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Reproductive partitioning in sea level quinoa (*Chenopodium quinoa* Willd.) cultivars

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ABSTRACT

The proportion of growth allocated to reproductive organs can be an important determinant of yield variation between cultivars and environments. The main aim of this paper was to evaluate the adequacy of a model assuming constancy in partitioning coefficients (PC, the slope of organ weight to total weight relationship) within periods whose limits are associated with phenological phases to describe variation in reproductive growth (including seeds when present) in the Andean seed crop quinoa. A second objective was to analyze the dynamics of panicle and stem growth to advance our understanding of factors determining yield in this species. To do this, we used data from two experiments conducted in 2 years under field conditions in the Argentinean pampas, using four cultivars belonging to the Sea Level Type and adapted to temperate environments, under three densities. Reproductive partitioning followed a bi-phasic pattern; panicle biomass increased gradually until reaching a total biomass value, and then there was an increase in the slope of panicle vs. total aerial biomass relationship. Partitioning coefficients for the initial stage varied between some cultivars and densities in the first year, but not in the second. No significant differences were detected when PCs for the second stage were considered. The start of panicle growth was associated with thermal time to first anthesis ($R^2 = 0.62$) while thermal time to change in partitioning from low to high PC and that to end of flowering were strongly related ($R^2 = 0.93$). Combining data across cultivars, years and densities gave a PC of 0.15 for the initial stage and 0.90 for the second stage. Using these relationships and parameters dynamics of panicle biomass accumulation was predicted satisfactorily in an independent data set for a different environment, confirming the usefulness of a single model approach to describe partitioning across cvs. and environments in this crop. Besides, crop yield estimations improved when compared to those obtained by a seed number estimation model, predictions were only 7.25% lower than observed values compared to −24.5% using a seed number approach. There is a trade-off between final partitioning to reproductive structures (higher in short-cycle cvs.) and total crop biomass, one of the factors contributing to this trade-off being a negative association between the panicle–stem relationship at harvest and duration in thermal time units of stem growth; so, selection for high partitioning rate should be targeted at long duration cvs. within this germplasm.

1. Introduction

Biomass growth is one of the two aspects determining crop yield; the other one is partitioning to the seed. Although less explored as a research subject than the processes affecting growth, changes in partitioning to reproductive structures were the basis of yield progress during the second half of the 20th century in species like wheat, barley and rice (Evans, 1993; Slafer et al., 1990). Central to this increase in yield was a reduction in stem partitioning that led to an increase in that to the spike associated with the use of genes which control plant height (Hedden, 2003). In wheat and barley, for example, final seed number and yield are strongly associated with spike biomass at anthesis (Bindraban et al., 1998; Moreno-Sotomayor and Weiss, 2004; Prystupa et al., 2004) and that is related to the spike–stem ratio at that time (Gonzalez et al., 2005). The capacity to reach a higher spike–stem ratio at anthesis is also determined by the relative spike dry weight at the onset of maximum stem growth rate (Gonzalez et al., 2003). Timing (i.e. when spikes and stems do start growing at their maximum rate, as is the case of wheat) and the values of these growth rates during the critical periods for yield determination appear as important subjects of analysis for the understanding of reproductive partitioning.

No previous studies have been published analyzing partitioning to reproductive structures along the crop cycle in the Andean seed crop quinoa (*Chenopodium quinoa* Willd.). Sea level quinoas have traditionally been grown at low altitudes in Central and Southern Chile (Tapia et al., 1979) and their low photoperiod sensitivity

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makes them suitable for cultivation in temperate environments (Bertero et al., 1999). The term sea level quinoa was first used by Tapia et al. (1979) and it is not clear whether they are the result of a past introduction to Chile from the Central Andes or of an independent domestication event (Wilson, 1990; Maughan et al., 2006). Evidence for quinoa association to a hunter–gatherers context in Central Chile is as old as 3000 BP (Planella et al., 2005). They have been evaluated in several countries apart from Chile confirming its potential as an alternative new crop, as in England (Risi and Galwey, 1989), Denmark (Jacobsen and Stolen, 1993), United States (Johnson and Ward, 1993), Morocco (Benlhabib et al., 2004), Germany (Schulte auf'm Erley et al., 2005), India (Barghava et al., 2007), Japan (Ujiie et al., 2007) and Pakistan (Munir and Basora, 2010). A previous paper (Ruiz and Bertero, 2008) analyzed the dynamics of growth in cultivars adapted to temperate environments before seed filling in terms of its principal determinants: leaf area index (LAI), light extinction coefficient (k) and radiation use efficiencies (RUE), its variation between cultivars, years, phenological phases and densities. By allowing for some simplifications (i.e. assuming one k and two RUE values between emergence and the end of flowering), we suggested a unique model providing a robust description of crop growth variation across the explored range of treatments and environmental conditions. In addition, we used the association between growth during different phenological phases and seed number as an indirect approach to the identification of the critical period for seed determination. This approach allowed us to propose that the flowering phase, from first anthesis to the end of anthesis, is the critical period for yield determination in this crop (Bertero and Ruiz, 2008). Although changes in harvest index or partitioning to reproductive structures have still not been explicitly considered as breeding objectives in this species, studying the temporal dynamics in partitioning to vegetative and reproductive structures, and its constancy or variation between existing cultivars could help orientate future breeding efforts. The main objectives are:

(i) To test whether a common partitioning model adequately describes biomass partitioning to reproductive structures across cultivars, densities and years.
(ii) To evaluate the association between the timing of change in partitioning rates and the phenological phases.
(iii) To study the relation between panicle and stem growth.

2. Materials and methods

2.1. Experimental design and growing conditions

Experimental conditions, cultivars and sampling procedures have been described in detail previously (Bertero and Ruiz, 2008). In short, four Sea-level Group cvs. (Bertero et al., 2004): NL-6, RU-5, CO-407 and Faro, in decreasing order of precocity, adapted to temperate climates, were cultivated during 2 years (2003 and 2004) under combinations of three plant densities (22, 33 and 66 plants m^{-2}) in Pergamino (33°56′S, 60°35′W), province of Buenos Aires, Argentina. A germplasm accession (2-Want) was included in the validation experiments and is described in Section 2.4. Pergamino is located in the Rolling Pampas (Hall et al., 1992) and its climate is defined as temperate humid with a very hot summer (Köppen, 1931). Plants received supplementary irrigation and fertilization at sowing (20 kg P and 18 kg N ha^{-1}) and two urea applications (totaling 200 kg 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 kg N ha^{-1} (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 were removed by hand. As these products were applied before observing any insect or fungal attack, no evaluation of their incidence was performed.

2.2. Partitioning dynamics

Starting one month after emergence, plants were sampled every week (2003) or fortnightly (2004) in order to measure aboveground biomass and leaf area index (LAI). Five contiguous plants per plot were harvested. Biomass was separated into green leaves (main stem and branches), senescent leaves, stem (main stem and branches) and inflorescences (panicles) when present. As this article focus is on the analysis of reproductive partitioning, only results on partitioning to panicles, and its relationship with stem growth, are presented. Samples were dried in an air-forced drying oven at 70 °C to constant weight.

Determination of partition coefficients followed the methodology of Trápani et al. (1994). Plots of panicle biomass (including seeds) against total biomass were generated for each combination of cultivar × density × experiment. Partitioning coefficients were estimated through regression using bilinear models as:

$$PB = a1 + PC1\ TB \quad \text{if } (TB \leq TB2) \tag{1a}$$

$$PB = a2 + PC2\ TB \quad \text{if } (TB > TB2) \tag{1b}$$

where PB is accumulated panicle biomass (in g m^{-2}, including seeds), TB is accumulated aerial biomass (g m^{-2}), $a1$ and $a2$ are intercepts, parameters PC1 and PC2 are partitioning coefficients to the panicle (g g^{-1}) – i.e. the slopes of the linear regression corresponding to the first (PC1, for values of TB less than TB2) and the second stages (PC2, for values of TB greater than TB2), respectively – and TB2 is the unknown breakpoint of the function indicating the total biomass value at which PCs changed from its initial value (PC1) to its maximum value (PC2). Additionally, total biomass when panicle starts to grow (TB1) was estimated from Eq. (1b) as $TB1 = -a1/PC1$.

Once regression parameters were determined, data were separated into two groups corresponding to values lower or greater than TB2 within each cultivar × density × experiment combination. Tests of comparison of slopes (PCs) and intercepts were performed using dummy variables in pooled data both (i) between densities within each cultivar × year combination and (ii) among cultivars across years and densities. Confidence intervals were used to compare TB1 and TB2 values among cultivars.

Thermal times associated with TB1 and TB2 were determined as follows: for each cultivar × density × experiment combination, logistic regressions were fitted to the TB vs. cumulative thermal time (TT, -°Cd-) from emergence (using 3 °C as base temperature, Bertero et al., 1999) relationship (data not shown). Parameters of those functions were used to estimate the thermal times at which crops reached the biomass corresponding to TB1 and TB2.

2.3. Temporal dynamics of panicle and stem growth

The model outlined previously was adapted to the description of the dynamics of inflorescence growth against thermal time, in a way similar to the study of the temporal dynamics of spike and stem growth in wheat (Gonzalez et al., 2003) where:

$$PB = a + b\ TT \quad \text{if } (TT \leq TT2) \tag{2a}$$

$$PB = c + d\ TT \quad \text{if } (TT > TT2) \tag{2b}$$

In this case, PB represents accumulated panicle biomass (g m^{-2}), TT is cumulative TT from emergence, a and c are intercepts, b and d represent panicle growth rates (g m^{-2} °C d^{-1}) for different growth stages, and TT2 is the unknown breakpoint of the function indicating the thermal time value at which panicle growth rate changed

from minimum to maximum. The period of panicle growth at maximum rate was termed active panicle growth period. The TT at which panicle starts growing (TT1, panicle biomass > 0 g m^{-2}) and partitioning changes from zero to a positive value was calculated as $-a/b$. Functions were fitted to means of all treatments.

For stem growth, a bilinear model with plateau was applied:

$$SB = a + b\ TT \quad \text{if } x \leq TT2 \tag{3a}$$

$$SB = c + d\,TT \quad \text{if } TT2 < x \leq TT3 \tag{3b}$$

$$SB = e \quad \text{if } x > TT3 \tag{3c}$$

where SB is stem biomass (g m^{-2}); a, b, c and d are the same as just described for panicle growth against thermal time (only replacing panicle biomass for stem biomass), and TT3 is the thermal time value above which stem biomass remains constant, maximum and equal to e. Data for samplings conducted before the start of either panicle or stem growth were not included in the analysis. Models presented in Eqs. (1)–(3) and logistic regressions were fitted using Table Curve V 3.0 (Jandel, TBLCURVE, 1992).

2.4. Validation of panicle biomass growth predictions

The ability of the partitioning framework proposed in the present work to adequately describe the temporal dynamics of panicle growth was tested by comparing the observed dynamic of inflorescence growth in an independent set of experiments with predictions arising from the relationships presented in this analysis. These experiments were conducted under field conditions in 2005 and 2006 at the Faculty of Agronomy of the University of Buenos Aires, Argentina (34°35′S, 58°29′W). Sowing dates were September 27th in 2005 and October 11th in 2006. These crops were irrigated and fertilized at sowing (20 kg P and 18 kg N ha^{-1}) and after plant thinning at about 20 days after emergence (82 kg N ha). Insecticides and fungicides were applied regularly to prevent insect attacks and fungal diseases and weeds were removed by hand. Plant density was similar in both experiments (50 pl m^{-2}). One cultivar and one germplasm accession (NL-6 and 2-Want) were used in 2005 and only one (2-Want) in 2006. NL-6 is the same cultivar included in the experiments conducted in Pergamino, and 2-Want is a germplasm accession obtained from the USDA quinoa germplasm collection, apparently derived from an spontaneous cross between a Bolivian and a Chilean accession (Christensen et al., 2007). Biomass accumulation dynamics and its partitioning between organs (green and senescent leaves, stems and inflorescences when present) were established from samplings conducted fortnightly in 2005 (five for NL-6 and seven for 2-Want) and at four phenological stages (visible floral bud, first anthesis, end of anthesis and physiological maturity) in 2006, and define four developmental phases: vegetative, reproductive, flowering and seed filling. These data belonged to control treatments in experiments involving other treatments not reported here, and each data is the mean of 3 (2005) and 2 (2006) replicate plots. Five contiguous plants per plot were harvested at each sampling date with the exception of that conducted at final harvest, when 10 plants were used. Samples were dried in an air-forced drying oven at 70 °C to constant weight. Seed number m^{-2} was estimated from the final harvest data as the ratio of seed yield (g m^{-2}) to average individual seed weight (g seed^{-1}), and individual seed weight was estimated using three replicates of 100 seeds in each replicate plot.

Panicle biomass predictions were made using actual aerial biomass data from the validation data set, and allocations to organs were calculated using the partitioning coefficients (PC1 and PC2) presented in this work and the critical dates for change in partitioning to the inflorescence: the start of panicle growth and the date of change from minimum to maximum partitioning rates. Such critical dates were estimated from observed thermal times to first and end of anthesis in the validation experiments and from the relationships between thermal time to critical dates and thermal time to start and end of flowering derived from the Pergamino experiments.

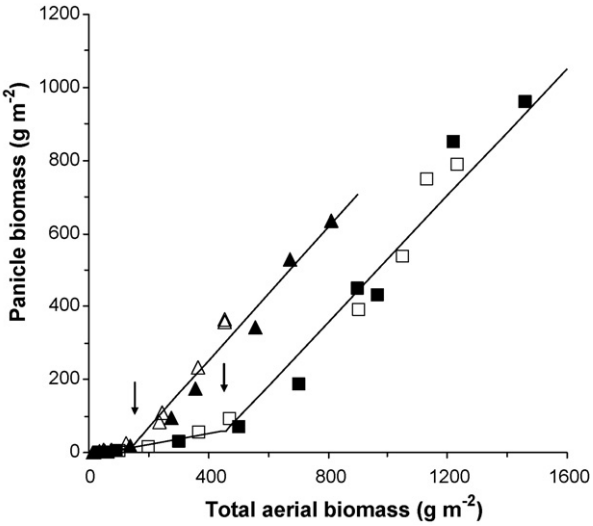

Fig. 1. Association between cumulative panicle biomass and cumulative total aerial biomass (in g m^{-2}) for the 2003 experiment. Symbols: cv. NL-6 (▲) and Faro (■). Open symbols: 22 pl m^{-2}, closed symbols 33 pl m^{-2}. Arrows indicates the values for PB2. Data are averages of four replicated plots.

3. Results

3.1. Association between panicle and biomass growth

Table 1 shows biomass accumulation up to first and end of anthesis for four sea-level genotypes of quinoa. Significant differences ($p < 0.05$) were observed among genotypes at both phenological stages within years. Trends in biomass accumulation agreed with cycle length. The greater the thermal time up to the developmental event, the higher the total biomass accumulation. Density effects on biomass were significant ($p < 0.05$) in 2003. Those effects tended to be significant ($p < 0.10$) only at the end of anthesis in 2004. Fig. 1 shows the association between cumulative panicle biomass and cumulative total aerial biomass for the experiment conducted in 2003 using as an example two cultivars of contrasting phenology (see Table 1). Bilinear models fitted well that relationship for each cultivar. This pattern was common to each combination cultivar × density × year. The partitioning coefficient to panicle was low when total biomass was less than TB2 (stage 1), but notably increased when total biomass was larger than TB2 (stage 2). Table 2 shows model parameters for every combination. Both PC1 and PC2 scarcely changed among combinations. Within cultivars, parameter PC1 differed between densities for NL-6, RU-5 and CO-407 in 2003; no differences were detected between densities in 2004. Across densities and years, PC1 was higher ($p < 0.05$) in short-cycle cultivars (NL-6: 0.28 ± 0.032; RU-5: 0.29 ± 0.035) than in long-cycle cultivar Faro (0.14 ± 0.013), whereas in cultivar CO-407 PC1 was intermediate (0.22 ± 0.041). On the other hand, values for PC2 were quite similar among cultivars (NL-6: 0.94 ± 0.044; RU-5: 0.86 ± 0.031; CO-407: 0.80 ± 0.056; Faro: 0.85 ± 0.039). In 2003 significant differences in TB2 ($p < 0.05$) were observed between short-cycle cultivar NL-6 (148 ± 27.0) and long-cycle cultivar Faro (457 ± 55.3) while values for RU-5 and CO-407 were intermediate (220 ± 31.9 and 320 ± 47.4, respectively). In 2004 a similar trend was observed although no significant differences were detected (NL-6: 249 ± 66.6; RU-5: 213 ± 74.8; CO-407: 370 ± 127.5; Faro:

Table 1
Thermal time (TT) from emergence (Tb = 3 °C) and total biomass accumulated up to first anthesis (FA) and end of anthesis (EoA). Means for four sea-level cultivars of quinoa at two densities in 2 years. SEM: standard error of the mean. d1: 22 plants m^{-2}, d2: 33 plants m^{-2}, d3: 66 plants m^{-2}. Different letters within a column and year indicate significant differences ($p < 0.05$) among cultivars. * and (o) indicate significant differences at $p < 0.05$ and $p < 0.10$ between densities. ns, no significant.

	TT FA (°Cd)	TT EoA (°Cd)	Biomass FA (g m^{-2})	Biomass EoA (g m^{-2})
2003				
Cultivar				
NL-6	634	968	45.6 c	187.9 d
RU-5	854	1184	94.6 c	312.9 c
CO-407	968	1278	183.5 b	497.5 b
Faro	1073	1360	251.8 a	637.4 a
SEM			17.40	39.63
Density				
d1			118.0	362.3
d2			169.7*	455.5*
SEM			12.3	28.02
2004				
Cultivar				
NL-6	647	836	61.3 c	206.3 b
RU-5	730	981	85.6 c	221.8 b
CO-407	784	1006	196.8 b	409.3 a
Faro	845	1116	289.7 a	510.6 a
SEM			22.52	50.56
Density				
d2			146.1	291.2
d3			170.6 ns	382.8 (o)
SEM			15.92	35.75

405 ± 81.2). For parameter TB1 (total biomass when panicle starts growing) significant differences ($p < 0.05$) were found between NL-6 (20 ± 5.6) and Faro (58 ± 11.4) in 2003. As well as for TB2, values for TB1 were similar among cultivars in 2004 (NL-6: 22 ± 17.7 and Faro: 73 ± 27.4).

On the basis of our results we combined data for all cultivars to evaluate whether a single model can describe partitioning to panicles across a range of conditions (Fig. 2). For stage 1, total biomass was corrected by TB1 (Fig. 2a). For stage 2 (Fig. 2b), total biomass and actual panicle biomass were corrected by TB2 and estimated panicle biomass for TB2, respectively. A fairly robust relationship was fitted to data in both Fig. 2a and b ($R^2 = 0.68$ and 0.93 respectively), giving a value of 0.15 ± 0.011 for PC1 and 0.90 ± 0.019 for PC2. Data from both years were randomly distributed around the regression line.

The associations between the estimated dates of start of panicle growth (thermal time to TB1) and change in partitioning from stage 1 to stage 2 (thermal time to TB2) with critical phenological events are shown in Fig. 3. There is a significant association between thermal time to TB1 and thermal time to first anthesis (Fig. 3a). Although detectable changes in panicle biomass are observed between floral initiation and first anthesis, no significant relationships could be established in these experiments between estimates of time to visible floral bud stage (Bertero et al., 1999) and time to TB1. Fig. 3b shows the close association between thermal time to the end of anthesis and the estimated thermal time to TB2; the start of active seed filling is closely related to that event in quinoa (unpublished data).

These data allow the prediction of panicle biomass growth across a wide range of conditions using aerial biomass data, the

Table 2
Parameters (±standard error) of the model that related panicle biomass to total biomass. Total biomass at which panicle begins to grow (TB1), total biomass when partitioning to panicle changes (TB2) and panicle partitioning coefficients for the first (PC1) and the second stage (PC2). Values for 2 years, four cultivars and three densities (d1: 22 plants m^{-2}, d2: 33 plants m^{-2} and d3: 66 plants m^{-2}). *, ns indicate significant ($p < 0.05$) or non-significant differences for PCs between densities within a year × cultivar combination.

Year	Cultivar	Density	TB1 (g m^{-2})	PC1 (g g^{-1})	TB2 (g m^{-2})	PC2 (g g^{-1})	R^2
2003	CO-407	d1	33 ± 11	0.10 ± 0.012 *	261 ± 62	0.80 ± 0.046 ns	0.95
		d2	45 ± 1	0.14 ± 0.012	369 ± 78	0.89 ± 0.094	0.93
	Faro	d1	57 ± 15	0.15 ± 0.017 ns	443 ± 67	0.86 ± 0.043 ns	0.97
		d2	60 ± 18	0.15 ± 0.015	471 ± 89	0.87 ± 0.059	0.93
	NL-6	d1	20 ± 6	0.22 ± 0.026 *	168 ± 34	1.07 ± 0.061 ns	0.96
		d2	21 ± 7	0.14 ± 0.013	178 ± 35	0.93 ± 0.036	0.98
	RU-5	d1	24 ± 7	0.24 ± 0.020 *	213 ± 42	0.87 ± 0.044 ns	0.97
		d2	31 ± 8	0.17 ± 0.022	185 ± 48	0.84 ± 0.030	0.98
2004	CO-407	d2	63 ± 59	0.38 ± 0.116 ns	554 ± 83	1.12 ± 0.206 ns	0.99
		d3	43 ± 21	0.08 ± 0.019	272 ± 197	0.68 ± 0.120	0.84
	Faro	d2	12 ± 12	0.10 ± 0.093 ns	253 ± 48	0.82 ± 0.065 ns	0.99
		d3	19 ± 11	0.02 ± 0.020	377 ± 176	0.79 ± 0.061	0.99
	NL-6	d2	31 ± 21	0.26 ± 0.052 ns	238 ± 95	0.86 ± 0.108 ns	0.91
		d3	12 ± 27	0.33 ± 0.073	294 ± 85	1.02 ± 0.172	0.94
	RU-5	d2	12 ± 4	0.09 ± 0.010 ns	96 ± 39	0.83 ± 0.088 ns	0.97
		d3	29 ± 24	0.39 ± 0.088	265 ± 201	0.86 ± 0.272	0.88

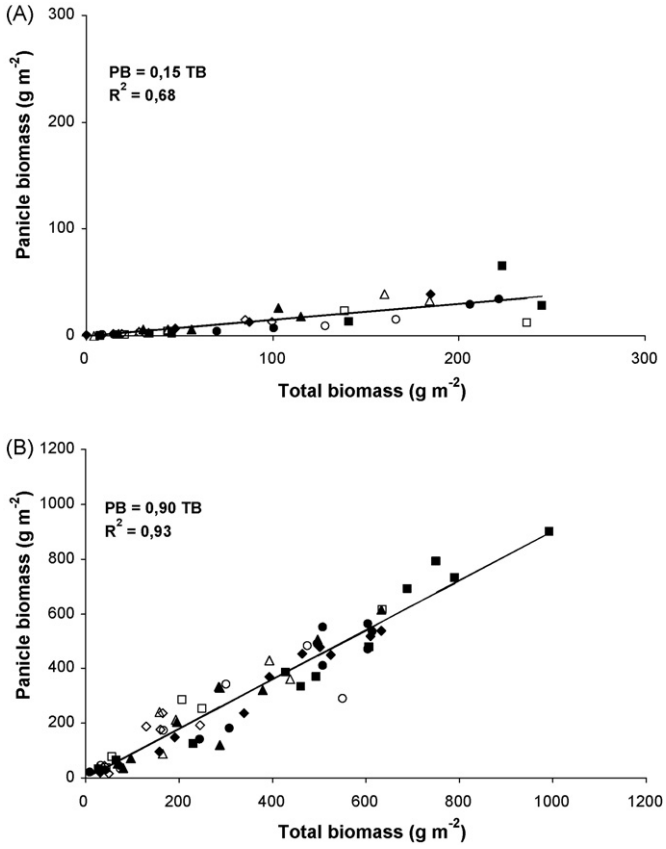

Fig. 2. Associations between cumulative panicle and total aerial biomass for experiments conducted in both years 2003 and 2004. Fig. 2a shows the relationship for data lower than the breakpoint TB2, while Fig. 2b shows the relationship for biomass values higher than TB2 (after substracting panicle and aerial biomass values at the breakpoint). Data are averages of four replicated plots. The line indicates the linear regression (forced through the origin, as intercept values were not significantly different from zero). Symbols: cv. NL-6 (▲), cv. RU-5 (♦), cv. CO-407 (●) and Faro (■); year 2003 (closed symbols), year 2004 (open symbols). R^2s are expressed as adjusted R^2s (Dike, 1997).

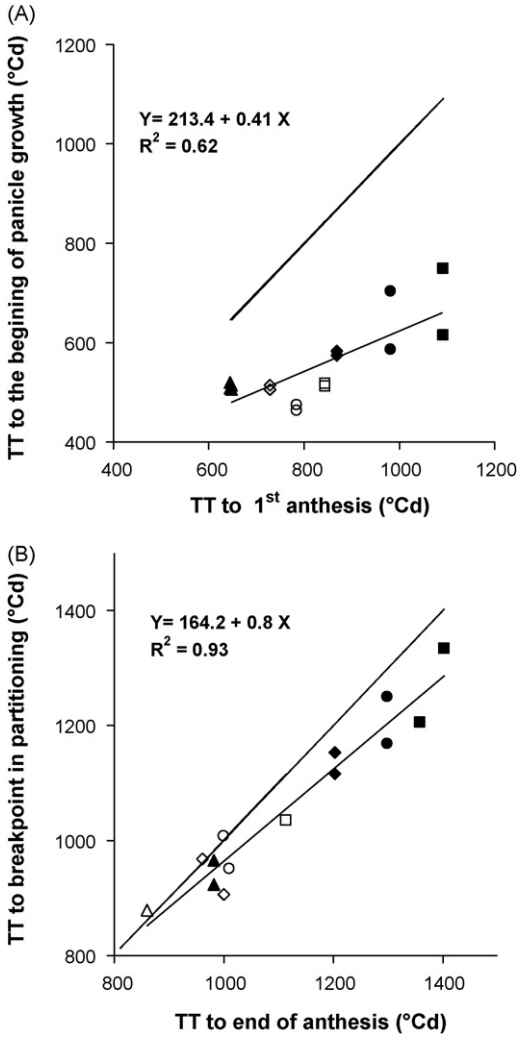

Fig. 3. Association between thermal time (TT, °Cd) from emergence to first anthesis and that to the beginning of panicle growth (a), and between TT to the end of anthesis and TT to the break point in partitioning to the inflorescence (b). Data are averages of four replicated plots. Symbols: cv. NL-6 (▲), cv. RU-5 (♦), cv. CO-407 (●) and Faro (■); year 2003 (closed symbols), year 2004 (open symbols). The dotted line indicates the 1:1 relationship, $n = 16$. R^2s are expressed as adjusted R^2s (Dike, 1997).

partitioning coefficients presented earlier and the critical dates for change in partitioning to the inflorescence. The single model was fitted to data from experiments conducted at the Faculty of Agronomy of the University of Buenos Aires during 2005 and 2006. Panicle growth was predicted satisfactorily (Fig. 4).

At this point, we had developed two different models to predict reproductive components from the same data set: the partitioning approach just described to predict panicle growth and the seed number approach that uses crop growth during flowering to predict seed number (Bertero and Ruiz, 2008). To make estimations from both models comparable we had to predict yield from seed number or panicle biomass at harvest. We used actual seed weight and the relationship between yield and panicle biomass from the 2005 and 2006 experiment to transform seed number and panicle biomass data into yield data. The results of these estimations are shown in Fig. 4 (inset).

Estimates of seed yield for cv. NL-6 were almost identical using both models and very similar to observed data. However, for both experiments using 2-Want, yields were underestimated in a higher degree using the seed number approach (average 87.7 g m^{-2} less) compared to the panicle biomass approach (-16.3 g m^{-2}). In relative terms, this means $a-24.5$ and $a-7.25$% yield difference between predicted and observed yields for each approach, respectively. The failure of the seed number approach to predict yield in this cultivar arose from its low panicle biomass growth during flowering compared to cultivars of similar phenology involved in the 2003 and 2004 experiment; on the other hand, high crop growth values during seed filling were translated into high panicle biomass, and hence yield (data not shown).

3.2. Association between stem and panicle growth

Panicle biomass at the end of flowering depended more on crop growth during flowering ($R^2 = 0.89$) than on the panicle–stem relationship at the end of flowering ($R^2 = 0.22$). This was also reflected in the weak association between yield and harvest index detected in these experiments ($R^2 = 0.38$, data not shown).

There is variability in the relative proportions of panicle and stem biomass during the crop cycle, as in the example for the contrasting cultivars NL-6 and Faro (Fig. 5a and b). Fig. 5c shows the relationship between partitioning to reproductive structures at harvest and the panicle–stem relationship at that time for both 2003 and 2004 (panicle + stem biomass represent between 92 and 100% of total aerial biomass at harvest). Besides variation between years in the absolute values, the earlier to mature cultivars NL-6 (triangles) and RU-5 (diamonds) reached higher partitioning values and panicle–stem relationships.

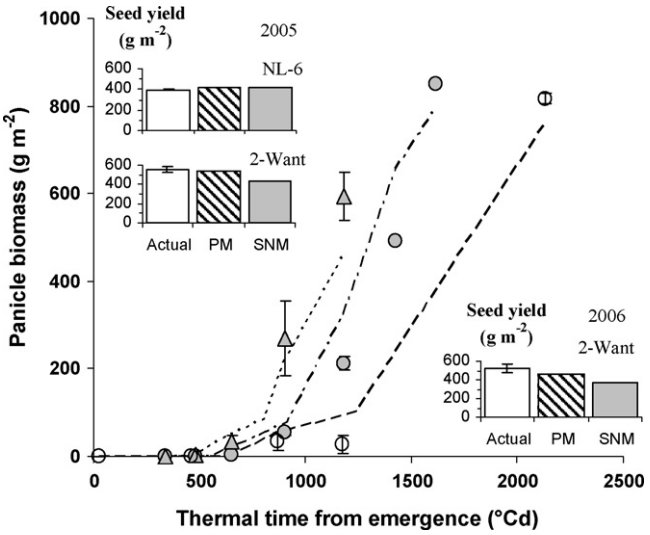

Fig. 4. Prediction of panicle biomass accumulation as a function of thermal time (TT, °Cd) from emergence. Symbols are observed values. Dotted lines are simulations. Symbols: cv. NL-6, 2005 (▲), accession 2-Want, 2005 (●), accession 2-Want, 2006 (○). Inset: actual seed yield and predicted seed yield using the partition model (PM) and the seed number model (SNM). Vertical bars are standard error of the means.

As shown in Fig. 5a and b, panicle growth passes through two stages, a period of slow growth and another of fast growth, ending at maturity. The first period starts between floral initiation and anthesis, while the second one (active panicle growth) starts near the end of anthesis (data not shown), in close correspondence with the date of the breakpoint in partitioning. This could be expected in terms of the relationship shown in Fig. 3b. For stem growth, a triphase model was fitted, as stem growth ends during seed filling. After a period of slow growth, stems enter a period of fast growth (active stem growth) and reach its maximum size once a plateau is observed earlier in seed filling. Active stem growth begins before the start of active panicle growth (both events showed a close correspondence, $R^2 = 0.82$), and ends after the end of anthesis (R^2 for the association between these variables = 0.84). On average, active stem growth starts 309 °Cd before active panicle growth and ends 112 °Cd after the end of anthesis, or 107 °Cd after the start of active panicle growth. An earlier start of active panicle growth (expressed as a smaller thermal time difference between the start of active panicle growth and that of active stem growth) is associated with a higher panicle–stem relationship at the end of flowering ($R^2 = 0.66$). However, the relevance of an earlier start of panicle growth is lower when analyzing its association with the panicle–stem relationship at harvest ($R^2 = 0.38$). The panicle–stem relationship at harvest exhibited a negative association with the absolute duration in thermal time units of stem growth ($R^2 = 0.60$) but no significant associations were found between that relationship at harvest and both duration of panicle growth (in °Cd) and the ratio dura-

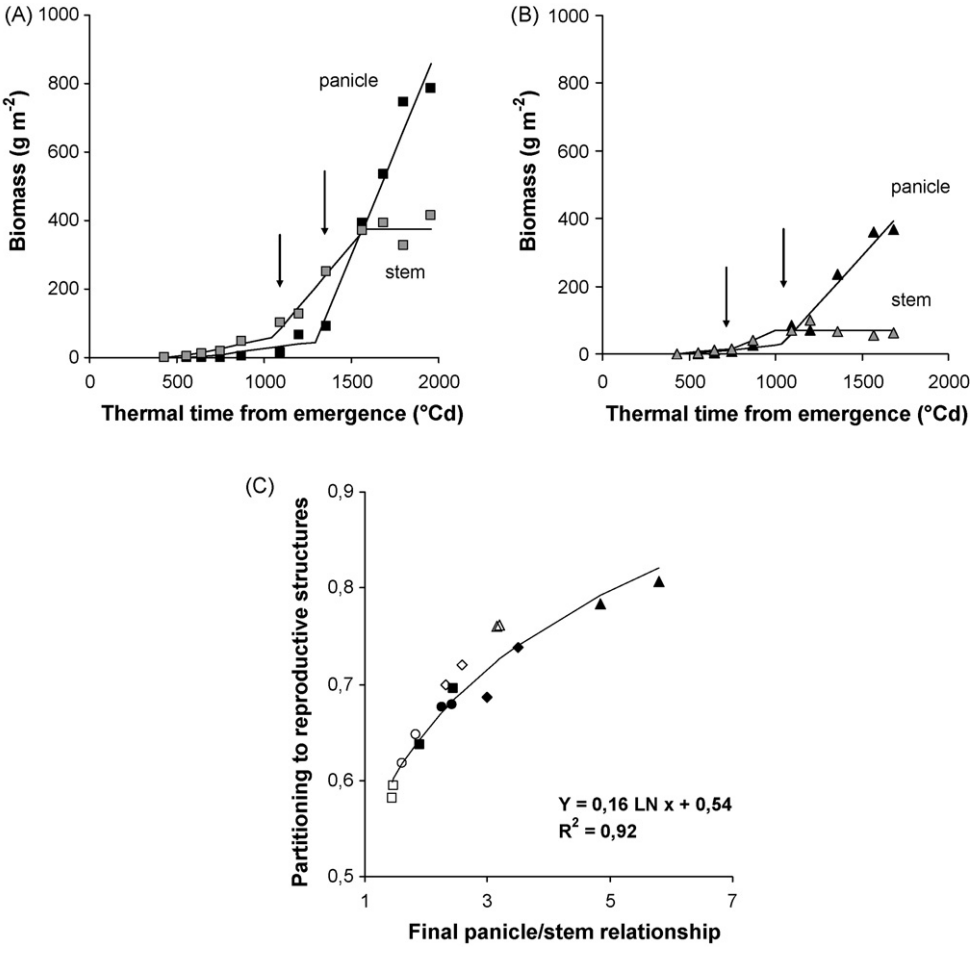

Fig. 5. Temporal dynamics of panicle and stem growth in cvs. Faro (a) and NL-6 (b) and association between partitioning to reproductive structures and panicle–stem relationship at harvest (c). Symbols: cv. NL-6 (▲), cv. RU-5 (♦), cv. CO-407 (●) and Faro (■); year 2003 (closed symbols), year 2004 (open symbols); the gray squares and triangles indicate stem biomass in (a) and (b). The arrows indicate the dates of anthesis and end of flowering. Data are averages of four replicated plots.

tion of panicle growth/duration of stem growth (in °Cd) (data not shown). Durations are not the only factor explaining differences in panicle–stem relationship however. For the two contrasting cvs. in Fig. 5a and b, stem growth rates during active stem growth are 3.3 times higher in Faro than NL-6, while maximum panicle growth rates are only 1.7 times higher.

4. Discussion

Although significant differences between cvs. in PC1 were detected for the experiment conducted during 2003, we have shown that a common reproductive allocation model that relates changes in partitioning rates to phenology explains most variation in the association between panicle and crop growth (Fig. 2). In this aspect, quinoa resembles crops like sunflower (Trápani et al., 1994) or soybean (Egli et al., 1985) and differs from species like maize, in which reproductive partitioning is highly sensitive to crop growth rate (Vega et al., 2001; Pagano and Maddonni, 2007). We cannot conclude that these partitioning coefficients will remain stable under water deficit of nutrient stress and should only be considered valid for the type of cultivars (Sea Level Type) studied. Nevertheless, waterlogging conditions experienced during part of the cycle in 2004 (Bertero and Ruiz, 2008) strongly affected biomass accumulation and yield but did not cause notable effects on partitioning coefficients (Fig. 2). In a recent paper (Gonzalez et al., 2009) reproductive partitioning values obtained 50 days after emergence were available for crops grown under well-watered, drought and waterlogging stress. The panicle/total biomass ratio was the same for both well-watered and drought treatments (5.6 and 5.7%) and only 1% lower under waterlogging (4.6%) These are low values and indicate that inflorescences were sampled at an early stage of growth (probably within the first stage of reproductive partitioning). In agreement with our results, stress effect was comparatively higher on total biomass than on reproductive partitioning (average reduction 23.4 against 8%, respectively), but comparisons with our results are limited because no data for a longer period were available.

One factor that has still not been analyzed is the role of stem reserves during seed filling in this crop. Values from Fig. 2b indicate that, on average, crop growth during seed filling is higher than panicle growth, and a model assuming a plateau in stem biomass once a maximum value is reached (e.g. Fig. 5a and b) fitted better to data than one assuming a decline in stem biomass later in seed filling (data not shown). A reduction in stem biomass would be expected if stem reserves were used to sustain grain growth. On the other hand, some treatments exhibited PC2 values higher than one (Table 2), suggesting that panicle growth could be higher than crop growth during seed filling. However, these values were not significantly different from other treatments with PCs lower than one. Stem reserves can be important for stress tolerance during seed filling (Ludlow and Muchow, 1990; Kiniry et al., 1992; Blum, 1998; Royo et al., 1999) and water deficits late in the crop cycle are common in locations were this species is traditionally grown (Etchevers and Avila, 1981; García et al., 2007) indicating that more detailed studies on this aspect are needed.

Panicle growth was described adequately by the model when we tested the validity of the approach for an independent data set with three cv × environment combinations (Fig. 4). Although an accession line not present in the original data set (2-Want) was included, a wider range of conditions should be considered for this validation. The use of this model and actual yield/panicle biomass ratio improved seed yield estimations when compared to those obtained by predicting seed number on the basis of crop growth during flowering and actual seed weight, and this means a significant improving in our capacity to predict seed yield in this species. One factor that can explain this difference is that conditions experienced after anthesis can affect final yield and seed number through changes in seed set (López and Bertero, 2006; Mignone and Bertero, 2007), a fact that was not taken into account by Bertero and Ruiz (2008). Partition coefficients seemed to be robust not only when describing panicle growth in different environments but also for a population (2-Want) not included in the original set. So, genotypic effects could be coarsely considered as affecting only the occurrence of critical dates for panicle growth (related to phenological events) and total aerial biomass production. Variation in final panicle biomass explained 89% of variation in yield, while final crop biomass did so for 79% of that variation, a 10% difference in favor of attempting to predict panicle biomass instead of just crop biomass to estimate yield. Yield can also be predicted from the simulation of harvest index increase during seed filling (e.g. Soltani et al., 2005), but total grain biomass early in seed filling is almost impossible to measure in quinoa; the description of the dynamics of harvest index increase reported by Geerts et al. (2008) is in fact one of panicle growth, as a recognition of that difficulty.

At the present stage of quinoa breeding and management, crop biomass is still the main variable affecting yield (Bertero et al., 2004). Furthermore, under some conditions (Bertero et al., 2004; Bertero and Ruiz, 2008), the longer the duration of the crop cycle, the higher the biomass and yield; while harvest index exhibits a negative association with crop duration (Bertero et al., 2004; Ruiz and Bertero, 2006). This trade-off between the final value of partitioning to reproductive structures and total crop biomass (e.g. Fig. 5, and Bertero et al., 2004) precludes selection for a higher panicle/stem ratio if it involves a reduction in duration of the crop cycle, and can just by chance (and hardly) be obtained by selection for yield only in a breeding program. Selection for a high partitioning rate can be targeted at long duration cultivars within germplasm adapted to the Pampas Region. When cultivated at high densities (Mignone et al., 2007), these cultivars can reach full radiation interception early in the crop cycle and maintain it until physiological maturity. This possible strategy was partially supported by recent experimental data. When partitioning to reproductive structures was manipulated by the application of a giberellic acid synthesis inhibitor (Paclobutrazol) to crops of 2-Want, a 50% increase in yield (from 517 to 791 g m^{-2}) was found without affecting total biomass accumulation and phenology (Mignone et al., 2007).

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