center of one row to midway between rows, and a second set of measurements was obtained from mid-row to the next row center. Thus, the sampling represented 20 and 10% of the total area for the D1 and D2 treatments, respectively. The means were automatically recorded and assigned a mean time.

Above-canopy readings were made before and after measuring each of the plots, and the means calculated. On each measuring day, seven solar positions distributed at equal intervals from sunrise to sunset were chosen. The first, fourth and seventh measurements were performed at sunrise, solar noon, and sunset, respectively. Daily incoming PAR and daily transmitted PAR were obtained by integrating the seven values of I_i and I_{oi} , respectively, by the rectangular rule. Therefore Q_d was:

$$Q_d = 1 - \int I_t dt / \int I_{oi} dt. \quad (2)$$

Every day when Q_d was measured, Q_{dif} was obtained at sunset. A plot of Q_d against Q_{dif} yielded the following linear relationship:

$$Q_d = 0.009 + 1.025 Q_{dif} \quad (3)$$

$(r^2 = 0.95 \quad n = 160 \quad SEE = 0.07).$

Estimates of the fraction of incident PAR intercepted by the trees (Q_d') for totally clear days were obtained by applying Equation 3 to the values of Q_{dif}' .

The daily fraction of incident radiation received as direct-beam radiation (beam fraction) was calculated as described by Spitters et al. (1986). Values of the fraction of incident PAR intercepted by the trees (Q_{di}) were estimated for each day during 1995, 1996 and 1997, based on Q_{dif}' for days with overcast sky conditions, Q_d' for clear days and an interpolated value for partially cloudy sky conditions. The cumulative PAR intercepted by the crop between consecutive dates of the growing cycle (I_R) was calculated as:

$$I_R = \sum I Q_{di}. \quad (4)$$

where I ($MJ \text{ PAR } m^{-2} \text{ day}^{-1}$) is daily incident PAR (45% of shortwave radiation).

Biomass, partitioning coefficients and conversion factor

Harvest of aboveground biomass was made on six dates: (1) September 25, 1995 (establishment period); (2) February 19, 1996 (end of winter); (3) May 13, 1996 (period of rapid vegetative growth); (4) September 10, 1996 (period of rapid

Table 1. Parameters (*a*, *b*, *c*, *d*) of Equation 1 describing the seasonal time-course of diffuse PAR intercepted by olive trees var. 'Picual,' for two planting densities (0.5 and 2.0 trees m⁻²) and two growing seasons. Determination coefficients (*r*²) and standard error of estimates (SEE) are also presented.

Planting density (trees m ⁻²)	Growing season	<i>a</i>	<i>b</i>	<i>c</i>	<i>d</i>	<i>r</i> ²	SEE
0.5	1995–1996	0.02	0.12	252.0	47.4	0.84	0.02
0.5	1996–1997	0.12	0.66	538.3	36.6	0.96	0.06
2.0	1995–1996	0.03	0.38	203.9	38.5	0.93	0.04
2.0	1996–1997	0.39	0.54	485.8	20.7	0.97	0.04

vegetative growth); (5) December 11, 1996 (beginning of winter) and (6) March 04, 1997 (end of winter). Two trees per density treatment and block were cut at ground level and separated into branches, trunk and leaves. After the fourth harvest, branches with diameters smaller than 5 mm were measured separately. Dry matter was obtained after drying the tree components separately to constant weight at 70 °C. Leaf area of the samples was measured with an electronic planimeter (Li-Cor LI-3100). Diameters and lengths of branches and trunks were determined and, assuming conic and cylindrical shapes, their area was considered as one-half of the lateral area of these shapes. Plant area index was derived as the ratio between plant area (leaves, trunk and branches) and ground area per tree (2 and 0.5 m² for D1 and D2, respectively). Specific leaf area (SLA) was determined as the ratio of area to dry weight. Because of the large size of the trees, in the fifth and sixth harvests only, a subsample of 10% of the fresh weight for each organ was separated.

The data for the six harvests were pooled and the biomass partitioning coefficients for each planting density were obtained as follows: from the slope of the regression (*b*₁) between leaf biomass and wood biomass, the leaf biomass partitioning coefficient (LPC_b) was calculated as $b_1/(1 + b_1)$. Similarly, the wood biomass partitioning coefficient (WPC_b) was estimated as $b_2/(1 + b_2)$, where *b*₂ is the slope of the regression of wood biomass and leaf biomass. Comparisons among the slopes were performed by the *t*-test procedure (Steel and Torrie 1960). The leaf area partitioning coefficient (LPC_a) was calculated as described for the calculation of LPC_b by using area data instead of biomass data.

Root biomass was obtained only in D1. Roots were separated from a soil volume of 1.4 × 1.4 × 0.7 m with the aid of water and dried at 70 °C to constant weight. A soil volume of 0.7 × 0.7 × 0.7 m around the trunk was removed, wetted and sieved through a 2-mm mesh. In the remaining soil volume, 72 soil samples of 0.09 × 0.12 m were removed, wetted and sieved. The root biomass partitioning coefficient (RPC) was calculated as described for the calculation of LPC_b with above-ground biomass as the independent variable and root biomass as the dependent variable.

The conversion factor or production value (cvf: the amount of dry matter produced per gram of glucose, g g⁻¹) was calculated for each organ according to the equation (Penning de Vries et al. 1974):

$$\frac{1}{\text{cvf}} = 1.242f_c + 1.704f_p + 3.106f_g + 2.174f_i + 0.05f_m \quad (5)$$

where *f*_c, *f*_p, *f*_g, *f*_i, and *f*_m denote the fractions of carbohydrates, proteins, fats, lignin and minerals in the dry matter of each organ (Table 2). The values corresponding to olive leaves and fine branches were taken from Banco de Muestras Valoradas de la Universidad de Córdoba, (V. Fernández, personal communication). The values corresponding to trunk and bulk branches were taken from Kropff and Spitters (1988). Above-ground dry matter expressed in glucose units (g) was calculated as:

$$g = \sum_{i=1,n} \text{dm}_i / \text{cvf}_i \quad (6)$$

where *n* is number of tree organs, dm_{*i*} is dry matter and cvf_{*i*} is the corresponding coefficient for each organ.

The relationships obtained at harvest between trunk diameter (*d*, cm) and biomass (*b*, g tree⁻¹) were: $b = 54.02d^{2.48}$ (*r*² = 0.90) for a planting density of 0.5 trees m⁻²; and $b = 29.80d^{2.85}$ (*r*² = 0.92) for a planting density of 2.0 trees m⁻².

Monthly values of aboveground biomass were estimated by applying Equations 7 and 8 to the trunk diameter measurement for the trees that were monitored throughout the experiment.

Radiation-use efficiency

Radiation-use efficiency (g (MJ PAR)⁻¹) was calculated as the slope of the regression of the tree biomass obtained in the six harvests versus cumulative intercepted PAR. Monthly values of RUE were calculated as the ratio between the monthly biomass increase (g m⁻²) calculated by trunk diameter, and the

Table 2. Fractions (g g⁻¹ of dry matter) of carbohydrates (*f*_c), proteins (*f*_p), fats (*f*_g), lignin (*f*_i), and minerals (*f*_m) in some organs of olive trees.

Fraction	Leaf	Fine branches	Trunk and bulk branches
<i>f</i> _c	0.570	0.615	0.660
<i>f</i> _p	0.115	0.061	0.020
<i>f</i> _g	0.058	0.037	0.010
<i>f</i> _i	0.184	0.205	0.300
<i>f</i> _m	0.079	0.082	0.010

PAR intercepted by trees during the same period (MJ PAR m^{-2}).

Results

Development of tree height, trunk diameter and PAI

The time courses of tree height and trunk diameter (Figure 1) followed a double-sigmoid pattern, with two periods of slow growth during the winters of 1995–1996 (Days 300–400) and 1996–1997 (Days 700–800). Plant area index (PAI) was negligible at planting. During summer 1995, PAI increased slowly, then remained constant during winter 1995–1996. It increased rapidly until summer 1996 and then stabilized in winter 1996–1997 (Figure 2). The high planting densities allowed PAI to reach values greater than those measured in commercial orchards. Plant area index was proportional to planting density ($D1/D2 = 1/4$) until July 1996, indicating that once rapid growth began, greater inter-tree competition in D2 than in D1 resulted in smaller trees in D2. Height growth appeared to be restricted in the D2 treatment slightly before treatment differences in trunk diameter appeared (Figure 1).

Biomass production

Dry matter per unit area increased with planting density. During the first year, aboveground dry matter increased to 109 ± 11 and 458 ± 34 $g\ m^{-2}$ in D1 and D2, respectively. During the second year of the experiment (February 1996–February 1997), the corresponding dry matter values were 2011 ± 68 and 3633 ± 355 $g\ m^{-2}$ (Table 3). Loomis and Connor (1992) reported a maximum production of $4000\ g\ m^{-2}$ for herbaceous C_3 species, at a comparable latitude and length of growing season, which is close to the final biomass obtained in D2.

No significant differences ($P > 0.05$) between biomasses of the fifth and sixth tree harvests were observed in D2, indicating that biomass accumulation was negligible during winter. However, differences were observed between biomasses of the fifth and sixth harvests in D1. Root biomass:aboveground biomass ratios were 0.35 ± 0.01 and 0.38 ± 0.03 for the fifth and sixth

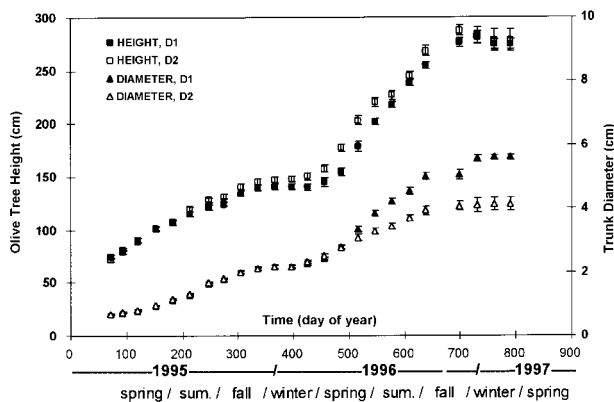


Figure 1. Time course of tree height and trunk diameter (mean and standard error) of olive trees var. 'Picual' grown at densities of $0.5\ trees\ m^{-2}$ (D1) and $2.0\ trees\ m^{-2}$ (D2).

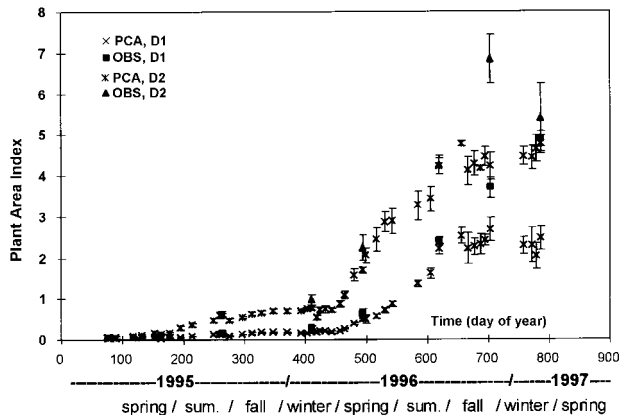


Figure 2. Time course of plant area index (PAI, mean and standard error) of olive trees var. 'Picual' grown at densities of $0.5\ trees\ m^{-2}$ (D1) and $2.0\ trees\ m^{-2}$ (D2). Values of PAI were estimated with a PCA and also directly obtained at six harvest dates (OBS).

harvests, respectively, and did not differ significantly ($P > 0.05$). Thus, the reduction in olive shoot growth during winter is apparently not related to an increase in partitioning to support root growth instead of shoot growth.

Biomass partitioning coefficients

A strong linear relationship between dry matter of the different organs was found in all cases. Partitioning coefficients were derived from these relationships (Table 4). The leaf partitioning coefficient (LPC_b) and wood partitioning coefficient (WPC_b) were 0.37 and 0.60 in D1, respectively. These values were significantly different ($P < 0.05$) from those obtained in D2 (LPC_b of 0.28 and WPC_b of 0.69).

Two periods were differentiated in the relationship between root biomass and aboveground biomass (Figure 3). In the first phase, from the planting date to winter 1995–1996, RPC was 0.39. In the second phase (the second year), the root partitioning coefficient (RPC) decreased significantly ($P < 0.05$) to 0.26.

Area partitioning and specific leaf area

Around 90% of the plant area corresponded to leaves, independent of planting density (Table 5). Villalobos et al. (1995) found similar values for area partitioning of mature olive trees var. 'Picual', indicating that the fraction of plant area corresponding to leaf is a constant value in well-managed trees and that it becomes established soon after planting. Specific leaf area (SLA) was similar at the two planting densities (51.0 ± 0.8 and $50.9 \pm 1.2\ cm^2\ g^{-1}$ in D1 and D2, respectively, Table 5). No obvious trend in SLA over time was observed (data not shown). Our SLA values are within the range found by Tombesi and Cartechini (1986) for three Italian olive varieties ($44\text{--}55\ cm^2\ g^{-1}$) and close to those for *Quercus ilex* L. in northeastern Spain ($50\ cm^2\ g^{-1}$, Sala et al. 1994).

Table 3. Dry matter production of olive trees var. 'Picual' at two planting densities (D1 = 0.5 trees m⁻² and D2 = 2.0 trees m⁻²) in Córdoba, Spain. Each value is the mean of eight olive trees.

Harvest	Aboveground biomass (g tree ⁻¹)				Aboveground biomass (g m ⁻²)			
	D1		D2		D1		D2	
	Mean	SEE	Mean	SEE	Mean	SEE	Mean	SEE
1	136.1	20.8	128.6	7.9	69.4	10.6	262.5	16.2
2	284.4	32.0	236.0	25.2	145.1	16.3	481.6	51.5
3	552.4	84.6	492.7	79.5	281.8	43.2	1005.6	162.3
4	2312.6	116.3	994.2	68.8	1179.9	59.3	2029.0	140.3
5	3132.0	123.1	1816.7	202.1	1597.9	62.8	3707.6	412.5
6	4225.8	185.2	2016.1	244.8	2156.0	94.5	4114.4	499.7

Table 4. Dry matter partitioning coefficients for leaves (LPC_b) and wood (WPC_b) of olive trees var. 'Picual' planted at 0.5 and 2.0 trees m⁻². The linear regressions from which the partitioning coefficients were calculated, determination coefficients (r^2) and the standard error of estimates (SEE) are also presented. Partitioning coefficient values followed by the same letter do not differ at the 0.05 probability level. An asterisk indicates significant at 5%.

Planting density (trees m ⁻²)	Organ	Partitioning coefficient	Equation	r^2	SEE
0.5	Leaves	0.37 a	$y = 42.2 + 0.598x$	0.89*	211.5
0.5	Wood	0.60 c	$y = 56.6 + 1.487x$	0.89*	333.5
2.0	Leaves	0.28 b	$y = 54.5 + 0.381x$	0.85*	96.8
2.0	Wood	0.69 d	$y = -24.8 + 2.23x$	0.85*	234.2

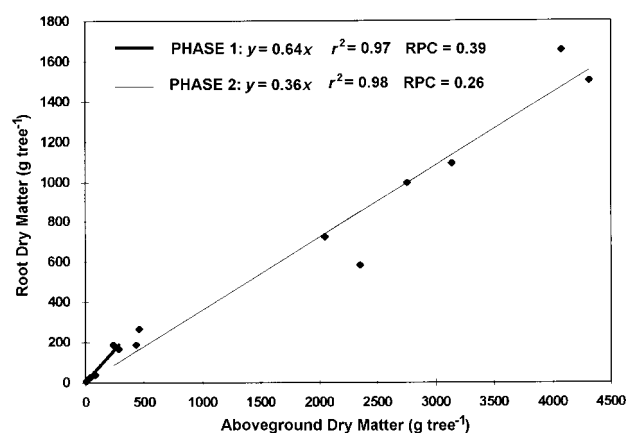


Figure 3. Root biomass versus aboveground biomass of olive trees var. 'Picual' grown at a density of 0.5 trees m⁻². The linear regressions for the first (Phase 1) and second (Phase 2) year of the experiment, and the root partitioning coefficient (RPC) are also presented.

Cost of dry matter production

The conversion factor (cvf) was 0.672 for leaves, 0.699 for fine branches, and 0.650 for bulk branches and trunk. The small difference in cvf among organs implies that biomass partitioning has only a small effect on RUE. A conversion factor was calculated for the olive trees as a whole, taking into account the biomass of each organ and its cvf. These values were $0.669 \pm 0.0006 \text{ g g}^{-1}$ in D1 and $0.667 \pm 0.0005 \text{ g g}^{-1}$ in D2 ($P < 0.05$). The differences between planting densities are explained by

Table 5. Leaf area partitioning coefficients (LPC_a) and specific leaf area (SLA) of olive trees var. 'Picual,' planted at 0.5 and 2.0 trees m⁻², at Córdoba, Spain. Values followed by the same letter do not differ at the 0.05 probability level.

Planting density (trees m ⁻²)	Partitioning coefficient	SLA (cm ² g ⁻¹)
0.5	0.91 a	$51.0 \pm 0.8 \text{ c}$
2.0	0.89 a	$50.9 \pm 1.2 \text{ c}$

the greater investment in supporting organs in D2 than in D1. Biosynthesis of products rich in proteins or lignin requires more energy than components with low concentrations of these products (Penning de Vries et al. 1974). The energy content of olive dry matter is relatively high. It is close to the cvf of some seeds; for example, it is between the cvf of corn (0.71) and chickpea seeds (0.65) (McDermitt and Loomis 1981).

PAR Interception

The time courses of daily PAR interception (Q_d) and diffuse interception (Q_{dif}) followed sigmoid patterns for each year of the experiment, with stabilization during each winter (Figure 4). During the rooting process, at the time of establishment, much biomass was invested in roots so that the trees remained small. At the end of the first year, maximum Q_d values were 0.15 and 0.40 for D1 and D2, respectively. However, rapid growth during the second year resulted in large increases in Q_d , from 0.15 to 0.70 in D1 and from 0.40 to 0.90 in D2. Because

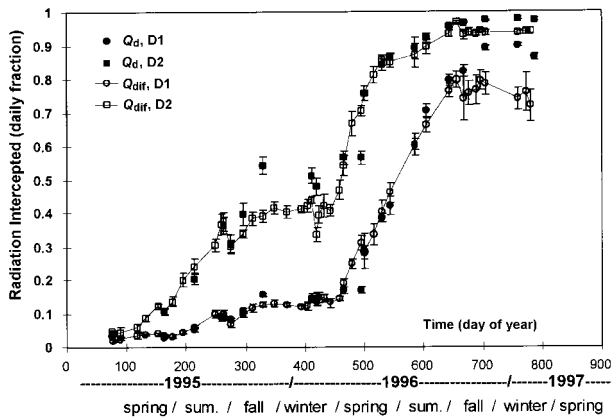


Figure 4. Time course of the daily fraction of PAR intercepted (Q_d) and diffuse radiation intercepted (Q_{dif}) for olive trees var. 'Picual' grown at densities of 0.5 tree m^{-2} (D1) and 2.0 trees m^{-2} (D2). Means and standard errors are presented.

of the D2-treatment-induced changes in canopy development, D2 always showed higher Q_d than D1, intercepting almost 100% of incoming radiation at the beginning of the second winter. The maximum interception of D1 was 0.70. Over the whole experiment (794 days), cumulative intercepted PAR by the olive canopies was 1705 $MJ m^{-2}$ for D1 and 2984 $MJ m^{-2}$ for D2, and cumulative incoming PAR was 5403 $MJ m^{-2}$.

RUE: Seasonal pattern and annual RUE

The aboveground biomass of olive trees was linearly related to the cumulative intercepted PAR (Figure 5). The slopes of the regressions (RUE) between these variables were 1.25 and 1.42 $g (MJ PAR)^{-1}$ for D1 and D2, respectively; however, these relationships were not significantly different ($P > 0.05$), and pooling the data from both densities yielded a seasonal RUE of 1.35 $g (MJ PAR)^{-1}$.

The value of RUE may change over the life of the plant. Because data corresponding to the harvests did not permit an

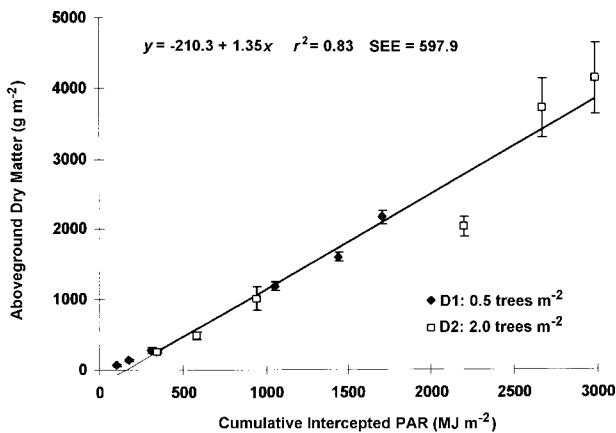


Figure 5. Aboveground biomass ($g m^{-2}$) versus cumulative intercepted PAR ($MJ m^{-2}$) for olive trees var. 'Picual' grown at densities of 0.5 tree m^{-2} (D1) and 2.0 trees m^{-2} (D2).

analysis of the time course of RUE, it was estimated from the relationship between trunk diameter and dry matter (Figure 6). Radiation-use efficiency was low ($< 0.5 g (MJ PAR)^{-1}$) during spring 1995. Thereafter, RUE increased gradually until fall 1995, when values close to 2 $g (MJ PAR)^{-1}$ were achieved. Subsequently, RUE decreased to almost zero in winter 1995–1996. During the second year, RUE decreased slightly during summer, and decreased to almost zero in winter 1996–1997.

Despite the large differences in PAI between planting densities (Figure 2), trees in both treatments had similar values and seasonal patterns of RUE. Because RUE was similar in fall 1995, spring 1996 and fall 1996, whereas PAI increased from 0.2 in fall 1995 to 4 in fall 1996, we conclude that PAI did not affect RUE.

Discussion

Biomass partitioning

Values of LPC_b and WPC_b at each planting density indicate that young olive trees (non-bearing) invest more aboveground biomass in supporting organs than in leaves (WPC_b of 0.60 and 0.69 in D1 and D2, respectively, Table 4). Partitioning to wood increased as tree-to-tree competition increased. For fractions of radiation interception close to 1, the wood partitioning coefficient tended toward 0.69. The WPC_b increased at the expense of LPC_b (0.37 versus 0.28), limiting the capacity for assimilation and growth per tree. Planting density did not affect area partitioning, although it did affect biomass partitioning, indicating that the fraction of area corresponding to leaves is relatively insensitive to changes in biomass partitioning between leaves and wood.

The root biomass partitioning coefficient (RPC) decreased over time. In the second year, RPC was 0.26 (Figure 3). Data on distribution of dry matter to roots in olive trees are scarce. Celano et al. (1997) showed a root:aboveground biomass ratio of 0.18 for 2-year-old olive trees var. 'Coratina' (root partitioning coefficient = 0.15). It seems that the proportion of assimi-

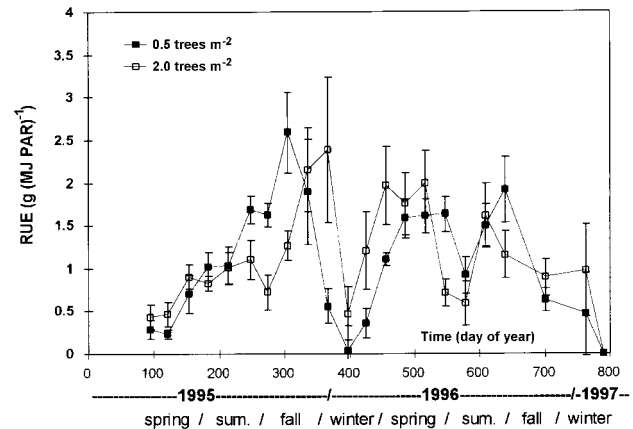


Figure 6. Time course of radiation-use efficiency ($g (MJ PAR)^{-1}$) of olive trees var. 'Picual' during the experiment. Means and standard errors are presented.

lates distributed to the roots of var. 'Coratina' was less than we observed; however, var. 'Coratina' yielded 0.5 kg of fruit per tree, whereas var. 'Picual' did not bear fruit. Despite the discrepancies in absolute values, Celano et al. (1997) showed that the root:aboveground biomass ratio decreases with time, in agreement with our results. In the absence of a clear understanding of how biomass production is distributed within the olive tree, dry matter partitioning coefficients could provide an initial estimate of plant growth.

Radiation-use efficiency

Dry matter production by olive trees is linearly related to the amount of PAR intercepted (Figure 5). Olive trees var. 'Picual' growing under non-limiting conditions of water and nutrients had a RUE of $1.35 \text{ g (MJ PAR)}^{-1}$ in the Andalusian environment. This RUE, although lower than values reported for herbaceous crops (e.g., Kiniry et al. 1989), is within the range reported for other woody species. For example, Linder (1985) reported a RUE of $0.5 \text{ g (MJ PAR)}^{-1}$ of global radiation (about $1 \text{ g (MJ PAR)}^{-1}$) for young *Eucalyptus*, and Wang et al. (1991) estimated a RUE of 0.43 g mol^{-1} (about $1.9 \text{ g (MJ PAR)}^{-1}$) for Douglas-fir. However, it is difficult to compare estimates for different species because of disparities in the measurement techniques, climatic conditions, amounts of biomass taken into account (aboveground or total), and in the nature of the observations.

There are several possible explanations for the low RUE of olive trees. In a woody stand, the respiration of supporting organs negatively affects RUE (Russell et al. 1989). The biochemical composition of woody biomass may also cause a low RUE (Russell et al. 1989). Sinclair and Horie (1989) showed theoretically that RUE depends on maximum leaf photosynthetic rate (P_m). However, this relationship is nonlinear, and at high P_m , small variations in RUE are expected as P_m changes. The P_m for leaves of olive trees var. 'Picual' ranges between 12 and $18 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (Gimenez et al. 1997), which is low compared with rates in other crops (Schulze and Hall 1982). Thus, low P_m could explain the low RUE in olive.

The value of RUE changed over time (Figure 6), partially as a consequence of changes in canopy photosynthetic rates. Radiation-use efficiency was low (less than $0.5 \text{ g (MJ PAR)}^{-1}$) during spring 1995, which could be associated with the rooting process during establishment. Radiation-use efficiency decreased to almost zero in winter 1995–1996 and winter 1996–1997. Bartelink et al. (1997) also estimated low values (even negative) of RUE in Douglas-fir in the winter period with the FORGRO model, and suggested that low RUE was a result of unfavorable temperatures and low PAR availability, when maintenance requirements in evergreen stands become greater than canopy assimilation. However, in Andalusia, winter temperature and PAR are not as low as the conditions modeled by FORGRO, indicating that other factors may have caused the low RUE values in winter. Gimenez et al. (1997) showed that daily values of stomatal conductance and photosynthesis during winter are low in relation to those during fall and spring. Temporary flooding may also contribute to a decrease in olive leaf photosynthesis (Nicoli and Tombesi 1984). Radiation-use

efficiency decreased slightly during summer 1996, probably as a result of partial stomatal closure and a reduction in photosynthesis in response to high vapor pressure deficits (Bongi et al. 1987, Angelopoulos et al. 1996, Gimenez et al. 1997). Also, an increase in temperature may result in a greater increase in maintenance respiration than in leaf photosynthesis.

Neither PAI nor planting density affected RUE, indicating that canopy structure and incident radiation determined the quantity of radiation intercepted by the canopy, whereas the efficiency of dry matter production was insensitive to differences in canopy structure and radiation environment. This behavior contrasts with other crops (e.g., Trapani et al. 1992). However, the response of canopy photosynthesis to radiation is complex and depends on incident radiation flux density and individual leaf photosynthetic response. Radiation-use efficiency may be affected by how these variables change as PAI increases. For example, Rosenthal et al. (1993) did not find changes in sorghum RUE with planting densities ranging between 5 and 26 plants m^{-2} , whereas Morrison and Stewart (1995) reported that RUE decreased in *Brassica napus* L. when plant density increased.

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