



HAL
open science

Plant response to environmental conditions: assessing potential production, water demand and negative effects of water deficit

Francois Tardieu

► **To cite this version:**

Francois Tardieu. Plant response to environmental conditions: assessing potential production, water demand and negative effects of water deficit. Drought phenotyping in crops: from theory to practice, CGIAR Generation Challenge Programme, 228 p., 2011, 978-970-648-178-8. hal-01190045

HAL Id: hal-01190045

<https://hal.science/hal-01190045>

Submitted on 1 Sep 2015

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1.5 Plant response to environmental conditions: assessing potential production, water demand and negative effects of water deficit

François Tardieu (INRA, France)

Introduction

Plants are machines which transform primary elements, namely light and CO_2 , into biomass. This occurs during a given period of time, the duration of which depends essentially on the air temperature and on the precocity of the genotype in question. During the same period of time, the plant requires an amount of water which depends on environmental conditions (light, air humidity, wind) and on plant variables such as stomatal conductance and leaf area. It follows that the biomass accumulated by a plant primarily depends on environmental conditions, but also depends on plants traits with genetic variability. The objective of this chapter is to provide a basis for analysing yield from a knowledge of environmental conditions, thereby enabling characterisation of the differences in behaviour between genotypes.

Variability of yield depending on light and water availability

The maximum yield that can be obtained in a given field depends on the amount of intercepted light.

Biomass accumulation is proportional to the amount of light that the plant intercepts over a period of time. Why is biomass accumulation proportional to light while photosynthesis is not? Photosynthesis depends on light intensity, with a relationship that is approximately linear for low light intensities (about $0\text{--}700\mu\text{mol m}^{-2}\text{ s}^{-1}$), but curvilinear at higher intensities. The linear relationship between biomass and light is due first to some of the leaves being shaded, so they receive light in the range where photosynthesis is nearly proportional to light. Second, the light intensity exceeds $700\mu\text{mol m}^{-2}\text{ s}^{-1}$ during the late morning and early afternoon, but is below this value during the rest of the day. Hence, the resulting relationship between photosynthesis and light is linear at the field level and during the entire day.

The biomass accumulation by a crop on a given day (Bio_j) depends on:

- The amount of light on the considered day in the range of wavelengths used by photosynthesis (PPFD).¹ Most light sensors directly record the amount of light in this range.
- The proportion of light that is intercepted by the plant leaves. The light that reaches the soil is not used for photosynthesis. The proportion of intercepted light depends on the leaf area of the plant on the day in question and is characterised by the leaf area index (LAI), which is the number of layers of leaves per unit soil area.² For instance, an LAI of 1 would correspond to a plant canopy with 1 m^2 of leaves per m^2 of soil. The proportion of light intercepted by plants increases with LAI (Figure 1) until an LAI of 3 or 4 depending on the species. At a higher LAI, nearly all the light is intercepted (there are no spots of unused light on the soil). The relationship between LAI and the proportion of intercepted light differs among species (Figure 1).

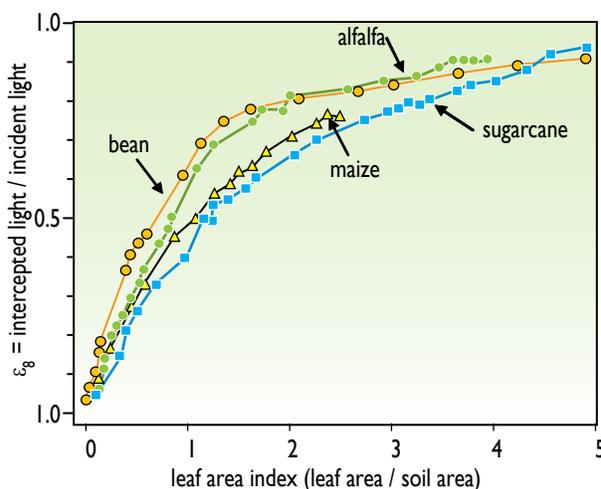


Figure 1. Relationship between leaf area and light interception (Redrawn from Gosse et al, 1986).

¹ The acronym standing for photosynthetic photon flux density.

² LAI can be measured by collecting all leaves on a sample soil area and measuring their area. It can also be measured indirectly and non-destructively using sensors that directly measure the proportion of intercepted light.

Plants intercept more light per unit area of leaf in species that have horizontal leaves, such as clover or cassava, than in species that have erect leaves, such as cereals.

- The efficiency of transformation of intercepted light into biomass, which depends essentially on the photosynthesis rate of leaves. This efficiency differs between species; it is maximal in C_4 species such as maize, sorghum or millet, which have a very efficient photosynthetic apparatus. It is roughly similar in all C_3 species that are neither legumes nor oil-rich seeds, such as wheat, canola or rice. It is lower in species that have a special metabolism such as legumes, which use part of the photosynthesised sugars for nitrogen fixation. It is also lower in oil-producing seeds, which have high energy content per unit biomass of seeds.

These three effects can be summarised in a simple equation:

$$\text{Bio}_i = \text{PPFD}_i \cdot \varepsilon_a \cdot \varepsilon_b \quad [1]$$

where Bio_i is the biomass accumulated on a given day, PPFD is the photosynthetic photon flux density, also called light intensity (in W m^{-2} or $\mu\text{mol m}^{-2} \text{s}^{-1}$), ε_a is the proportion of intercepted light (in percentage), and ε_b is the efficiency of transformation (in g per unit light intensity). The biomass accumulated during the whole season (Bio_{tot}) is the sum of biomasses accumulated each day:

$$\text{Bio}_{\text{tot}} = \sum (\text{PPFD}_i \cdot \varepsilon_a \cdot \varepsilon_b) \quad [2]$$

The yield is the fraction of Bio_{tot} that is transferred to harvested organs, such as grains or tubers. The proportion of harvested biomass divided by the total biomass is usually termed the 'harvest index' (HI), expressed as a percentage:

$$\text{Yield} = \sum (\text{PPFD}_i \cdot \varepsilon_a \cdot \varepsilon_b) \text{ HI} \quad [3]$$

This expression (Monteith, 1977) is very useful for analysing the yield performance of a given genotype and to compare genotypes. In particular:

The best genotypes are those that give a high priority to the harvested organs in the biomass partitioning. A large part of the genetic progress of several species has consisted of increasing HI.

In contrast, the efficiency of conversion of intercepted light into biomass is less variable between genotypes of a given species. In particular, the genetic progress of photosynthesis has been slow, if not negligible.

Another large source of genetic variation is the proportion of light that is intercepted by plants. The genetic variation in leaf area then translates into a change in accumulated biomass and, in turn, into yield in the range of LAI from 1 to 4. However, confounding effects, as analysed below, may obscure this relationship.

Finally, yield largely depends on the number of days during which biomass accumulates (term Σ in Equation 3). It is intuitive that the longer the crop cycle the higher the maximum potential yield. This number of days depends on the temperature sensed by plants during the crop cycle. Increasing temperature tends to cause shorter crop cycles, thereby decreasing the potential yield. It also depends on the genotype via two traits: first the precocity of the considered genotype, which defines the time for flowering and the duration of the period between flowering and maturity; and second the degree of maintenance of this second period under stressing conditions.

An alternative way of expressing yield as a function of water availability and water-use efficiency.

Water availability does not appear directly in the analysis presented above, because water is not involved per se in the process of biomass accumulation. In contrast to light which has a nearly proportional effect on the accumulation of biomass, water 'only' serves to allow biomass accumulation to occur in good conditions by favouring stomatal opening, organ growth and plant metabolism. In order to express yield as a function of water use, an alternative expression of yield has been proposed by Passioura (1977). This states that the biomass accumulation on one day depends on the transpiration rate multiplied by the water-use efficiency (WUE) ie, the ratio of biomass accumulation to transpiration). As in Equation 2, the biomass accumulated over the plant cycle is the sum of that accumulated every day of the cycle. The yield is the fraction of the accumulated biomass that is transferred to harvested organs, such as grains or tubers (ie, the HI):

$$\text{Yield} = \sum (T_i \cdot \text{WUE}_i) \text{ HI} \quad [4]$$

where T_i is the transpiration on day i , WUE_i is the water-use efficiency on day i and Σ indicates that the biomass is accumulated over the whole crop cycle.

Transpiration rate

T_i changes every day depending on evaporative demand and on leaf area. Evaporative demand depends essentially on light, on the degree of water saturation of the air, measured as vapour pressure deficit (VPD), and on wind speed. Most weather stations provide the evaporative demand, termed 'potential evapotranspiration' or 'reference evapotranspiration'. Otherwise, evaporative demand can be calculated using a spreadsheet by using Penman's formula.

Leaf area affects the transpiration rate in the same way as it affects the intercepted light (Figure 1). Thus, transpiration is nearly proportional to leaf area for low LAI, and saturates for LAI higher than 3 or 4.

$$T = ET_r \cdot \varepsilon_a \quad [5]$$

where ET_r is the reference evapotranspiration, as provided by a weather station or calculated using Penman's formula, and ε_a is the proportion of transpiration of the studied field to the reference evapotranspiration, which has the same value as that in Equation 1.

The root system also affects the transpiration rate, via several traits such as total root length, rooting depth, or the hydraulic conductivity of roots. It should be noted that this is the case only if roots have access to a large volume of soil. In contrast, an increase in root length has virtually no effect in a shallow soil. A breeding programme for drought carried out by Bolaños et al (1993) had the surprising result that the root length was reduced in drought-tolerant genotypes compared with drought-sensitive ones.

Water-use efficiency

WUE is defined here as the ratio of the biomass accumulated on one day to the transpiration rate on the same day. Defined in this way, it is difficult and tedious to measure. A surrogate measurement consists of the ratio between the photosynthetic rate and the transpiration rate, or between photosynthesis and stomatal conductance as measured using gas exchange equipment. The latter can be measured indirectly via the ratio of two natural isotopes of carbon in leaves or grains (carbon isotope discrimination, often called $\Delta^{13}C$), providing rapid estimates with a high throughput.

Environmental conditions greatly affect WUE (defined as in Equation 6). In particular, WUE decreases when evaporative demand increases, because transpiration is higher at high evaporative demands for a given photosynthesis. It follows that WUE is higher in regions with wet air, and that crops that are grown during winter or during rainy seasons have a higher WUE than those grown during summer or during dry seasons (Figure 2). Large differences in WUE exist between species. WUE is higher in C_4 species, such as maize, sorghum or millet, than in C_3 species. It is noteworthy that the method based on carbon isotope discrimination cannot be used in C_4 species.

Finally, it should be noted that the concept of WUE, and therefore Equation 4, can be misleading, depending on the definition that is taken for WUE and on the time scale. Depending on the study or paper in question, WUE is defined in different ways that are not equivalent, have different genetic variabilities, and respond differently to environmental conditions. Defined as the ratio of photosynthesis to transpiration, WUE has a lower genotype-by-environment interaction (GEI),

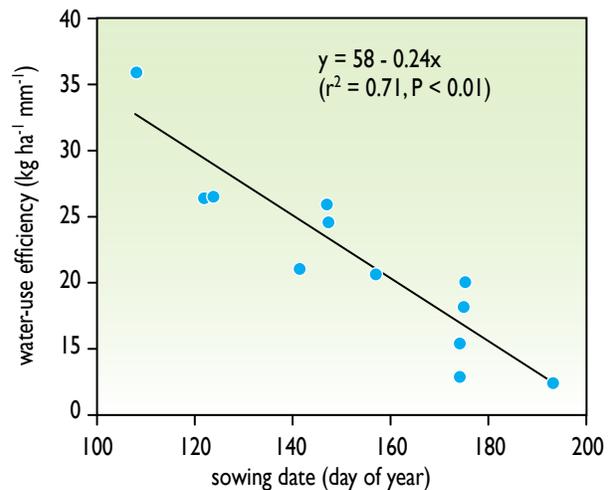


Figure 2. An example of change in WUE during the growing period of the plant. The later in the growing period, the higher is the evaporative demand. Because the accumulated biomass does not increase in the same proportion, the WUE is lower during periods with high evaporative demand. Data obtained with wheat lines sown at different times of the year in Australia (Redrawn from Richards et al, 2002).

but it cannot be used directly as the efficiency of transforming transpiration into biomass. At the other extreme, WUE can be defined at the scale of the crop cycle as the ratio of the total biomass (or yield) to the total transpiration. It should be noted that, in this case, WUE is not a direct consequence of stomatal and photosynthetic functioning, and is affected by growth conditions. For instance, a short stress that causes abortion of reproductive organs affects total biomass accumulation, with a lesser effect on transpiration. Therefore, it affects WUE at the whole cycle scale, although it has a small effect on gas exchange.

A third expression of yield as a series of yield components: roles of individual phases of the crop cycle

Agronomists have long expressed yield by a multiplicative series of yield components: the number of plants per m²; the number of immature reproductive organs per plant (eg, the number of seeds per tiller multiplied by the number of tillers per plant, or the number of tubers per stem multiplied by the number of stems per plant); the proportion of non-aborted reproductive organs; and the individual weight of seeds or tubers. Thus:

$$\text{Yield} = N (1-A) W_r \quad [6]$$

where N is the number of immature reproductive organs (eg, ovules), A is the proportion of aborted reproductive organs, and W_r is the mean weight of individual reproductive organs.

This expression has the advantage of breaking down the yield into several phase of the crop cycle. The setting of reproductive organs occurs during the

pre-flowering time, the proportion of non-aborted reproductive organs is determined during a phase around flowering, and the individual weight of seeds or tubers is determined between flowering and maturity. Therefore, it is possible to express the result of each phase as a function of environmental conditions during that phase. For instance, one can relate the abortion rate to the water availability during the same period (Claasen and Shaw, 1970), or to the biomass accumulation during that period (Vega et al, 2001; Figure 3). In the same way, seed number usually correlates well to the intercepted light during the pre-flowering period. These relationships help to identify the behaviours of genotypes, which can either have common behaviours (common relationships) or different behaviours (different relationships).

How does each term of yield expression vary with water availability, and where is the genetic variability of responses to water deficit?

Each of the three approaches of yield provided by Equations 3, 4 and 6 has its own interests, and each represents a view of the yield setting. The first equation is more mechanistic and is the one used in all crop models, but the effect of water deficit does not appear explicitly. The second is perhaps more intuitive for understanding the effects of water deficit but can be misleading, depending on the definition that is taken for WUE. The third is the most intuitive, but cannot be related to physiological functions of plants. These three views should be considered as frameworks of analysis to help identify where a given trait is involved in yield formation and what the effects are of a water deficit.

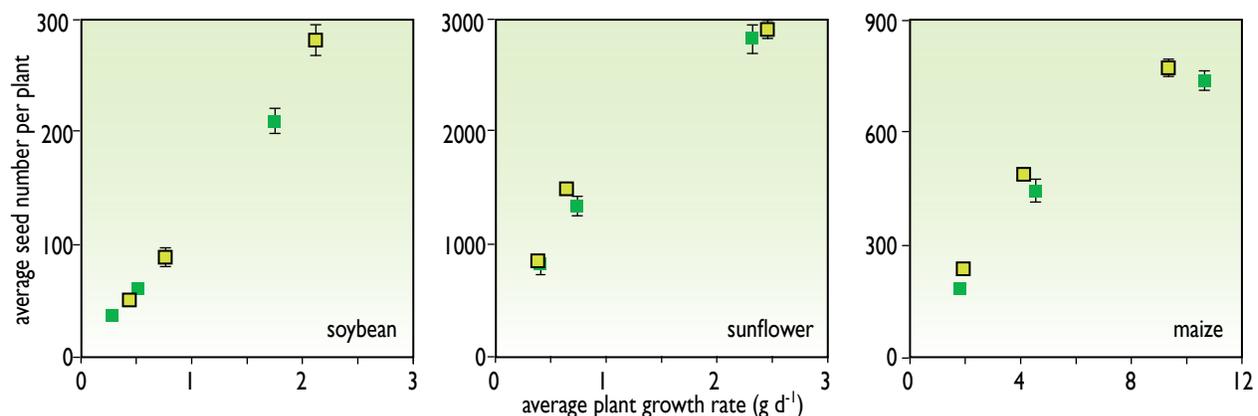


Figure 3. The relationship between seed number per plant at maturity and average plant growth rate at flowering time in soybeans, sunflowers and maize (Redrawn from Vega et al, 2001).

Growth reduction of expanding tissues

The first effect of a water shortage is to drastically reduce the growth of expanding tissues, with effects on terms ε_a , T and N, and indirect effects on other terms. Expansive growth is one of the processes most sensitive to water deficit in leaves, internodes (eg, the peduncle in cereals) or reproductive organs (eg, the silks in maize, or tubers in potatoes). This occurs because turgour – the driving force for cell expansion – is reduced in the case of water deficit, but also because of other indirect processes such as a reduction in cell division rate or in the extensibility of cell walls. A water deficit during the vegetative stages affects leaf growth and hence light interception but, in most species, it also affects the growth of immature storage organs (seeds or tubers).

Via this mechanism of reduced growth, a water deficit can affect the term ε_a of Equation 3, because it reduces LAI and, therefore, both light interception (Equation 3) and transpiration (Equation 4). The reduction in growth also affects the number of reproductive organs and their abortion ratio (N and A respectively in Equation 6) via a reduction in biomass accumulation (Gambin and Borrás, 2007), but also because vegetative and reproductive growth can depend on common mechanisms and common genetic determinism (Welcker et al, 2007). Other terms can also be affected by a reduction in growth, in particular HI if young reproductive organs or young tubers abort. In this case, biomass cannot accumulate in harvested organs in later stages of the crop cycle, and is stored in stems or roots.

There is a very large genetic variability of the sensitivity of growth to water deficit. For instance, quantitative trait loci (QTLs) have been identified for the degree of maintenance of growth under water deficit of leaves (Reymond et al, 2003), silks (Ribaut et al, 1997) or the peduncle (Maccaferri et al, 2008). The sensitivity of leaf growth to evaporative demand and to soil water deficit, which can be determined in controlled conditions, translates into differences in leaf area and into biomass accumulation observed in the field (Chenu et al, 2008). Several QTLs for growth maintenance have been shown to translate into QTLs for yield (Ribaut et al, 1997).

Stomatal closure

A second effect of water shortage is to close stomata, thereby affecting the terms ε_b , WUE, N and W_r . Plants subjected to water deficit close their stomata, with the involvement of hydraulic and chemical messages such as the plant hormone abscisic acid (ABA; Tardieu and Davies, 1993). This reduces the loss of water by the plant, thereby saving soil water and improving leaf water status, but also reducing the rate of photosynthesis and increasing leaf temperature. These effects can be measured via gas exchange equipment, but measurement of leaf temperature can provide a convenient surrogate for gas exchange if used carefully (Jones, 2007).

There is some genetic variability for stomatal sensitivity to water deficit, but probably less marked than that for growth maintenance. In contrast, there is an interesting genetic variability for WUE, when defined as the ratio of photosynthesis to transpiration rate. Genetic analyses and breeding programmes have been carried out on WUE via its relation to carbon isotope discrimination, resulting in appreciable gains in yield in wheat grown in dry conditions (Condon et al, 2004).

A water deficit decreases the term ε_b of Equation 3, because the plant accumulates less biomass per unit leaf area than a well-watered plant. This is reversible, because stomata can reopen when more water is available after a rain or watering. In contrast, the heat stress caused by stomatal closure can result in permanent damage to the photosynthetic apparatus, thereby decreasing ε_b for the rest of the crop cycle. Conversely, WUE usually increases with stomatal closure, because photosynthesis and stomatal conductance are linked with a non-linear relationship. The reduction in photosynthesis affects kernel weight and also the proportion of reproductive organs that develop into seeds. In a number of species, the latter is related to sugar metabolism (Zinselmayr et al, 1999).

Duration of the crop cycle

A third effect of water deficit is to reduce the duration of the crop cycle, thereby affecting the terms Σ , T and W. In most species, water deficit

affects the duration of the crop cycle by accelerating senescence. This is due to an early expression of genes associated with remobilisation of proteins, which are redirected from leaves to reproductive organs (Pic et al, 2002). This reduction in the duration of the crop cycle is an adaptive mechanism, since it allows the plant to finish its cycle earlier while there is still water in the soil, and redirects assimilates to the reproductive organs. This reduces the total intercepted light and, therefore, the biomass accumulation in Equation 3, and the total transpiration in Equation 4. It may also affect the seed weight (Equation 6) if the seed number is not reduced in the same proportion as the reduction in biomass accumulation.

Genetic variability exists in the degree of maintenance of the green leaf area (Borrell et al, 2000), and a breeding strategy has been developed, aimed at maintaining photosynthesis in leaves for a longer duration ('stay-green'). This strategy is adequate for soils with an appreciable water reserve, and may otherwise cause severe stress at the end of the crop cycle through increased transpiration (Hammer et al, 2006).

Genetic strategies for yield maintenance under water deficit

The above paragraphs provide an understanding of possible strategies for improving yield under water deficit. They also suggest that the maintenance of biomass accumulation under water deficit should be considered as an optimisation process between transpiration, biomass accumulation and its partitioning between root and shoot, rather than as a tolerance process per se. It follows that a given trait can have positive, null or negative consequences, depending on the drought scenario (Chapman et al, 2003; Vargas et al, 2006).

Escape strategy

The escape strategy consists of adapting the crop cycle to water availability and evaporative demand, usually by reducing its duration, thereby reducing the total demand for water and avoiding severe terminal stresses. It leads farmers to choose species and genotypes according to local environmental conditions. It is also a strategy adopted by some desert plants that have a very rapid cycle after rain, and finish this cycle before the occurrence of water deficit. For a given genotype, it also consists of

reducing the duration of the cycle, thereby reducing the total demand for water and avoiding severe terminal stresses. This strategy saves water but also reduces the accumulated photosynthesis during the crop cycle (Equation 3). Therefore, it consists of a trade-off between a lower risk of terminal stress against a reduced potential yield.

Avoidance strategy

The avoidance strategy consists either of the maintenance of transpiration rate under water deficit achieved by improving the size, architecture or hydraulic conductance of the root system (de Dorlodot et al, 2007), or a reduction in the demand for transpiration by stomatal closure or reduction in leaf area.

Maintenance of transpiration rate under water deficit via the root system

This strategy is observed when the improvement of the root system increases access to soil moisture, ie, in deep soils. In contrast, when roots grow in a limited volume of soil because of physical barriers (eg, a hard layer due to compaction) or chemical barriers (eg, acid soil), improvement of in the architecture of the root system can be detrimental. This is because soil depletion occurs more rapidly, thereby causing severe stress at the end of the season (Tardieu et al, 1992), and because the assimilates invested in roots would be better invested in other organs. Accordingly, while a number of genetic studies of root systems have shown a positive association between yield and certain root features (Tuberosa et al, 2002), some programmes to improve yield under water deficit have resulted in a reduced root biomass (Bolaños and Edmeades, 1993; Bolaños et al, 1993; Bruce et al, 2002), or decreased conductivity of the root system (Richards and Passioura, 1989). Therefore, this strategy is a trade-off between a greater carbon investment in roots against an expectation of higher water uptake, which only occurs if soil properties allow the higher uptake.

Reduction in transpiration by stomatal closure or reduction in leaf area

Reduction in transpiration has been selected by evolution to reduce the risk of failure at the end of the growing season, because they both reduce the plant's demand for water. However, they intrinsically reduce the yield expectation by decreasing the

proportion of light intercepted by leaves (ϵ_a , Equation 3), and/or the efficiency of the transformation of light into biomass, which follows stomatal conductance (ϵ_b , Equation 3). It is noteworthy that many experiments in pots that identify 'drought-tolerant' plants, in fact, use this strategy (eg, Iuchi et al, 2001). Therefore, this strategy trades off a lower risk of plant failure against lower potential biomass production.

Growth maintenance

Unlike in the other strategies described so far, that of growth maintenance consists of continued growth of the most important organs, thereby maintaining yield. However, the maintained transpiration may cause a crop failure at the end of the crop season. Therefore, this strategy exchanges the maintenance of yield potential for a high risk of crop failure.

Maintenance of leaf growth

The maintenance of leaf growth under water deficit allows better light interception, thereby increasing photosynthesis but also increasing the transpiration rate and soil water depletion. Therefore, it is appropriate in many cases, although not for severe, terminal water deficits. It is noteworthy that, in one mapping population, half of the QTLs for sensitivity of leaf growth overlapped with those of silk growth (Welcker et al, 2007), suggesting that mechanisms favouring expansive growth may also favour reproductive development.

Maintenance of reproductive growth

The maintenance of reproductive growth around the time of flowering allows the maintenance of capacity for storage of photoassimilates later in the crop cycle, thereby increasing HI (Equations 3 and 4) and decreasing A, the proportion of aborted reproductive organs (Equation 6). This strategy has been successful in several species, in particular maize, via the assessment of the anthesis–silking interval (ASI), which is typically increased by water deficit and negatively correlated with yield. Phenotypic selection under well-managed stress environments for low ASI has produced large genetic gains and resulted in significant impacts (Bolaños and Edmeades, 1996; Ribaut et al, 2004).

Increase in water-use efficiency

An increase in WUE may seem to be the ideal candidate mechanism for drought-prone environments. In crops, WUE has been regarded as a 'conservative strategy' involving reduced transpiration,

such that the positive influence of a higher WUE on yield may be reduced under moderately favourable environments and become a penalty under the most favourable conditions (Rebetzke et al, 2002). This strategy has been used in wheat for Australian environments, where water must be used conservatively to allow the crop to complete its life cycle. It has led to the release of two cultivars (Condon et al, 2004).

Increase in harvest index

Finally, an increase in HI (Equations 3 and 4) has been a major way of increasing yield, even under water deficit (Turner, 1997). Furthermore, a change in biomass allocation between stem, roots and seeds has been a clear route to progress.

The progression of developmental stages of a plant can be predicted by using thermal time

Why use thermal time and plant development models?

The above paragraphs show that environmental stress has different consequences depending on the phenological stage at which it occurs in the plant. In particular, some stages such as flowering present a high sensitivity to stresses, while others such as grain filling present a lower sensitivity. It follows that a genetic comparison can be biased severely if the stress occurs at different stages in each genotype, because some genotypes will encounter the stress at a sensitive stage while others will encounter it at a stage with lower sensitivity. This results in non-reproducible experiments.

Therefore, it is essential that the main phenological stages of each genotype are precisely recorded. This raises two problems. The first is that, because a key stage such as flowering can occur over one or more weeks in a population of genotypes, it is usually impossible to visit each day to obtain the flowering date of every individual genotype. The second is that some key stages are difficult and lengthy to determine. While emergence, leaf number or flowering time can be obtained in a straightforward way, determining other stages such as flower initiation requires a detailed analysis. However, these stages can often be determined from other phenological stages such as the number of leaves.

When an experiment is repeated in naturally fluctuating conditions, phenological stages occur at different dates in each experiment. The number of days after emergence cannot, therefore, provide a good prediction of the stages. For instance, the progression of leaf initiation on the stem generally differs between different experiments in the field or in the greenhouse. Therefore, we need a tool that can: (i) simulate the exact date of a given stage from several datapoints obtained at different dates; (ii) compare the behaviour of a given genotype in different experiments; and (iii) estimate the dates of 'hidden' stages, eg, flower initiation or the beginning of stem elongation, from other stages that are easier to determine.

What is thermal time?

Rates are linearly related to organ temperature

Biological processes have a rate that follows temperature. For instance, Figure 4 shows the rate of initiation of leaves in peas (Turc and Lecoer, 1997) and sunflowers (Granier et Tardieu, 1998). In the latter, the same relationship held for plants grown in the growth chamber, in the greenhouse or in the field. In a study of the relationship between meristem temperature and maize leaf elongation rate over 15 field experiments, three growth chamber experiments and three greenhouse experiments at night (ie, in the absence of evaporative demand), using a single genotype (hybrid Dea), the same relationship

was found to apply to all three conditions (Tardieu, 2003). Marked differences in slopes between inbred lines were observed consistently over successive experiments. The slope is therefore a stable characteristic of a genotype. These relationships only apply during the night. Elongation rates at a given temperature are lower during the day owing to the effect of evaporative demand, which is taken into account by a second relationship.

Several conclusions can be drawn:

- If the same relationship holds for experiments in different places, years and experimental conditions, this means that the temperature dependence of rates is a stable characteristic of a genotype. Therefore, regardless of the experiment, we can assume that the relationship will apply and can be used as a tool.
- The linear relationships presented in Figure 4 implies that rates can be deduced from the temperature. For example, in Figure 4, twice as many leaves will have been initiated at 26°C than at 16°C. Alternatively, it can be stated that the time sensed by the plant elapses twice as rapidly at 26°C as at 16°C. This is the intuitive basis for thermal time: thus, plants 'sense' thermal time rather than calendar time, and thermal time depends on temperature. The x-intercept of this relationship is termed the 'threshold temperature'. If the relationship were linear across the whole range, this threshold temperature would be the temperature at which

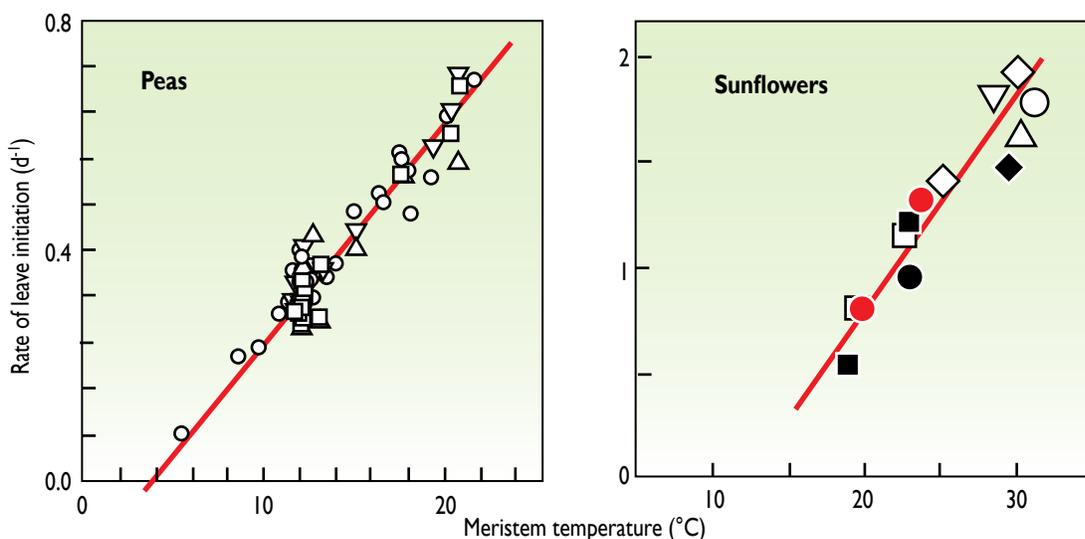


Figure 4. The relationship between temperature and initiation rate of leaves on the apex (ie, the reciprocal of the time elapsed between the initiation of two consecutive leaves). For peas, each datapoint corresponds to a different experiment (Redrawn from Turc and Lecoer, 1997). For sunflowers, plants grown in a growth chamber are represented by filled symbols, those grown in the greenhouse by open symbols, and those grown in the field by red symbols (Redrawn from Granier et Tardieu, 1998).

the rate is zero. This is not usually the case, since the response tends to be curvilinear at low temperatures, hence the threshold temperature has rather a statistical definition.

- Several processes such as leaf appearance rate, cell division rate or leaf growth rate have a common relationship with temperature, with a common x-intercept. This means that thermal time as sensed by several processes or organs is the same. It is, therefore, the ‘physiological age’ of the plant.

Calculation of thermal time

Thermal time depends on the existence of the linear relationships described above. The first relates temperature to the rates of processes involved in leaf growth:

$$dP/dt = a (T - T_0) \quad [7]$$

where P is the studied process (eg. expansion, cell division or leaf initiation), T is the current temperature, a and T₀ are the slope and the x-intercept, respectively, of the relationship between dP/dt and T. The second relationship involves the reciprocal of the duration of the studied process:

$$1/d = b (T - T_0) \quad [8]$$

where d is the time during which expansion (or any other developmental process) occurs in a given leaf, or the time during which leaf initiation occurs on the apex. It follows that, at time d:

$$P = a \int_0^d (T - T_0) dt \quad [9]$$

$\int_0^d (T - T_0) dt$ is commonly named thermal time (unit of °Cd, when calculated with a daily timestep).

This calculation can easily be carried out using a spreadsheet, where each line represents a date. First, the mean temperature for each day must be calculated. An efficient way for that is to consider the average of the maximum and minimum temperatures, which are usually available in weather stations. The thermal time elapsed during a given day is the difference between the mean temperature of the day and threshold temperature of the considered species. This is available in the literature (eg, 10°C for maize, 11°C for sorghum, 13°C for rice etc). The thermal time for a given period of time is the sum of the thermal times of all days in question.

The development of plants follows a programme which is stable for a given genotype

A development model can be built at the whole plant level, using the method presented previously. The occurrence of several phenological stages of the plant can be predicted, depending on thermal time. For example, Figure 5 (Chenu et al, 2008) presents the number of leaves that have been initiated, the number that are visible, and the number that have stopped growth as a function of thermal time after emergence.

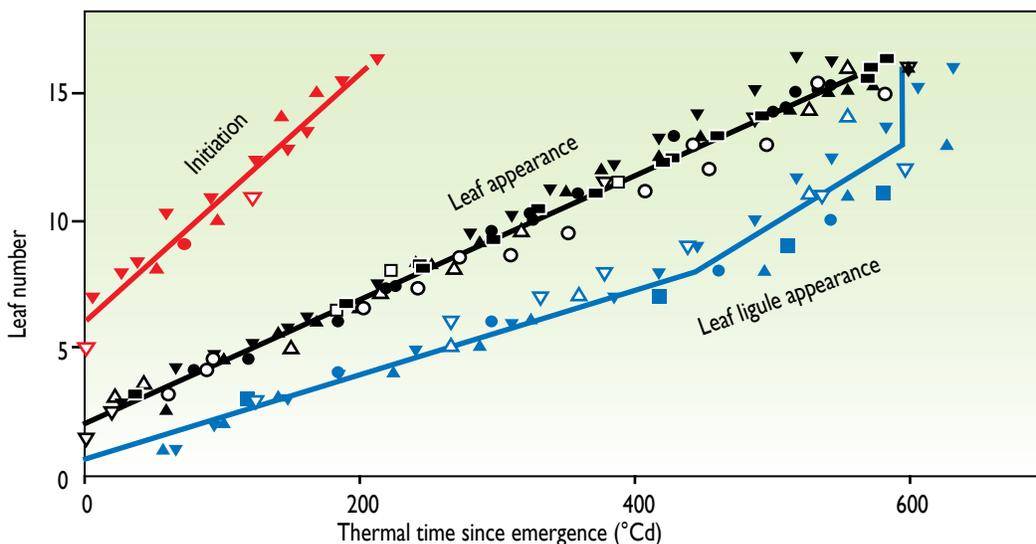


Figure 5. Example of a plant development model in maize. Initiation, leaf appearance and ligule appearance in maize are expressed as a function of thermal time. The y axis represents each position of the leaf on the stem. For each leaf, the beginning and end of linear elongation occurred at a common thermal time in all experiments (Redrawn from Chenu et al, 2008).

It summarises different experiments and different plants in each experiment. For instance, leaf 10 was initiated at 90°Cd, was visible at 320°Cd and ceased elongation at 490°Cd. If we consider all experimental points, three regression lines appear, which allow prediction of the phenological stages. When the progression of stages is common to several experiments, it can be used in a new experiment where no stage was recorded. It can therefore be assumed that, in any experiment in any place in the world, leaf 10 of this genotype stops elongation 490°Cd after emergence. As an example, it has been checked that a common development model for sorghum was valid in both Mali and in Montpellier, France (Lafarge and Tardieu, 2002).

The development model summarised in Figure 5 can be read in two ways. First, if it is considered vertically, for instance at 400°Cd, it indicates the number of initiated leaves and leaves that have ceased expansion on that day. Thus, it is a 'snapshot' of the plant on a given day. Then, if the graph is considered horizontally, it indicates the development of each organ. This development model responds to the needs presented at the beginning of this chapter.

If a phenological stage has not been recorded exactly when it occurred, it can be inferred from measurements carried out before and after the date in question. For instance, if the date of plant emergence occurs between two visits to the experiment, it can be reconstructed by recording the leaf number at two or three dates, and calculating the date at which the leaf number would be zero.

Several experiments can be analysed jointly, and the timing of stresses of each experiment and each genotype can be placed on a single scale of development. This is of considerable help in the interpretation of a network of experiments, which would otherwise have apparently erratic behaviour.

Practical ways for comparing the productivity of genotypes in field environments

A minimum dataset for using methods described here

The above methods allow comparison between experiments, genotypes and treatments, provided that a minimum set of measurements is collected. These are described below.

Key dates of the crop cycle

Although this information is relatively straightforward, it is frequently missing, meaning that none of the methods presented above can be used. The most important dates are sowing, emergence, flowering and physiological maturity (harvest). It is useful to record intermediate stages such as leaf number, which allow recalculation of missing stages by using thermal-time based interpolation as described above.

Daily irradiance or photosynthetic photon flux density

This information about available light is essential because: (i) it is an input for calculating the soil water balance; and (ii) it allows estimation of the potential biomass accumulation in the environment in question. Irradiance (I_r , measured in $W\ m^{-2}$) is better suited for the first use and is provided by pyranometers, while PPF (mol $m^{-2}\ s^{-1}$) is better suited to the second use, and is provided by photosynthetically active radiation (PAR) sensors. Because either variable can be translated into the other under field conditions, both are acceptable. It can also be acceptable to use an inexpensive sensor of daily sunlight duration which, combined with constants linked to the latitude, allows a rough calculation of I_r and PPF. While this is not encouraged, it can be helpful.

Light intensity has a relatively low site specificity. It is acceptable to record data from a weather station located at several km distance provided that: (i) the weather station is in the same geographical situation as the experimental field (altitude etc); and (ii) there can be reasonable confidence in the data (especially if missing data are not too frequent, if the sensors are of satisfactory quality, etc). In contrast, special care has to be taken in greenhouse and growth chamber experiments because of the high spatial variability (both horizontal and vertical) of light in these environments. A map of light intensity, or at least the use of several sensors, is recommended.

Air temperature

Together with irradiance, information on the air temperature (T) is necessary for calculating the soil water balance. It also allows estimation of thermal time if plant temperature is close to air temperature. This is usually acceptable for well-watered adult plants, but is prone to large errors during early phases in monocot species and in plants subjected to water deficit. It allows estimation of

the occurrence of high temperature stresses (eg, at $T > 40^{\circ}\text{C}$), of risks of oxidative stresses (eg, at $T < 3^{\circ}\text{C}$ and $\text{PPFD} > 1000 \text{ mol m}^{-2} \text{ s}^{-1}$), and of phenological stages, with the use of thermal time. This information must be recorded close to the experimental field using a local weather station or a data logger with thermocouples. Data can be recorded at daily intervals as minimum and maximum temperatures. The data need to be measured at plant height in greenhouse or growth chamber experiments.

Air relative humidity, vapour pressure deficit and reference evapotranspiration

These three variables quantify the evaporative demand, which is essential for estimating stress levels, for characterisation, and for calculation of the soil water balance. They provide essentially the same information, but with different time scales and usefulness. Relative humidity (RH), expressed as a percentage and VPD (in kPa) are calculated on short timescales (minute to hour), and ET_0 (in mm per day) is on a daily timescale. The variable recorded in the database would be ET_0 , either calculated from other climatic data (I_r , VPD, T wind speed) recorded in a datalogger (see above), or directly calculated by the weather station. ET_0 is species-independent and calculated by energy balance.

RH and wind speed have relatively low site specificities. As in the case of air temperature, it is acceptable to record these data from a weather station located at several km distance. RH in greenhouse and growth chamber experiments should be recorded with replications, because of the large spatial variability. A method for calculating ET_0 is available at: [http://www.fao.org/docrep/X0490E/x0490e04.htm#reference%20crop%20evapotranspiration%20\(eto\)](http://www.fao.org/docrep/X0490E/x0490e04.htm#reference%20crop%20evapotranspiration%20(eto)).

It might be useful here to emphasis on two frequent errors:

- RH should not be interpreted per se, because it does not characterise the evaporative demand when the air temperature is fluctuating. The use of both RH and air temperature allow a very simple calculation of VPD, which is the driving force for transpiration. Extreme events such as the sirocco should be recorded as daily maximum VPD over a period of three or four hours.

- Mean daily air VPD or RH recordings are not acceptable for characterising the daily evaporative demand; ET_0 should be used.

Rainfall and irrigation

Recordings must be made near the field (< 300m distant) because of very high spatial variability. Simple rain gauges are efficient and inexpensive but require frequent visits, while automatic rain gauges connected to a datalogger are more expensive but are useful in distantly located experiments.

Initial soil water content in the field

The water balance data begin at a given date (eg, emergence), at which time the soil water content must be recorded. This can be done with augers over a depth similar to the final rooting depth, with particular attention to spatial variability in the field. This measurement is important especially in experiments where the rainfall is zero or negligible. Some 'shortcuts' can be acceptable, especially when either the rainfall or irrigation before the experiment is sufficient to guarantee that the soil is at retention (or field) capacity.

Soil hydraulic properties

These are essentially the variables that allow calculation of the limits of soil water reserves, namely the field capacity and the limit of water extraction. These should be measured in experimental fields where drought experiments often take place, using equipment that measures soil water content, eg, neutron probes or using time domain reflectometry (TDR). These properties can also be inferred from the soil texture (eg, loamy sand, clay loam etc) and the estimated rooting depth.

Conclusions

It is not possible to present in detail here how to use each method for each species. Readers are referred to the sections of this book dealing with individual crops. However, it can be stressed that the tools presented here help in the interpretation of data gathered from networks of experiments.

The potential production of each site can be calculated from the development model, which provides an estimate of leaf area, and the available light. For instance, the biomass accumulation in

cloudy years is lower than that of bright years, if water is not seriously limiting yield. In the same way, a hot year reduces yield even in the absence of heat stress or water stress, by reducing the duration of the crop cycle. It is particularly useful to compare the potential productivity of experimental sites and years, in order to distinguish the natural variability of yield linked to light availability from the effects of stressing events.

The soil water balance can be calculated for each genotype, provided that a minimum dataset has been

collected. This requires estimation of the change with time in leaf area of each genotype. The latter information can be inferred from measurements of 'probe genotypes' having approximately the same cycle duration as a class of genotypes under examination. Once leaf area has been estimated, it is possible to calculate the proportion of evapotranspiration needed by the genotype in question in comparison with the reference level of evapotranspiration.

References

- Bolaños J and Edmeades GO (1993). Eight cycles of selection for drought tolerance in lowland tropical maize. I. Responses in grain yield, biomass, and radiation utilization. *Field Crops Research* 31:233–252.
- Bolaños J and Edmeades GO (1996). The importance of the anthesis-silking interval in breeding for drought tolerance in tropical maize. *Field Crops Research* 48:65–80.
- Bolaños J, Edmeades GO and Martinez L (1993). Eight cycles of selection for drought tolerance in lowland tropical maize. 3. Responses in drought-adaptive physiological and morphological traits. *Field Crops Research* 31:269–286.
- Borrell AK, Hammer GL and Douglas ACL (2000). Does maintaining green leaf area in sorghum improve yield under drought? I. Leaf growth and senescence. *Crop Science* 40:1026–1037.
- Bruce WB, Edmeades GO and Barker TC (2002). Molecular and physiological approaches to maize improvement for drought tolerance. *Journal of Experimental Botany* 53: 13–25.
- Chapman S, Cooper M, Podlich D and Hammer G (2003). Evaluating plant breeding strategies by simulating gene action and dryland environment effects. *Agronomy Journal* 95:99–113.
- Chenu K, Chapman SC, Hammer GL, McLean G, Salah HBH and Tardieu F (2008). Short-term responses of leaf growth rate to water deficit scale up to whole-plant and crop levels: an integrated modelling approach in maize. *Plant, Cell & Environment* 31:378–391.
- Claassen MM and Shaw RH (1970). Water deficit effects on corn. I. Vegetative components. *Agronomy Journal* 62:649–652.
- Condon AG, Richards RA, Rebetzke GJ and Farquhar GD (2004). Breeding for high water-use efficiency. *Journal of Experimental Botany* 55:2447–2460.
- de Dorlodot S, Forster B, Pages L, Price A, Tuberosa R and Draye X (2007). Root system architecture: opportunities and constraints for genetic improvement of crops. *Trends in Plant Science* 12:474–481.
- Gambin BL and Borrás L (2007). Plasticity of sorghum kernel weight to increased assimilate availability. *Field Crops Research* 100:272–284.
- Gosse G, Varlet Grancher C, Bonhomme R, Chartier M, Allirand JM, Lemaire G (1986). Maximum dry-matter production and solar-radiation intercepted by a canopy. *Agronomie* 6:47–56.
- Granier C and Tardieu F (1998). Is thermal time adequate for expressing the effects of temperature on sunflower leaf development? *Plant, Cell & Environment* 21:695–703.
- Hammer G, Cooper M, Tardieu F, Welch S, Walsh B, van Eeuwijk F, Chapman S and Podlich D (2006). Models for navigating biological complexity in breeding improved crop plants. *Trends in Plant Science* 11:587–593.
- Iuchi S, Kobayashi M, Taji T, Naramoto M, Seki M, Kato T, Tabata S, Kakubari Y, Yamaguchi-Shinozaki K, Shinozaki K (2001). Regulation of drought tolerance by gene manipulation of 9-cis-epoxycarotenoid dioxygenase, a key enzyme in abscisic acid biosynthesis in *Arabidopsis*. *The Plant Journal* 27:325–333.
- Jones HG (2007). Monitoring plant and soil water status: established and novel methods revisited and their relevance to studies of drought tolerance. *Journal of Experimental Botany* 58:119–130.
- Lafarge T and Tardieu F (2002). A model co-ordinating the elongation of all leaves of a sorghum cultivar was applied to both Mediterranean and Sahelian conditions. *Journal of Experimental Botany* 53:715–725.
- Maccaferri M, Sanguineti MC, Corneti S, Ortega JLA, Ben Salem M, Bort J, DeAmbrogio E, del Moral LFG, Demontis A, El-Ahmed A, Maalouf F, Machlab H, Martos V, Moragues M, Motawaj J, Nachit M, Nserallah N, Ouabbou H, Royo C, Slama A and Tuberosa R (2008). Quantitative trait loci for grain yield and adaptation of durum wheat (*Triticum durum* Desf) across a wide range of water availability. *Genetics* 178:489–511.
- Monteith JL (1977). Climate and the efficiency of crop production in Britain. *Philosophical Transactions of the Royal Society of London, B* 281:277–294.
- Passioura JB (1977). Grain-yield, harvest index, and water-use of wheat. *Journal of the Australian Institute of Agricultural Science* 43:117–120.
- Pic E, de la Serve BT, Tardieu F and Turc O (2002). Leaf senescence induced by mild water deficit follows the same sequence of macroscopic, biochemical, and molecular events as monocarpic senescence in pea. *Plant Physiology* 128:236–246.
- Rebetzke GJ, Condon AG, Richards RA and Farquhar GD (2002). Selection for reduced carbon isotope discrimination increases aerial biomass and grain yield of rainfed bread wheat. *Crop Science* 42:739–745.
- Reymond M, Muller B, Leonardi A, Charcosset A and Tardieu F (2003). Combining quantitative trait loci analysis and an ecophysiological model to analyze the genetic variability of the responses of maize leaf growth to temperature and water deficit. *Plant Physiology* 131:664–675.
- Ribaut J-M, Bänziger M, Setter T, Edmeades GO and Hoisington DA (2004). Genetic dissection of drought tolerance in maize: a case study. In: *Physiology and biotechnology integration for plant breeding* (Nguyen H and Blum A, eds). Marcel Dekker Inc, New York, USA, pp 571–611.
- Ribaut J-M, Jiang C, Gonzalez-de-Leon D, Edmeades GO and Hoisington DA (1997). Identification of quantitative trait loci under drought conditions in tropical maize. 2. Yield components and marker-assisted selection strategies. *Theoretical and Applied Genetics* 94:887–896.
- Richards RA and Passioura JB (1989). A breeding program to reduce the diameter of the major xylem vessel in the seminal roots of wheat and its effect on grain-yield in rain-fed environments. *Australian Journal of Agricultural Research* 40:943–950.
- Richards RA, Rebetzke GJ, Condon AG and van Herwaarden AF (2002). Breeding opportunities for increasing the efficiency of water use and crop yield in temperate cereals. *Crop Science* 42:111–121.
- Tardieu F (2003). Virtual plants: modelling as a tool for the genomics of tolerance to water deficit. *Trends in Plant Science* 8:9–14.
- Tardieu F, Bruckler L and Lafolie F (1992). Root clumping may affect the root water potential and the resistance to soil-root water transport. *Plant and Soil* 140:291–301.
- Tardieu F and Davies WJ (1993). Integration of hydraulic and chemical signaling in the control of stomatal conductance and water status of droughted plants. *Plant, Cell & Environment* 16:341–349.
- Tuberosa R, Sanguineti MC, Landi P, Michela Giuliani M, Salvi S and Conti S (2002). Identification of QTLs for root characteristics in maize grown in hydroponics and analysis of their overlap with QTLs for grain yield in the field at two water regimes. *Plant Molecular Biology* 48:697–712.
- Turc O and Lecoer J (1997). Leaf primordium initiation and expanded leaf production are co-ordinated through similar response to air temperature in pea (*Pisum sativum* L). *Annals of Botany* 80:265–273.
- Turner NC (1997). Further progress in crop water relations. *Advances in Agronomy* 58:293–338.
- Vargas M, van Eeuwijk FA, Crossa J and Ribaut J-M (2006). Mapping QTLs and QTL x environment interaction for CIMMYT maize drought stress program using factorial regression and partial least squares methods. *Theoretical and Applied Genetics* 112:1009–1023.
- Vega CRC, Andrade FH, Sadras VO, Uhart SA and Valentinuz OR (2001). Seed number as a function of growth. A comparative study in soybean, sunflower, and maize. *Crop Science* 41:748–754.
- Welcker C, Boussuge B, Bencivenni C, Ribaut JM and Tardieu F (2007). Are source and sink strengths genetically linked in maize plants subjected to water deficit? A QTL study of the responses of leaf growth and of anthesis-silking interval to water deficit. *Journal of Experimental Botany* 58:339–349.
- Zinselmeier C, Jeong BR and Boyer JS (1999). Starch and the control of kernel number in maize at low water potentials. *Plant Physiology* 121:25–35.

© 2011 CGIAR Generation Challenge Programme/CIMMYT

Published under the Creative Commons Attribution-NonCommercial-ShareAlike 2.5 Mexico licence. This licence allows all users to read, copy (in full or in part), distribute or adapt this work, providing that they: (i) acknowledge GCP as the original author of the work; (ii) do not use it for commercial purposes; and, (iii) require other users to observe conditions (i) and (ii), (ie, other parties must also acknowledge GCP and only use the work for non-commercial purposes).

Correct citation: *Drought phenotyping in crops: from theory to practice* (Monneveux Philippe and Ribaut Jean-Marcel, eds). CGIAR Generation Challenge Programme, Texcoco, Mexico.

ISBN: 978-970-648-178-8

Dewey Decimal Classification: 631.53

AGROVOC Descriptors: crops; phenotypes; mapping; genotypes; drought; drought resistance; drought stress; drought tolerance; experimental design; environmental conditions; rice; wheat; maize; sorghum; pearl millet; common beans; chickpeas; pigeonpeas; cowpeas; groundnuts; cassava; sweet potatoes; bananas and plantains

Additional keywords: CIMMYT; CGIAR Generation Challenge Programme

AGRIS category codes: F30 Plant Genetics and Breeding, H50 Miscellaneous Plant Disorders

Edited by: Lyndsey Withers

Editorial management, photo sourcing and selection: Gillian Summers and Antonia Okono

Cover illustration: Recomposition by Miguel Mellado based on original artwork by Rhoda Okono entitled *In the house of life* and *Desert bloom Meztnopalli*.

Art direction: Miguel Mellado, CIMMYT

Design and layout: Miguel Mellado, Eliot Sanchez, and Marcelo Ortiz, CIMMYT

Available online at: www.generationcp.org/drought_phenotyping