



Light interception and radiation use efficiency in temperate quinoa (*Chenopodium quinoa* Willd.) cultivars

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ABSTRACT

Sea level quinoas are grown at low altitudes in Central and Southern Chile. Both sensitivity to photoperiod and response to temperature largely determine quinoa adaptation, but crop biomass production must be quantified to evaluate agronomic performance. The objectives of this work are: (i) to characterize development effects on leaf area evolution for genotypes of sea level quinoa differing in cycle length, (ii) to quantify the extinction coefficient (k) for photosynthetically active radiation (PAR) and radiation use efficiency (RUE) from emergence up to the beginning of grain filling and (iii) to identify which crop attributes related to canopy architecture should be considered to improve biomass production. Four cultivars (NL-6, RU-5, CO-407 and Faro) were cropped in Pergamino (33°56'S, 60°35'W, 65 m a.s.l.), Argentina, at three densities (from 22 to 66 plants m^{-2}) in two consecutive years under field conditions with adequate water and nutrient supply. Thermal time to first anthesis and maximum leaf number on the main stem were linearly correlated ($r^2 = 0.87$; $p < 0.0001$). Leaf area continued to increase during the flowering phase, notably in NL-6, the earliest genotype. There were significant differences in maximum plant leaf area between cultivars. Increasing density reduced plant leaf area but effects were comparatively small. Estimated k was 0.59 ± 0.02 across genotypes and was higher ($p < 0.05$) for 66 plants m^{-2} . Values for RUE changed as cumulative intercepted PAR (IPAR) increased; at initial stages of development RUE was 1.25 ± 0.09 g MJ IPAR⁻¹, but if cumulative IPAR was higher than 107.5 ± 10.4 MJ IPAR m^{-2} , RUE was 2.68 ± 0.15 g MJ IPAR⁻¹. That change occurred when leaf area index (LAI) and fraction of PAR intercepted were still low and ranged from 0.61 to 1.38 and from 0.33 to 0.51, respectively. No significant association was found with any developmental stage. Our results agreed to the notion that RUE variation during pre-anthesis phases is largely determined by LAI through its effect on radiation distribution within the canopy. Biomass production could be improved if periods of interception below 50% of incoming PAR were reduced to ensure high RUE. This seems to be possible in temperate areas both by the use of late genotypes with a higher number of leaves on the main stem and by early genotypes provided adequate plant density is chosen. Early increment in LAI and overlapping of the leaf area increase period with the flowering phase are desirable strategies for earliest genotypes to maximize yield.

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1. Introduction

In recent years, the cultivation of crops like quinoa, amaranth and buckwheat has gained rising attention, due to the attractive nutritive value of these species, as well as the effort to expand the

number of species which contribute to human nutrition (Schulte auf'm Erley et al., 2005). Quinoa (*Chenopodium quinoa*, Willd.) is an Andean seed crop with different ecotypes adapted to different conditions (Tapia et al., 1979). There is a wide range of humidity and temperature requirements for the cultivation of quinoa. In fact, some genotypes of quinoa are grown under conditions of severe drought while others need more humid conditions (Jacobsen, 2003). Sea level quinoas are grown at low altitudes in Central and Southern Chile (Tapia et al., 1979) and their low photoperiod sensitivity makes them suitable for cultivation in temperate environments (Bertero et al., 1999). Breeding programs in Europe and the USA have released new genotypes, some of them selected from Chilean lines (Jacobsen, 2003). There is a special interest in this crop because of its environmental stress tolerance and economic pos-

Abbreviations: F, fraction of PAR intercepted at midday; Fd, daily fractional interception; IPAR, intercepted PAR (MJ $m^{-2} d^{-1}$); k , extinction coefficient; LAI, leaf area index ($m^2 m^{-2}$); PAR, photosynthetically active radiation (MJ $m^{-2} d^{-1}$); RUE, radiation use efficiency (g MJ PAR⁻¹); TPLA, total plant leaf area ($m^2 plant^{-1}$); TPLA_{max}, maximum total plant leaf area ($m^2 plant^{-1}$).

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sibilities both in local and international markets. Although some crop management (notably that related to crop establishment), and harvest and post-harvest technology determine certain constraints, quinoa could become an interesting alternative to winter cereals (Bertero, 2001a) or be included in a double crop sequence when an early harvest is required to sow a second crop, as it usually occurs in the Pampas region of Argentina (Calviño et al., 2003).

Sensitivity to photoperiod as well as response to temperature during the growing period largely determine quinoa adaptation to new environments. Both attributes were described for various sets of cultivars of different origin and were useful to select promising cultivars for a certain environment and management combination (Bertero et al., 1999). However, actual crop biomass production must be quantified in order to draw accurate conclusions about those cultivars agronomic adaptation. In sea level quinoa cultivars, the period of active inflorescence growth before seed filling appears to be the most sensitive to environmental conditions in terms of seed number determination (Bertero and Ruiz, 2008). So, it is desirable to reach the maximum crop growth rate before and to sustain it during the flowering phase to maximize this yield component.

In the absence of biotic and abiotic stresses, crop biomass accumulation depends on the quantity of PAR (photosynthetically active radiation) intercepted by the canopy (e.g., Monteith, 1977; Kiniry et al., 1989; Sinclair and Muchow, 1999). The relationship between crop biomass and IPAR (intercepted PAR) has been termed RUE (radiation use efficiency) (g MJ^{-1} ; Monteith, 1977). Interception of PAR by a crop can be further described in terms of the total amount of incident PAR on the crop, and the fraction of this radiation which is intercepted by the canopy. The total incident PAR is a function of location, year, sowing date and crop phenology, whereas the fraction of incident PAR intercepted is a function of LAI (leaf area index) and k (Monteith, 1965). Thus, the successful modeling of plant growth relies on an adequate description of LAI, the light extinction coefficient for PAR, and RUE. These major canopy characteristics of important grain crops are well established from unstressed field experiments for wheat (Kiniry et al., 1989; Siddique et al., 1989), barley (Gallagher and Biscoe, 1978), maize (Sivakumar and Virmani, 1984; Kiniry et al., 1989), peanut (Kiniry et al., 2005), sorghum (Sivakumar and Virmani, 1984; Kiniry et al., 1989), rice (Kiniry et al., 1989), sunflower (Connor et al., 1985) and soybean (Sinclair and Shiraiwa, 1993), and also from rainfed crops in semi arid environments (O'Connell et al., 2004). By contrast, as far as quinoa is concerned, data on these attributes are scarce (Bertero et al., 2004). A number of crop growth simulation models have been developed using the RUE concept to predict crop growth and yield under different environments and management conditions (e.g., Jones and Kiniry, 1986; Muchow et al., 1990; Brisson et al., 2003). Increased understanding of factors controlling biomass production is required to accurately simulate growth. This will help quantify productivity in different environments and, thus, limitations due to stress or to canopy architecture as well as leaf area dynamics could be better understood (Kiniry et al., 1999).

The objectives of this work are:

- (i) To characterize development effects on leaf area evolution for sea level quinoa genotypes differing in cycle length.
- (ii) To quantify the extinction coefficient for PAR and RUE from emergence up to the beginning of grain filling.
- (iii) To identify which crop attributes related to canopy architecture should be considered to improve biomass production.

2. Materials and methods

2.1. Experimental design and growing conditions

Sea level quinoa (*C. quinoa* Willd.) genotypes from Chile or selected from lines of that origin were cropped in Argentina, at the Instituto Nacional de Tecnología Agropecuaria (INTA) Experimental Station in Pergamino ($33^{\circ}56'S$, $60^{\circ}35'W$, altitude 65 m a.s.l., 225 km NW from Buenos Aires), on a silty clay loam soil (Typic Argiudoll, Soil Taxonomy, U.S. Department of Agriculture) in two consecutive years. Mean soil properties in the first 20 cm of soil depth at sowing were: pH (in water 1:2.5) 5.5; organic matter 28.5 g kg^{-1} ; organic nitrogen 1.4 g kg^{-1} ; mineral phosphorus 41 mg kg^{-1} and electric conductivity 0.144 dS m^{-1} .

Four cultivars – NL-6 (from Holland), RU-5 (from the UK), CO-407 (from the USA) and Faro (from Chile) – were sown at two densities in a factorial experiment arranged in a randomized complete block design with four replicates. Sowing dates were August 28, 2003 and September 7, 2004. Plots were hand-planted and thinned to 22 (d1) and 33 (d2) pl m^{-2} in rows 0.45 and 0.30 m apart in 2003 and to 33 (d2) and 66 (d3) pl m^{-2} in rows 0.30 and 0.15 m apart, respectively in 2004. Plots were 9 (d1), 15 (d2) and 17 (d3) rows wide and 5 m long, and size ranged from 12 to 23 m^2 , depending on the density. Soil nitrate availability at sowing was low (below 15 kg N ha^{-1} as NO_3^- for the 0–60 cm depth). Plots received supplementary irrigation and fertilization at sowing (20 kg P and 18 kg N ha^{-1} as diammonium phosphate) and two urea applications (in order to reach $200 \text{ kg available N ha}^{-1}$) at 30 and 60 days after emergence to minimize nutrient restrictions. Nitrogen doses were decided on the basis of previous reports of maximum yields being achieved between 160 (Jacobsen et al., 1994) and 225 kg N ha^{-1} (Berti et al., 2000). To prevent insect pests and fungal diseases, insecticides and fungicides were applied regularly and weeds removed by hand. Emergence dates were September 4, 2003 and September 21, 2004.

Average temperatures during the crop cycle were similar for both years (18.4 and 18.8°C for 2003 and 2004, respectively), but radiation was lower in 2004 (9.4 and $7.8 \text{ MJ PAR m}^{-2} \text{ d}^{-1}$ for 2003 and 2004, respectively). The 2004 experiment suffered from waterlogging around mid-November, coinciding with the flowering phase in some of the cultivars (Fig. 1).

2.2. Light interception

Photosynthetically active radiation interception was measured with a 0.8-m long ceptometer (Decagon Devices Inc., Pullman, Washington) between 11:30 and 14:00 h on clear days. Six measurements were taken in each replicate. The first and last measurements were taken above the canopy to determine incident PAR (I_0). The other four measurements were taken at soil surface level placing the sensor below the canopy and moving it parallel to rows at regular intervals in order to determine transmitted PAR (I_t) as indicated by Charles-Edwards and Lawn (1984). The fraction of PAR intercepted at midday (F) was calculated as:

$$F = \frac{(I_0 - I_t)}{I_0} \quad (1)$$

where I_0 and I_t are the means of the measurements above and below the canopy.

Daily fraction of PAR intercepted (F_d) was calculated from mid-day values, as proposed by Charles-Edwards and Lawn (1984) as:

$$F_d = \frac{2F}{(1 + F)} \quad (2)$$

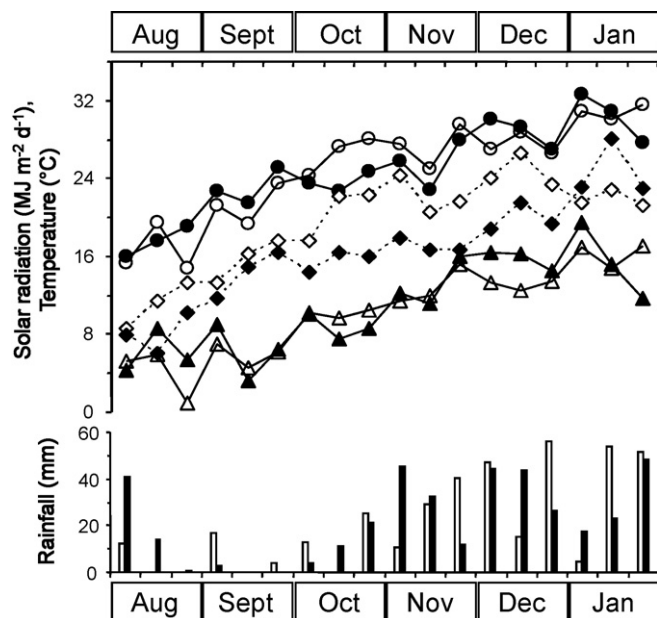


Fig. 1. Incident solar radiation (diamonds, dotted line), maximum temperature (circles, solid line), minimum temperature (triangles, solid line) and rainfall (bars) during the two experiments: 2003 (open symbols) and 2004 (closed symbols) in Pergamino. Values are means (radiation and temperature) or total (rainfall) of 10-day periods.

Daily fraction of PAR intercepted between measurements was obtained by linear interpolation and applied to the corresponding daily values of PAR to estimate IPAR. To calculate daily incident PAR, the incident total solar radiation was measured with a standard weather station 200 m from the plots and then multiplied by 0.45 (Monteith, 1965). Daily values were summed from emergence for each plot to obtain cumulative IPAR.

2.3. Biomass, LAI and developmental stage

Starting 1 month after emergence, plants were sampled weekly (2003) or fortnightly (2004) to estimate above-ground biomass and LAI. Five plants per plot (those adjacent to the site where radiation interception was measured) were harvested. Biomass was separated into green leaves (main stem and branches), senescent leaves, stem (main stem and branches) and inflorescence when present. Samples were dried in a force-air drying oven at 70 °C until constant weight.

Leaf area was measured with a Li-cor LI-3100 leaf area meter (LI-Cor Inc., Lincoln, Nebraska) and expressed on a per ground area basis. When sample size was large, total leaf area in branches was estimated by using an aliquot of about 20% of total fresh leaf weight. Leaf area was measured on that aliquot and total leaf area estimated by multiplying total leaf biomass by the leaf area:biomass ratio of the aliquot.

Number of leaves (>1 cm long) on the main stem were counted and developmental stages determined on the same plants sampled to estimate biomass. Developmental stages (recorded when 3 out of 5 sampled plants within each plot reached the stage) were determined as: emergence, visible flower bud (Bertero et al., 1999), first anthesis (at least one flower opened), end of anthesis (no more flowers opened determined by observations on the main inflorescence), and physiological maturity (visually determined by examination of seeds on the medium third of the inflorescence). These stages are in agreement with stages 0, 2, 8 and 18 in the scale of Jacobsen and Stølen (1993), respectively and define four developmental phases: vegetative, reproductive, flowering and seed filling.

Total plant leaf area (main stem + branches, TPLA, cm² plant⁻¹) evolution was described as a logistic function of thermal time (TT, °Cd) from emergence (Chapman et al., 1993):

$$TPLA = \frac{TPLA_{max}}{1 + \exp[-a * (TT - b)]} \quad (3)$$

where TPLA_{max} is maximum total plant leaf area and *a* and *b* are fitted coefficients. The coefficient *b* is the thermal time required for TPLA to reach 50% of TPLA_{max}, while *a* determines the steepness of the curve. Leaf area evolution was restricted up to end of anthesis; no model was fitted to describe leaf area senescence. Daily TT increment was estimated as the difference between daily average temperature and *T_b* (base temperature); for days where average temperatures were lower than a *T_b* value of 3 °C, this increment was assumed to be zero (Bertero et al., 1999).

2.4. Light attenuation and radiation use efficiency

The light extinction coefficient (*k*) for Beer's law was determined from the *F* and the LAI values. Values for *k* were calculated for every sample date of each genotype and density as:

$$k = \frac{[\ln(1 - F)]}{LAI} \quad (\text{Kiniry et al., 2005}) \quad (4)$$

Only data up to the beginning of grain filling were considered. Means and standard errors of *k* and LAI were calculated using the measured values for every replication of each genotype and density.

An exponential function (Trapani et al., 1992) was fitted between means of *F* and LAI to obtain an estimate of *k* for the period analyzed:

$$F = 1 - \exp(-k LAI) \quad (5)$$

Linear and bilinear regression models (forced through the origin) were applied to cumulative biomass vs. cumulative IPAR relationship to estimate radiation use efficiency. The nonlinear routine of Table Curve V 3.0 (Jandel, TBLCURVE, 1992) was utilized to fit bilinear regression models. A conditional model with two stages (Eqs. (6) and (7)) was used:

$$y = b_1x \quad \text{for } x < c \quad (6)$$

$$y = a + b_2(x - c) \quad \text{for } x \geq c \quad (7)$$

where *y* is cumulative biomass (g m⁻²), *b*₁ and *b*₂ are the slopes (i.e., RUE, g MJ IPAR⁻¹), respectively, of the linear regression corresponding to the first and the second stage, *x* is cumulative IPAR from emergence (MJ IPAR m⁻²), *a* is cumulative biomass when *x* = *c*, and the constant *c* is the unknown breakpoint of the function indicating the cumulative IPAR value where RUE has changed. Functions were fitted to means of all treatments. Statistical comparisons between

Table 1

Duration of development phases (°Cd), maximum number of leaves on the main stem and phyllochron (°Cd leaf⁻¹, *T_b* = 3 °C) for four sea-level genotypes of quinoa in 2 years

Genotype	VP (°Cd)	RP (°Cd)	FL (°Cd)	GFP (°Cd)	Number of leaves	Phyllochron (°Cd leaf ⁻¹)
2003						
NL-6	423	211	334	579	27.7	21.7
RU-5	539	315	330	483	35.8	18.6
CO-407	563	405	310	511	40.1	18.1
Faro	563	510	287	588	44.3	21.5
2004						
NL-6	464	183	189	497	26.5	20.1
RU-5	500	230	251	454	31.4	16.3
CO-407	569	215	222	429	36.1	17.4
Faro	640	205	271	624	40.2	15.5

Means of two densities. VP: vegetative phase, RP: reproductive phase, FL: flowering phase, GFP: grain filling phase.

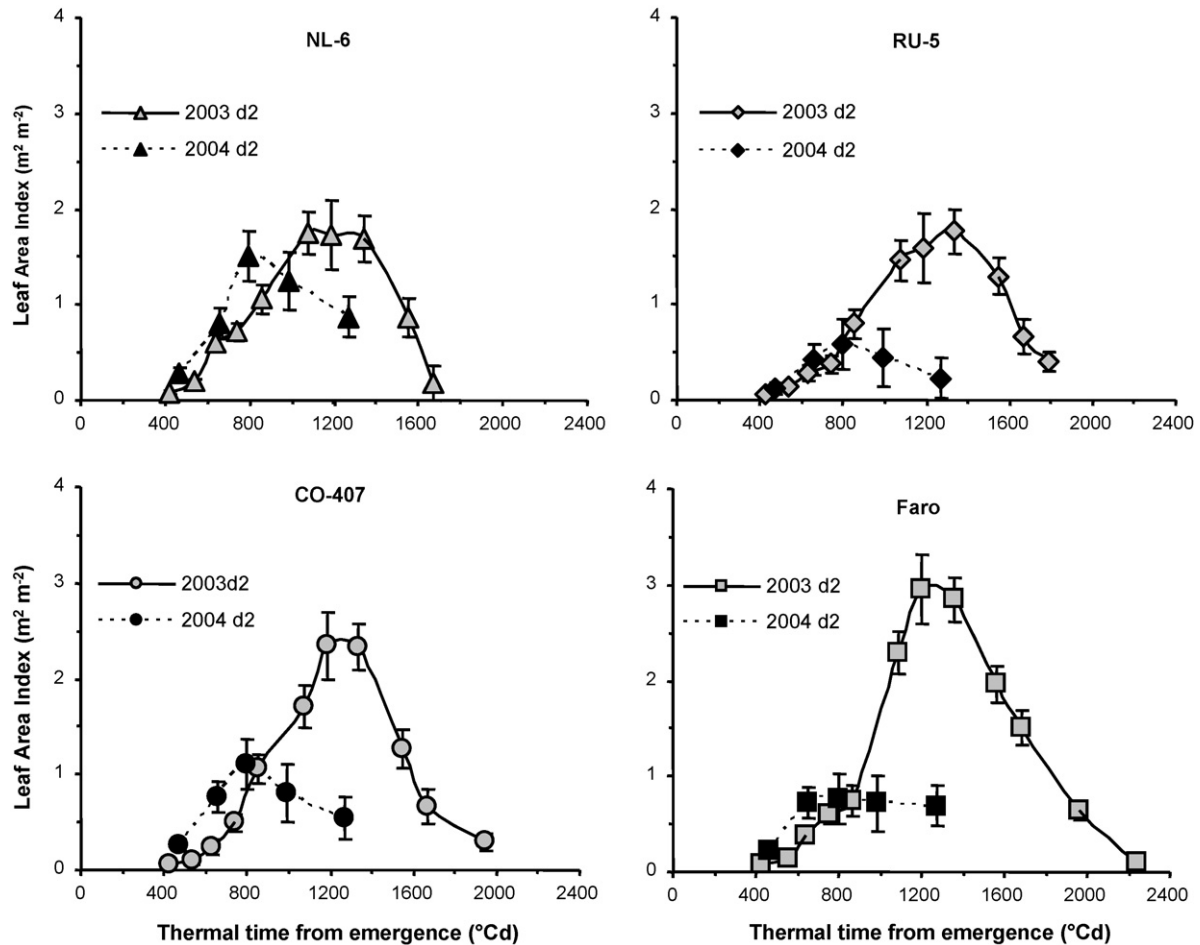


Fig. 2. Leaf Area Index as a function of thermal time from emergence ($T_b = 3^\circ\text{C}$) for four sea-level genotypes of quinoa at a density of 33 pl m^{-2} (d2) in 2 years.

the bilinear and simple linear models were performed by calculating the root mean square error (RMSE) described in Potter and Williams (1994).

Different attributes recorded on a plot basis were analyzed to identify any possible association between the occurrence of the breakpoint and a generalized observation across genotypes, densities and years. For each plot (a particular combination of genotype, density, replicate and year), we selected two values of cumulative IPAR—one immediately above and the other immediately below the breakpoint estimated by the bilinear model (Eqs. (6) and (7)). We chose the closer value and identified the sampling date. A database was built recording the corresponding LAI and F values for every selected IPAR value. We also recorded the developmental stage and number of leaves of five plants harvested from each plot in the same date. All developmental data corresponding to the same genotype were pooled across densities and years. Then, we built cumulative frequency distributions for developmental stage and leaf number for each genotype ($n=70$), and for F and LAI across treatments and years ($n=56$). For each attribute, we calculated the 20th, 50th and 80th percentiles.

3. Results

3.1. Development

While genotypes differed in cycle length, no significant density effects were observed on development in neither of the 2 years.

Cultivar Faro had the longest cycle, followed by CO-407 and RU-5. Cultivar NL-6 had the shortest cycle and the shortest thermal time to anthesis (Table 1). The most variable phase (in terms of thermal time) among genotypes was largely the vegetative one, which extended about one third of total cycle length (range: 27–32% in 2003 and 34–39% in 2004), while the flowering phase was roughly similar. Maximum leaf number in the main stem differed among genotypes and showed the same trend as cycle length. Phyllochron values were between 15.5 and 21.7 $^\circ\text{Cd}$ ($T_b = 3^\circ\text{C}$) across genotypes, densities and years. In 2004 both phyllochron and maximum leaf number were lower than in 2003 resulting in a shorter reproductive phase (Table 1).

3.2. Leaf area index and crop development

Leaf area index values were higher in 2003 than in 2004 (Fig. 2). A high rainfall period stopped sharply the increase of leaf area in the second year. In 2003 average maximum LAIs across genotypes were higher in d2 than in d1 (2.20 vs. 1.77; $p < 0.02$). Maximum LAIs differed among genotypes ($p < 0.01$). Faro presented the highest value (2.60, average over densities), CO-407 the intermediate (2.11); NL-6 and RU-5 the lowest (1.63 and 1.61, respectively). In 2004 maximum LAIs only reached 0.99 and 1.35 (average across genotypes) for d2 and d3 ($p > 0.12$). Only Faro (a late genotype) had significant different values ($p < 0.05$) between densities (0.75 vs. 2.09 for d2 and d3). Maximum LAIs did not differ among genotypes (range 0.93–1.42) for the second year.

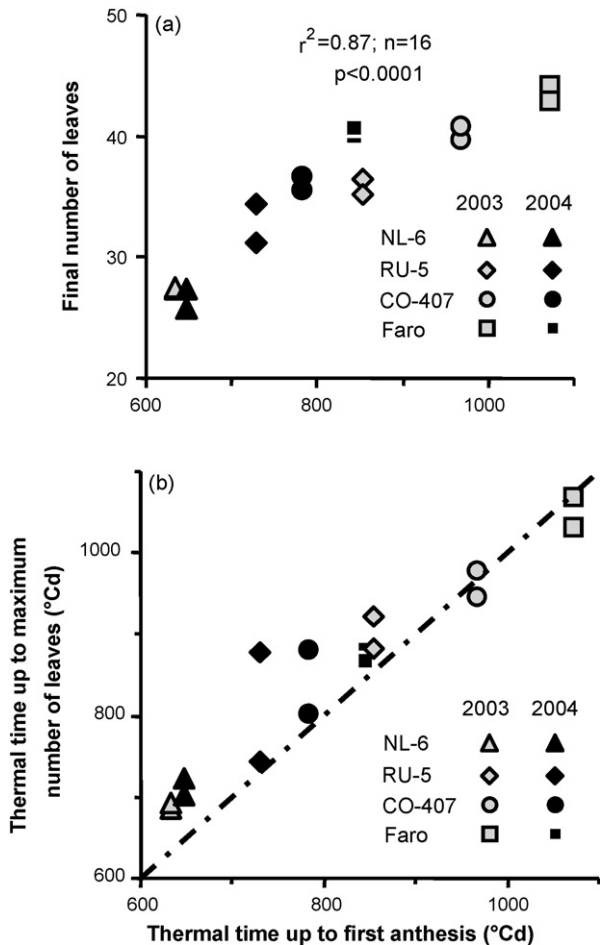


Fig. 3. (a) Association between final number of leaves on the main stem and thermal time up to first anthesis ($T_b = 3\text{ }^\circ\text{C}$) for four genotypes of quinoa at two densities in 2 years. (b) Association between thermal time up to maximum number of leaves and thermal time up to first anthesis ($T_b = 3\text{ }^\circ\text{C}$) for four genotypes of quinoa at two densities in 2 years. The dotted line indicates the 1:1 relationship.

Thermal time to first anthesis and maximum leaf number in the main stem were linearly correlated ($r^2 = 0.87$, $n = 16$; $p < 0.0001$). First anthesis of early genotypes (NL-6 and RU-5) occurred a little thermal time (about $60\text{ }^\circ\text{Cd}$) before the last leaf appeared on the main stem. In late genotypes (CO-407 and Faro), the occurrence of maximum leaf number coincided with first anthesis (Fig. 3).

Description of LAI was restricted to the first year since in 2004 waterlogging affected LAI evolution. In 2003 leaf area increase continued until shortly after first anthesis in the main stem and up to beginning of grain filling in branches. Occurrence of maximum leaf area both in main stem and in branches correlated with development stages. Days to maximum leaf area on the main stem were highly correlated with days to first anthesis ($r^2 = 0.99$, $n = 8$, $p < 0.00001$) and days to maximum leaf area in branches were highly correlated with days to end of anthesis ($r^2 = 0.86$; $n = 8$, $p < 0.001$). Maximum leaf area in the main stem occurred, on average, 18 days after first flower opened, while maximum leaf area in branches was observed 6 days after the completion of anthesis (Fig. 4).

Logistic models adequately described total plant leaf area evolution (r^2 s > 0.96 ; $p < 0.0005$) (Fig. 5). No losses due to senescence were modeled; senescent leaf biomass was less than 5% of total (green+dead) leaf biomass during the period analyzed. Parameters “ b ” of the model (thermal time needed to reach 50% of TPLA_{max}) were highly correlated with maximum main stem leaf

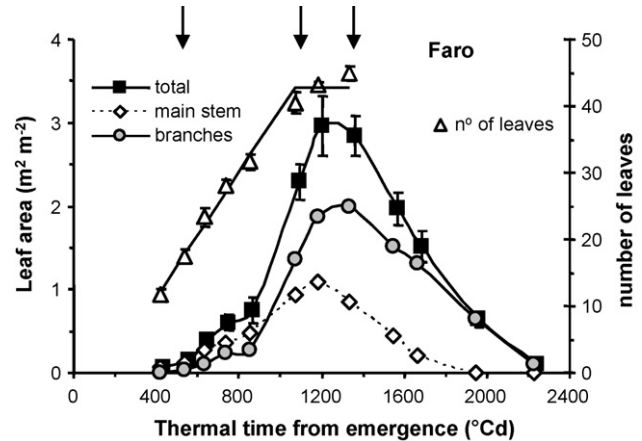


Fig. 4. Leaf Area and number of leaves on the main stem as a function of thermal time from emergence for genotype Faro at a density of 33 pl m^{-2} in 2003. Total leaf area, leaf area in main stem, and leaf area in branches are shown. Arrows indicate (from left to right) thermal time of visible flower bud, first anthesis and end of anthesis. Vertical bars are standard errors of the mean.

number ($r^2 = 0.94$; $n = 8$, $P < 0.001$), and tended to be higher than thermal time to first anthesis as cultivar cycle length decreased. Leaf area continued to increase during the flowering phase, notably in the earliest genotype NL-6. There were significant differences in TPLA_{max} between genotypes. Despite differences in total leaf number, early genotypes NL-6 and RU-5 had similar TPLA_{max} ; while late genotypes reached significantly ($p < 0.05$) higher TPLA_{max} , as total leaf number increased. Genotype NL-6 combined an early LAI increase and a TPLA_{max} similar to that of RU-5. Therefore, NL-6 had a significantly ($p < 0.05$) higher LAI than that of longer duration cultivars (i.e., RU-5 and CO-407) in both densities, during early development phases up to about $750\text{ }^\circ\text{Cd}$ after emergence (Fig. 5). Increasing density reduced TPLA_{max} , but effects were comparatively small, values of TPLA_{max} for 33 plants m^{-2} were 80–87% of those for 22 plants m^{-2} regarding the earliest and the latest genotypes, respectively.

3.3. Light attenuation

Estimated k values for each sample date, genotype and density showed no clear association with LAI ($r^2 = 0.02$, $p > 0.18$, $n = 84$). When all F and LAI data were pooled across genotypes and densities to fit an exponential model (Eq. (5)), the value of k was 0.589 ± 0.016 ($r^2 = 0.93$, $n = 84$, $p < 0.0001$) resulting in a critical LAI value (equivalent to $F = 0.95$) of 5.09 (Fig. 5). This estimate should be considered with caution as this LAI was not reached at any plot in these experiments. Maximum LAI recorded in the experiment at a replicate was 3.78 and corresponded to an F value of 0.926. Across genotypes mean values of k differed slightly between d1 and d2 (0.52 vs. 0.58, $p < 0.10$) but were higher for d3 (0.74, $p < 0.05$) (Fig. 6).

3.4. Radiation use efficiency

A linear model forced through the origin was fitted to estimate RUE ($n = 84$; $r^2 = 0.90$; $p < 0.00001$). Radiation use efficiency (the slope of the model) was $1.75 \pm 0.047\text{ g MJ IPAR}^{-1}$ across genotypes and densities. However, for lower IPAR values, it was observed some degree of overestimation regarding biomass produced for a given amount of intercepted radiation. The bias was particularly evident when cumulative IPAR $< 150\text{ MJ IPAR m}^{-2}$ (about 80% of total data). When RUE across genotypes and densities was calculated by fitting a bilinear model between cumulative total biomass

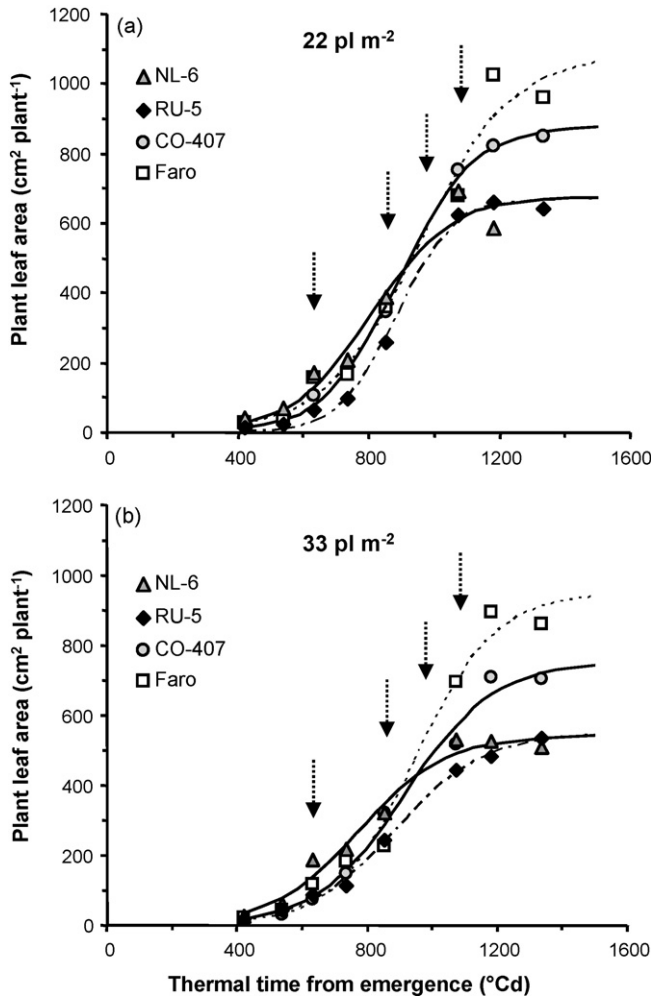


Fig. 5. Total plant leaf area as a function of thermal time from emergence for four genotypes of quinoa in 2003. (a) 22 pl m⁻² and (b) 33 pl m⁻². Lines indicate logistic models fitted to each genotype. Arrows indicate thermal time of first anthesis for (from left to right) genotypes NL-6, RU-5, CO-407 and Faro. For 22 pl m⁻²: NL-6: $TPLA = 677 / \{1 + \exp[-0.00832 (TT-807)]\}$ ($r^2 = 0.96$, $p < 0.001$). RU-5: $TPLA = 668 / \{1 + \exp[-0.01199 (TT-886)]\}$ ($r^2 = 0.99$, $p < 0.00001$). CO-407: $TPLA = 880 / \{1 + \exp[-0.00888 (TT-892)]\}$ ($r^2 = 0.99$, $p < 0.00001$). Faro: $TPLA = 1084 / \{1 + \exp[-0.00709 (TT-957)]\}$ ($r^2 = 0.98$, $p < 0.00001$). For 33 pl m⁻²: NL-6: $TPLA = 544 / \{1 + \exp[-0.00750 (TT-778)]\}$ ($r^2 = 0.98$, $p < 0.0001$). RU-5: $TPLA = 550 / \{1 + \exp[-0.00734 (TT-893)]\}$ ($r^2 = 0.99$, $p < 0.00001$). CO-407: $TPLA = 753 / \{1 + \exp[-0.00737 (TT-919)]\}$ ($r^2 = 0.99$, $p < 0.00001$). Faro: $TPLA = 950 / \{1 + \exp[-0.00824 (TT-951)]\}$ ($r^2 = 0.98$, $p < 0.0001$).

and cumulative IPAR ($n = 84$; $r^2 = 0.95$; $p < 0.0001$), a significant breakpoint was found and two different slopes could be identified (Fig. 7). Radiation use efficiency at initial stages of development was $1.25 \pm 0.09 \text{ g MJ IPAR}^{-1}$, but increased up to $2.68 \pm 0.15 \text{ g MJ IPAR}^{-1}$ for cumulative IPAR higher than $107.5 \pm 10.4 \text{ MJ IPAR m}^{-2}$.

Fitting a bilinear model instead of a linear one improved adjusted r^2 (from 0.90 to 0.95) and reduced RMSE (from 46.1 to 33.4 g m^{-2}); mean deviation changed from 14.4 to 1.8 g m^{-2} . Improvement on the estimation was clear when values of cumulative IPAR $< 150 \text{ MJ IPAR m}^{-2}$ ($n = 69$) were considered. Both RMSE and mean deviation decreased (from 34.7 to 23.1 g m^{-2} and from 24.6 to 2.1 g m^{-2} , respectively).

The functional cause of this breakpoint is not clear, and some possible determinants were analyzed as follows. When RUE changed (cumulative IPAR range: 64–130 MJ IPAR m⁻²), different attributes were considered to identify any link between the occur-

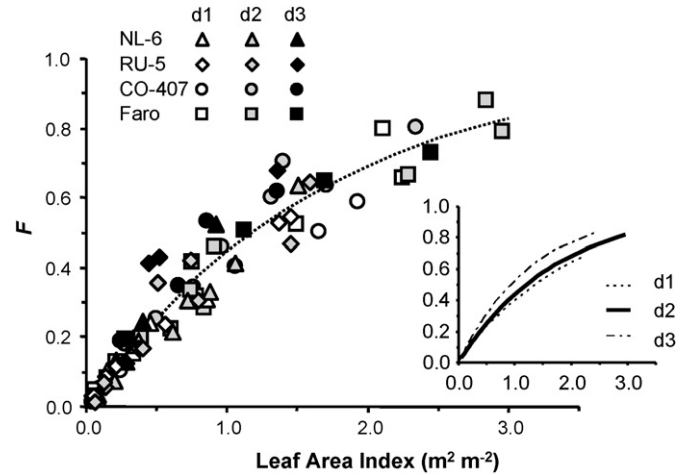


Fig. 6. Fraction of photosynthetically active radiation intercepted (F) as a function of leaf area index (LAI) for four genotypes at three densities in 2 years. The dotted line indicates fitted model: $F = 1 - \exp(-k \text{ LAI})$, $r^2 = 0.94$, $p < 0.00001$. $n = 84$, where k is 0.59. Inset: F as a function of LAI for three densities d1: 22 pl m⁻², d2: 33 pl m⁻², d3: 66 pl m⁻².

rence of the breakpoint and a generalized observation across genotypes and densities. The values representing the 20th and 80th percentiles for those selected variables were LAI: 0.61–1.38; F : 0.33–0.51; leaf number, NL-6: 24–30, RU-5: 27–38, CO-407: 27–36 and Faro: 27–39. The 50th percentiles (median) for development stage of individual plants were anthesis for NL-6 and RU-5, and visible flower bud for CO-407 and Faro (Fig. 8d). No evident developmental stage seemed to be related to changes in RUE across genotypes, but both LAI and F showed a narrow range of variation between plots coinciding with the occurrence of the breakpoint (Fig. 8a and b). Among genotypes, differences in leaf number could be related to LAI evolution. When data of individual plants are pooled considering only plant densities, the 50th percentiles of leaf number observed on the main stem were 34 for d1, 32 for d2, and 24.5 for d3. So, increasing plant density shortened the period of low RUE. Genotype NL-6 reached the time RUE changed with a lower main stem leaf number than the others, probably as a consequence of its early increment in LAI (Fig. 5).

Estimates of RUE were also calculated for each genotype separately. By the time the breakpoint was observed, cultivar NL-6 was very close to the beginning of the grain filling period. For that rea-

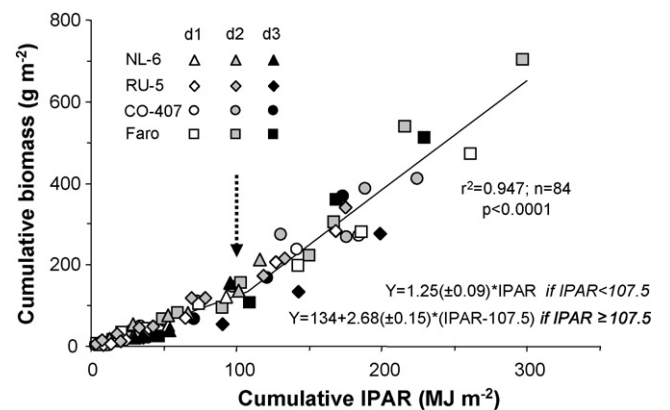


Fig. 7. Cumulative biomass as a function of cumulative intercepted photosynthetically active radiation (IPAR) for four genotypes of quinoa at three densities (d1: 22 pl m⁻², d2: 33 pl m⁻², d3: 66 pl m⁻²) in 2 years. Solid lines indicate bilinear model fitted to data. The arrow indicates the cumulative IPAR at which the slope changes.

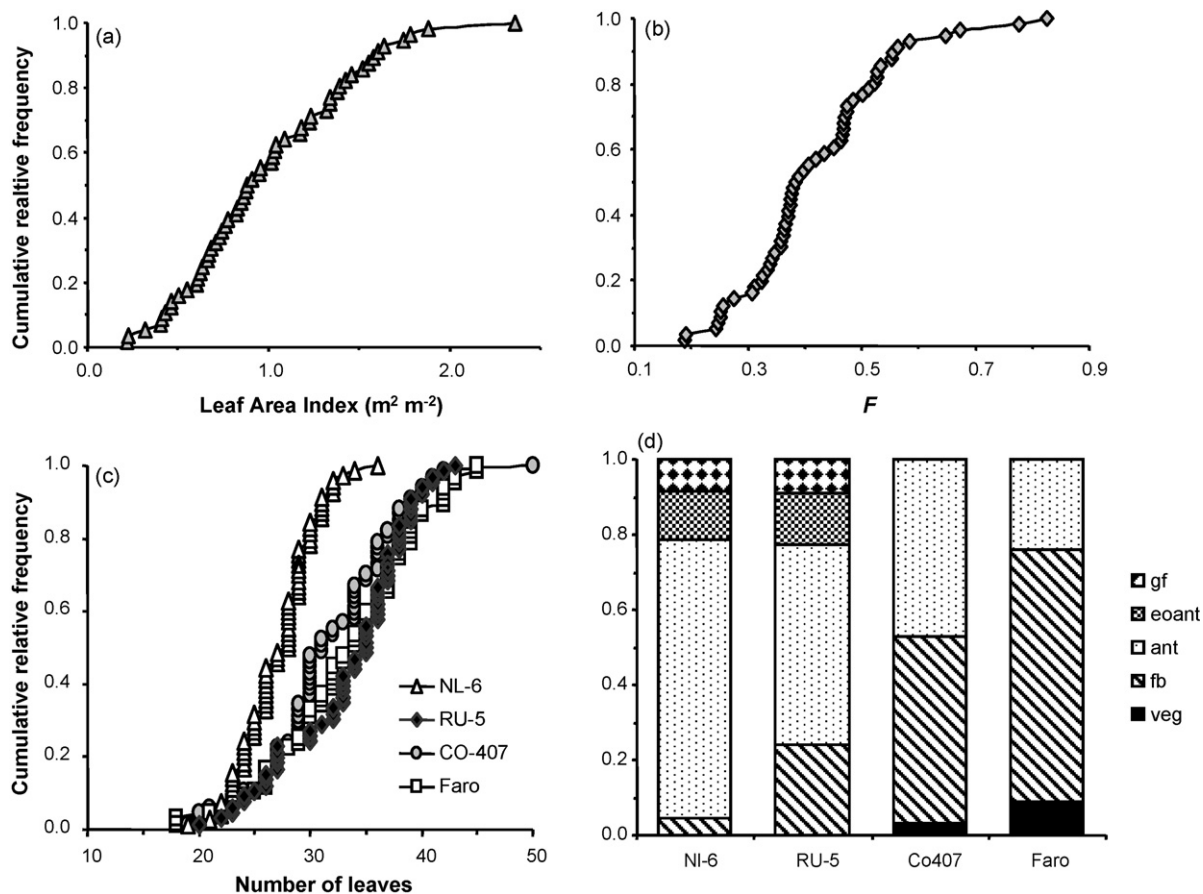


Fig. 8. Observed cumulative relative frequency for (a) Leaf area index, (b) Fraction of photosynthetically active radiation intercepted (F), (c) number of leaves on the main stem, (d) stage of development, when radiation use efficiency breakpoint occurred. Data are recorded on a plot basis (a and b) or on a plant basis (c and d). Veg: vegetative stage, fb: visible flower bud, ant: anthesis, eoa: end of anthesis.

son, only a linear model forced through the origin could be fitted to this genotype. Estimate of RUE for NL-6 (1.30 ± 0.07) only tended to differ ($p < 0.08$) from that of CO-407 (1.02 ± 0.34) but was similar to those of other cultivars for cumulative IPAR lower than the breakpoint (1.15 ± 0.19 and 1.19 ± 0.18 for RU-5 and Faro, respectively). For cumulative IPAR higher than the breakpoint, no significant differences were observed among cultivars (2.04 ± 0.45 , 2.12 ± 0.18 , and 2.95 ± 0.27 for RU-5, CO-407 and Faro, respectively).

4. Discussion

Leaf area evolution in terms of thermal time (without losses due to senescence) has been adequately described by a logistic function, as observed for crops both with (Hammer and Muchow, 1994) and without branches or tillers (Chapman et al., 1993). As previously reported for other crops (Sadras and Hall, 1988), differences in $TPLA_{max}$ in quinoa were also related to genotype and density effects. For late cultivars, genotype effects on $TPLA_{max}$ largely reflected different thermal time to first anthesis. This correlated with total main stem leaf number, but leaf area continued to increase during the flowering phase (mainly in branches). The earliest genotype NL-6 reached a high $TPLA_{max}$ due to a longer thermal time from first anthesis to the end of leaf expansion (see Fig. 4).

Leaf appearance rate was relatively stable and phyllochron values compared well with those observed previously for sea-level genotypes (Bertero, 2003). However, maximum number of leaves and phyllochron values decreased in the second year (with the exception of the earliest genotype NL-6). The reproductive phase

and thermal time to anthesis also shortened. No photoperiod effects were expected since sowing date was similar between years. An increase in global radiation could reduce phyllochron values in quinoa genotypes (Bertero, 2001b), specially for those of moderate sensitivity to photoperiod, like these Southern Chilean cultivars. However, in our experiment, global radiation was lower in 2004 than in 2003, even if we consider an $800^\circ C d$ period from emergence that includes the vegetative phase and most of the reproductive phase for all cultivars. So, the changes observed in the phyllochron could not be explained by this factor.

Extinction coefficients for quinoa were intermediate compared to others reported for different crops (Flenet et al., 1996; Maddonni and Otegui, 1996; Westgate et al., 1997; Kemanian et al., 2004; O'Connell et al., 2004; Kiniry et al., 2005). Increasing density from 22 to 66 plants m^{-2} increased k values. This opposed a number of reports for other species (Kemanian et al., 2004; Francescangeli et al., 2006) where a decrease in k with increasing plant density was found. In our experiments, as density increased, row spacing decreased and within-row spacing remained constant. Plant rectangularity (the ratio between row spacing and within-row distance between plants) was 1.5 in d3 but increased up to 3 and 4.5 for d2 and d1. Westgate et al. (1997) showed that, in maize, the extinction coefficient decreased with increasing density but did not vary with row spacing prior to canopy closure. Flenet et al. (1996) observed greater light interception efficiency in narrow rows (without changing density), probably as a result of a more even distribution of the plants and hence of the foliage. Maddonni et al. (2001) observed in maize crops significant row spacing effects on

k only when a more square planting pattern (rectangularity close to 1) promoted a significant increase in k . Lindquist et al. (2005) suggested that larger estimates of k observed during late stages of reproduction in maize are likely to be the result of an increasing proportion of dead leaves intercepting radiation, since dead leaf tissue is not removed from the field. In our experiments, no interference of dead leaves was expected. Estimates of k were restricted up to the beginning of grain filling and senescent leaves (those attached to plants when collected) represented less than 5% of total leaf biomass.

Radiation use efficiency of quinoa was clearly different between early stages of development and subsequent stages close to flowering, when twofold increase could be recorded. Variability in RUE was found within a species and, in the same experiment, throughout the crop cycle (Albrizio and Steduto, 2005). Several works reported a decrease in RUE ascribed to decline in canopy photosynthetic efficiency as a consequence of senescence (Sinclair and Horie, 1989) or increase in respiratory load during the grain-filling stage (Penning de Vries et al., 1983; Whitfield et al., 1989; Giménez et al., 1994). This was not the case since we observed an increase in RUE estimates as development progressed. On the other hand, only biomass production up to the beginning of grain filling was considered and senescence was not generalized. Although no analysis in energy content of biochemical constituents was done, a change of biomass production value with progress in development (Sinclair and Muchow, 1999) could not be invoked since the breakpoint occurred at different developmental stages among genotypes (from flower bud visible up to end of anthesis). Biomass partitioning between roots and shoots (Kiniry et al., 1989; Trapani et al., 1992; Giménez et al., 1994) could contribute to explain that difference. No measurements were made, but a different development pattern among genotypes should be assumed to support such an explanation for the changes observed in RUE. Although estimation errors related to measurement methodology can exist, they cannot explain observed differences along the crop cycle. Underestimations of cumulative intercepted radiation are said to be an important source of error but a correction was applied to avoid that topic. If intercepted radiation was underestimated then RUE could be even lower at early stages where bias in intercepted radiation is expected to be of certain magnitude (Charles-Edwards and Lawn, 1984). Temperature effects (García et al., 1988; Andrade et al., 1993) were disregarded as mean temperature of 15-day periods pre- and post-breakpoint occurrence rarely differed in more than 2°C.

Concerning the light environment, RUE should increase if the saturation of photosynthesis decreased (Sinclair and Horie, 1989). RUE should increase with a reduction in incident radiation or an increase in the fraction of diffuse to total radiation because, in both cases, the proportion of photosynthetic area operating at nonsaturating radiation increases (Bange et al., 1997; Kemanian et al., 2004). In our experiments, RUE values were high when solar radiation increased and no cloudy conditions prevailed during that period, however. On the other hand, a higher RUE could be expected with increasing LAI since less intense radiation in the lower leaf layers means that the photosynthesis there is less saturated, whereas the upper leaves are often light saturated. In annual crops, low RUE values should be evident in the first stages of development, when F (and LAI) is low (Kemanian et al., 2004). Results of model analyses performed by Hall et al. (1996) in sunflower were consistent with the notion that RUE and its variation during the pre-anthesis phase of the crop season are largely determined by the effect of LAI on radiation distribution within the canopy. In our experiment RUE changes occurred in LAI values from 0.61 to 1.38 and F values from 0.33 to 0.51 when leaf area both in main stem and branches was increasing. We conclude that light distribution within the canopy

is the major cause of our observed results. Density effects on the number of main stem leaves at which this breakpoint occurred are consistent with the above statement; as LAI for a given number of leaves on the main stem was also modified.

Radiation use efficiency estimates were within the typical range of C_3 crops. Our values for RUE after the breakpoint ($2.68 \pm 0.15 \text{ g MJ IPAR}^{-1}$) compare well with those of cereals like wheat ($2.70 \text{ g MJ IPAR}^{-1}$, Abbate et al., 1997), or barley ($2.63 \text{ g MJ IPAR}^{-1}$, Bingham et al., 2007) and also with that of sunflower for rapid growth phase prior to anthesis ($2.4 \text{ g MJ IPAR}^{-1}$, Trapani et al., 1992). On the contrary, they are higher than those of grain legumes, such as peanut ($2.0 \text{ g MJ IPAR}^{-1}$, Kiniry et al., 2005), pea ($1.52 \text{ g MJ IPAR}^{-1}$, O'Connell et al., 2004) or soybeans ($1.2\text{--}2.0 \text{ g MJ IPAR}^{-1}$, Egli and Bruening, 2000).

Although estimates of RUE differed among cultivars, major differences could be explained in terms of the unequal weighting of cumulative IPAR before and after a minimum LAI was reached. If late genotypes are considered, a greater proportion of IPAR will accumulate when $\text{LAI} \geq 1$, as a consequence of higher F , a higher incident PAR and a longer period up to end of anthesis. High weighted RUE values are expected for those genotypes. Early genotypes, on the other hand, tended to halve IPAR accumulation equally during early stages of development and periods close to anthesis. Low weighted RUE values are expected in that case.

From our results, leaf area dynamics become a key characteristic since it determines both F evolution and RUE values. Differences were found among analyzed genotypes. Cultivar NL-6 had lower thermal time to reach 50% of TPLA_{max} than RU-5 but TPL_{max} were similar (Fig. 6). This indicated a higher leaf area increment during early stages that contributed to shorten periods of low cover ($F \leq 0.4\text{--}0.5$) when IPAR accumulation was slow and hastened time to enhance RUE. So, NL-6 had a lower number of appeared leaves when RUE changed (Fig. 8). Choosing an adequate plant density could also be a way to reach this objective. Increasing plant density not only determined a significant increment in LAI but also allowed the crop to reach the RUE breaking point at an earlier stage of development.

5. Conclusions

Our results contribute to emphasize the importance of F and RUE as factors controlling biomass production of quinoa in the Pampas region of Argentina. Sea level quinoa genotypes adapted to a short crop season, thus allowing an early harvest if required. The use of cultivars like CO-407 or Faro in late winter or early spring sowings ensures adequate interception efficiency (F close to 0.95) around mid to late spring. Consequently, it also reaches maximum RUE during the flowering phase when daily incoming PAR maximizes without compromising the early harvest requirement. On the other hand, short-cycle cultivars with short thermal time to first anthesis (and low number of leaves in the main stem, like NL-6 and RU-5) could hardly reach full interception and maximum RUE during the critical period of active panicle growth. For the latter cultivars, biomass production (at least up to end of anthesis) was reduced both due to a relative high proportion of the pre-anthesis period with low cover and low RUE and due to short duration itself and low daily incoming PAR during early spring. Plant density is a key management decision for those short-cycle cultivars; no less than 33 pl m^{-2} (or higher) are required for a reasonable crop. Cultivar NL-6 has some desirable characteristics for short-cycle cultivars, like an early increment in LAI and an extended period of leaf area increase that overlaps the flowering phase. Combining these characteristics with a longer time to first anthesis is an interesting goal for a breeding program.

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