CSIRO PUBLISHING
www.publish.csiro.au/journals/fpb *Functional Plant Biology*, 2011, **38**, 420–430

Can yield potential be increased by manipulation of reproductive partitioning in quinoa (*Chenopodium quinoa*)? Evidence from gibberellic acid synthesis inhibition using Paclobutrazol

M. B. Gómez[A], *P. Aguirre Castro*[A], *C. Mignone*[A] *and H. D. Bertero*[A,B,C]

[A]Cátedra de Producción Vegetal, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453 (C1417DSE), Buenos Aires, Argentina.
[B]Consejo Nacional de Investigaciones Científicas y Técnicas, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453 (C1417DSE), Buenos Aires, Argentina.
[C]Corresponding author. Email: bertero@agro.uba.ar

Abstract. One factor conditioning quinoa (*Chenopodium quinoa* Willd.) adoption is the need to increase yield. This paper analyses the effect that Paclobutrazol, a GA synthesis inhibitor, produces on yield, biomass, partitioning, seed number and weight in quinoa. Two experiments were conducted under field conditions: one compared a tall genotype (2-Want) with a shorter genotype (NL-6); while the other analysed seed yield and its components using the 2-Want genotype. As a consequence of Paclobutrazol application in the one-genotype experiment, plant height decreased from 197 to 138 cm, yield increased from 517 to 791 g m^{-2}, seed numbers rose from 308 000 to 432 000 seeds per m^2, and the harvest index increased from 0.282 to 0.398 g g^{-1}. Biomass accumulation and seed weight were not affected. The leaf area index was reduced by Paclobutrazol but radiation interception was only marginally reduced; soil plant analysis development (SPAD) values and specific leaf weight were increased, but radiation use efficiency was not affected by treatments. Root biomass and lateral roots tended to increase under Paclobutrazol treatment. Genotypes were compared until the end of flowering and similar responses were obtained. Higher yields could be obtained in quinoa if reproductive partitioning was increased, turning it into a good candidate in the search for high quality protein sources.

Additional keywords: floral development, harvest index, panicle growth, plant growth regulators, root growth, seed number.

Introduction

One of the most outstanding crop breeding achievements during the 20th century was the development of semi-dwarf wheat (*Triticum aestivum* L.) and rice (*Oryza sativa* L.) cultivars, which allowed crop production to cope with population growth and led some developing countries to become self-sufficient in the production of these crops, as described by one of its main participants (Borlaug 2007). Besides wide adaptation, the main trait affected by breeding was plant height, which was achieved through the introgression of genes that impaired GA biosynthesis (GA biosynthesis mutants) or interfered with the GA signal transduction pathway (GA sensitivity mutants) (Chandler and Robertson 1999; Peng *et al*. 1999; Rebetzke and Richards 2000; Silverstone and Sun 2000; Hedden 2003; Swaminathan 2006).

Understanding yield determination from a crop physiology standpoint was greatly improved by using a top-down approach (e.g. Passioura 1981; Slafer and Savin 2006) and recognising the existence of a critical period for yield determination, the crop cycle window when yield is most sensitive to environmental factors (Fischer 1985; Slafer and Savin 2006; Slafer *et al*. 2006). Using a top-down approach, crop yield is explained as the product of final crop aerial biomass and the harvest index (HI). For cultivars growing under optimal conditions (no water or nutrient limitation), radiation is the driving force of crop growth. Biomass accumulation depends on the amount of incident radiation intercepted by the crop canopy and on radiation use efficiency (RUE, g aerial biomass per unit of intercepted radiation, g m^{-2} MJ PAR^{-1}). Intercepted radiation during the crop cycle, as well as crop duration and daily incident radiation, depends on radiation interception efficiency (RIE), which is determined by the leaf area index (LAI, the photosynthetically active leaf surface per unit of soil surface) and the light attenuation coefficient (k). Considering the critical period for yield determination implies focusing on growth and partitioning during the window of phenological time in which yield (or grain number) is most responsive to environmental changes (see Slafer *et al*. 2006 for a highly detailed analysis of grain number determination in several grain crops using this approach). As the higher HI in semi-dwarfs of wheat, rice or other crops is the final result of partitioning changes during the crop cycle, it is also relevant to evaluate the temporal dynamics of partitioning to reproductive structures when comparing genotypes or treatments for yield

10.1071/FP10168 1445-4408/11/050420

determination processes (i.e. González *et al*. 2003; Bertero and Ruiz 2010).

The Andean seed crop quinoa (*Chenopodium quinoa* Willd.) possesses grains that are used in a similar way to those of cereals. Moreover, it has a high nutritive value associated with an excellent amino acid balance – better than that of cereal and leguminous plants – and a high content of lysine, an essential amino acid (Ruales and Nair 1992). Quinoa can be grown with limited water and tolerates low temperatures, prevailing conditions in the highlands of Bolivia, Peru, Chile and the Argentinean north-west; these traits have aroused interest in its evaluation as a new crop in different countries (Jacobsen and Stolen 1993). Research on this crop started several years ago at the University of Buenos Aires with the aim of cultivating it in the Argentinean Pampas. As part of a research project aimed at analysing growth and yield determination in quinoa cultivars grown in temperate environments, yields of up to 5200 kg ha^{-1} were obtained under potential conditions in late winter-early spring sowings in that region (Mignone and Bertero 2007; Bertero and Ruiz 2008).

One factor limiting crop expansion in this species is the need for cultivars with high yield potential; crop breeding in this species has recently started (Jacobsen and Mujica 2002) and a high potential for yield increase by genetic manipulation is expected considering the high level of genetic variability being detected (Mason *et al*. 2005; Christensen *et al*. 2007 and breeders' reports (S. Ward, pers. comm.)). In comparison with modern crops of wheat, rice or maize (*Zea mays* L.) (Evans 1993; Ashraf *et al*. 1994; Slafer *et al*. 1994), the average HIs of quinoa are low (i.e. 0.30, Bertero *et al*. 2004), similar to those of wheat and rice before the green revolution (Sakamoto and Matsuoka 2004). Given the previous history of crop breeding (wheat and rice, for instance), an increase in yield is expected to be achieved by affecting GA metabolism, and thus manipulating plant height. The underlying hypothesis is that yield in quinoa is limited by a low sink capacity (Miralles and Slafer 2007; Reynolds *et al*. 2009) and that a reduction in competition between stem and panicle for photoassimilates will result in higher seed number and yield, as a consequence of increased reproductive partitioning. No reports are available on the existence of mutants for plant stature in quinoa so a direct evaluation of this hypothesis is currently not possible. Plants treated with GA biosynthesis inhibitors are phenotypically similar to GA biosynthesis mutants (Sarkar *et al*. 2004). Consequently, they can be used to evaluate the potential impact of genetic manipulation of GA content in this species. We have chosen Paclobutrazol (Crestar, ICI, Buenos Aires, Argentina) because of its wide use as a plant growth regulator and previous experience with its use in other quinoa experiments (Bertero *et al*. 2001). This work is mainly aimed at evaluating the effect of a reduction in plant height using the GA synthesis inhibitor Paclobutrazol on quinoa yield and the processes involved in its determination. The objectives of this work are the following:

(*a*) to analyse the effect of Paclobutrazol treatments on determining crop biomass (e.g. LAI, RIE and RUE), reproductive partitioning, seed number and seed weight; and
(*b*) to evaluate the effect of treatments on two genotypes of different initial stature.

Materials and methods

Experimental design and growing conditions

Two experiments were conducted during 2006 and 2007 at the Faculty of Agronomy of the University of Buenos Aires, Argentina (34°35′S, 58°29′W, 20 m above sea level). The Faculty is located in the Pampas (Hall *et al*. 1992) and its climate is defined as temperate humid with a very hot summer (Köppen 1931). One genotype (*Chenopodium quinoa* Willd. cv. 2-Want) was used during the first year and two (2-Want and *Chenopodium quinoa* Willd. cv. NL-6) were studied during the second. 2-Want is a tall (~2 m height) germplasm accession obtained from the United States Department of Agriculture quinoa germplasm collection (identified as AMES 13737 at: http://www.ars-grin.gov/cgi-bin/npgs/html), probably deriving from a spontaneous cross between a Bolivian and a Chilean accession (Christensen *et al*. 2007). This accession exhibited a high yield potential (5200 kg ha^{-1}) when cultivated in Buenos Aires, Argentina (Mignone and Bertero 2007). NL-6 is an earlier flowering, shorter cultivar (~1.2 m height) selected at Wageningen University, the Netherlands (S. Jacobsen, pers. comm.), yielding up to 4000 kg ha^{-1} under local conditions (Mignone and Bertero 2007). To minimise nutrient restrictions, plants received supplementary irrigation and fertilisation at sowing (20 kg P and 18 kg N ha^{-1}) and one urea application (totaling 100 kg N ha^{-1}) 30 days after emergence. Weeds were removed by hand, and fungicides and insecticides applied upon detection in the field.

The one-genotype experiment was the only one that went to completion until physiological maturity. The other experiment (two genotypes) was interrupted after end of flowering because of a severe mildew (*Peronospora farinosa* f. sp. *Chenopodii* (Fr.) Fr.) attack. This is the reason why the results are presented in inverse order, and are named the one- and two-genotype experiment, respectively.

Two-genotype experiment

This experiment involved accession 2-Want and cultivar NL-6, sown on 16 November 2007, and was conducted with the aim of comparing treatment responses in genotypes differing in final plant height. Plots were hand-planted and thinned to 28.6 plants per m^2 in rows 0.35 m apart. Plots were six rows wide (4.2 m^2) and there were three replicate plots per treatment in a split-plot design, with Paclobutrazol (Crestar) levels (applications and control) as main plots and genotypes as subplots. GA inhibition treatments consisted of two levels of Paclobutrazol application (treatment and controls). Paclobutrazol was applied as a 3.4 mM solution totaling four applications at 4-day intervals, and 2 days after the visible floral bud (VFB) stage (Bertero *et al*. 1999). It started to be applied as foliar spray; plastic sheets were used to separate plots during spraying. This dose was chosen on the basis of Steinbach *et al*. (1997), where Paclobutrazol was used to manipulate dormancy in sorghum (*Sorghum bicolour* (L.) Moench.) and on Bertero *et al*. (2001), who used it on quinoa for the same purpose. VFB was chosen because it is the stage at which active stem growth starts in quinoa; active panicle growth starts at first anthesis (Bertero and Ruiz 2008).

Developmental stages (recorded when four out of seven sampled plants within each plot reached the stage) were determined as: emergence, VFB (Bertero *et al*. 1999), first anthesis (at least one flower opened), end of anthesis (no more flowers opened, determined by observation of the main inflorescence) and physiological maturity (visually determined by examination of seeds on the medium third of the inflorescence) (Bertero and Ruiz 2008). These stages define four developmental phases: vegetative, reproductive, flowering and seed filling, and coincide with stages 0, 2, 8 and 18 in the scale of Jacobsen and Stolen (1993). These determinations (except for emergence) were made by observations conducted every 3 days on seven plants per plot tagged after thinning (10 days after emergence). Plant height (cm) was measured every 5 days on the same plants, considering the distance from the soil to the panicle top, starting at VFB stage and ending when a stable height was reached (~mid-seed filling; Bertero and Ruiz 2010). Soil plant analysis development values (SPAD-502, Minolta Corporation, Osaka, Japan) were measured in three plants per plot sampled at random every ~10 days, on fully expanded upper leaves exposed to direct radiation, in order to estimate the relative variation in chlorophyll (Minolta 1989) and leaf N content. Previous work with quinoa confirmed a strong linear relationship ($R^2 = 0.88$) between total chlorophyll content and SPAD values in the range of 25–75 SPAD units (Bertero 2001) and also with leaf N concentration (mg N mg leaf biomass^{-1}, SPAD range 20–65; Raffaillac *et al*. 2007). Intercepted radiation was measured every 3 days at midday on clear days (as described in Ruiz and Bertero 2008) and values were converted to daily fractional interception (RIE) as outlined by Charles-Edwards and Lawn (1984).

At VFB, first anthesis and end of anthesis, plants were sampled in order to measure aboveground biomass and LAI. Five contiguous plants per plot were harvested from the central rows in each plot (to avoid border effects) at each sampling date. Biomass was separated into green leaves (main stem and branches), stem (main stem and branches) and inflorescences. Samples were dried in an air-forced drying oven at 70°C to constant weight. Leaf area was measured with an LI-3100 leaf area meter (LI-Cor Inc., Lincoln, NE, USA) and expressed on a per ground area basis. Specific leaf weight (SLW) (g cm^{-2}) was estimated from the leaf weight to leaf area relationship.

At the end of anthesis, three plants were sampled in each treatment in NL-6 to count the number of fertile flowers for three node positions (20, 25 and 30); these plants were dissected under a stereomicroscope (Leica steromicroscope MZ6, Leica, Wetzlar, Germany) and a flower was considered fertile if it was at floral stage G7 (differentiation of stigmatic branches) or higher in the scale of Bertero *et al*. (1996). Roots were also included in this sampling; they were carefully removed from the soil and thoroughly washed to remove soil parts before drying.

One-genotype experiment

This experiment was sown on 11 October 2006, using 2-Want. Plots were hand-planted and thinned to 50 plants per m^2 in rows 0.20 m apart. Plots were 10 rows wide (3.6 m^{-2}) and there were two replicate plots per treatment in a fully randomised design.

Samplings for measuring aboveground biomass and LAI were conducted in the same way described for the two-genotype experiment at VFB, first anthesis, end of anthesis and physiological maturity stages, with the exception of the maturity harvest, when 10 plants were used. Seed numbers per m^2 was estimated considering the final harvest data as the ratio of seed yield (g m^{-2}) to average individual seed weight (g per seed). Individual seed weight (mg) was estimated using 5 replicates of 50 seeds in each replicate plot. HI was estimated as the ratio of grain yield to total aerial biomass at harvest. Partitioning to organs (panicle or roots [but for roots only in the two-genotype experiment]) was estimated as the organ to total aerial biomass ratio at each sampling date. At the end of anthesis, three plants per plot were sampled to estimate the number of fertile flowers. The number of fertile flowers was counted every five nodes, and the total flower number per plant was estimated as the area below the curve by fitting an asymmetric double sigmoid curve to the flower number per node *v.* node position relationship, using TableCurve V3.0 (Jandel TBLCURVE 1992).

Data analysis

ANOVA was used for the evaluation of treatment (Paclobutrazol level × genotype) effects, and associations between variables were estimated using linear regressions. *P*-values <0.1 were considered significant for one-genotype experiment based on the low number (two) of replicates used in this experiment, whereas *P*-values <0.05 were considered significant for the two-genotype experiment. RUEs for the emergence–end of anthesis period (to allow for comparisons between experiments) were estimated as the slope of the linear regression (forced through the origin, since intercepts were not different from zero) of the accumulated aerial biomass (g m^{-2}) *v.* the accumulated intercepted PAR (MJ m^{-2} d^{-1}), and RUE values (slopes) were compared by ANOVA and Student's *t*-test (Steel and Torrie 1960). Daily RIE values were estimated using the *Evaluation* option of TableCurve V3.0 (Jandel TBLCURVE 1992) and applied to a double sigmoid function fitted to the RIE *v.* time from emergence relationship. Daily intercepted radiation was obtained as the product of daily intercepted PAR and RIE. Climatic data (temperature and radiation) were obtained from an automated meteorological station located ~50 m away from the experiment.

Results

General results

Data from the sampling conducted at the end of flowering in the two-genoype experiment are shown in Table 1. There were significant differences between treatments (cultivar × Paclobutrazol level combinations) in biomass, panicle weight, plant height and reproductive partitioning (panicle biomass total biomass^{-1}) but Paclobutrazol effects within a cultivar were significant only for partitioning in NL-6. In the case of the one-genoype experiment, final biomass (g m^{-2}), plant height (cm), seed yield (g m^{-2}), HI (g g^{-1}), seed number (thousand seeds per m^2) and weight (mg per seed) data were available (Table 2) and are discussed in below.

Table 1. Panicle biomass, total aerial biomass, reproductive partitioning (g panicle g aerial biomass $^{-1}$) at the end of flowering and final plant height for the two-genotype experiment

Different letters within a column indicate significant differences ($P < 0.05$) between Paclobutrazol treatments, genotypes or both. Data are means ±1 s.e.

Treatments	Panicle weight (g m^{-2})	Aerial biomass (g m^{-2})	Partitioning to panicles (g g^{-1})	Final height (cm)
2-Want Paclobutrazol	196 ± 34a	822 ± 146a	0.24 ± 0.02a	132 ± 10ab
2-Want control	118 ± 71ab	625 ± 141ab	0.17 ± 0.05ab	156 ± 21a
NL-6 Paclobutrazol	104 ± 15ab	436 ± 55bc	0.25 ± 0.04a	71 ± 5c
NL-6 control	43 ± 3b	311 ± 35c	0.14 ± 0.01b	99 ± 7bc

Table 2. Yield, final aerial biomass, harvest index, plant height, seed number and individual seed weight at physiological maturity for the one-genotype experiment

Different letters within a column indicate significant differences ($P < 0.10$) between Paclobutrazol treatments. Data are means ±1 s.e.

Treatments	Yield (g m^{-2})	Aerial biomass (g m^{-2})	Harvest index (g g^{-1})	Final height (cm)	Seed number (thousand seeds m^{-2})	Seed weight (mg)
Paclobutrazol	791 ± 83a	1983 ± 202a	0.398 ± 0.001a	138 ± 6b	432 ± 37a	1.8300 ± 0.0003a
Control	518 ± 45a	1859 ± 143a	0.282 ± 0.050a	197 ± 1a	308 ± 8b	1.6778 ± 0.0004a

Yield, seed number and HI exhibited higher values under Paclobutrazol treatment, but these differences were significant only for seed number ($P < 0.08$) and were near significance for yield ($P = 0.1$) and HI ($P = 0.12$). Total aerial biomass (an average of 1770 g m^{-2}) and seed weight (an average of 1.63 mg per seed) values were not affected ($P > 0.28$). Plant height reduction under Paclobutrazol was highly significant ($P < 0.01$). Plant height decreased by ~30% (from 197 to 138 cm); however, seed yield increased by ~50% (from 517 to 791 g m^{-2}), seed number by ~40% (from 308 000 to 432 000 seeds per m^2) and HI by ~43% (from 0.282 to 0.398 g g^{-1}). Seed yield showed a very strong, linear and positive association with seed number ($R^2 = 0.98$) so changes in yield were explained by those in seed number. Paclobutrazol application did not affect development in either of the experiments or genotypes, with the exception of seed filling in the one-genotype experiment, which was reduced by 6 days, probably associated with earlier senescence under Paclobutrazol (data not shown).

Growth components

Plants treated with Paclobutrazol exhibited an important reduction in plant height and in stem biomass in both genotypes and experiments, which was more marked during the one-genotype experiment (Fig. 1). Plant height started to differ between treatments shortly after application, and maximum height was reached shortly after the beginning of seed filling. In the two-genotype experiment, although not significant, reductions were 15% for 2-Want and 29% for NL-6; in the one-genotype experiment, height was reduced by 30% by Paclobutrazol (from 197 to 138 cm). Interestingly, changes in total stem biomass were not significant ($P > 0.25$) in both experiments and genotypes. In the two-genotype experiment, stem biomass increased 17% under treatment in 2-Want and remained unchanged (2% reduction) in NL-6; substantiality (shoot DW per unit of plant height, Yim *et al.* 1997) increased by 36.5% (NL-6) and 38.7% (2-Want). Stem biomass was reduced from 856 to 637 g m^{-2} in the one-genotype experiment,

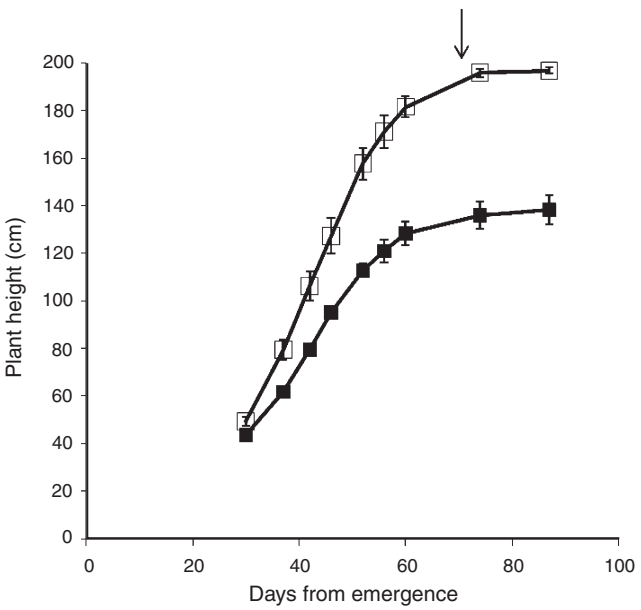

Fig. 1. Plant height as a function of days from emergence in the 2-Want cultivar (one-genotype experiment). Closed symbols, plants treated with Paclobutrazol; open symbols, control. The arrow indicates the beginning of the seed filling phase. Data are averages ± 1 s.e.

with a similar tendency for branch biomass (from 113 to 77 g m^{-2}), but stem substantiality was increased by 6% as a consequence of treatment. Main stem node number was counted at harvest in the two-genotype experiment and related to plant height, showing that height variability between treatments for both genotypes was related to changes in node number and not in length per node (data not shown).

Fig. 2 presents the LAI results for samplings conducted at the end of flowering for both experiments, and represent the maximum attainable value under each condition (Ruiz and Bertero 2008). Differences between Paclobutrazol treatments

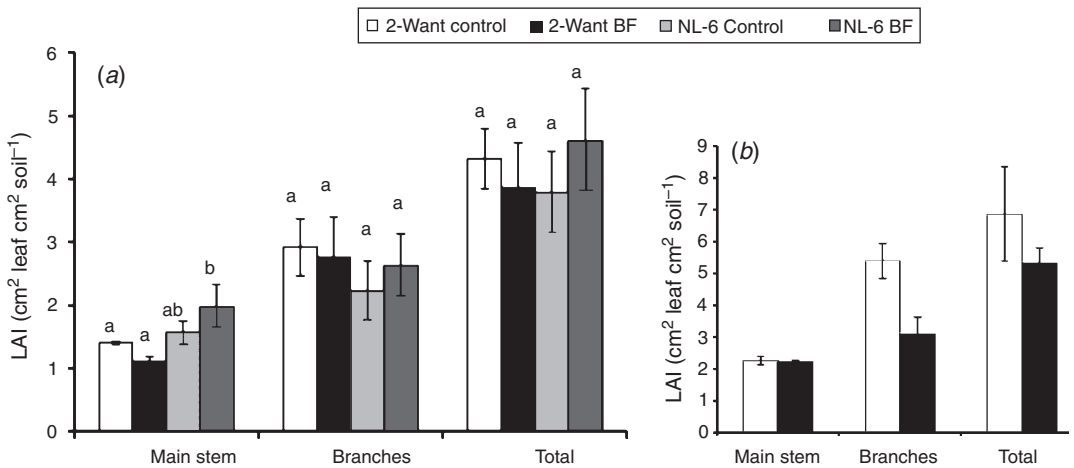

Fig. 2. Leaf area index (LAI) values at the end of flowering on the main stem, branches and totals. (*a*) 2-Want and NL-6 in the two-genotype experiment; (*b*) 2-Want in the one-genotype experiment. Closed bars, 2-Want treated with Paclobutrazol; open bars, 2-Want control; light gray bars, NL-6 control; dark gray bars, NL-6 treated with Paclobutrazol. Data are averages ± 1 s.e. Different letters indicate significant differences ($P < 0.1$ for the one-genotype experiment and $P < 0.05$ for the two-genotype experiment) within an experiment and leaf area category.

were not significant for either leaf area category or for either genotypes in the two-genotype experiment ($P > 0.8$; Fig. 2*b*). Total LAI was reduced by 27% (not significant) under Paclobutrazol in the one-genotype experiment, but these effects were seen only in the branches (a 46% reduction, $P = 0.09$), as main stem leaf area was not affected (Fig. 2*a*). The relative importance of leaf area in branches is high: 76% in the control and 58% in treated plants. When RIE was analysed in the two-genotype experiment, 2-Want reached a maximum RIE of 0.92 and 0.95 during flowering (63 days after emergence) for the control and Paclobutrazol treatments, respectively, and the maximum values for NL-6 were 0.91 and 0.86 on Day 56, near the end of flowering again for treatment and control, respectively. No differences were found for most of the cycle in the one-genotype experiment (Fig. 3), and RIE only decreased for the Paclobutrazol treatment for measurements conducted 2 weeks after first anthesis. The crop reached full radiation interception (RIE >0.95) 37 days after emergence and maintained it at least until Day 60, covering the whole reproductive and flowering phase.

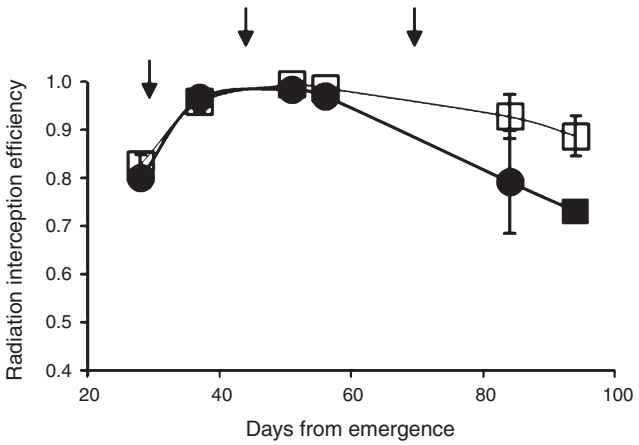

Fig. 3. Radiation interception efficiency (RIE) as a function of days from emergence in 2-Want (one-genotype experiment). Closed symbols, plants treated with Paclobutrazol; open symbols, control. Arrows (from left to right) indicate the dates of the visible floral buds (VFB), first anthesis and end of flowering stages. Data are averages ± 1 s.e.

Photosynthesis-related variables

Radiation use efficiency values did not differ between genotypes and Paclobutrazol levels in the two-genotype experiment or between treatments in the one-genotype experiment, reaching average RUE values of 1.46 and 2.24 g MJ^{-1}, respectively. Because of the sampling frequency, changes in RUE during development, as outlined by Ruiz and Bertero (2008), could not be identified, and a single linear relationship adequately described the biomass *v.* intercepted radiation relationship (data not shown). The estimated RUE values were similar to those estimated by Ruiz and Bertero (2008). However, the two-genotype experiment values were closer to the minimum and the one-experiment values were closer to the maximum reported in that work.

Paclobutrazol effects on SPAD values are exemplified using data from the two-genotype experiment (Fig. 4); those from the one-genotype experiment exhibited a similar trend (data not shown). Differences between treated and control plants increased from the VFB stage onwards and reached a maximum (~10 SPAD units) around anthesis, remaining stable thereafter. SLW, the third variable associated with photosynthetic capacity, was significantly higher ($P < 0.05$) under Paclobutrazol but only for main stem leaves ($P < 0.01$) in the two-genotype experiment, in agreement with the SPAD values (data not shown), and SLW was not changed by treatments in the one genotype experiment (with a tendency to higher values in treated plants). Finally, leaf conductance, a variable associated with higher photosynthetic capacity, cooler canopies and higher

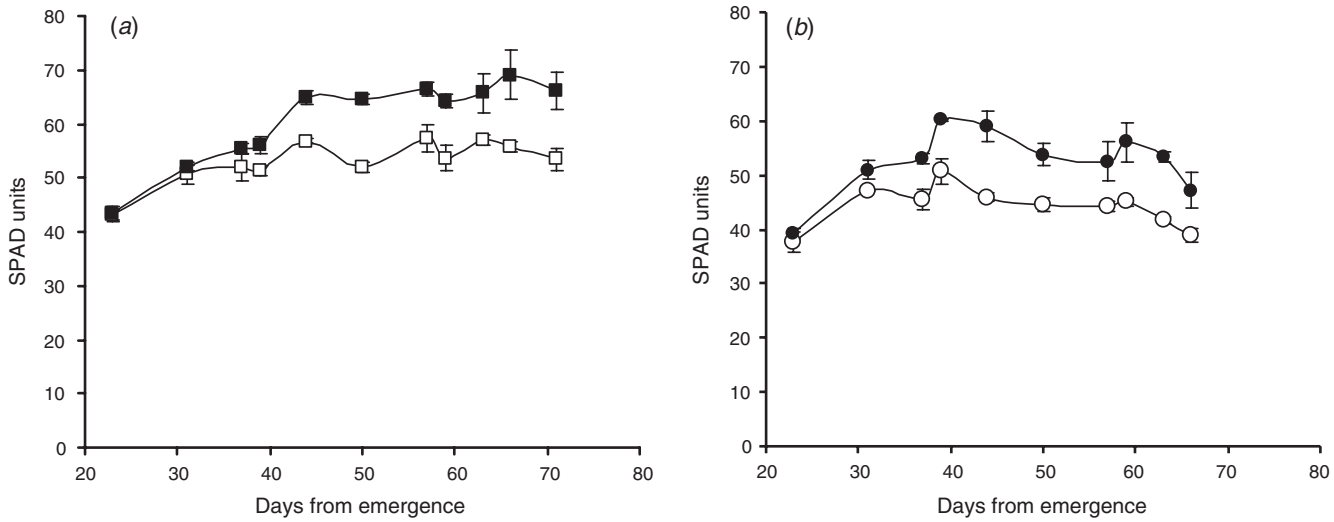

Fig. 4. SPAD values as a function of days from emergence in the two-genotype experiment. (*a*) 2-Want; (*b*) NL-6. Data are averages ± 1 s.e.

yield potential in species like cotton (*Gossypium barbadense* L.) and wheat (Lu *et al*. 1994; Fischer *et al*. 1998), was measured for both genotypes and treatments in the two genotype experiment, but no differences between treatments were detected (data not shown).

Reproductive and root growth and partitioning

A higher partitioning to panicles was observed in Paclobutrazol-treated plants, beginning with the sampling conducted at first anthesis and maintained until physiological maturity in all experiments and cultivars (Fig. 5; Fig. S1, available as an Accessory Publication to this paper). Values for the two-genotype experiment (end of flowering sampling) were 0.17 and 0.24 for 2-Want, and 0.14 *v.* 0.25 for NL-6 for the control and treated plants, respectively. For the one-genotype experiment, reproductive partitioning at physiological maturity (panicles per total biomass) was 0.44 and 0.61 for the control and treated plants, respectively.

In the two-genotype experiment, root biomass values were measured at the end of flowering, a stage when root biomass reaches its maximum in several crops (Gregory 2004). Root biomass tended to be higher in 2-Want than in NL-6, consistent with its higher aerial biomass, and a tendency towards higher root biomass and partitioning to roots was detected in treated plants in both genotypes. It is important to highlight that treated plants had much more abundant lateral roots when visually compared with controls (data not shown).

Floral development

Fig. 6*a* presents the flower number profile across node positions for the sampling conducted at the end of flowering in the one-genotype experiment. Node numbers are assigned from the base (older) to the top of the plant, so the figure mirrors flower density in the same order. Flower number increases sharply and reaches a maximum around node 30 then decreases gradually up to the panicle top. Differences between treatments were marked and concentrated in the lower third of the panicle. An estimation of total flowers per plant resulted in 13 300 flowers per plant for control and 26 400 flowers per plant for treated plants, a 98% difference. Fig. 6*b* shows the relationship between flower number per node and node biomass, combining data across node positions for both treatments. A single linear relationship provides a good description of the relationship ($R^2 = 0.94$), suggesting that a stable reproductive efficiency can be assumed across nodes and treatments. During the two-genotype experiment, flowers were counted in NL-6 for three node positions (20, 25 and 30); values were 74% higher under Paclobutrazol for Node 20, and differences disappeared for higher nodes (data not shown).

Discussion and conclusions

This article analysed Paclobutrazol effects on quinoa at different hierarchical levels. An important yield increase can be obtained by the inhibition of GA synthesis (Table 2) through increases in HI that are not compensated by a reduction in crop biomass. Yield reached under Paclobutrazol (as in the one-genotype experiment ($790\ g\ m^{-2}$)) had never been measured in previous experiments carried out in the Argentinean Pampas (Bertero and Ruiz 2008) and was higher than almost all values reported in related literature (Jacobsen *et al*. 1994; Berti *et al*. 2000; Mastebroek *et al*. 2002; Bertero *et al*. 2004; Schulte auf'm Erley *et al*. 2005; Spehar and De Barros Santos 2005; Bhargava *et al*. 2006; Lebonvallet 2008; Geerts *et al*. 2009). At a lower hierarchy level, biomass accumulation can be understood in terms of crop duration and crop growth rate determinants (CGR; $g\ m^{-2}\ d^{-1}$). With the exception of the final part of the cycle in the one-genotype experiment, no changes in duration of development were detected, and this reduction of seed filling duration under Paclobutrazol was not associated with a lower seed weight (Table 2). RIE and RUE are the components of CGR on the crop side: changes in RIE were minimal and concentrated in the late seed filling stage (Fig. 3), while RUE did not change under Paclobutrazol but changed between experiments. However, there is room for changes in

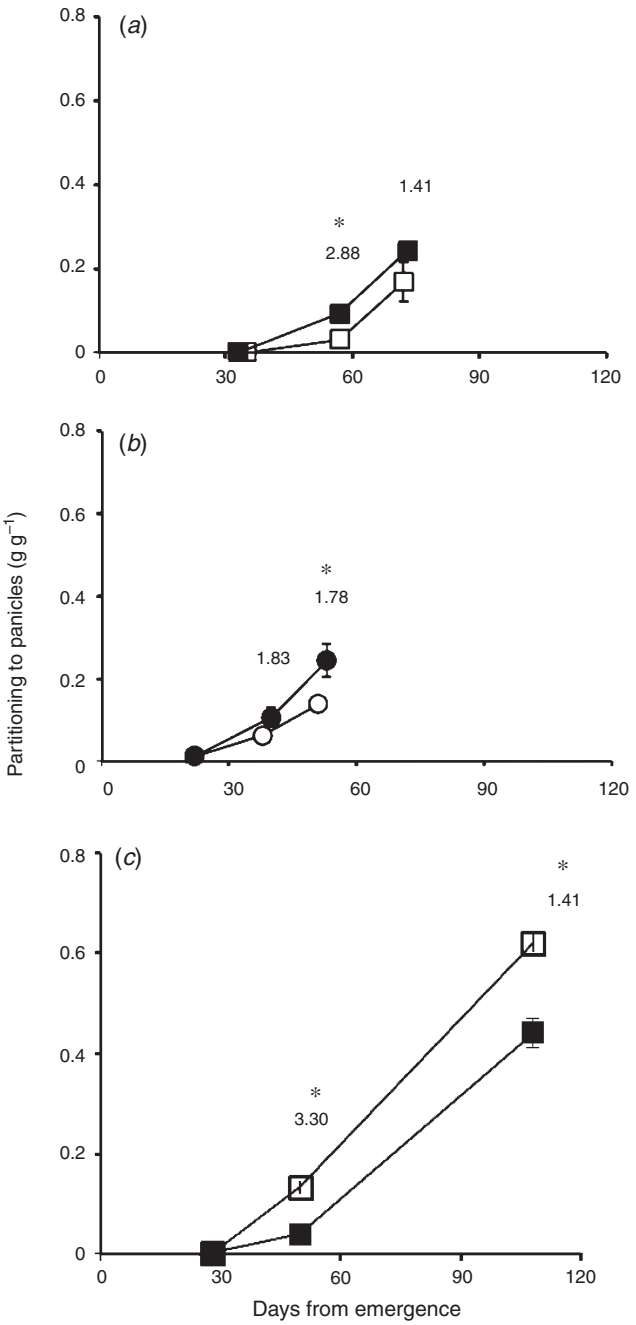

Fig. 5. Biomass partitioning to panicles as a function of days from emergence: (*a*) 2-Want in the two-genotype experiment; (*b*) NL-6 in the two-genotype experiment; (*c*) 2-Want in the one-genotype experiment. Samplings were conducted at VFB, first anthesis and end of anthesis in the two-genotype experiment, and at VFB, end of anthesis and physiological maturity during the one-genotype experiment. Values above the points are the Paclobutrazol : control ratios at each sampling date except for VFB. Asterisks indicate significant differences ($P < 0.1$ for the one-genotype and $P < 0.05$ for the two-genotype experiment). Data are averages ± 1 s.e.

photosynthetic rates during part of the cycle and in some specific positions (as those reported for wheat by Fischer *et al.* 1998). This notion is supported by a recent article (González *et al.* 2010) that reported a positive association between yield and photosynthesis during seed filling. Some possible interpretations of higher RUE values in the one-genotype experiment are that higher densities, which caused crops to reach faster and higher RIE values, made plants be within the second (higher) RUE stage most of the time (Ruiz and Bertero 2008). Another possibility is that higher temperatures during the evaluated period (an average of 23.5°C in the two-genotype experiment; 21.5°C in the one-genotype experiment [PAR values were similar at ~11.3 MJ m^2 d^{-1}]) reduced RUE by inhibiting photosynthesis; no experimental test of this last possibility has been conducted in quinoa and temperature differences were small. LAI, the main determinant of variation between genotypes and environments in RIE, was only marginally reduced (Fig. 2) but, as LAI values were high, they were not associated with a RIE reduction. A practical implication of these experiments for quinoa management is that, at high densities and reduced distances between rows, as those explored in the one-genotype experiment, the crop reaches a high LAI (7 in controls) and maintains maximum RIE (>0.95) during the critical period for yield determination (Bertero and Ruiz 2008). These RIE values were reached later and for a shorter period in the two-genotype experiment. Some RUE-related variables were modified by treatments: SPAD was increased for both experiments and genotypes (Fig. 4) while SLW values were significantly increased only for the two-genotype experiment. Reproductive growth changes were detected at different levels as an increase in seed number for a given crop biomass without concomitant reductions in seed weight (Table 2), increased reproductive partitioning (Fig. 5) or flower number (Fig. 6).

Comparisons between the genotypes of different height were limited because the two-genotype experiment was stopped before maturity, but reproductive partitioning was modified in a similar fashion for both genotypes up to the end of flowering. Attention should be paid to a short cycle cultivar like NL-6; however, evidence of source limitations (as reflected in an important photoassimilate retranslocation during seed filling) was detected in a parallel experiment (Mignone and Bertero 2007). Finally, for some of the variables analysed, differences were barely significant or near significance; the strong consistency of the results obtained for both experiments and genotypes, however, give credit to their biological significance.

All these results are consistent with those obtained from other species in which GA synthesis was manipulated using plant growth regulators, as for yield (i.e. Zhou and Xi 1993; Gill and Singh 1993; Senoo and Isoda 2003*a*, 2003*b*; Mohapatra and Mohapatra 2005), number and biomass of reproductive organs (Mohapatra and Mohapatra 2005), and increased SPAD values (Senoo and Isoda 2003*a*, 2003*b*; Mohapatra and Mohapatra 2005). Reduction in branch leaf area and branch biomass under Paclobutrazol treatment resembles the results from perennial ryegrass (*Lolium perenne* L.; Young *et al.* 1996), rice (Yim *et al.* 1997) and wheat (Guoping 1997), and differs from peanut (*Arachis hypogaea* L.) and *Brassica carinata* A. Br., where branch numbers were increased (Zhou and Xi 1993; Setia *et al.* 1995; Senoo and Isoda 2003*a*). The measured increase in stem substantiality, arising from a lower proportional reduction in stem biomass relative to height, is similar to the

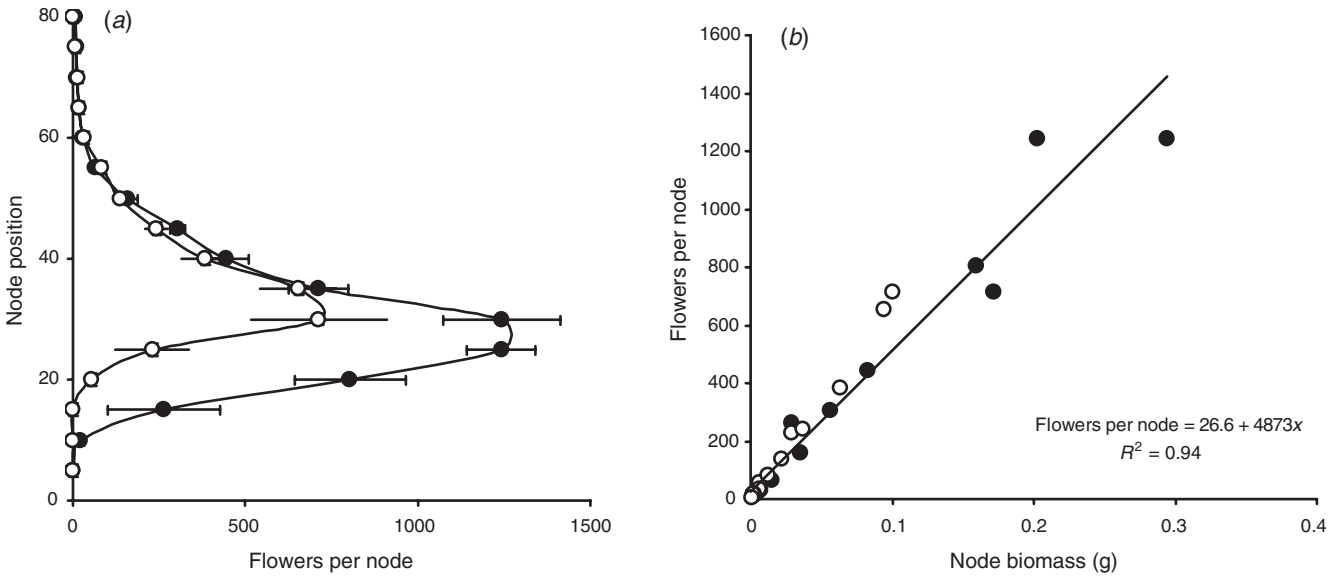

Fig. 6. (*a*) Fertile flowers profile across node position in the one-genotype experiment (2-Want) and (*b*) association between flowers per node and node biomass. Node positions are shown as seen in a real plant in (*a*) and data are averages ± 1 s.e.; data in (*b*) are averages.

results arising from rice (Yim *et al*. 1997), and changes in root growth have already been reported for soybean (*Glycine max* (L.) Merr.; Sankhla *et al*. 1985). Leaf longevity, as measured by SPAD values, was higher for treated plants, as in other species (Sankhla *et al*. 1985; Zhou and Xi 1993; Setia *et al*. 1995), but RIE was lower in the final part of the cycle (Fig. 3). An increased senescence (a faster decline in RIE values) could be attributed to the higher seed number, reflecting their higher N demand, particularly in a species like quinoa, with protein contents above cereal averages (Ruales and Nair 1992). The apparent contradiction between SPAD and RIE values can be explained by a hierarchical effect: even though leaves at a given position can have higher SPAD values under Paclobutrazol, the lower LAI under this treatment in the one-genotype experiment determined an earlier fall below critical LAI values. Of high potential interest is the manipulation of stress resistance as a consequence of lower GA content. This stress resistance was evaluated at lower hierarchies (e.g. antioxidant levels, electrolyte leakage, osmolite content or superoxide dismutase levels); however, effects at higher hierarchies, e.g.changes in root partitioning, were not reported. Surprisingly, these results are not mentioned in articles dealing with crop breeding for stressful environments and thus deserve more attention.

When compared with changes associated with the use of reduced height mutants, our results are similar to those seen in comparisons between standard height and semi-dwarfs in wheat (*Triticum aestivum* L.), rice or barley (*Hordeum vulgare* L.) (Ashraf *et al*. 1994; Slafer *et al*. 1994; Miralles and Slafer 1995; Miralles and Slafer 1997; Miralles *et al*. 1998; Swaminathan 2006). As a consequence of the way treatments were applied, changes in early vigour (Rebetzke and Richards 2000; Ellis *et al*. 2004) could not be explored.

One important concern is related to the meaning of the associations between changes in reproductive biomass *v.* those in stem height or biomass. Although there is a clear negative relationship expressed as more reproductive biomass for less stem height, the comparison between organ biomass changes is less clear; either in absolute or relative terms, the increase in panicle biomass is higher than the decrease (or even the lack of change) in stem biomass (Tables 1 and 2, Figs 1 and 5). The notion of reproductive organs as users of the carbohydrate leftovers of vegetative organs (e.g. the Sheldrake hydraulic model in Wardlaw 1990) seems too simplistic after so many years of research on sugar and hormone signals, their interactions and metabolism regulation (i.e. Gibson 2004; Razem *et al*. 2006; Rolland *et al*. 2006).

All previous results can be summarised stating that a higher yield could be obtained in quinoa if reproductive partitioning was increased (the evaluation of growth regulators at a commercial scale was beyond the aim of this article, but could be considered as a management option in some casese.g. in non-organic production systems). Manipulation of the GA metabolism appears to be a valid strategy; in these experiments, it was achieved without a reduction in capacity for capturing aerial resources (radiation) or changes in radiation utilisation efficiency, and even with an increase in capacity for capturing soil resources. There are methods available to carry this out (e.g. a search for natural mutants, mutation induction [González *et al*. 2001 for quinoa] or transgenics) and there have been instances where plant stature within a crop species has been transformed using genes from other species (Peng *et al*.1999). Increasing yield potential could imply many advantages for quinoa's future. Limitations on its increase led some crops to be abandoned or marginalised during the 20th century (Evans 1993) but quinoa could be a very good candidate in the search for high quality plant protein sources (Linnemann and Dijkstra 2002; Aiking 2011) considering current and near future food demands. On the other hand, the characteristics of the current international quinoa market (mostly organic, not allowing the use of

genetically transformed crops) must be considered when deciding the best way to carry this out.

Acknowledgements

To Ricardo Ruiz for his assistance with statistical analyses. This work was funded by a grant from the Argentine Ministry of Science (PICT 08–13935).

References

Aiking H (2011) Future protein supply. *Trends in Food Science & Technology* **22**, 112–120. doi:10.1016/j.eja.2007.07.002

Ashraf M, Akbar M, Salim M (1994) Genetic improvement in physiological traits of rice yield. In 'Genetic improvement of field crops'. (Ed. GA Slafer) pp. 413–435. (University of Buenos Aires: Buenos Aires)

Bertero HD (2001) Variabilidad intraespecífica en variables asociadas a la generación de biomasa. Asociación con el origen de los cultivares. In 'Memorias primer taller internacional en quinua: recursos genéticos y sistemas de producción'. (Eds SE Jacobsen, A Mujica, Z Portillo) pp. 265–272. (Universidad Nacional Agraria La Molina, Centro Internacional de la Papa, Universidad Nacional del Altiplano: Lima)

Bertero HD, Ruiz RA (2008) Determination of seed number in sea level quinoa (*Chenopodium quinoa* Willd.) cultivars. *European Journal of Agronomy* **28**, 186–194. doi:10.1016/j.eja.2007.07.002

Bertero HD, Ruiz RA (2010) Reproductive partitioning in sea level quinoa (*Chenopodium quinoa* Willd.) cultivars. *Field Crops Research* **118**, 94–101. doi:10.1016/j.fcr.2010.04.009

Bertero HD, Medan D, Hall AJ (1996) Changes in apical morphology during floral initiation and reproductive development in quinoa (*Chenopodium quinoa* Willd.*) Annals of Botany* **78**, 317–324. doi:10.1006/anbo.1996.0126

Bertero HD, King RW, Hall AJ (1999) Modelling photoperiod and temperature responses in quinoa (*Chenopodium quinoa* Willd.). *Field Crops Research* **63**, 19–34. doi:10.1016/S0378-4290(99)00024-6

Bertero HD, Píriz R, Aiscorbe D, Benech Arnold R (2001) Effect of ABA (fluoridone) and GA (Paclobutrazol) synthesis inhibitors on germination responses of developing quinoa (*Chenopodium quinoa* Willd.) seeds. In 'Proceedings of the 9th international symposium on pre-harvest sprouting in cereals, 24–28 June 2001, Kruger National Park, South Africa'.

Bertero HD, De la Vega AJ, Correa G, Jacobsen SE, Mujica A (2004) Genotype and genotype-by-environment interaction effects for grain yield and grain size of quinoa (*Chenopodium quinoa* Willd.) as revealed by pattern analysis of international multi-environment trials. *Field Crops Research* **89**, 299–318. doi:10.1016/j.fcr.2004.02.006

Berti M, Wilckens R, Hevia F, Serri H, Vidal I, Mendez C (2000) Fertilización nitrogenada en quinoa (*Chenopodium quinoa* Willd.). *Ciencia e Investigación Agraria* **27**, 81–90.

Bhargava A, Shukla S, Ohri D (2006) *Chenopodium quinoa* – an Indian perspective. *Industrial Crops and Products* **23**, 73–87. doi:10.1016/j.indcrop.2005.04.002

Borlaug NE (2007) Sixty-two years of fighting hunger: personal recollections. *Euphytica* **157**, 287–297. doi:10.1007/s10681-007-9480-9

Chandler PM, Robertson M (1999) Gibberellin dose-response curves and the characterization of dwarf mutants of barley. *Plant Physiology* **120**, 623–632. doi:10.1104/pp.120.2.623

Charles-Edwards DA, Lawn RJ (1984) Light interception by grain legume row crops. *Plant, Cell & Environment* **7**, 241–251.

Christensen SA, Pratt DB, Pratt C, Nelson PT, Stevens MR, Jellen EN, Coleman CE, Fairbanks DJ, Bonifacio A, Maughan PJ (2007) Assessment of genetic diversity in the USDA and CIP-FAO international nursery collections of quinoa (*Chenopodium quinoa* Willd.) using microsatellite markers. *Plant Genetic Resources: Characterization and Utilization* **5**, 82–95. doi:10.1017/S1479262107672293

Ellis MH, Rebetzke GJ, Chandler P, Bonnett D, Spielmeyer W, Richards RA (2004) The effect of different height reducing genes on the early growth of wheat. *Functional Plant Biology* **31**, 583–589. doi:10.1071/FP03207

Evans LT (1993) 'Crop evolution, adaptation and yield'. (Cambridge University Press: Cambridge, UK)

Fischer RA (1985) Number of kernels in wheat crops and the influence of solar radiation and temperature. *The Journal of Agricultural Science* **105**, 447–461. doi:10.1017/S0021859600056495

Fischer RA, Rees D, Sayre KD, Lu ZM, Condon GA, Saavedra LA (1998) Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopies. *Crop Science* **38**, 1467–1475. doi:10.2135/cropsci1998.0011183X003800060011x

Geerts S, Raes D, Garcia M, Taboada C, Miranda R, Cusicanqui J, Mhizha T, Vacher J (2009) Modeling the potential for closing quinoa yield gaps under varying water availability in the Bolivian Altiplano. *Agricultural Water Management* **96**, 1652–1658. doi:10.1016/j.agwat.2009.06.020

Gibson SI (2004) Sugar and phytohormone response pathways: navigating a signalling network. *Journal of Experimental Botany* **55**, 253–264. doi:10.1093/jxb/erh048

Gill DS, Singh OS (1993) Modification of growth, yield and lodging response of lentil to phosphorus by paclobutrazol. *The Annals of Applied Biology* **123**, 667–671. doi:10.1111/j.1744-7348.1993.tb04936.x

González JJ, de la Cruz Torres I, Rublio A, Garcia JM (2001) Situación actual del estudio de quínoa en México. In 'Proceedings of the X congreso internacional de cultivos Andinos, 04–07 July 2001, Jujuy, Argentina'. (CD-ROM)

González FG, Slafer GA, Miralles DJ (2003) Grain and floret number in response to photoperiod during stem elongation in fully and slightly vernalized wheats. *Field Crops Research* **81**, 17–27. doi:10.1016/S0378-4290(02)00195-8

González JA, Bruno M, Valoy M, Prado FE (2010) Genotypic variation of gas exchange parameters and leaf stable carbon and nitrogen isotopes in ten quinoa cultivars grown under drought. *Journal of Agronomy & Crop Science* doi:10.1111/j.1439-037X.2010.00466.x

Gregory PJ (2004) Resource capture by root networks. In 'Resource capture by crops. Proceedings of the 52nd Easter School'. (Eds JL Monteith, RK Scott, MH Unsworth) pp. 77–97. (Nottingham University Press: Nottingham, UK)

Guoping Z (1997) Gibberellic $acid_3$ modifies some growth physiologic effects of Paclobutrazol (PP_{333}) on wheat. *Journal of Plant Growth Regulation* **16**, 21–25. doi:10.1007/PL00006970

Hall AJ, Rebella CM, Ghersa CM, Culot JP (1992) Field-crop systems of the Pampas. In 'Ecosystems of the world 18. Field crops ecosystems'. (Ed. CJ Pearson) pp. 413–450. (Elsevier Science Publishers: Amsterdam)

Hedden P (2003) The genes of the Green Revolution. *Trends in Genetics* **19**, 5–9. doi:10.1016/S0168-9525(02)00009-4

Jacobsen SE, Mujica A (2002) Genetic resources and breeding of the Andean grain crop quinoa (*Chenopodium quinoa* Willd.). *Plant Genetic Resources Newsletter (Rome, Italy)* **130**, 54–61.

Jacobsen SE, Stolen O (1993) Quinoa. Morphology, phenology and prospects for its production as a new crop in Europe. *European Journal of Agronomy* **2**, 19–29.

Jacobsen SE, Jorgensen I, Stolen O (1994) Cultivation of quinoa (*Chenopodium quinoa*) under temperate climatic conditions in Denmark. *The Journal of Agricultural Science* **122**, 47–52. doi:10.1017/S0021859600065783

Jandel TBLCURVE (1992) 'TableCurve 3.0. Curve fitting software'. (Jandel Scientific: Corte Madera, CA)

Köppen W (1931) 'Grundriss der Klimakunde Vol. 12'. (Walter de Gruyter: Berlin)

Lebonvallet S (2008) Implantation du quinoa et simulation de sa culture sur l'Altiplano Bolivien. PhD Thesis, Institut des Sciences et Industries du Vivant et de l'Environnement (Agro Paris Tech), Paris.

Linnemann AR, Dijkstra DS (2002) Towards sustainable production of protein-rich foods: appraisal of eight crops for Western Europe. PART I. Analysis of the primary links of the production chain. *Critical Reviews in Food Science and Nutrition* **42**, 377–401. doi:10.1080/20024091054193

Lu Z, Radin JW, Turcotte EL, Percy R, Zeiger E (1994) High yield in advances lines of Pima cotton are associated with higher stomatal conductance, reduced leaf area and lower leaf temperature. *Physiologia Plantarum* **92**, 266–272. doi:10.1111/j.1399-3054.1994.tb05336.x

Mason SL, Stevens MR, Jellen EN, Bonifacio A, Fairbanks DJ, Coleman CE, McCarty RR, Rasmussen AG, Maughan PJ (2005) Development and use of microsatellite markers for germplasm characterization in quinoa (*Chenopodium quinoa* Willd.). *Crop Science* **45**, 1618–1630. doi:10.2135/cropsci2004.0295

Mastebroek HD, Van Loo EN, Doestra O (2002) Combining ability for seed yield traits of *Chenopodium quinoa* breeding lines. *Euphytica* **125**, 427–432. doi:10.1023/A:1016030129541

Mignone CM, Bertero HD (2007) Identificación del período crítico de determinación del rendimiento en quínoas de nivel del mar. In 'Proceedings of the congreso internacional de la quinua, 23–26 October 2007, Iquique, Chile'. (CD-ROM)

Minolta (1989) 'Chlorophyll meter SPAD-501. Instruction manual'. (Minolta Co. Ltd., Radiometric Instruments Operations: Osaka, Japan)

Miralles DJ, Slafer GA (1995) Yield, biomass and yield components in dwarf, semi-dwarf and tall isogenic lines of spring wheat under recommended and late sowing dates. *Plant Breeding* **114**, 392–396. doi:10.1111/j.1439-0523.1995.tb00818.x

Miralles DJ, Slafer GA (1997) Radiation interception and radiation use efficiency of near-isogenic wheat lines with different heights. *Euphytica* **97**, 201–208. doi:10.1023/A:1003061706059

Miralles DJ, Slafer GA (2007) Sink limitations to yield of wheat. How could it be reduced? *The Journal of Agricultural Science* **145**, 139–149. doi:10.1017/S0021859607006752

Miralles DJ, Katz SD, Colloca A, Slafer GA (1998) Floret development in near isogenic wheat lines differing in plant height. *Field Crops Research* **59**, 21–30. doi:10.1016/S0378-4290(98)00103-8

Mohapatra PK, Mohapatra R (2005) Sink–source relationships and yield potential of rice: effect of ethylene on grain filling of late-flowering spikelets. In 'Rice is life: scientific perspectives for the 21st century. Proceedings of the world rice research conference held in Tokyo and Tsukuba, Japan. 4–7 November 2004'. (Ed. K Toriyama, KL Heong, B Hardy). (International Rice Research Institute: Los Baños, The Philippines)

Passioura JB (1981) The interaction between the physiology and the breeding of wheat. In 'Wheat science – today and tomorrow'. (Eds LT Evans, WJ Peacock) pp. 191–201. (Cambridge University Press: Cambridge, UK)

Peng J, Richards DE, Hartley NM, Murphy GP, Devos KM, Flintham JE, Beales J, Fish LJ, Wolrand AJ, Pelica F, Sudhakar D, Christou P, Sbape JW, Gale MD, Harberd NP (1999) "Green Revolution" genes encode mutant gibberellin response modulators. *Nature* **400**, 256–261. doi:10.1038/22307

Raffaillac JP, Barrientos E, Mamaní F, Rodríguez JP (2007) Una red agronómica de la quínoa en el Altiplano Boliviano. In 'Proceedings of the congreso internacional de la quínoa, 23–26 October 2007, Iquique, Chile'. (CD-ROM)

Razem FA, Baron K, Hill RD (2006) Turning on giberellin and abscisic acid signaling. *Current Opinion in Plant Biology* **9**, 454–459. doi:10.1016/j.pbi.2006.07.007

Rebetzke GJ, Richards RA (2000) Gibberellic acid-sensitive dwarfing genes reduce plant height to increase kernel number and grain yield of wheat. *Australian Journal of Agricultural Research* **51**, 235–245. doi:10.1071/AR99043

Reynolds M, Foulkes MJ, Slafer GA, Berry P, Parry MAJ, Snape JW, Angus WJ (2009) Raising yield potential of wheat. *Journal of Experimental Botany* **60**, 1899–1918. doi:10.1093/jxb/erp016

Rolland F, Baena-González E, Sheen J (2006) Sugar sensing and signaling in plants: conserved and novel mechanisms. *Annual Review of Plant Biology* **57**, 675–709. doi:10.1146/annurev.arplant.57.032905.105441

Ruales J, Nair BN (1992) Nutritional quality of the protein in quinoa (*Chenopodium quinoa* Willd.) seeds. *Plant Foods for Human Nutrition (Dordrecht, Netherlands)* **42**, 1–11. doi:10.1007/BF02196067

Ruiz RA, Bertero HD (2008) Light interception and radiation use efficiency in temperate quinoa (*Chenopodium quinoa* Willd.) cultivars. *European Journal of Agronomy* **29**, 144–152. doi:10.1016/j.eja.2008.05.003

Sakamoto T, Matsuoka M (2004) Generating high-yielding varieties by genetic manipulation of plant architecture. *Current Opinion in Biotechnology* **15**, 144–147. doi:10.1016/j.copbio.2004.02.003

Sankhla N, Davis TD, Upadhyaya A, Sankhla D, Walser RH, Smith BN (1985) Growth and metabolism of soybean as affected by Paclobutrazol. *Plant & Cell Physiology* **26**, 913–921.

Sarkar S, Perras MR, Falk DE, Zhang R, Pharis RP, Fletcher A (2004) Relationship between gibberellins, height, and stress tolerance in barley (*Hordeum vulgare* L.) seedlings. *Plant Growth Regulation* **42**, 125–135. doi:10.1023/B:GROW.0000017492.56792.64

Schulte auf'm Erley G, Kaul G, Kruse M, Aufhammer W (2005) Yield and nitrogen utilization efficiency of the pseudocereals amaranth, quinoa and buckwheat under different nitrogen fertilization. *European Journal of Agronomy* **22**, 95–100.

Senoo S, Isoda A (2003*a*) Effects of Paclobutrazol on dry matter distribution and yield in peanut. *Plant Production Science* **6**, 90–94. doi:10.1626/pps.6.90

Senoo S, Isoda A (2003*b*) Effects of Paclobutrazol on podding and photosynthetic characteristics in peanut. *Plant Production Science* **6**, 190–194. doi:10.1626/pps.6.190

Setia RC, Brathal G, Setia N (1995) Influence of Paclobutrazol on growth and yield of *Brassica carinata* A. Br. *Plant Growth Regulation* **16**, 121–127. doi:10.1007/BF00029532

Silverstone LA, Sun T (2000) Gibberellins and the green revolution. *Trends in Plant Science* **5**, 1–2. doi:10.1016/S1360-1385(99)01516-2

Slafer GA, Savin R (2006) Physiology of crop yield. In 'Encyclopedia of plant and crop science'. (Ed. RE Goodman) pp. 1–4. (Taylor and Francis: New York)

Slafer GA, Satorre EH, Andrade FH (1994) Increases in grain yield in bread wheat from breeding and associated physiological changes. In 'Genetic improvement of field crops'. (Ed. GA Slafer) pp. 1–54. (University of Buenos Aires: Buenos Aires)

Slafer GA, González FG, Kantolic AG, Whitechurch EM, Abeledo GL, Miralles DJ, Savin R (2006) Grain number determination in major grain crops. In 'Handbook of seed science and technology'. (Ed. SB Amarjit) pp. 95–123. (Food Products Press: New York)

Spehar C, De Barros Santos LR (2005) Agronomic performance of quinoa selected in the Brazilian Savannah. *Pesquisa Agropecuaria Brasileira* **40**, 609–612. doi:10.1590/S0100-204X2005000600012

Steel RGD, Torrie JH (1960) 'Principles and procedures of statistics, with special reference to the biological sciences'. (McGraw Hill: New York)

Steinbach HS, Benech-Arnold RL, Sanchez RA (1997) Hormonal regulation of dormancy in developing sorghum seeds. *Plant Physiology* **113**, 149–154.

Swaminathan MS (2006) An evergreen revolution. *Crop Science* **46**, 2293–2303. doi:10.2135/cropsci2006.9999

Wardlaw IF (1990) The control of carbon partitioning in plants. *New Phytologist* **116**, 341–381. doi:10.1111/j.1469-8137.1990.tb00524.x

Yim K, Kwon YW, Bayer DE (1997) Growth responses and allocation of assimilates of rice seedlings by Paclobutrazol and gibberellin treatment. *Journal of Plant Growth Regulation* **16**, 35–41. doi:10.1007/PL00006972

Young WC, Chilcote DO, Youngberg HW (1996) Seed yield response of perennial ryegrass to low rates of Paclobutrazol. *Agronomy Journal* **88**, 951–955. doi:10.2134/agronj1996.00021962003600060018x

Zhou WJ, Xi HF (1993) Effects of mixtalol and Paclobutrazol on photosynthesis and yield of rape (*Brassica napus*). *Journal of Plant Growth Regulation* **12**, 157–161. doi:10.1007/BF00189647

Manuscript received 13 August 2010, accepted 18 March 2011