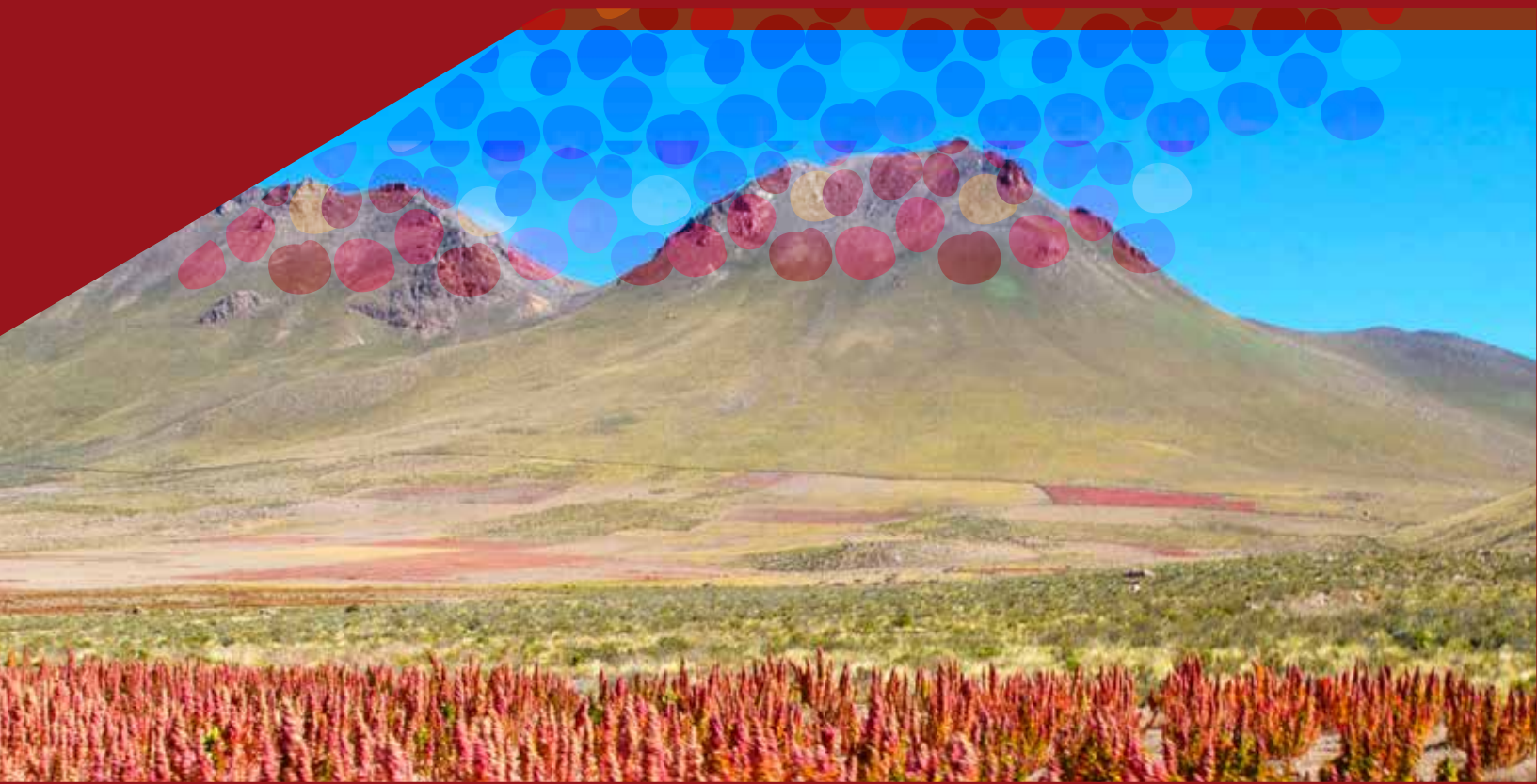# Section 2

Agronomic and Ecological Aspects

CHAPTER: 2.1

Environmental control of development

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Abstract

The duration of development stages is one of the key determining factors of the adaptation of a species, conditioning adjustment to the growing season, the distribution of photoassimilates, water and nutrient absorption and lastly, the yield achieved. Four factors affect the progression of quinoa development: temperature, photoperiod, hydric status and radiation; the last two variables have been barely analysed in terms of its impact on development and there is documented genetic variability regarding sensitivity for the first two. Temperature is the environmental factor with the highest relative impact on duration of development. Sensitivity to temperature was evaluated for the time to visible floral buds and leaf appearance rate; variability for both variables is associated with characteristics of the original environments, being higher in environments with limited water and low temperatures, indicating that adaptation to short growing seasons is expressed through higher earlyness, partly offset by a higher leaf appearance rate, whilst most late genotypes are found in more humid and warmer environments. Quinoa behaves as a short-day plant and the higher photoperiod sensitivity is expressed in valley genotypes, grown between Argentina and Colombia. At the opposite extreme, those in the southern Altiplano, including Bolivia and north-western Argentina, together with Chilean sea-level genotypes, show little or no sensitivity to this factor in respect of time to flowering. Photoperiod sensitivity is manifested from the early stages of development up to advanced stages of grain filling; there is also variability in the duration of the sensitive period.

1. Environmental control of development and intraspecific variability in sensitivity to environmental factors

Optimizing productivity implies adjusting ontogenesis (the sequence of development stages) in such a way that the crop explores the best environmental conditions (e.g.: favourable temperatures or proper availability of water) and when the unfavourable conditions are unavoidable, minimizing their coincidence with the more vulnerable stages of the crop. Therefore and unsurprisingly, phenology (the influence of environment on ontogenesis) is a most important factor in determining genotype adaptation (Lawn e Imrie, 1994). Ontogenesis can be adapted to the environment through two ways: by breeding through manipulation of the genes that cause sensitivity to the environment or through management of sowing dates and sites (Richards, 1989).

The previous paragraph stresses the importance of variation in duration of development as a key aspect of the adaptation of crops to the environment (Evans, 1993), and this is also valid for quinoa. Knowledge of the environmental factors that regulate duration of development of crops constitutes a key element for predicting their agronomical behaviour and yield in an area of known climate regime (Miralles et al., 2001). The most relevant environmental factors in controlling crop development are temperature and photoperiod, and their relative importance depends on the sensitivity of the plant in each phase (Hall, 2001).

2. Importance of knowledge about development control in quinoa

In a crop cycle, we can distinguish between separate periods characterized by the initiation of specific organs and the pattern of distribution of photo-assimilates. These periods are known as phases or stages, where a phase can be defined as the period spanning two clearly-identifiable development events. These events are often observable at the meristematic level (in the apical or axillary meristem, depending on the crop) and involve changes in organ generation and photo-assimilate distribution. The most important events in the life cycle of an annual crop are: emergence, floral initiation, flowering (usually identified as the date of anthesis, i.e. the appearance of anthers) and physiological maturity. These events are used to determine three major development phases: (i) vegetative phase (between emergence and floral initiation), (ii) reproductive phase (between floral initiation and flowering) and (iii) maturity or grain-filling phase (between flowering and physiological maturity) (Ritchie, 1991). These phases can also be broken down into sub-phases.

Since certain scales used to characterise crop development are based on phenomena such as the appearance of leaves, while others are based on changes in the activity level of apical meristems, a distinction has been made between phasic and morphological development (Ritchie, 1991). The first involves changes in growth stages (succession of phases) and the second refers to the onset and end of the generation of organs within the life cycle of a plant (e.g. the time between the appearance of two leaves).

The duration of the cycle or specific stages of development is one of the most important variables to explain genotype-by-environment interaction patterns for yield (Bertero *et al.*, 2004) or genetic variability in quinoa germplasm collections (Ortiz et al., 1998, Rojas 2003, Curti *et al.*, 2012). The BLUPS - estimators of genotypic effects - for sowing-maturity duration showed a strong positive association with yield (R2=0.88) and total above-ground biomass (R2=0.87) and negative association with the harvest index (HI, proportion of above-ground biomass in grain, R2=0.7) in a network of experiments conducted in the inter-tropical zone (Bertero *et al.*,

2004). When this analysis was conducted by environmental group (environments that have a similar impact on the behaviour of genotypes in terms of yield), the duration of development showed higher variation and better association with yield components in colder environments, while duration were shorter with less variation in high temperature and short-day tropical environments (e.g. Brasilia, Brasil and Gia Loc, Vietnam, Bertero et al., 2004). The genetic component (genotype/ genotype-by-environment, G/GxA) have a relatively high weight for duration of development (1.69) vs. 0.25, 0.89, 0.44 and 0.0026 for yield, grain weight, biomass and Harvest Index respectively, indicating better hereditability of these traits and the possibility of responding to selection (Bertero et al, 2004); with even higher weights for evaluations made in more delimited geographical regions such as North-Western Argentina (R. Curti, com. pers.). On the other hand, the time to floral initiation, 50% a anthesis and maturity have the highest weight in explaining genetic variance and discrimination on the first axis of the main components analysis (which explains 30% of the total systematic variance) for a collection of 1,512 accessions in Bolivia, explaining 78, 87.5 and 56% of the variance, respectively (Rojas, 2003). Similar results were obtained for the Peruvian (Ortiz *et al.,* 1988) and Argentinian collection (Curti *et al.*, 2012). An interesting aspect of this variability is the tenuous association found between phase durations, which suggests that it could be independently manipulated (Risi and Galwey, 1989).

The duration and sequence of developmental phases are the most relevant parameters in controlling the time-dependent dynamics of leaf area generation. For instance, the number of leaves on the main stem is determined at anthesis (Bertero *et al.*, 1999a, Ruiz and Bertero, 2008), the leaf area on the main stem around anthesis and those on branches during the flowering period (Ruiz and Bertero, 2008). While there is a strong coordination between phasic development and morphology, there is no unique relationship, with genotypes that can continue generating leaf area for a longer period after anthesis, with a lesser relative reduction of the leaf area compared with genotypes of similar precocity, and of interest regarding genotypes selection for short crop seasons (Ruíz and Bertero, 2008). The association between the duration of development

phases and the start and interruption date (from lowest to highest) in photo-assimilate distribution to quinoa panicle and stems was quantified (Bertero and Ruiz, 2010). Like other crops (e.g. González *et al.*, 2003), active stem growth starts earlier than that of panicles in quinoa, possibly conditioning the competition between these two organs. This information was subsequently used to define the moments for applying growth regulators to enhance photo-assimilate distribution and yield (Gómez *et al.*, 2011). The distinction between developmental stages allowed the identification of the flowering period (between 1st anthesis and end of flowering) as the most important in determining the number of grains in Chilean quinoa genotypes (Bertero and Ruiz, 2008).

3. Development scales

LDevelopment scales are important for quantifying the effect of environment, the association of development with the generation of yield or crop management (identification of periods of tolerance to frost or drought, application of herbicides or periods of tolerance to weeds or application of fertilisers). There are various scales to study quinoa development; and a few are described below. Flores (1977) defined five sub-periods between sowing and physiological maturity separated by four events: emergence, appearance of the first pair of true leaves (marking the onset of leaf area generation), appearance of inflorescence and anthesis. The duration of the second sub-period (emergence-appearance of first pair of leaves) has an average duration of approximately 160 °Cd (base temperature (Tb) = 2 °C) and is used to model the appearance of leaves (Bertero, 2001a). The length of this sub-period shows a close association with early vigour (ability to cover the ground and quickly reach a high growth rate), important for genotype selection (Bertero, 2001b and unpublished data) (Figure 1).

Jacobsen and Stölen (1993) proposed a development scale involving 23 stages, the most relevant events of which are panicle formation, anthesis, floral dehiscence, fruit set and maturity. Unlike other scales, this one includes combinations of development and growth aspects (e.g. the time when a specific panicle width is reached). Bertero *et al.* (1996), based on apical meristem scale observations using
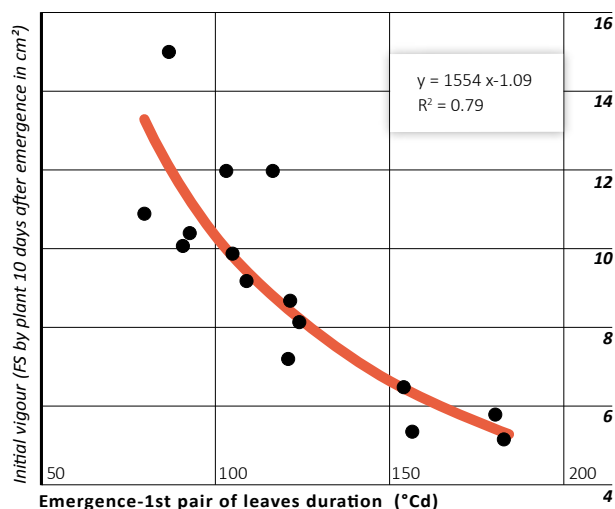

Figure 1: Association between the duration of the emergence-appearance of the first pair of green leaves (in °Cd, bT = 2 °C) stage and initial vigour, measured as the leaf area (FS) by plant 10 days after emergence, for 15 genotypes grown in temperate climates.
Source: Bertero, unpublished data.

stereomicroscope and scanning electron microscopy, generated a development scale that distinguishes between amarantiform (7 stages) and glomerulate type (8 stages) panicles.

When the proposed scores were analyzed using a thermal time scale (Tb= 3.7 and 6.4 °C for the amarantiform and glomerulate scale respectively), they were distributed at regular intervals between stages. In a subsequent analysis Bertero *et al.* (1999a) proposed a division into four sub-periods for the emergence-anthesis period named: Vg (between emergence and floral initiation), Rp1 (between floral initiation and the end of leaf primordia initiation in the apical meristem), Rp2 (between the end of Rp1 and differentiation of stigmatic branches in the apical meristem (G7 on the scale of Bertero et al., 1996)), and Rp3, between the end of Rp2 and anthesis. More than 50% of total leaf primordia were initiated during Rp1. Mujica *et al.* (2001) proposed a scale based on 12 stages for the American and European Quinoa Trial. Lastly, Bertero and Ruiz (2008) used a scale based on external characters (non invasive) and distinguished four phases: emergence-visible floral bud (VFB), visible floral bud-anthesis, anthesis-end of flowering and end of flowering-maturity for the identification of the critical period for yield generation. Variations

in a few aspects of these scales were used by García Cárdenas (2003) and Geerts (2008). The lack of precision in the description of the events of the various scales, or the lack of availability of information in easily accessible publications, poses difficulty in establishing analogies between scales (e.g. for determining whether, for example, the stages inflorescence appearance (Flores, 1977), panicle formation (Jacobsen and Stölen, 1993) and VFB (Bertero and Ruiz, 2008) correspond to the same event).

4. Response of phasic development to environmental factors

Quinoa is a plant with a short-day quantitative response to photoperiod (Sívori, 1945, Fuller, 1949)); this implies that duration of some development stages is longer when plants are grown during longer days, but reach flowering in all the range of photoperiods explored. Furthermore, the duration of development is sensitive to temperature and these two factors interact to determine its duration under field conditions (Bertero et al., 1999b). This chapter analyzes existing knowledge for all assessed stages, using the Bertero and Ruiz scale (2008), due to its greater simplicity. Existing knowledge for the sowing-emergence period is analyzed in detail
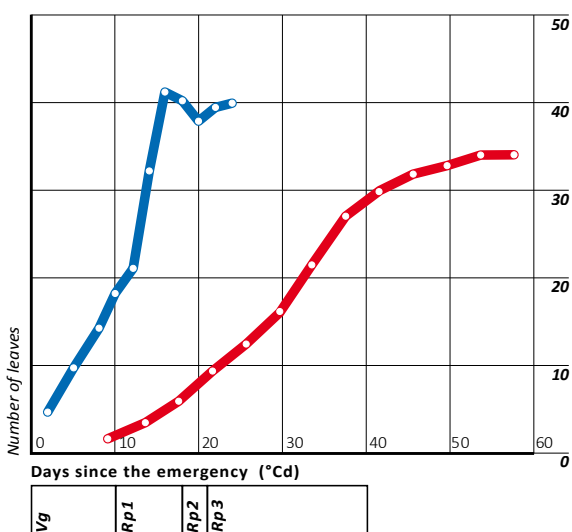

Figure 2: Association between the duration of sub-periods in development (Bertero et al., 1999a) and leaf initiation and appearance (cv. Kanckcolla, Peruvian Altiplano). The pictures correspond to the following stages: G0 (vegetative), G1 (early reproductive), G3 (start of differentiation of the terminal flower) and G7 (start of differentiation of stigmatic branches) for a glomerulate type panicle. Adapted from Bertero et al. (1996) and Bertero et al. (1999a)

in chapter 2.6, hence the treatment of only a few aspects in this chapter.

The duration of the photoperiod-sensitive periods were analyzed in a few genotypes. The juvenile phase (period after emergence when the crop is not in condition to allow the detection and response to changes in photoperiod) shows variability between genotypes and this is associated with the latitude of origin of the genotypes (longer duration at lower latitudes), varying between 0 and 9 days for plants growing under a temperature of 21°C (Bertero et al., 1999b). This is in contrasted with an estimate of 16 days at 16°C for variety Real according to Christiansen et al. (2010).

Expressed by a common base temperature of 3°C (Bertero, 2003) this would imply a duration of 208°Cd, against a maximum of 162° Cd estimated by the Colombian variety Nariño, and by ~ 80 °Cd, according to the equation proposed by Bertero (2003) which links the duration of the juvenile phase with the latitude of origin of a variety. It's possible that this difference is due to the response variables used, floral initiation in the first and anthesis in the second work. The end of the period of sensitivity to photoperiod is less known. Christiansen et al. (2010) found variation in the duration of grain filling as a consequence of plant transfers between photoperiods, but the sensitivity period to transfers ends ~ 25 days after sowing (Figure 2 of the article quoted for the Real variety), before the start of anthesis. In other experiments (Bertero et al., 1999a, Píriz et al., 2002), quinoa displayed the capacity to respond to photoperiod changes effected after flowering, and this period appears to stretch at least between 10 and 15 days after anthesis, as observed upon analysing the impact of plants transfer between photoperiods after anthesis on grain filling rate.

A first look at genotypic variation in sensitivity to the environment is shown by Figure 4. It shows the response of development rate (sowing-maturity days -1) to temperature for four genotypic groups identified based on their GxA interaction patterns for yield (Bertero et al., 2004). Rhis figure includes results of field experiments carried out in tropical environments, but the average photoperiod showed little variation between environments (~1 h), so that much of the presented variation is attributable to the effect of temperature.

4.1 Sowing-emergence

Jacobsen and Bach (1998) studied the influence of temperature on germination rate in a Chilean origin variety selected in Denmark. They identified a Tb of 3 °C and an optimum temperature (associated with the maximum development rate) of between 30 and 35 °C. The seeds achieve 100% germination within 30 ° Cd (Thermal time units), which implies that under high temperatures and adequate humidity all the seeds will germinate within approximately one day. Bois et al. (2006), studied the variability in response to temperature in 10 Bolivian cultivars and detected variation in Tb and time of up to 50% of the germination, Tb varied between 0.24 and -1.97 °C, several degrees lower than the figure reported by Jacobsen and Bach (1998). Interestingly, lower temperatures seem to characterize cultivars originally from colder and drier climates (example, the Bolivian Altiplano compared with the south of Chile).

The variation between cultivars is more obvious when seeds were incubated at 2 °C, in that environment, the time to 50% germination (T50) varied between 45 and 67 hrs. Quinoa can be grown at the end of winter in southern Bolivia (Joffre and Acho, 2008) that is why the impact of this variation on the crop's ability to adapt to lower temperatures deserves to be explored.
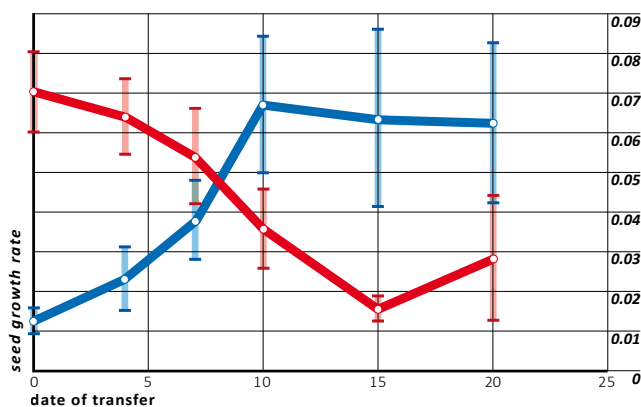
Higher Tb values were obtained in a comparison of four Bolivian quinoa genotypes (Boero *et al.*, 2000) but in this case the same ratios were estimated using polynomial type relationships, unlike the linear relationships used in the usual approximations. An example of this variability is observed in Figure 5,
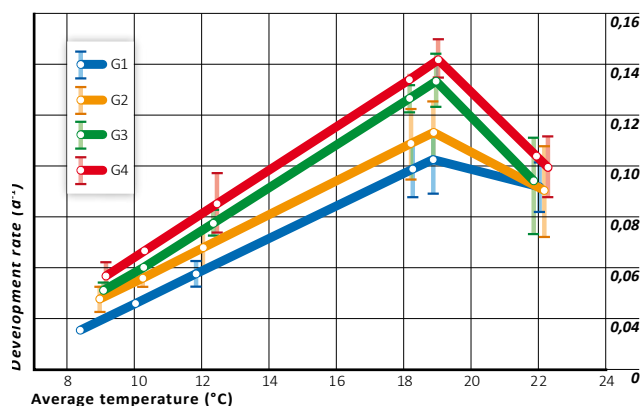

Figure 4: Association between the average development rate (d-1) measured by genotypic group for the sowing - maturity period in five cropping environments included in the American and European Quinoa Trial (Mujica *et al.*, 2001). The symbols correspond to: genotypes natives to the Inter-Andean Valleys (G1), Peruvian Altiplano (G2), Bolivian Altiplano (G3) and Sea level (central and southern part of Chile, G4) according to Bertero *et al.* (2004).
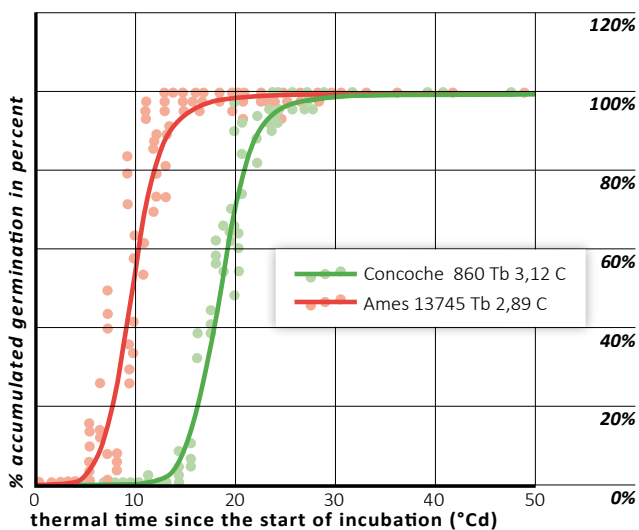

Figure 3: Effect of transfers between photoperiods (from 16 to 10.25 (◆) and from 10.25 to 16 hrs (■) a regular intervals from anthesis, on the rate of increase in grain volume (mm d^{-1}) measured as changes in the maximum diameter of seeds. The plants grew under a temperature of 25 °C in a greenhouse with controlled temperature and photoperiod and natural radiation. Blanca de Junín cultivar (Inter-Andean valleys of Peru, more details on this experimental procedure in Bertero *et al.*, 1999a)

Figure 5: Progression in accumulated germination as a function of thermal time since the start of incubation (°Cd, see base temperature values in the diagram) for two contrasting response genotypes: Concoche, native of Valdivia, Chile, and AMES 13745, native of Bolivia (Christensen *et al.*, 2007). The data corresponds to seeds incubated at 6, 11, 15 and 19 °C.
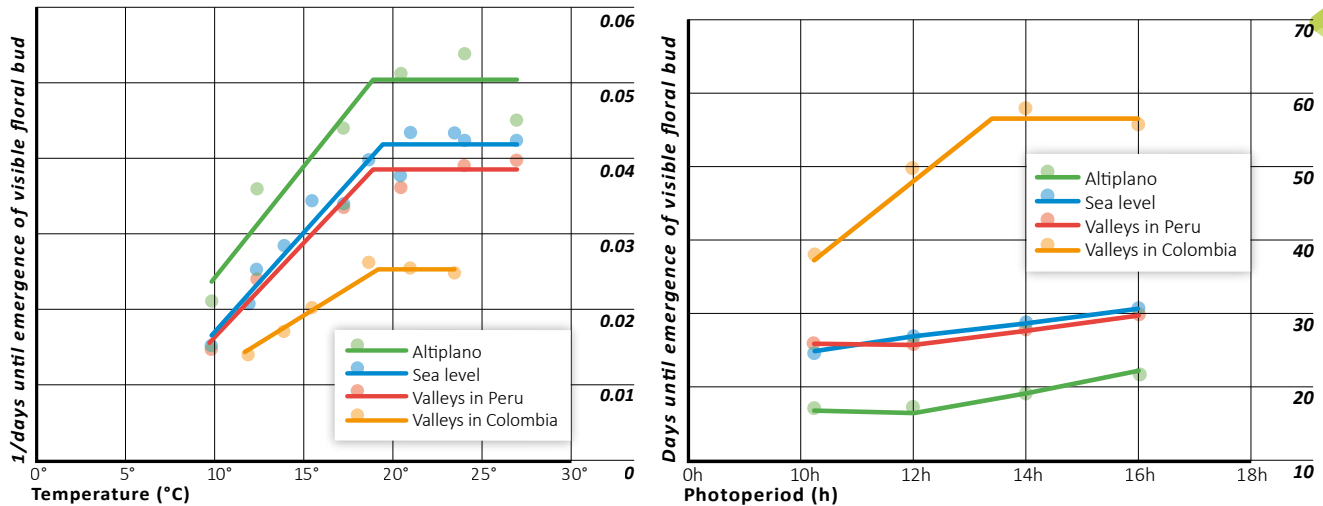
Figure 6: Variability in the response of development rate to temperature (a) and of duration from emergence to visible floral bud (VFB, b) to photoperiod, in four genotypes representative of the range of responses to these factors, evaluated under controlled conditions. The represented genotypes are: Nariño (◆), Colombia, Inter-Andean Valleys), Amarilla de Maranganí (■), Peru, Inter-Andean Valleys), Blanca de Julí (◆) Peru, Altiplano) and Baer (■) Chile, sea level). The response to temperature was analyzed for a photoperiod of 10.25 hours and that to photoperiod for a temperature of 21 °C. All the genotypes show a maximum development rate at a temperature of ~20 °C, whereas in the response to photoperiod, a threshold photoperiod of ~12 h could be observed for Blanca de Juli and a critical photoperiod of ~14 h for Nariño. More details on the experimental procedure in Bertero *et al.*, (1999b)

which compares the germination dynamic between two contrasting response genotypes, one Chilean and the other Bolivian. In this example T50 varied between ~ 10 and 18 °Cd, between 1 and 2/3 of values estimated by Jacobsen and Bach (1998) using similar Tbs.

4.2 Emergence-visible floral buds

This phase includes the Vg and Rp1 stages (Bertero *et al.*, 1999a) and therefore the entire leaf primordia initiation period, both stages are affected by the length of the day. The quantity of primodia, but not its initiation rate (primordial day $^{-1}$) varied between photoperiods in the two genotypes that were analyzed (Bertero *et al.*, 1999a).

Regarding genetic variability for duration of this stage two parameters that characterize responses to temperature and photoperiod, the basic vegetative phase (BVP), estimator of the temperature sensitivity (1/BVP) and photoperiod sensitivity (PS) are the most useful for explaining the differences between genotypes (Figure 6).

The BVP is the minimum duration of the phase, found under short days in short-day plants, whilst photoperiod sensitivity is the change in the dura-

tion of a phase per unit of change in photoperiod, expressed in °Cd for variable temperature conditions or in days h^{-1} for constant temperatures. Both parameters changed through a latitude gradient: a tropical cultivar (Nariño, from Colombia) displayed longer BVP duration and higher PS values (700 °Cd and 65 ° Cd h^{-1} (Tb = 1.5 ° C)) and the lowest values were observed in cultivar Baer (380 ° Cd and 12 ° Cd h^{-1} (Tb = 3.4 ° C)) from southern Chile (Bertero, 2003). Lower BVP and PS values were observed in the early flowering cultivars from the Peruvian and Bolivian Altiplanos, as an adaptation to the short vegetative period experimented in these environments. Unlike other stages (see anthesis-physiological maturity below), such as grain filling, the effects of temperature and photoperiod can be regarded as independent (Bertero *et al.*, 1999b).

4.3 Visible floral bud-anthesis.

This phase is also affected by photoperiod, sometimes directly or as by photoperiods experimented in the previous phases (Bertero *et al.*, 1999a). This in turn has an impact on the dynamic of leaf appearance. Although the number of primordia is determined at the onset of this stage, the number of leaves expanded from Rp2 until the end of the

leaf appearance period changes with photoperiod, through modifications in the proportion of primordia which expand to form leaves (Bertero, 2003).

Photoperiod sensitivity is greater in this stage than in the previous one (Bertero et al., 1999a) and is reflected in the range of variation shown in Fig. 7 (from insensitivity to more than three times the maximum value estimated by the same combination of genotypes for the emergence –VFB phase). A regression adjusted to the relationship between photoperiod sensitivity and latitude of origin for the 0-20 °S range allowed the estimate of an slope of -11.1 °Cd h^{-1} lat^{-1}, compared with -1.5 °Cd h^{-1} lat^{-1} for the emergence period-VFB (Bertero, 2003). Preliminary evidence suggests that pollen viability might be reduced through the effect of photoperiod (less under long days, unpublished data).

4.4 Anthesis-physiological maturity

Perhaps the most decisive limitation to phenological adaptation to non-tropical environments is linked to photoperiod sensitivity and the temperature experienced during seed filling. A temperature x photoperiod interaction affects seed filling, which is strongly inhibited by the combination of long days and high temperatures (Bertero et al., 1999a). While some Andean cultivars can be grown and matured in high latitudes (Carmen, 1984, Risi and Galwey, 1991), only limited by the duration of the growing season, seed production is strongly inhibited in mean latitudes when flowering occurs under long days and high temperatures. In the American and European Quinoa Trial (Mujica et al., 2001) all temperate environments were excluded from the analysis due to the fact that the cultivars adapted to the tropics produced a large amount of plant biomass but little or no grains (Bertero et al., 2004; Correa Tedesco, 2005). An interesting point for the adaptation to temperate climates is that this inhibition does not appear to occur, or has a lesser impact (Christiansen et al., 2010) on sea level and some highland cultivars, which can be cultivated in these environments.

High temperatures also appear to explain the poor adaptation of varieties from the Chilean and Bolivian Altiplano, cultivated at an altitude of around 2,500 m in Colorado, USA., even though they performed well at 2,800 m in other locations in the same State (Johnson and McCamant, 1986). Making even more
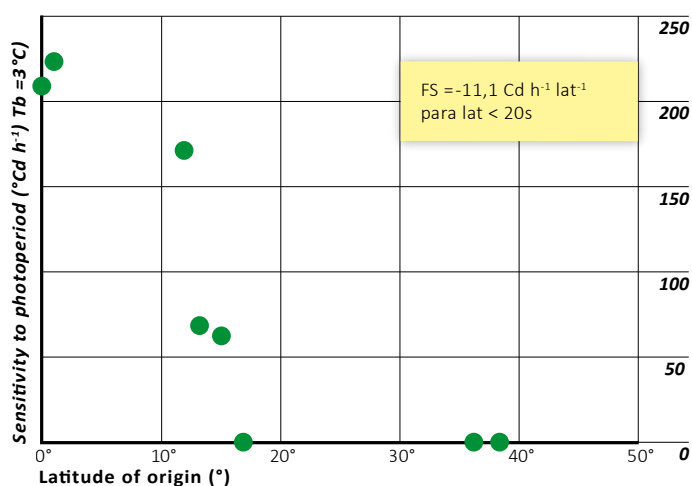

Figure 7: Association between photoperiod sensitivity (PS) for the VFB-anthesis phase and the latitude of origin of the genotypes (same as included in Bertero et al., 1999b). PS was estimated for plants growing in different sowing dates in Buenos Aires, Argentina, in the 10-14.4 h range of average photoperiod per phase for each planting date. PS is expressed in °Cd h^{-1}, for a Tb = 3 °C.

complex the interaction between photoperiod and temperature during seed filling, plants grown under short days before flowering present less inhibition for photoperiod during seed filling than those from long days (Bertero et al., 1999a, Bertero et al, 2002) (Fig. 8). An additional aspect of the effect of photoperiod on grain filling is delayed senescence (Bertero et al., 2002, Christiansen et al., 2010) possibly a consequence of alterations in the source-sink relationship linked to the inhibition of photoassimilate partitioning (and nitrogen?) to the grain (Fig. 8). This is manifested as a stay-green behaviour which does not generate an advantage in terms of grain weight or yield, since the latter is inhibited. The difference between the sample (S) and F2 (extension of photoperiod from anthesis to maturity) appears to be associated with differences in time to physiological maturity between these treatments, while the leaves shown in F1 (extension from floral bud to maturity) correspond to plants which, shortly after the beginning of samplings, were shaded by new leaves which continued to appear on the main stem, and the acceleration observed in senescence can be interpreted as a consequence of this shading. With respect to S, senescence was faster than in F2, associated with differences in maturity date. For both F2 and S, at physiological maturity senescence is associated with the start of a significant drop in SPAD values (Fig. 8). Plants under the treat-
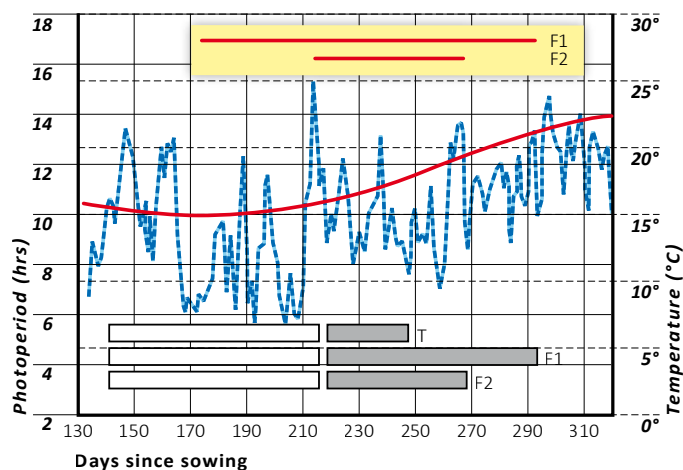
Figure 8: Effect of the manipulation of photoperiod under field conditions (Faculty of Agronomy, University of Buenos Aires) on the duration of development stages. The clear horizontal bars correspond to the duration of the emergence-anthesis period, while the dark ones correspond to anthesis-physiological maturity. Treatments are: plants grown under natural photoperiod (T), photoperiod extension from VFB to maturity (F1) and from anthesis to maturity (F2). The upper horizontal line indicates the duration of the photoperiod extension treatments (16 hrs), the dotted line to temperature averages over ten day periods and the rest to the progression of natural photoperiod (calculated according to Charles-Edwards et al., 1986). Sajama cultivar (Bolivian Altiplano. F1 does not cause changes in the time to flowering, indicating the insensitivity of this stage of the genotype to photoperiod).

ment of photoperiod extension never mature, the stems stay green and growth of new ramifications from the inflorescence can be observed (Christiansen *et al.*, 2010).

5. Response of morphological development to environmental factors

Other development processes are those linked to the appearance of leaves. The leaf appearance rate (day leaves-1) is affected by temperature and photoperiod in quinoa, even though the effects of temperature are more relevant in relative terms (Bertero et al., 2000) (Figure 9).

The variation in phyllochron (thermal period between the appearance of two successive leaves on the main stem, in ° Cd) shows a similar pattern to that of time to flowering: late flowering plants are also those with a higher phyllocron (and therefore, lower leaf appearance rate), while the opposite is
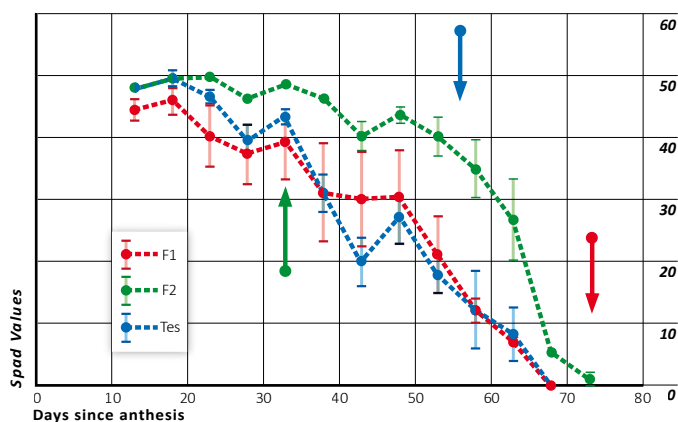
Figure 9: Effect of photoperiod on the chlorophyll content (SPAD arbitrary units, Minolta 1989) during grain filling, leaf No.13. The arrows indicate the time of physiological maturity, and the treatments are the same as for Fig. 7. Cultivar Sajama.

observed in Altiplano and Southern Chile accessions. This indicates that, in short season environments, as in the Altiplano (Geerts *et al.*, 2006) the genotypes flower in less thermal time, but this reduction in available time can be partly offset.

By the production of a higher number of leaves per time unit than varieties from warmer and more humid environments. An interesting fact is that the phyllocron is shorter (25%) in nine varieties selected in the Bolivian highlands compared to a traditional landrace variety (Bois *et al.*, 2006), perhaps a consequence of the selection for a higher crop growth rate and biomass production.

However, as a general rule, early flowering plants pay a cost in terms of yield potential due to the shorter available time to capture resources (above and below ground) as indicated by the positive association between crop biomass and cycle length (Bertero et al., 2004). The accumulation of biomass is also a function of changes in crop growth rate however, and the lower phyllocron could lead to a faster generation of leaf area, greater interception of radiation and growth, which would allow the design of cultivars that achieve similar biomass values with shorter cycles or high biomass values with similar cycles, as proposed for maize (Padilla and Otegui, 2005). The partial superposition between leaf appearance and reproductive development, mentioned previously, is also an interesting option
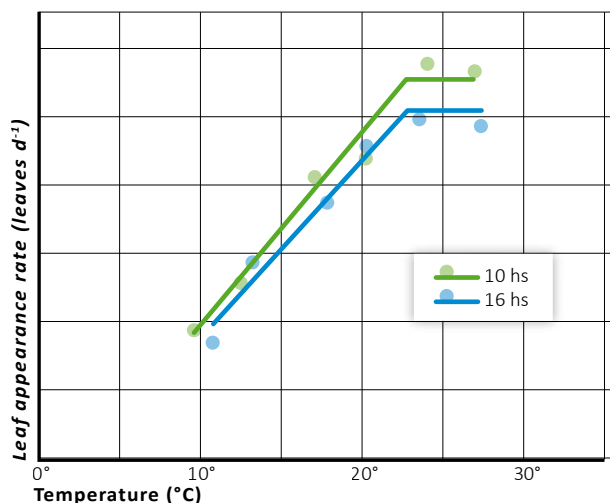
Figure 10: Response of leaf appearance rate (leaves day -1) to temperature and photoperiod, cv. Amarilla de Maranganí (Cuzco valleys, Peru). The data correspond to experiments conducted under controlled conditions in two photoperiods (10.25 and 16 hrs) and in the range between 10-27 °C in greenhouses under natural radiation. The estimated Tb is 3.1 °C, the optimum is 23 °C, and phyllocron responds to the equation: phyllocron (°Cd)=15 + 0.29 x photoperiod. More details on the experimental procedure in Bertero et al., (2000).

and, in fact, in quinoa, the generation of leaf area and panicle growth are partially simultaneous (Ruiz and Bertero, 2008).

6. Other factors

Another factor that appears to play a key role in development control, at least for varieties from the Bolivian Altiplano, is water scarcity. Geerts et al. (2008) reported 30 (from 65 to 95) days of delay in the time until the first anthesis with an increase in water deficit, while a similar stress can accelerate maturity if it occurs during seed development. This discovery has several implications. Extended dry periods can occur during the growing season coinciding with flowering and the filling of seeds in this milieu (García *et al.*, 2007). Flowering is more sensitive to stress (García, 2003), and also part of the critical period for yield deterinination (Bertero and Ruiz, 2008, Mignone and Bertero, 2008); postponing flowering could act as an escape mechanism if this means exposing flowering to a condition of more favourable water availability after the stress.

An additional factor of complexity is the effect of radiation on duration of development and the appearance rate of leaves (Bertero et al., 1999b,

Bertero 2001a). When models generated under controlled conditions were used to predict the time to VFB and the leaf appearance rate under field conditions, a systematic underestimation of both variables was detected when simulating the behaviour of crops growing at high temperatures. One of the differences between conditions was that under controlled conditions, a plateau is reached in development rate for temperature values ~ at 20 °C, which was not observed in the field (Bertero *et al.*, 1999b); and this "saturation of the rate of increase in development rate" is associated with lower incident radiation under controlled conditions (see Figure 3 in Bertero et al., 1999b). Based on this, a hypothesis is proposed that, in the presence of high temperature conditions, radiation is a limiting factor in the acceleration of development rate, in a manner equivalent to source limitations when analyzing carbon demand for growth processes (Borrás et al., 2004). When these variables were simulated assuming a single linear relationship between development rate and temperature, without a plateau, the systematic differences between observed values and predictions were eliminated, and greater prediction accuracy was achieved. An additional confirmation of this hypothesis was the analysis of the relationship between time to VFB and incident radiation (generated through different planting dates in a greenhouse under high temperature
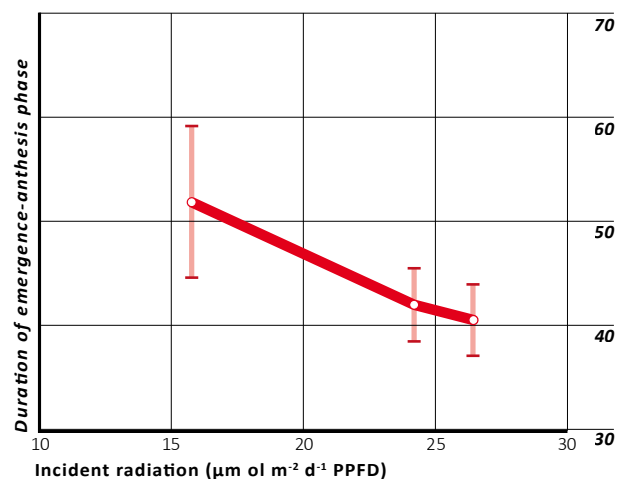

Figure 11: Association between incident radiation (mol PPFD m-2 d-1) and duration of the emergence-anthesis phase, for plants growing under constant temperature and photoperiod (27°and 16 hrs, respectively) in a greenhouse. Cultivar Sajama

and constant photoperiod) (Fig. 10) which possibly explains the apparent long day response found in Chilean quinoa genotypes when photoperiod was reduced through shading (Tejeda et al. 2007, Urbina *et al.* 2010).

Concluding remarks

The results presented in this chapter highlight the complexity of environmental control of quinoa development. The most studied factors are photoperiod, followed by temperature, covering a range of genotypic variation, while water deficits and radiation have only been partially studied in a few genotypes (and then for a few development stages). Given that the impact of factors such as water deficit and radiation are usually associated with growth process, we can speculate that the availability of nutrients will also affect the phenology of quinoa. We are yet to know the mechanism through which these last factors affect development. Among the affected phases, grain filling appears as the most critical in affecting latitudinal adaptation, as it may be strongly inhibited by high temperatures and/or long days. Experiments simulating the duration of phases and leaf appearance in field conditions have been reasonably successful (e.g. Bertero *et al.*, 1999b, Bertero, 2001, Geerts *et al.*, 2008, Lebonvallet, 2008), even though grain filling requires a better understanding to succeed in precisely simulating it. All this available information can be useful for taking decisions about crop management, adaptation to new environments or genetic improvement, decisions which so far have been taken empirically. High genetic control (G/GxE) of the duration of development may result in a high success rate for selection and management. The genetic control of quinoa development is yet to be addressed and represents the next chapter in quinoa development studies.

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