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Characterizing the crop environment – nature, significance and applications

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1 INTRODUCTION

Progress in plant improvement for yield relies on the identification of genotypes better adapted to their production environment. However, the complexity of genotype \times environment ($G \times E$) interactions typically reduces heritability of yield, resulting in slow breeding progress, especially in production environments where complex abiotic stresses, such as drought, are frequent. Over the last decades, productivity improvement in crops like wheat has been limited, especially in rain-fed regions (Graybosch and Peterson, 2010; Richards et al., 2010). A possible factor inhibiting progress may be that breeders tend to focus on selection for disease resistance, and then yield and quality (Richards, 1996), but they generally lack reliable methods for selecting tolerance to abiotic stresses, such as drought.

A range of abiotic stresses affect to varying degrees different genes and physiological

processes depending on the timing, intensity, duration and history (acclimation) of the stress in regards to the crop cycle (Slafer, 2003; Hammer et al., 2006; Fischer, 2011). For drought, $G \times E$ interactions may originate from environmental variations in the timing and severity of the water deficit (Cooper et al., 1999a; Chenu et al., 2011), from genetic variations, e.g. in flowering time or in rate of water uptake (Pantuwan et al., 2002; Chenu et al., 2009a), and from interactions with nutrient supply and biotic stresses (Cooper et al., 1999b; Bänziger and Cooper, 2001; Chapter 7). As a result, the pertinence of gene, trait and germplasm evaluation is highly dependent on how relevant the growing environment is compared to the target population of environments (TPE; Comstock, 1977).

In breeding trials, the source of yield variation arises primarily from the environment (E), secondly from the ($G \times E$) interactions and, finally, from the genotype (G), i.e. $E > G \times E > G$.

For instance, for a series of crops grown in different environments including field pea in Canada (Yang et al., 2005), sunflower in Argentina (de la Vega et al., 2007), wheat in Queensland (Cooper et al., 1995), sugar beet in Europe (Hoffmann et al., 2009), and maize in Midwestern USA (Alwala et al., 2010), the yield variation explained by the environment (E) was between 48 and 93%, compared to 4–35% for $G \times E$ interactions and 1–16% for the genotype (G). However, the resources invested to deal with these sources of variation rank in the opposite order: $G > G \times E > E$ (Bernardo, 2001; Sadras et al., 2009; Varshney et al., 2011) and refined methods used to characterize genotypes often contrast with the coarse methods applied to characterize breeding-trial environments (Varshney et al., 2011). Different methods have been developed and deployed to deal with environmental variability and $G \times E$ in breeding and genetic studies. They include increasingly sophisticated statistical tools (Cooper et al., 1995; Basford and Cooper, 1998; Lacaze et al., 2009; van Eeuwijk et al., 2010), and environmental characterization as described here.

This chapter focuses on characterization of the crop environment in a breeding context, with an emphasis on drought stresses. The first section examines characterization of the target population of environments (TPE) to understand better the prevalent types of crop production environments over long-term periods. The second section focuses on characterization of local environments (e.g. trials) and how these can be used to extrapolate locally observed phenotypes to overall performances expected in the TPE. In the third section, managed environment facilities are discussed as another way to deal with environmental variability, as management interventions can be used to target environments that best reflect the TPE or that maximize relevant germplasm discrimination. The final section (4) illustrates how environment characterization can assist the identification of adapted traits for the TPE.

2 CHARACTERIZATION OF THE TARGET POPULATION OF ENVIRONMENTS (TPE) – A BETTER UNDERSTANDING OF THE NATURE, DISTRIBUTION AND FREQUENCY OF THE MAIN ENVIRONMENT CLASSES

2.1 Importance of characterizing the TPE

Multi-environment trials (MET) of small breeding programs typically involve trials over a few years at several locations, and are often considered to reflect the overall TPE. While screening for genotype performance in MET allows germplasm improvement for the tested environments, MET may misrepresent the TPE and thus lead to the release of germplasm that is poorly adapted to the true production environment. Hence, breeder's elite pool of germplasm can oscillate between adapted and non-adapted depending, for example, on how seasonal conditions affect the MET. For instance, selecting for yield during a few consecutive wet years in a generally drought-prone TPE can bias the selection towards slow-maturing genotypes, as these can accumulate more resources over their longer lifespan than quick-maturing genotypes, and thus better perform during *good* years. However in *bad* years, slow-maturing genotypes are more likely to suffer severe terminal drought. Selection can thus potentially alternate between late and early maturity or between low and high values of other adaptive traits, as crop environments vary across seasons. To avoid such bias, breeders should consider how their MET compare to the overall TPE. This requires understanding of the TPE.

2.2 Different types of environment classification

The characterization of a TPE is typically conducted to identify key environment classes affecting genotype performance. These

environment classes (e.g. 'mega-environments', 'macro-environments', 'environment types') are groupings of environments that are relatively homogeneous within the TPE, in which genotypes are expected to perform similarly. Environments may be grouped according to geographical locations (country, region), physical characteristics (e.g. altitude, photoperiod, temperature, rainfall), stress factors (e.g. drought, heat) or directly by their effect on genotype performance. These criteria have been used in a variety of combinations and, more recently, with additional input from crop modeling. Ultimately, environment classes are typically described as either

1. '*groups of locations*', also called '*mega-environments*' when they refer to a broad spatial area. These classes generally encompass various types of stresses, and year-to-year variations. The international maize and wheat improvement center (CIMMYT) defines a mega-environment as a 'broad, not necessarily contiguous area, occurring in more than one country and frequently transcontinental, defined by similar biotic and abiotic stresses, cropping system requirements, consumer preferences and, for convenience, by a volume of production' (e.g. [Braun et al., 1996](#))
2. '*environment types*' when they refer to specific environments experienced by crops. These are not location specific but are defined by *explicit ranges of climatic factors or stress patterns which affect the crops*. Thus, environment types are based on specific site-year-management-genotype combinations rather than on locations. Accordingly, various environment types can be found at a specific location or within a given mega-environment.

Overall, methods used to characterize a TPE are mostly based either on (1) yield, which is the *end-product* trait broadly integrating all environmental factors that influence crops over

their lifespan ([Chapman et al., 1997](#); [Chauhan et al., 2008](#); [Hernandez-Segundo et al., 2009](#)), (2) multifactor pedo-climatic analysis ([Runge, 1968](#); [Pollak and Corbett, 1993](#); [Chapman and Barreto, 1996](#); [Hodson and White, 2007](#)), or (3) stress index reflecting the intensity and timing of key stress(es) to which crops are exposed (e.g. [Lacaze and Roumet, 2004](#); [Chapman, 2008](#)).

In all cases, the quality of the TPE characterization depends on the relevance of the database (e.g. representativeness of the sites, years and management practices) and on the criteria and method used to define the environment classes.

2.2.1 Yield-based characterization

TRIAL-BASED CHARACTERIZATION – CAPTURING G × E INTERACTIONS

The advantage of using yield to characterize the TPE is that this trait is usually the main target, and reflects the integration of environmental factors that influenced crop growth (e.g. temperature, drought, nutrient availability). Accordingly, breeders typically define environment groups based on similarities in germplasm yield response rather than using environmental variations *per se* and use performance in multi-year, multilocation trials to characterize their TPE. Hence, environment classes are generally defined by homogeneous subsets of trials or sites identified using clustering techniques applied to genotype performance data ([Horner and Frey, 1957](#); [Abou-El-Fittouh et al., 1969](#); [Ghaderi et al., 1980](#); [Brown et al., 1983](#); [Collaku et al., 2002](#)). Such groupings allow G × E interactions to be minimized within groups, while maximized among groups ([Malhotra and Singh, 1991](#); [Russell et al., 2003](#)). This approach has been in use for decades. For example, [Horner and Frey \(1957\)](#) reduced G × E variances of oat trials by 11, 21, 30 and 40% by dividing the state of Iowa (USA) into 2, 3, 4 and 5 subregions, respectively. More sophisticated grouping methods have been developed since ([DeLacy and Cooper, 1990](#); [Crossa et al., 1993](#); [Trethowan et al., 2001](#); [Yang et al., 2005](#)).

A major limitation of yield-based approaches is that, in many breeding programs, they are applied to only a limited set of years and sites that are likely to misrepresent the TPE, as longer-term weather patterns of the TPE are not considered. [Yang et al. \(2005\)](#) illustrated how characterization of an extreme case, using single-year data, led to site grouping that was highly varied from year to year. Their results highlight the importance of working with a relevant set of trials, preferably over a long period, when characterizing a TPE. While germplasm pools are constantly evolving in breeding programs with frequent turn-over of genotypes, long-term consistency can be achieved by comparing germplasm performance to a check variety that is grown consistently over the years and is used as a sort of ‘environmental probe’ ([Cooper and Fox, 1996](#); [Brancourt-Hulmel, 1999](#); [Mathews et al., 2011](#); [Forkman, 2013](#)).

Long-term analyses of field trials have been used by major breeding programs to define large TPEs. For instance, the ICARDA–CIMMYT barley breeding program used yield data of 25–50 genotypes from 750 trials (235 locations in 75 countries over 27 years with 10–50 trials per year) to identify three mega-environments across the world ([Hernandez-Segundo et al., 2009](#)). For convenience, the mega-environments were also coarsely described in terms of environmental factors (temperature and precipitation). Numerous similar studies have been performed for various crops, usually at smaller scales, for fewer years and within specific production regions or countries (e.g. [de la Vega et al., 2001](#); [Yang et al., 2005](#)).

As both biotic and abiotic factors can influence the determination of environment classes (e.g. [Hernandez-Segundo et al., 2009](#)), trials affected by pest and diseases are often excluded from the TPE characterization, while tolerance to biotic factors is screened separately (e.g. [Mathews et al., 2011](#)). In practice, disease occurrence is often predominately associated with specific environment classes (e.g. [Bänziger et al., 2006](#); [Hernandez-Segundo et al., 2009](#)).

MODELLING-BASED CHARACTERIZATION – SIMULATION OF A WIDE RANGE OF ENVIRONMENTS

Modeling tools offer another avenue to characterize TPEs as they allow more comprehensive environmental sampling than is possible with experiments (e.g. [Löffler et al., 2005](#); [Hammer and Jordan, 2007](#)). While the relevance of sites (soil and climate) and management practices chosen to represent the cropping production system of the region remain criteria of prime importance, crop productivity can be simulated over decades or more using crop modeling, provided soil and historical climatic data are available. Characterizations based on simulated yield have been done for maize and mungbean in Australia ([Fig. 13.1](#); [Chauhan et al., 2013, 2014](#)) and for chickpea in India and Australia ([Chauhan et al., 2008](#)). In addition to yield, these authors also considered flowering time and maturity to at least partly account for phenology impact on yield. While simulation approaches help to explore spatial and temporal variability for yield (or other traits), these characterizations remain constrained by the limits of the models used (e.g. generally do not account for extreme temperatures and toxicities). In addition, simulation-based characterizations are currently restricted to a limited number of genotypes with studies generally conducted for a standard well-characterized genotype. However, such TPE characterizations can be complemented by experimental data with multiple genotypes to ensure their relevance (e.g. [Löffler et al., 2005](#); [Chenu et al., 2011](#)). To be useful, environment classes are expected to be such that $G \times E$ (or the ratio $G \times E/G$) is substantially lower in trials within, compared to across, environment classes.

Yield-based TPE can be characterized by environment classes that are either spatially contiguous (e.g. [Bänziger et al., 2006](#); [Chauhan et al., 2013](#)) or not (e.g. [Yang et al., 2005](#); [Hernandez-Segundo et al., 2009](#)). In some cases, the identification of continuous or discontinuous

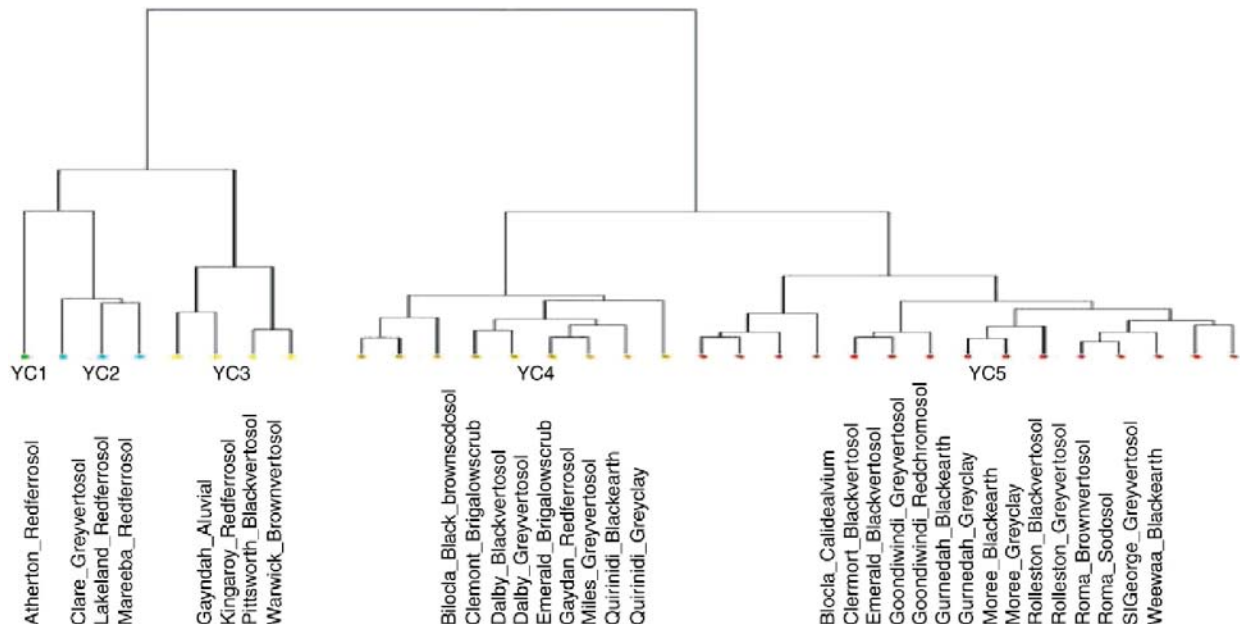


FIG. 13.1 Maize environment characterization based on yield variation. Sites of the maize breeding program from north-eastern Australia were classified based on long-term simulation, using hierarchical clustering on cumulative probability of simulated yield. Source: [Chauhan et al. \(2013\)](#).

classes may only depend on the method used for the characterization (Chauhan et al., 2014), highlighting the sensitivity and thus importance of the method used to characterize a TPE.

2.2.2 *Pedo-climatic characterization*

Physical variables (soil and climate characteristics) can be considered logical bases for TPE characterization (e.g. [Pollak and Corbett, 1993](#); [Berger and Turner, 2007](#)), given their long-established influence on crop performance (e.g. [Yates and Cochran, 1938](#); [Grafius and Kiesling, 1960](#)) and on $G \times E$ interactions (e.g. [Nor and Cady, 1979](#); [Malosetti et al., 2004](#); [Drecer et al., 2008](#); [van Eeuwijk et al., 2010](#)). TPE characterization based on site pedo-climatic conditions offers substantial advantages, as they allow wide spatial and temporal characterizations (provided data are available) without experimentation. Accordingly, new evaluation sites can also be potentially classified and integrated into an existing pedo-climatic characterization,

without any need for new multiple-year trials beforehand.

Facing the major challenge to breed wheat and maize for the benefit of the developing world, CIMMYT began defining mega-environments in the late 1980s to develop breeding programs targeting each mega-environment. In the case of bread and durum wheat, CIMMYT is interested in a crop which occupies an estimated 200 million ha globally, ranging from sea level to over 3500 m of altitude, and from the equator to Canada, Europe, and Asia in the northern hemisphere and to South America and Australia in the southern hemisphere ([FAOSTAT, 2005](#)). The CIMMYT wheat mega-environments were first defined generically on the bases of key components such as rainfall and temperature, e.g. 'high rainfall' vs 'low rainfall' or 'moderate cold' vs 'severe cold' ([Braun et al., 1996](#)). Since, advances in geographic information systems (GIS), agro-climatic datasets (e.g. [Hijmans et al., 2005](#)) and irrigated area

databases (Siebert et al., 2005) have permitted global mapping of wheat mega-environments based on more quantitative climate, soil, and management data that are now used for breeding (Hodson and White, 2007).

A slightly different approach has been used to characterize the production environment of maize in southern Africa, where the crop is grown on over 12 million hectares (FAOSTAT, 2003). Here, eight mega-environments were identified from a cluster analysis applied to the most prominent $G \times E$ grouped trial sites, using data from 290 genotypes over 3 years at 94 sites (Setimela et al., 2002; Bänziger et al., 2006). As the mega-environments could be distinguished by environmental factors such as season rainfall, maximum temperature and subsoil pH, a map was produced to delineate the geographic boundaries of the mega-environments using GIS (Fig. 13.2a; Hodson et al., 2002).

Private breeding companies have also defined and used TPE characterization. Pioneer Hi-Bred International Inc. identified five mega-environments for maize in the USA based on variation in photoperiod, maximum temperature and average radiation (Fig. 13.2b; Löffler et al., 2005). In their case, the environment classes were defined for different periods of the crop cycle and calculated through crop modeling.

While both pedo-climatic and yield-based characterizations may improve our understanding of production environments, these are typically used to group locations into mega-environments and are thus *de facto* considering environmental conditions as ‘static’. Methods have been developed to integrate the year-to-year variability in the characterization of sites. However, the classification of a site into a single mega-environment infers that all trials at this site will be classified as belonging to the same mega-environment, irrespective of specific weather and management conditions for each season. In reality, sites may belong to different mega-environments depending on the season (e.g. Trethowan et al., 2005a; Yang et al., 2005).

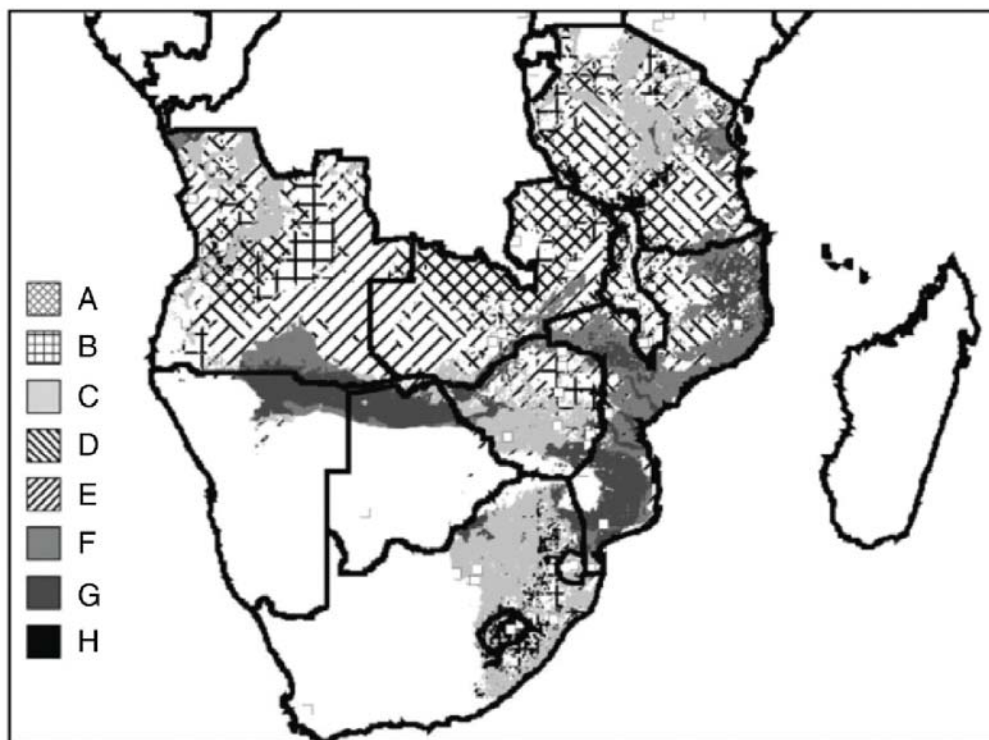
This highlights the need for a more ‘dynamic’ approach that relates to the environment that crops are experiencing during part of or the whole crop cycle. In contrast to the ‘site’ approaches, dynamic approaches apply to specific trials or even to specific genotypes in those trials (e.g. an early-maturing genotype may avoid a terminal stress). As for the ‘site’ approaches, characterizations can be based on yield or pedo-climatic data as long as environments are classified based on conditions that apply to the crop (i.e. in terms of the specific genotype–site–year–management combination) and not the site alone (i.e. with all environments at a site classified into a unique mega-environment).

2.2.3 Specific-stress characterization

To focus on the environment experienced by the crops *per se*, TPE characterization can be based on stress patterns or environmental factors occurring over the crop cycle or at specific phenological stages. Modeling approaches have been developed to estimate phenological stages (e.g. Löffler et al., 2005; Zheng et al., 2013), quantify the local plant/crop environment (e.g. Chelle, 2005; Chenu et al., 2008b), and capture the interactions between the plants and their environment (e.g. Chenu et al., 2008a). For instance in the case of drought, crop models capture feedbacks between plant growth and soil water depletion, e.g. genotypes with rapidly developing canopies will generally deplete soil water quicker than less vigorous genotypes. Accordingly, crop models have been shown to characterize water-limited environments better than standard climatic indices (Muchow et al., 1996). As a result, they have been used to characterize drought environments (see below), in a similar way as previously done with weather indices (e.g. Palmer, 1965; Chapman and Barreto, 1996).

TPE characterization has applied to different stresses (e.g. drought, heat). In the case of drought, long-term simulations have been carried out for various sites, soils and

a- Maize mega-environments in southern Africa



b- Maize environment classes in the U.S.A.

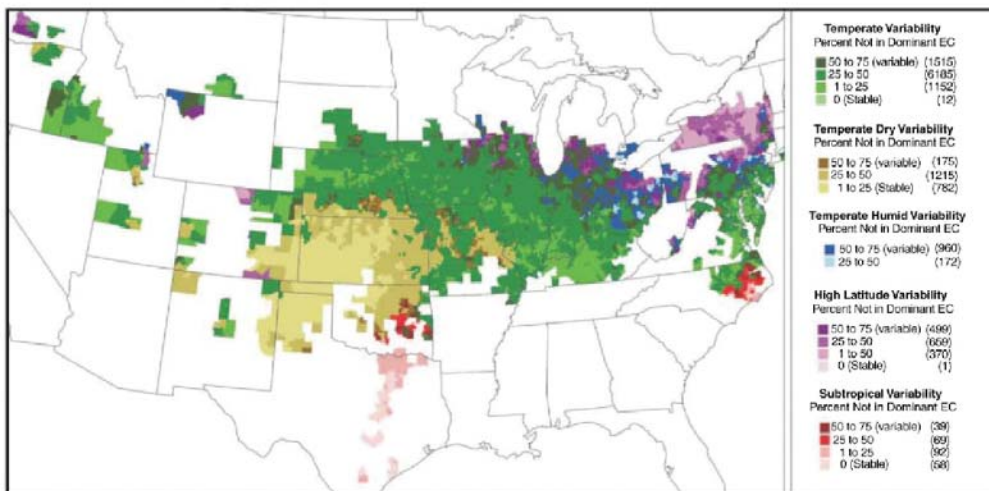


FIG. 13.2 Environment characterization based on pedo-climatic factors. (a) Public breeding organization CIMMYT identified eight maize mega-environments (A–H) in southern Africa that were defined by combination of maximum temperature, seasonal rainfall and subsoil pH. Figure from [Bänziger et al. \(2006\)](#). (b) Private breeding company Pioneer Hi-Bred International Inc. identified five major abiotic environment classes (EC) for the US Corn Belt, for which geographic distribution and variability are presented here. The major environment classes (‘Subtropical’, ‘High Latitude’, ‘Temperate Dry’, ‘Temperate Humid’ and ‘Temperate’) were defined in regards to photoperiod, maximum temperature and average solar radiation. Source: [Löffler et al. \(2005\)](#).

3. GENETIC IMPROVEMENT AND AGRONOMY

management strategies to determine the timing, intensity and frequency of drought that crops experience in a TPE (Fig. 13.3). Such studies have been carried out for various crops and regions, such as sorghum, wheat, barley, field pea, maize and mungbean in Australia (Chapman et al., 2000a; Chenu et al., 2009b, 2011, 2013a; Sadras et al., 2012; Chauhan et al., 2013, 2014); rice and maize in part of Brazil (Heinemann et al., 2008; Chenu et al., 2009a); millet in India (Kholová et al., 2013) and maize in Europe (Harrison et al., 2014). These drought characterizations are all based on the approach first proposed by Muchow et al. (1996) and Chapman et al. (2000a), where environments are clustered based on the drought seasonal pattern experienced by the crop, and usually centered at flowering. The drought pattern in this case corresponds to the fluctuation over time of a water-stress index calculated as the ratio between modeled water supply and demand (Chapman et al., 1993; Chenu et al., 2013a), which indicates the degree to which the soil water extractable by the roots ('water supply') is able to match the potential transpiration ('water demand'). Better to represent TPEs, Chenu et al. (2011) have proposed applying a weight to the simulations based on the degree to which they represent the production environments. Chenu et al. (2013a) also stressed the importance of the choice of soil, site (climate) and management (including the cultivar) given their substantial influence on the environment characterization (Fig. 13.4). However, the nature of the drought patterns can be quite consistent across regions, despite large variation in soil characteristics and rainfall patterns (Chenu et al., 2013a). This might be partly explained by the method applied (e.g. smoothing of the drought pattern by averaging stress indexes every 100°Cd) and by producer practices that restrain certain types of stresses (e.g. early vegetative stress). While the nature of the main drought patterns can be quite stable across regions, their frequency of occurrence varies greatly both spatially and temporally (Fig. 13.4; e.g. Chapman et al., 2000b, 2002a;

Chenu et al., 2011, 2013a). Interestingly, similarities in drought patterns can also be observed at a broader level, across crops and TPEs (Fig. 13.3). Most TPEs seem to include an environment type defined by little or no stress, while other environment types typically involve water stresses that begin before or at flowering (Fig. 13.3). The stresses are then generally released during grain filling in one environment type, while they are maintained till maturity in another environment type. In none of the previously mentioned studies was an early vegetative stress identified as a characteristic of a major environment type, partly due to the fact that stress around germination was not examined, as producers rarely sow in conditions where this type of risk is high. However, these early-season stresses may indeed occur in some TPEs (e.g. sowing of subsistence crops in developing countries, Chapter 5) and could become more frequent with the increasing adoption of dry sowing in places like Australia. From the studies mentioned above (Fig. 13.3), it appears that the earliest vegetative stresses of the environment types tend to begin 300–600°Cd before flowering in wheat, maize and field pea in Australia, and millet in India, when they are expected to greatly impact grain number and thus yield (e.g. Chenu et al., 2013a).

Minimum and maximum temperature for either critical stages or the whole crop cycle have also been used to characterize environments (e.g. Löffler et al., 2005; Sadras et al., 2012; Zheng et al., 2012). Correlations exist among climatic/stress variables, as they often co-vary in space and time (Rodríguez and Sadras, 2007). For instance, negative associations exist between water supply/demand ratio and maximum temperature (e.g. Sadras et al., 2012). However, despite the statistically significant association between these variables, severe water stress can occur under mild temperatures and, conversely, thermal stress can occur with mild water stress.

Different stresses and/or climatic variables can be combined either with a unique or with several environment characterizations, although

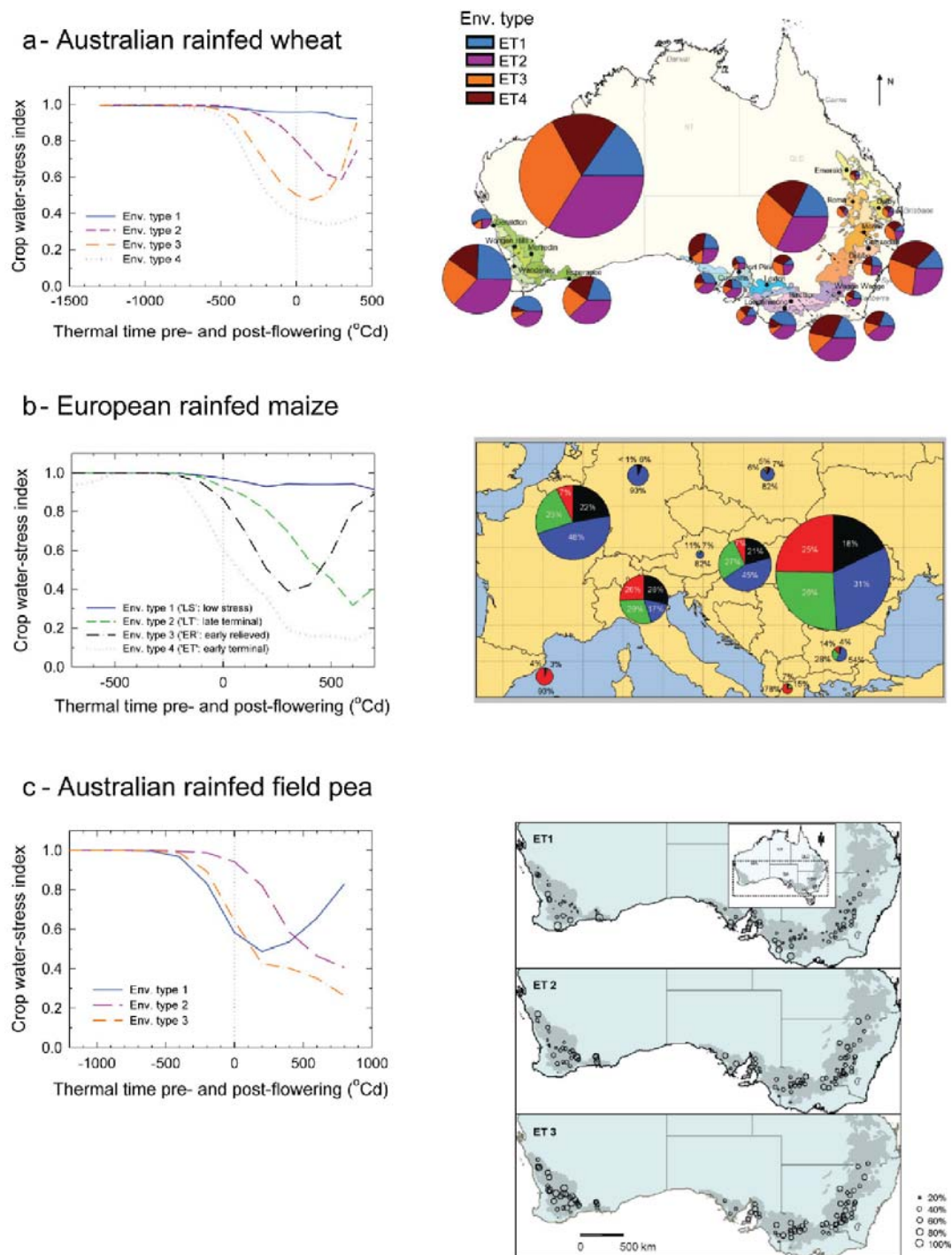


FIG. 13.3 Drought environment characterization for (a) rain-fed wheat in Australia, (b) maize in Europe and (c) field pea in Australia. Dominant water-stress index patterns expressed as thermal time before or after anthesis are presented on the left of the figure, while the distribution of their frequency is displayed on the right. In (a–b), the pie-chart size is proportional to the regional (for wheat) or national (for maize) average cropped area (wheat) or harvest (maize), while in (c), the size of the circle corresponds to the frequency of environment types (ET) at various locations. The crop water-stress index (or ‘water supply/demand ratio’) indicates the degree to which the potential water supply that depends on the volume and wetness of soil explored by roots (‘water supply’) is able to match the ‘water demand’ of the canopy, which is influenced by radiation and temperature and air humidity conditions. See [Chapman et al. \(1993\)](#) or [Chenu et al. \(2013a\)](#) for details.

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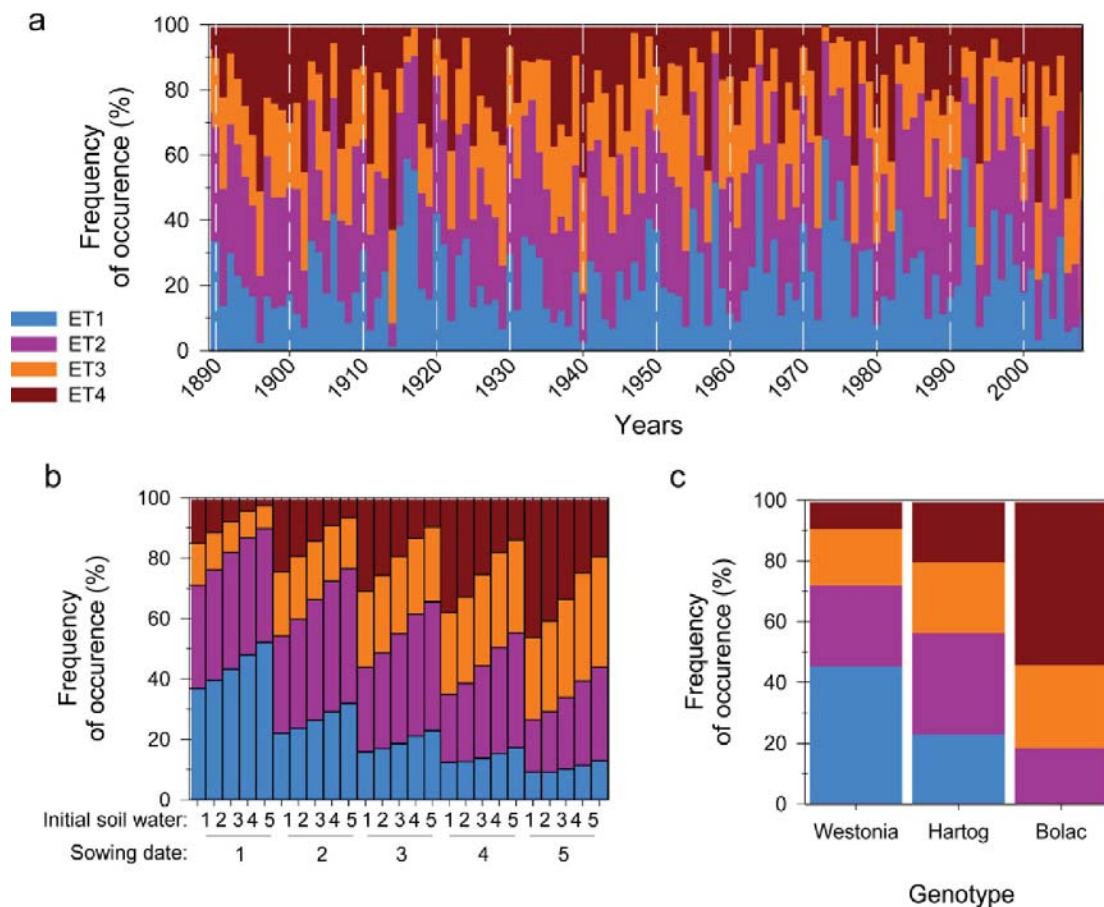


FIG. 13.4 Change in occurrence of drought-environment types for rain-fed Australian wheat (a) over time, (b) with different management practices and (c) for different genotypes. The environment types (ET1–4) correspond to those described in Figure 13.3a. Sowing dates are presented from the earliest (1) to the latest (5), with each sowing date representing 20% of the simulated sowing opportunities. Initial soil water increased from the lowest (1; most severe conditions) to the highest (5; less severe) values, each representing 20% of the simulated initial soil water availability. Simulations were performed for a standard, medium-maturing variety ('Hartog') in (a–b) as well as for an early-maturing ('Westonia') and a late-maturing ('Bolac') variety in (c). For details and information concerning spatial variability, see Chenu et al. (2013a). Source: Chenu et al. (2013a).

correlations between variables and interactions of their impact on crops complicate the task. In Australian rain-fed maize and mungbean, Chauhan et al. (2013, 2014) showed that environment classes for yield distribution were related to the environment types for drought, thus confirming the relevance of drought characterization in the search for crop adaptation in these TPEs.

How to characterize a TPE depends on the region, crop and management practices, as well as

the aim, e.g. broad vs specific adaptation. However, to be directly useful for breeders, the characterization should have a substantial influence on $G \times E$, and assist in better understanding of the genetic correlations for genotype performance among testing sites. Hence, most relevant characterizations are likely to concern major limiting stresses (e.g. drought in Australia) or combine a series of important environmental variables (e.g. Löffler et al., 2005).

2.3 Comparison of environments (regions), genotypes and management practices to assist site and management selection, germplasm exchange, global data analysis, and adaptation to future climates

2.3.1 Breeding-trial locations and management practices

Brown et al. (1983) defined an *optimum* selection environment as one in which (1) the targeted trait is expressed, (2) genetic variance is maximized, (3) environmental and $G \times E$ variances are minimized, (4) the growing region of the germplasm tested is accurately represented, (5) the environment is accessible for efficient and inexpensive screening and (6) conditions 1–5 are consistent over years. An environment characterization of the TPE provides a basis for choosing representative sites and management practices, and may also possibly allow the scaling down of testing programs by identifying smaller sets of representative test sites. For instance, based on groupings derived from correlations for traits between sites, Guitard (1960) found that the number of barley test locations in Alberta could be reduced from 10 to 5 without appreciable loss of information. Using similar analyses in sunflower, de la Vega and Chapman (2006) revealed that hybrid performance in remote northern Argentina could be well predicted by late-sown trials in central Argentina (the main breeding zone), which has since facilitated the early identification of candidate northern hybrids and allowed substantial savings of breeding resources.

The selection of most evaluation sites typically relies on the postulate that a genotype developed at one location (or with a managed stress) is expected to perform well at other locations within the same mega-environment (e.g. Malhotra and Singh, 1991). Although environments vary from one year to another due to climatic variability, developing germplasm in locations where major types of stress are predominant is expected to improve rates of yield gain over selection cycles (e.g. Chapman et al., 2003; Hammer et al., 2005).

Where year-to-year variations are high, evaluation trials should thus be located at sites known to experience high frequency of targeted environment types, and/or use managed environments (section 4).

2.3.2 Exchange of germplasm

In addition to rationalizing testing-trial locations and management, TPE characterization may be useful for improving the efficiency of national and international germplasm exchanges, and introducing high-yielding cultivars into new regions based on environmental similarities. Using such an approach, CIMMYT is running selection trials in worldwide mega-environments and developing widely-adapted germplasm (e.g. Mathews et al., 2007, 2011; Hernandez-Segundo et al., 2009). Large importations of CIMMYT wheat germplasm have occurred in Australia given the environmental similarities between certain CIMMYT testing sites and the drought-prone Australian production area (e.g. Cooper et al., 1997; Brennan and Fox, 1998; Brennan and Quade, 2006). In particular, wheat grown in Australia's north-eastern region experiences drought stresses similar to those of CIMMYT mega-environments ME1, ME4c and ME5, which are also generated via specific management practices in Mexico (e.g. Braun et al., 1996; Trethowan et al., 2005b; Rattey and Shorter, 2010). Accordingly, strong genetic correlations have been observed between Australian environments and those at CIMMYT stations in Mexico (Mathews et al., 2007). The value of germplasm exchange across breeding programs that share similar mega-environments is such that Australia now systematically introduces wheat germplasm from CIMMYT (CAIGE program; <http://gwis.lafs.uq.edu.au/index.php/cagections>).

Other tools have been developed to mine germplasm of potential interest for particular environment classes. For instance, based on the premise that adaptive traits should reflect the selection pressures of the environment from which accessions were originally sampled (e.g. Mackay

et al., 2005), the Focused Identification of Germplasm Strategy (FIGS) combines environmental and plant characteristics to facilitate the identification of germplasm with traits of potential interest for particular environments (e.g. Khazaei et al., 2013).

2.3.3 Adaptation to future climates

Using climatic forecasts in crop modeling is a way to simulate future expected changes within TPEs. Using this approach, a recent study revealed that no major change in the main range of drought patterns is foreseen for European maize, however, their occurrence is expected to shift toward more frequent incidence of the more severe drought patterns (Harrison et al., 2014). Similar results were found previously for wheat in Australia (Chenu and Chapman, 2012).

Simulations of adaptation to future climates are still in the early stages and need to be interpreted carefully, as (1) current studies typically do not account for adaptation in management practices (e.g. Zheng et al., 2012), (2) daily prediction of future climates (as required for crop modeling) remain uncertain with predictive climate models under constant evolution (e.g. Semenov et al., 2010), and (3) crop models are currently missing the capability to simulate extreme events (e.g. Lobell et al., 2012). Chapter 20 further discusses the application of modeling tools to characterize cropping systems under future climate scenarios.

3 TRIAL CHARACTERIZATION – ADDING VALUE TO FIELD DATA THROUGH IMPROVED UNDERSTANDING OF THE GENOTYPIC VARIABILITY

3.1 Environment characterization at the trial level

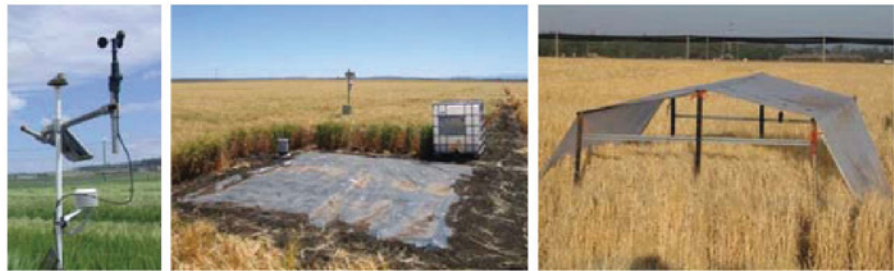
Breeders typically characterize the environment of selection trials indirectly, based on

genotype discrimination for crop performance as described in section 2.2.1. As for the TPE characterization, alternatives have been deployed, with trial characterization based on pedo-climatic or stress variables. The relevance of these alternative approaches depends on how variable the considered factors are (i.e. factors stable across trials are not helpful), and how these factors influence yield $G \times E$ interactions, especially cross-over interactions (i.e. variation in genotypes ranking among trials). Advantages of pedo-climatic and stress-based methods include: (1) independence from the performance of genotypes used in trials; and (2) capacity for comparison of trials from a breeding program (MET) with the targeted environments (TPE), thus indicating how well the TPE is represented by the trials.

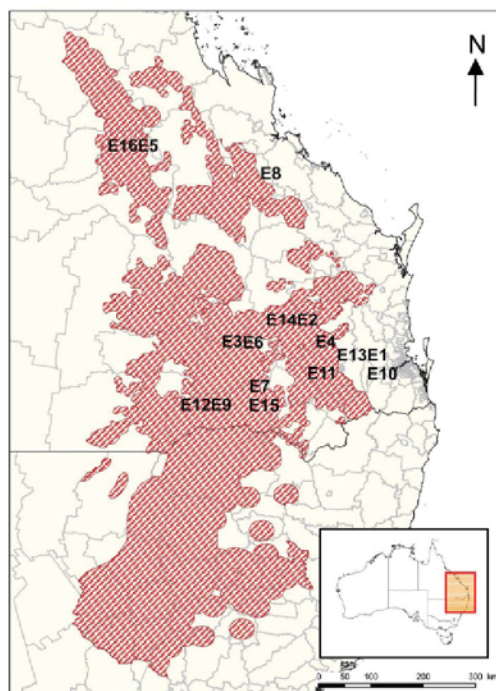
To enable MET–TPE comparison, trial characterization has to be performed in ways that relate to the TPE characterization. When the TPE is defined by continuous geographical area (Fig. 13.2a; Bänziger et al., 2006) or by climatic characteristics (e.g. Hodson and White, 2007), the trial characterization is generally based on the location or the long-term climatic records at the site (i.e. with no account of the particular seasonal environment specific to the trial). For characterizations using pedo-climatic variables or stress indexes, which account for the conditions that crops experience at a particular trial (e.g. Chenu et al., 2011), data specific to the trial are required. This trial information can come from measurements for certain pedo-climatic factors, or from modeling in the case of complex stresses such as drought, where interactions between the crops and their environment have to be accounted for (e.g. Chapman et al., 2000a; Chenu et al., 2011). An example of drought characterization for a MET is presented in Figure 13.5, including steps for soil and climate characterization, trial modeling, testing/validation of the model for those trials using a check genotype, classification of simulated drought patterns from the trials into their respective environment types, and finally $G \times E$ analysis. Other types of detailed

FIG. 13.5 Environment characterization for wheat breeding trials in north-eastern Australia. Measurements of weather and soil data, in particular estimation of the drained upper limit and the crop lower limit (a) were required to simulate crops at specific trials. The example presented here involves 16 wheat trials (E1–E16) of a breeding program in the Australian north-eastern production area (red hashed area) (b), for which drought patterns were characterized using crop modeling (c). Simulations were done for a standard cultivar with the APSIM crop model (Keating *et al.*, 2003). The main drought-environment types (ET1–3) of the studied TPE are presented with dashed lines in (c). Out of the 16 trials, three were classified as environment type 1 (ET1), four trials ET2, and nine trials ET3. Overall, compared to the TPE, this 16-trial MET slightly over-represented ET1 (22% vs 16% in the TPE) and slightly under-represented ET2 (28% vs 34%), while both the TPE and the MET had the same proportion of ET3 (50%). Including the drought characterization in the trial analysis assisted the interpretation of the observed genotype-environment interactions (d). Figure adapted from Chenu *et al.* (2011), with permission from Oxford University Press and the Queensland Government © 2011.

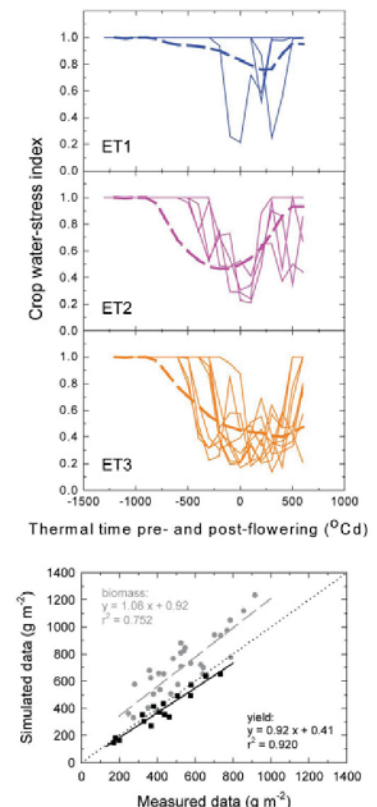
a- Weather and soil measurements



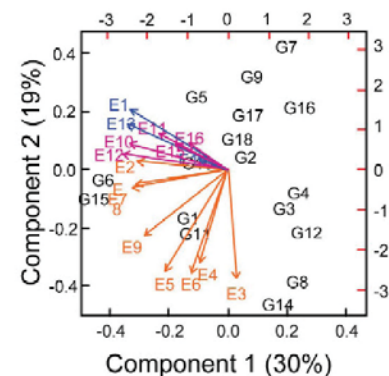
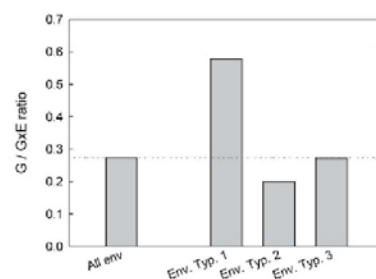
b- Multiple Environment Trials (MET)



c- Trial simulation



d- Genotype x Environment analysis



3. GENETIC IMPROVEMENT AND AGRONOMY

trial characterizations have been proposed for studies on plant physiology in both field and controlled environments (e.g. Chelle, 2005; Louarn et al., 2008; Chenu et al., 2008b).

While pests and diseases are usually excluded from the TPE characterization, they might strongly impact genotype performance in MET, and have to be considered appropriately. Affected trials might need to be analyzed separately (e.g. Mathews et al., 2011). Alternatively, the importance of a disease might justify its direct integration into the TPE and trial characterizations (e.g. Löffler et al., 2005).

Variations in genotype maturity are also to be considered and accounted for in the trial characterization or data analysis, as they strongly influence $G \times E$ interactions for yield (e.g. Bänziger and Cooper, 2001). Genotypes with contrasting phenology (e.g. short vs long crop cycle) are likely to experience different environments even within the same trial (e.g. stress occurring after vs before flowering). The environments of particular genotypes can be characterized separately, e.g. using crop modeling or, alternatively, yield in each trial can be adjusted for flowering date or other traits (e.g. Bänziger et al., 2006).

3.2 Genotype–environment interpretation

The main objective of grouping trials is to reduce the $G \times E$ within subgroups of trials (e.g. grouping by environment types) and identify adapted genotypes that perform consistently better in a group of environments. Thus, the aim is to minimize the $G \times E$ variance component while maximizing the G component.

Grouping trials from a MET based on genotype performance is common but may, as discussed previously, result in environment groups that are unstable over time (e.g. Malhotra and Singh, 1991). Alternatively, grouping trials based on previously defined environment classes (preferably from an independent dataset reflecting the broad TPE) is more challenging, but allows a more comprehensive analysis in respect to adaptation in the TPE. An example is given in Figure 13.5,

where drought patterns of wheat MET are compared to the TPE main drought-environment types. Here, grouping trials (18 genotypes, 16 trials from 11 sites over 3 years) into the TPE environment types allowed a better interpretation of the $G \times E$ interactions, in particular, by explaining a greater proportion of the genotypic variability in the generally non-stressed environment type (doubling in the $G/G \times E$ ratio in Figure 13.5d; Chenu et al., 2011). Another interesting example is given for maize in the USA, where grouping trials (18 genotypes grown in 266 environments from 90 sites over 3 years) by the TPE environment classes explained up to 30% of the $G \times E$ variance (Löffler et al., 2005). Here, genetic correlations between trials grouped within each environment class were generally greater than those between trials across environment classes. As expected, however, in both examples, a substantial portion of the $G \times E$ remained unexplained by the environment classification which focused on a restricted part of the environmental variation.

3.3 Trial representativeness and weighted selection

While increasing MET size may assist breeding programs better to sample the TPE, resources limit the number of trials. In practice, trials that diverge from the TPE are likely to bias genetic analysis and to divert selection from the optimum for the TPE. Cooper et al. (1996) demonstrated theoretically how mismatches between the frequencies of environment types sampled in a MET and their true frequencies in the TPE can reduce genetic improvement for the TPE.

‘Weighted selection’ is a breeding strategy that uses environment characterization to anticipate and adjust for deviations from the TPE. In this approach, trial data from a MET are weighted according to the frequency of the trial’s environment class within the TPE in order to ‘balance’ the MET. Such weighting of trial data based on the similarity of trials to the target environments (or ‘to a hypothetical most frequently encountered environment’) was proposed in the 1980s (Fox

and Rosielle, 1982; Brennan and Sheppard, 1985). Simulation analyses have since assessed the value of weighting genotype performance with respect to trial representativeness in the TPE (Fig. 13.6). The advantage of such weighted selection has been demonstrated *in silico* for variable environments, especially for MET of limited size or for germplasm pools with high cross-over interactions (Fig. 13.6a; Podlich et al., 1999). Chapman et al. (2000b) also showed that the expected yield of a genotype when weighting MET data was quite stable over the years and was similar to the expected average yield of this genotype in the TPE, whereas the unweighted average yield fluctuated greatly over the years (Fig. 13.6b).

Given the limited resources available to breeding programs, weighting germplasm performance is an effective way to increase the value of collected data and to improve selection towards elite germplasm with better performance in the TPE.

4 MANAGED ENVIRONMENTS – INCREASING THE RELEVANCE OF PHENOTYPING ENVIRONMENTS

While different tools exist to increase the relevance and exploitation of MET, the identification of superior genotypes may still be limited by the nature of the selection environments (MET), which only represent a limited sample of the multitude of complex environments that constitute the TPE. To deal with the variability and unpredictability of field environments, managed environments are being used by both public and private organizations, as they permit selection under more controlled conditions (e.g. Campos et al., 2004; Kirigwi et al., 2004; Trethowan et al., 2005b; Bänziger et al., 2006; Rebetzke et al., 2013).

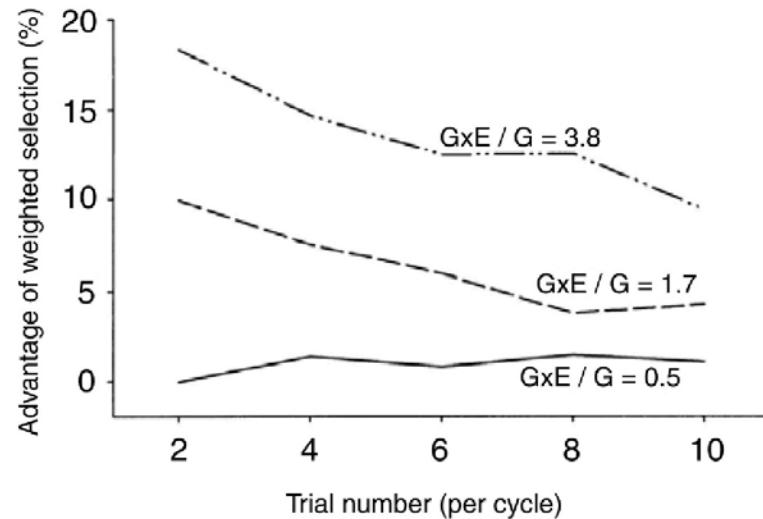
4.1 Managed environments to target specific stresses in the field

While breeders commonly inoculate dedicated trials to assess crop tolerance to specific

diseases, some breeding programs are now, in a similar way, managing abiotic stress at key sites. For instance, CIMMYT undertakes managed drought trials in Ciudad Obregón (Mexico), where the dry desert climate allows various kinds of drought stresses to be reliably imposed via irrigation scheduling (e.g. Edmeades et al., 1989, 1999). Byrne et al. (1995) demonstrated that significantly greater yield stability and higher rate of yield gain could be achieved when selecting under managed levels of drought in one location compared to conventional MET at a range of international locations. Using managed environments over several cycles of selection has contributed to improving yield simultaneously for drought and irrigated conditions (e.g. Chapman et al., 1997). Other types of managed environments have been designed, as in southern Africa, where selecting in environments managed for nitrogen and drought resulted in a consistent yield advantage over maize hybrids selected more conventionally, especially in low to medium yielding environments (Bänziger et al., 2006). In this case, the authors attributed their success partly to (1) selection in managed environments where high-priority stresses were imposed to keep heritability high and to maximize genotype-by-stress interactions (even if those stresses were more severe than typical stresses from the TPE), and (2) selection for stress tolerance at early breeding stages when genetic variance is large (which contrasts with classical breeding approaches where genotypes are usually exposed to abiotic stresses at later breeding stages, in MET).

Managed environments have also been created to target representative environments. For instance, in Australia, a web-based modeling application ('StressMaster') is used at representative sites to define irrigation strategies that target the predominant drought patterns of the TPE (Fig. 13.7; Chenu et al., 2013b). In this case, managed environments are used to assess the value of drought tolerant germplasm, traits and genes in representative environments

a- Advantage of weighted selection in a simulated breeding program



b- Yield evaluation in weighted multi-environment trials

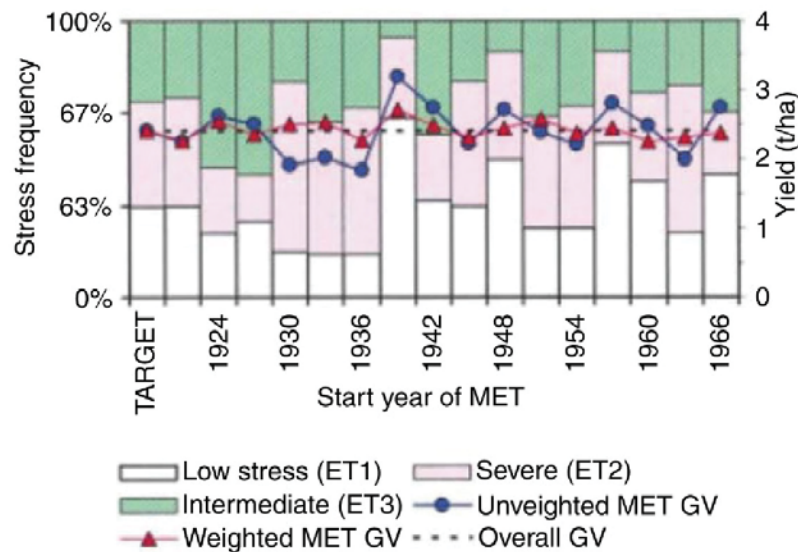
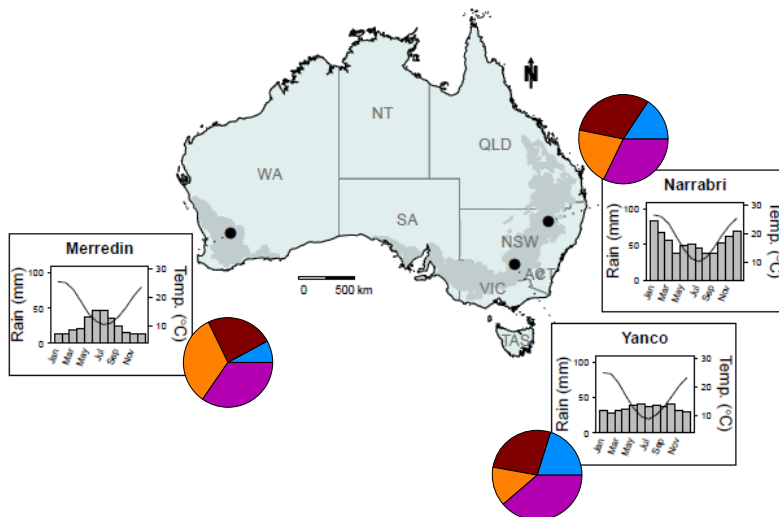


FIG. 13.6 Advantage of weighted selection illustrated in simulation studies for (a) contrasting levels of cross-over $G \times E$ interactions and different numbers of trials per testing cycle, in a wheat breeding program; and for (b) yield evaluation in weighted and unweighted multi-environment trials in sorghum. In (a), virtual genotypes were tested *in silico* in 2–10 trials over 2 years during 1 to 10 breeding cycles (the average over all cycles is presented here). The advantage of weighting the trial data according to the trial-environment expected frequency of occurrence in the TPE increases with the level of cross-over $G \times E$, while decreasing with the size of the MET. Source: [Podlich et al. \(1999\)](#). In (b), the genotype value (GV) was either unweighted (i.e. average yield, circle) or weighted (triangle) according to the frequency of occurrence of the specific drought-environment types (ET) in trials compared to the frequency in the TPE. The data are for simulations for 1 hybrid in 16 consecutive multi-environment trials (each of 6 locations over 3 years). Weighting trial data (triangle) resulted in a better prediction of the overall value of the genotype (dashed horizontal line) in the TPE ('Target' bar). Source: [Chapman et al. \(2000b\)](#).

a - Australian managed-environment facilities



c- Targeted genetic analysis

Traits	No. genetic backgrounds
Awn presence	Five
Canopy stay-green	Two
Canopy temperature	Two
Carbon isotope discrimination	Six
Early vigour	Six
Grain fertility	Three
Leaf glaucousness	Two
Plant development	Two
Reduced-tillering	Six
Root vigour	Two
Stem carbohydrates	Two

b - Modelled-assisted management of drought patterns (StressMaster application)

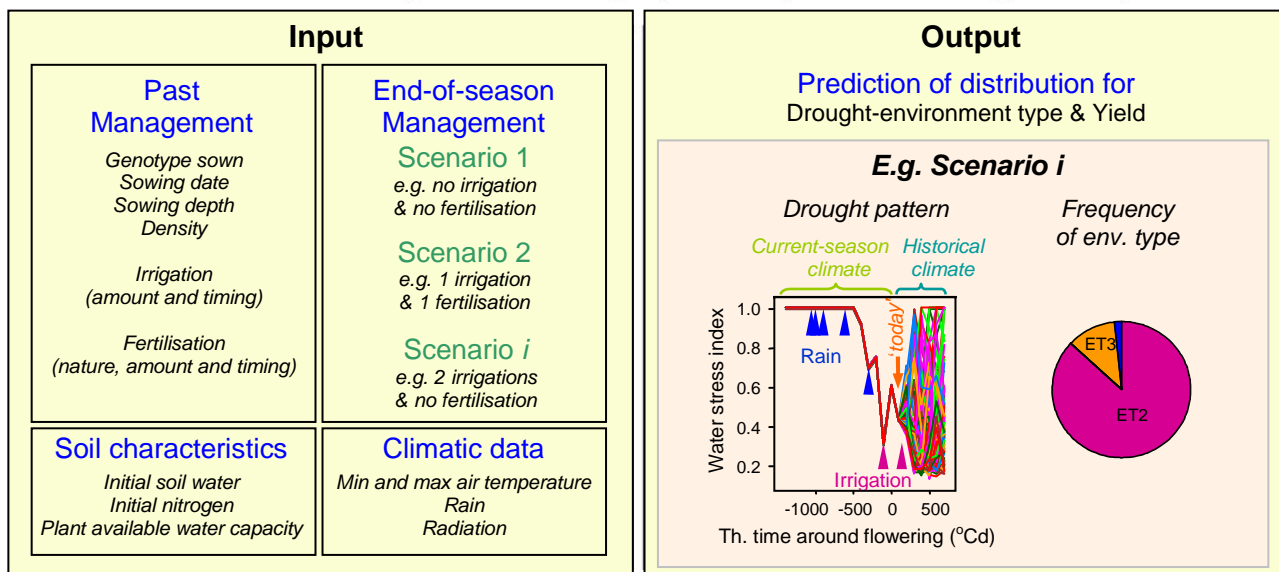


FIG. 13.7 Managed-environment facilities targeting representative drought patterns. Three locations have been chosen across Australia to represent the variability in soil and weather conditions observed across the wheat-belt (a). To adapt for the year-to-year variability that affects the occurrence of drought-environment types (pies in (a)); the environment types are defined in Fig. 13.3a), irrigation is applied to target specific drought types. Irrigation scheduling is assisted by a model-based application (StressMaster) that keeps track of the crop water-stress index as the season progresses, and that allows testing of various future end-of-the-season management scenarios (b). The managed-environment facilities are used to test the value of traits with potential for drought adaptation in diverse genetic backgrounds (c). Sources: [Rebetzke et al. \(2013\)](#) and [Chenu et al. \(2013b\)](#).

at relatively large scale (Fig. 13.7; Rebetzke et al., 2013).

4.2 Phenotyping platforms in artificial environments

Following the trends in genomics, phenomics platforms are now being developed worldwide for screening purposes as well as to provide new insights into gene function and environmental responses (e.g. Granier et al., 2006; Berger et al., 2010; Furbank and Tester, 2011). The advantage of such platforms is their ability to phenotype quickly large numbers of genotypes, and to impose different levels of stress in a controlled manner. They are typically used to identify genotypes, traits and genes of potential interest for crop-adaptation improvement, and to develop and test hypotheses concerning processes and their involvement in plant response. The value of these platforms to aid improvement for the industry depends on how the results transfer to the TPE (e.g. Passioura, 2012). The effect of genes and physiological processes involved in adaptation to complex stress such as drought vary greatly depending on the timing, severity, duration and history of stress (e.g. Slafer, 2003), e.g. plant survival and crop performance under drought are regulated by different processes and genetic controls (e.g. Skirycz et al., 2011). Typically, genes and traits beneficial to yield in some environments can have negative effects in others (e.g. Chenu et al., 2009a; Tardieu, 2012). Overall, given the complexity of the interactions across traits and the interactions with the environment (e.g. competition for light, water, nutrients), discoveries about complex traits made in growth chambers or glasshouses need to be validated in field environments and in genetic backgrounds of interest to test their relevance for breeding (e.g. Tardieu, 2012; Passioura, 2012; Rebetzke et al., 2014). Chapter 15 presents a case study in maize where physiologically-meaningful traits are quantified in breeding-relevant field trials.

5 CROP PLASTICITY AND ENVIRONMENT TYPES – IDENTIFICATION OF KEY TRAITS FOR POTENTIAL ADAPTATION

5.1 Which traits for which environment types?

Given the complex $G \times E$ interactions that occur over the crop cycle, the relative importance of traits (e.g. maturity, tillering, leaf and root growth) may vary depending on the environment (e.g. Hammer and Vanderlip, 1989; Van Oosterom et al., 2003; Chenu et al., 2009a; Veyradier et al., 2013). For instance, when a drought stress occurs early in development (e.g. ET3–4 for Australian wheat and ET2–3 for Australian field pea; Fig. 13.3a and c), improvement of vigor and maintenance of crop growth rate around flowering can contribute to seed set and yield. However, high biomass at flowering might also be detrimental, as excessive leaf area can prematurely exhaust soil water, thus limiting photosynthesis, reducing seed growth and decreasing yield if the stress is not relieved during the seed-filling period (e.g. ET4 for wheat, ET3 for field pea). Such trade-offs between advantageous/detrimental traits or genetic controls depending on the environment types are further illustrated in Chenu et al. (2009a).

Grouping environments into classes is expected to reveal groups of genotypes with common traits that contribute to adaptation to specific classes of environments. Accordingly, phenotypic selection in breeding has been applied either directly for yield, for other (secondary) traits, or a combination of both, depending on the environment targeted (e.g. Araus et al., 2008; Cattivelli et al., 2008). Selection indexes have also been created to weight the importance of traits, with traits and weights chosen based on the type of environments considered (e.g. Bänziger et al., 2006). Such trait-selection approaches are particularly interesting in conditions where yield has a low heritability

while secondary traits have high heritability and genetic variance.

For traits to be useful in selection, they must be associated with some interesting genetic variation (e.g. have the potential to improve yield), and be less subjected to $G \times E$ than yield in at least some relevant types of environments (e.g. Chapman et al., 2002b; Araus et al., 2008). In maize, this is the case for traits like increased seed number, synchronized male–female flowering, and adjusted crop maturity (Bolaños and Edmeades, 1996; Duvick, 2005; Cooper et al., 2009; Chapter 15). Harrison et al. (2014) have tested the value of these traits in their European TPE (Fig. 13.8) and found that traits having positive effects on yield in crops subjected to one type of drought-stress pattern did not necessarily have positive effects on yield in other drought patterns. This sort of result could explain the lack of consistent progress achieved in breeding when selecting for genotypes with high expression of key traits (Bolaños and Edmeades, 1996), even though such traits are highly correlated with yield (Campos et al., 2004).

While germplasm may share common traits within environment classes, each environmental class typically groups a wide range of environments, and different adaptation strategies may still be required to improve yield within environment classes. For instance, wheat under severe drought (e.g. ET3–4 in Fig. 13.3a) may benefit from deep roots in deep clay soils that store substantial soil moisture (Manschadi et al., 2006), but this may not be so valuable in light sandy soils, even where crops are experiencing the same type of drought (ET3–4). Environment classes encompass a lot of environmental variability and the effect of traits of interest may differ even within environment classes.

To aid identification of potential traits of interest, modeling approaches have been designed to predict potential consequences of trait \times management combinations in the TPE and generate information to help define ideotypes (e.g. Chapter 14). Numerous studies have

explored the putative value of potential trait variation in a range of species (e.g. Spitters and Schapendonk 1990; Muchow et al., 1991; Aggarwal et al., 1997; Boote et al., 2001; Asseng and van Herwaarden 2003; Sinclair et al., 2005), some looking more specifically at response to environment types (Fig. 13.8; Hammer et al., 2005; Chenu et al., 2009a; Harrison et al., 2014). While such approaches have merit, they nevertheless require confidence in the adequacy of the model to simulate the effects of trait variations, and may require additional experimental evidence to confirm the findings.

Direct evaluation of traits is taking place in numerous experimental studies, ranging from growth chambers to field, and from phenotyping on small numbers of genotypes to screening of large populations (e.g. Fig. 13.7). Ultimately, examples where the influence of traits is evaluated in representative environments of the TPE (via MET or managed environments) and in genetic backgrounds of relevance for breeding are important for bridging the gap between research and industry (Rebetzke et al., 2013).

5.2 Design and evaluation of breeding strategies

The value of traits in breeding, over several cycles of selection, can be evaluated when combining breeding-system and crop models. Such an approach has highlighted the importance to consider appropriately both (1) the traits to select for and (2) the selection environments (Fig. 13.9; Cooper et al., 2002; Chapman et al., 2003). Gene/trait impact and fixation rate over breeding cycles vary greatly with the type of environment. Hence, depending on the trait, alleles targeted when considering the whole TPE might differ from those targeted in a specific environment type (Fig. 13.9a). For instance, in Australian sorghum, a phenology-ideotype under terminal drought is genetically distant from the phenology-ideotype for the TPE (Fig. 13.9a(iii)). Accordingly, when selecting for increased yield,

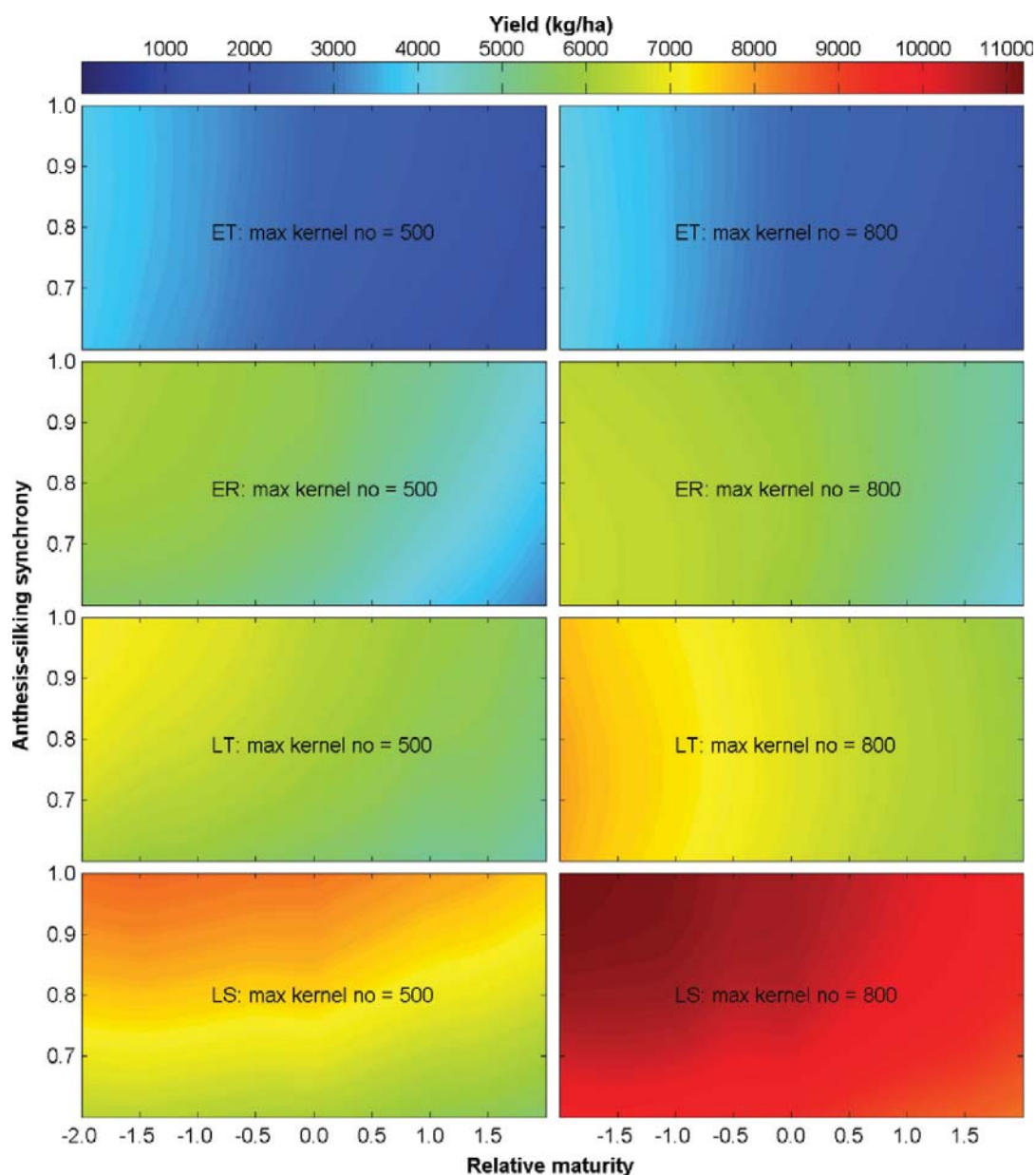
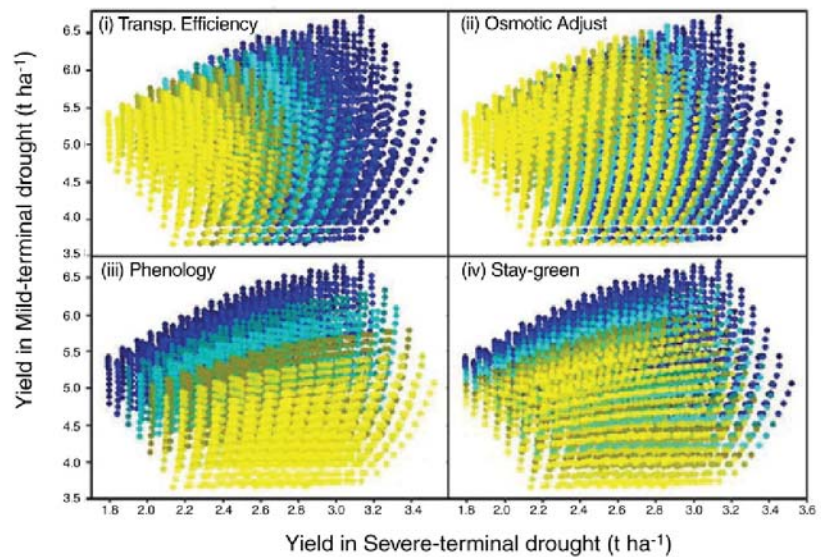


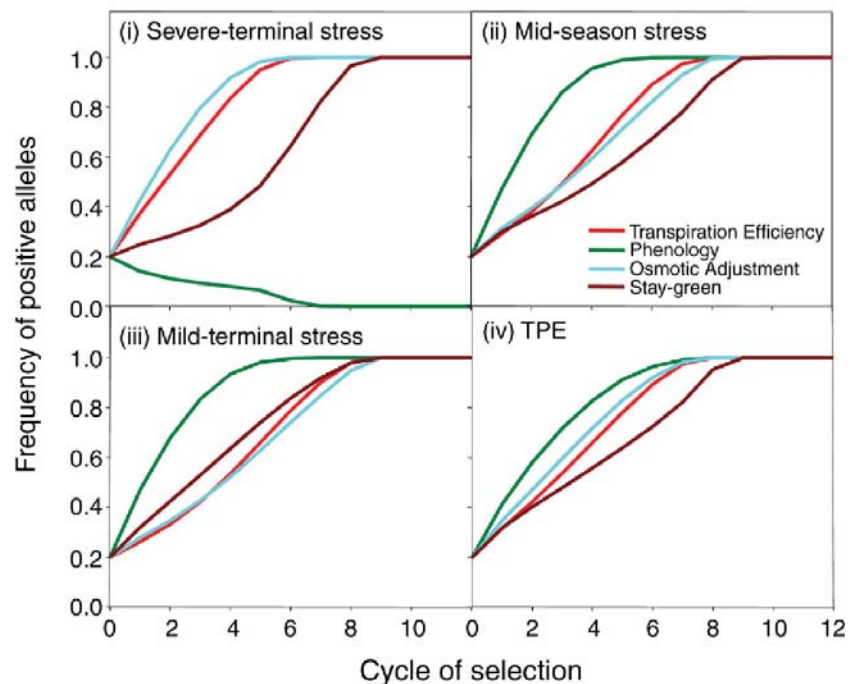
FIG. 13.8 Heat map of grain yield response to trait variation in the four main drought-environment types occurring in the European rain-fed maize cropping area. Each panel presents yield for variation in anthesis-silking synchrony (standard genotype = 0.8; higher values improve synchrony) and in relative maturity (expressed as number of leaves difference from the standard genotype). Panels in the left and right columns show yields for maximum grain number per plant of 500 and 800, respectively. Drought-environment types (ET = ET4, ER = ET3, LT = ET2 and LS = ET1) are as presented in Figure 13.3b. Source: Harrison *et al.* (2014).

FIG. 13.9 Effect of drought-environment types on (a) simulated yield for trait ideotypes and on (b) the change in allele frequency while selecting for simulated yield. Sorghum simulations generated for 15 genes associated with four adaptive traits identified by genetic and physiological studies as important for drought tolerance: transpiration efficiency (five genes), phenology (three genes), osmotic adjustment (two genes), and stay-green (five genes). In (a), the yield of virtual genotypes in the 'mild terminal stress' and the 'severe terminal stress' environment types is presented with a color code that indicates the genetic distance from the trait ideotype of the TPE (blue: no allele different from the ideotype, yellow: all alleles different). Colors are presented for ideotypes for (i) transpiration efficiency, (ii) osmotic adjustment, (iii) phenology and (iv) stay-green. In (b), change in frequency of alleles with a positive effect on the four traits over cycles of selection, when selection is conducted in the different environment types. Simulations for the sorghum region of north-eastern Australia. Figures adapted from Cooper *et al.* (2002) reprinted with permission from IOS Press, and from Chapman *et al.* (2003).

a- Yield for genotypes with different traits/alleles



b- Change in allele frequency in different selection environments



the frequency of late-flowering alleles decreased over breeding cycles in severe terminal stress (Fig. 13.9b(i)), while rapidly increasing when selecting in the other environment types (Fig. 13.9Bb(ii–iii)). While these results may appear trivial when considering flowering, the method applies to various traits of different complexity (Fig. 13.9).

In addition, combining crop models with breeding-system models also provides quantitative information on how the traits would likely be selected over time, in particular in different sampling of the environments (Chapman et al., 2003).

Integrated modeling gives a framework to explore the implications of interactions between the genetic architecture of traits, the selection environments, and breeding strategies (e.g. Cooper et al., 2002). It also provides hypotheses for further experimentation to test our current understanding, thus offering a foundation for defining priorities in research (physiology, genetics and modeling) and for assisting the design of efficient breeding strategies.

6 CONCLUDING REMARKS – PERSPECTIVE

The complexity of the phenotypic landscape arises from multiple and challenging $G \times E$ interactions, that impede progress in crop productivity. Environment characterization plays an important role in improving the efficiency of breeding programs, in particular in allowing (1) better understanding of the TPE, (2) informed choice for locations of selection trials, (3) global analysis of trials from similar environments, where germplasm may express interesting adaptation strategies, (4) weighing of germplasm performance (yield and/or secondary traits) based on the degree to which the trial environment represents the TPE, and also in assisting the identification of (5) relevant environmental indices for selection in the TPE, (6) accurate environmental targets for managed environments,

and (7) pertinent adaptive physiological traits and underlying genes of relevance for environment classes in the TPE.

Commonly, while assessing selection strategies, breeders may be too concerned with keeping high heritability for yield while ignoring the need to represent adequately the TPE. The effectiveness of genotype evaluation largely depends on the genetic correlation between their performance in multi-environment trials and in the TPE. Weighting trial data is a way to reduce bias in MET data and obtain a more reliable assessment of the genotype value for the TPE. In parallel, managed environments might be considered to target specific environments of value for the TPE, either because they are representative of TPE environment types or because they allow good germplasm discrimination for stresses of importance in the TPE. Secondary traits which affect yield while maintaining a high heritability under stress can also be useful to improve crop adaptation. And while it was not the focus of this chapter, the importance of improved statistical design and analysis techniques (e.g. Gilmour et al., 1997) should not be neglected.

Experimental and *in-silico* research are continuously developing methods, tools and knowledge to increase understanding of the processes involved in plant adaptation. Improved productivity of cropping systems is coming from breeding (genotype), agronomy (management), and economics (feasibility, market). Beyond crop improvement, environment characterization offers benefits such as managing financial risks associated with crop production, which can benefit not only growers but also financial institutions, input suppliers, and end users (Avey et al., 2011). Finally, in a context of seasonal climate variability and long-term climate change (Chapter 20), modeling frameworks are opening promising avenues to simulate and improve understanding of crop performance and adaptation where climate (E), farmer practices (M) and genotype responses (G) are constantly changing.

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References

- Abou-El-Fittouh, H.A., Rawlings, J.O., Miller, P.A., 1969. Classification of environments to control genotype by environment interactions with an application to cotton. *Crop Sci.* 9, 135–140.
- Aggarwal, P.K., Kropff, M.J., Cassman, K.G., ten Berge, H.F.M., 1997. Simulating genotypic strategies for increasing rice yield potential in irrigated, tropical environments. *Field Crops Res.* 51, 5–17.
- Alwala, S., Kwolek, T., McPherson, M., Pellow, J., Meyer, D., 2010. A comprehensive comparison between Eberhart and Russell joint regression and GGE biplot analyses to identify stable and high yielding maize hybrids. *Field Crops Res.* 119, 225–230.
- Araus, J.L., Slafer, G.A., Royo, C., Serret, M.D., 2008. Breeding for yield potential and stress adaptation in cereals. *Crit. Rev. Plant Sci.* 27, 377–412.
- Asseng, S., van Herwaarden, A.F., 2003. Analysis of the benefits to wheat yield from assimilates stored prior to grain filling in a range of environments. *Plant Soil* 256, 217–229.
- Avey, D.P., Bax, P.L., Brooke, R.G., et al., 2011. Method for using environmental classification for making crop production decisions, involves determining lending terms for lender to finance producer for crop production using agricultural input based on profile of producer. Pioneer Hi-Bred Int Inc. US Patent 8046280 B2.
- Bänziger, M., Cooper, M., 2001. Breeding for low input conditions and consequences for participatory plant breeding: Examples from tropical maize and wheat. *Euphytica* 122, 503–519.
- Bänziger, M., Setimela, P.S., Hodson, D., Vivek, B., 2006. Breeding for improved abiotic stress tolerance in maize adapted to southern Africa. *Agric. Water Manag.* 80, 212–224.
- Basford, K.E., Cooper, M., 1998. Genotype \times environment interactions and some considerations of their implications for wheat breeding in Australia. *Aust. J. Agric. Res.* 49, 153–174.
- Berger, J.D., Turner, N.C., 2007. The ecology of chickpea: evolution, distribution, stresses and adaptation from an agro-climatic perspective. In: Yadav, S., Redden, R., Chen, W., Sharma, B. (Eds.), *Chickpea breeding and management*. CAB International, Wallingford, pp. 47–71.
- Berger, B., Parent, B., Tester, M., 2010. High-throughput shoot imaging to study drought responses. *J. Exp. Bot.* 61, 3519–3528.
- Bernardo, R., 2001. What if we knew all the genes for a quantitative trait in hybrid crops? *Crop Sci.* 41, 1–4.
- Bolaños, J., Edmeades, G.O., 1996. The importance of the anthesis-silking interval in breeding for drought tolerance in tropical maize. *Field Crops Res.* 48, 65–80.
- Boote, K.J., Kropff, M.J., Bindraban, P.S., 2001. Physiology and modelling of traits in crop plants: implications for genetic improvement. *Agric. Syst.* 70, 395–420.
- Brancourt-Hulmel, M., 1999. Crop diagnosis and probe genotypes for interpreting genotype environment interaction in winter wheat trials. *Theor. Appl. Genet.* 99, 1018–1030.
- Braun, H.J., Rajaram, S., van Ginkel, M., 1996. CIMMYT's approach to breeding for wide adaptation. *Euphytica* 92, 175–183.
- Brennan, P.S., Sheppard, J.A., 1985. Retrospective assessment of environments in the determination of an objective strategy for the evaluation of the relative yield of wheat cultivars. *Euphytica* 34, 397–408.
- Brennan, J.P., Fox, P.N., 1998. Impact of CIMMYT varieties on the genetic diversity of wheat in Australia, 1973–1993. *Aust. J. Agric. Res.* 49, 175–178.
- Brennan, J.P., Quade, K.J., 2006. Evolving usage of materials from CIMMYT in developing Australian wheat varieties. *Aust. J. Agric. Res.* 57, 947–952.
- Brown, K.D., Sorrells, M.E., Coffman, W.R., 1983. A method for classification and evaluation of testing environments. *Crop Sci.* 23, 889–893.
- Byrne, P.F., Bolanos, J., Edmeades, G.O., Eaton, D.L., 1995. Gains from selection under drought versus multilocation testing in related tropical maize populations. *Crop Sci.* 35, 63–69.
- Campos, H., Cooper, M., Habben, J.E., Edmeades, G.O., Schussler, J.R., 2004. Improving drought tolerance in maize: a view from industry. *Field Crops Res.* 90, 19–34.
- Cattivelli, L., Rizza, F., Badeck, F.-W., et al., 2008. Drought tolerance improvement in crop plants: An integrated view from breeding to genomics. *Field Crops Res.* 105, 1–14.
- Chapman, S.C., Hammer, G.L., Meinke, H., 1993. A sunflower simulation model: I. Model development. *Agron. J.* 85, 725–735.
- Chapman, S.C., Barreto, H.J., 1996. Using simulation models and spatial databases to improve the efficiency of plant breeding programs. In: Cooper, M., Hammer, G.L., (eds), *Plant adaptation and crop improvement*. pp. 563–587. CAB international, Wallington, UK.
- Chapman, S.C., Crossa, J., Edmeades, G.O., 1997. Genotype by environment effects and selection for drought tolerance in tropical maize. 1. Two mode pattern analysis of yield. *Euphytica* 95, 1–9.
- Chapman, S.C., Cooper, M., Hammer, G.L., Butler, D.G., 2000a. Genotype by environment interactions affecting grain sorghum. II. Frequencies of different seasonal

- patterns of drought stress are related to location effects on hybrid yields. *Aust. J. Agric. Res.* 51, 209–221.
- Chapman, S.C., Hammer, G.L., Butler, D.G., Cooper, M., 2000b. Genotype by environment interactions affecting grain sorghum. III. Temporal sequences and spatial patterns in the target population of environments. *Aust. J. Agric. Res.* 51, 223–233, <http://www.publish.csiro.au/nid/40/paper/AR99022.htm>.
- Chapman, S.C., Cooper, M., Hammer, G.L., 2002a. Using crop simulation to generate genotype by environment interaction effects for sorghum in water-limited environments. *Aust. J. Agric. Res.* 53, 379–389.
- Chapman, S.C., Hammer, G.L., Podlich, D.W., Cooper, M., 2002b. Linking biophysical and genetic models to integrate physiology, molecular biology and plant breeding. In: Kang, M.S. (Ed.), *Quantitative genetics, genomics and plant breeding*. CAB International, Wallingford, pp. 167–187.
- Chapman, S., Cooper, M., Podlich, D., Hammer, G., 2003. Evaluating plant breeding strategies by simulating gene action and dryland environment effects. *Agron. J.* 95, 99–113.
- Chapman, S.C., 2008. Use of crop models to understand genotype by environment interactions for drought in real-world and simulated plant breeding trials. *Euphytica* 161, 195–208.
- Chauhan, Y.S., Rachaputi, R.C.N., 2014. Defining agro-ecological regions for field crops in variable target production environments: A case study on mungbean in the northern grains region of Australia. *Agric. Forest Meteorol.* 194, 207–221.
- Chauhan, Y., Wright, G., Rachaputi, N., McCosker, K., 2008. Identifying chickpea homoclims using the APSIM chickpea model. *Aust. J. Agric. Res.* 59, 260–269.
- Chauhan, Y.S., Solomon, K.F., Rodriguez, D., 2013. Characterization of north-eastern Australian environments using APSIM for increasing rainfed maize production. *Field Crops Res.* 144, 245–255.
- Chelle, M., 2005. Phylloclimate or the climate perceived by individual plant organs: What is it? How to model it? What for? *New Phytol.* 166, 781–790.
- Chenu, K., Chapman, S.C., Hammer, G.L., McLean, G., Ben-Haj-Salah, H., Tardieu, F., 2008a. 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 Environ.* 31, 378–391.
- Chenu, K., Rey, H., Dauzat, J., Lydie, G., Lecoeur, J., 2008b. Estimation of light interception in research environments: a joint approach using directional light sensors and 3D virtual plants applied to sunflower (*Helianthus annuus*) and *Arabidopsis thaliana* in natural and artificial conditions. *Funct. Plant Biol.* 35, 850–866.
- Chenu, K., Chapman, S.C., Tardieu, F., McLean, G., Welcker, C., Hammer, G.L., 2009a. Simulating the yield impacts of organ-level quantitative trait loci associated with drought response in maize: A “gene-to-phenotype” modeling approach. *Genetics* 183, 1507–1523.
- Chenu, K., McIntyre, K., Chapman, S.C., 2009b. Environment characterisation as an aid to improve barley adaptation in water-limited environments. Australian Barley Technical Symposium. 13–16 September 2009, Twin Waters, Australia. p. 9.
- Chenu, K., Cooper, M., Hammer, G.L., Mathews, K.L., Drecer, M.F., Chapman, S.C., 2011. Environment characterization as an aid to wheat improvement: interpreting genotype-environment interactions by modelling water-deficit patterns in North-Eastern Australia. *J. Exp. Bot.* 62, 1743–1755.
- Chenu, K., Chapman, S.C., 2012. Drought experienced by Australian wheat: current and future trends. 16th Australian Agronomy Conference. Armidale, NSW, Australia. p. 7.
- Chenu, K., Dehilmfard, R., Chapman, S.C., 2013a. Large-scale characterization of drought pattern: a continent-wide modelling approach applied to the Australian wheat belt spatial and temporal trends. *New Phytol.* 198, 801–820.
- Chenu, K., Doherty, A., Rebetzke, G.J., Chapman, S.C., 2013b. StressMaster: a web application for dynamic modelling of the environment to assist in crop improvement for drought adaptation. In: Sievänen, R., Nikinmaa, E., Godin, C., Lintunen, A., Nygren, P. (Eds.), *7th International Conference on Functional-Structural Plant Models*. Saarisekä, Finland. pp. 317–319.
- Collaku, A., Harrison, S.A., Finney, P.L., Van Sanford, D.A., 2002. Clustering of environments of southern soft red winter wheat region for milling and baking quality attributes. *Crop Sci.* 42, 58–63.
- Comstock, R.E., 1977. Quantitative genetics and the design of breeding programs. In: *Proceedings of the international conference on quantitative genetics*. Iowa State University Press, Ames, USA, pp. 705–718.
- Cooper, M., Woodruff, D.R., Eisemann, R.L., Brennan, P.S., Delacy, I.H., 1995. A selection strategy to accommodate genotype-by-environment interaction for grain yield of wheat: Managed environments for selection among genotypes. *Theor. Appl. Genet.* 90, 492–502.
- Cooper, M., DeLacy, I.H., Basford, K., 1996. Relationships among analytical methods used to analyse genotypic adaptation in multi-environment trials. In: Cooper, M., Hammer, G.L. (Eds.), *Plant adaptation and crop improvement*. CAB International, Wallingford, pp. 193–224.
- Cooper, M., Fox, P.N., 1996. Environmental characterization based on probe and reference genotypes. In: Cooper, M., Hammer, G.L. (eds), *Plant adaptation and crop improvement*. pp. 529–549. CAB International, Wallington, UK.

- Cooper, M., Stucker, R.E., DeLacy, I.H., Harch, B.D., 1997. Wheat breeding nurseries, target environments, and indirect selection for grain yield. *Crop Sci.* 37, 1168–1176.
- Cooper, M., Rajatasereekul, S., Immark, S., Fukai, S., Basnayake, J., 1999a. Rainfed lowland rice breeding strategies for Northeast Thailand. I. Genotypic variation and genotype \times environment interactions for grain yield. *Field Crops Res.* 64, 131–151.
- Cooper, M.E., Podlich, D.W., Fukai, S., 1999b. Combining information from multi-environment trials and molecular markers to select adaptive traits for yield improvement of rice in water-limited environments. In: Ito, O., O'Toole, J., Hardy, B. (Eds.), *Genetic improvement of rice for water-limited environments*. International Rice Research Institute, Makati City, The Philippines, pp. 13–33.
- Cooper, M., Chapman, S.C., Podlich, D.W., Hammer, G.L., 2002. The GP problem: Quantifying gene-to-phenotype relationships. *In Silico Biol.* 2, 151–164.
- Cooper, M., van Eeuwijk, F.A., Hammer, G.L., Podlich, D.W., Messina, C., 2009. Modeling QTL for complex traits: detection and context for plant breeding. *Curr. Opin. Plant Biol.* 12, 231–240.
- Crossa, J., Cornelius, P.L., Seyedsadr, M., Byrne, P., 1993. A shifted multiplicative model cluster analysis for grouping environments without genotypic rank change. *Theor. Appl. Genet.* 85, 577–586.
- de la Vega, A.J., Chapman, S.C., Hall, A.J., 2001. Genotype by environment interaction and indirect selection for yield in sunflower I. Two-mode pattern analysis of oil and biomass yield across environments in Argentina. *Field Crops Res.* 72, 17–38.
- de la Vega, A.J., Chapman, S.C., 2006. Defining sunflower selection strategies for a highly heterogeneous target population of environments. *Crop Sci.* 46, 136–144.
- de la Vega, A.J., DeLacy, I.H., Chapman, S.C., 2007. Changes in agronomic traits of sunflower hybrids over 20 years of breeding in central Argentina. *Field Crops Res.* 100, 73–81.
- DeLacy, I.H., Cooper, M., 1990. Pattern analysis for the analysis of regional variety trials. In: Kang, M.S. (Ed.), *Genotype-by-environment interaction and plant breeding*. Louisiana State University, Baton Rouge, LA, pp. 301–334.
- Dreccer, M.F., Chapman, S.C., Ogonnaya, F.C., Borgognone, M.G., Trethowan, R.M., 2008. Crop and environmental attributes underpinning genotype by environment interaction in synthetic-derived bread wheat evaluated in Mexico and Australia. *Aust. J. Agric. Res.* 59, 447–460.
- Duvick, D.N., 2005. The contribution of breeding to yield advances in maize (*Zea mays* L.). In: Sparks, D.L., (ed.), *Advances in agronomy*, 86. pp. 83–145. Academic Press, Elsevier. <https://www.elsevier.com/books/advances-in-agronomy/sparks/978-0-12-000784-4>
- Edmeades, G.O., Bolaños, J., Lafitte, H.R., Pfeiffer, W., Rajaram, S., Fischer, R.A., 1989. Traditional approaches in breeding for drought resistance in cereals. In: Baker, F.W.G. (Ed.), *Drought resistance in cereals*. ICSU Press/CABI, Paris/Wallingford, pp. 27–52.
- Edmeades, G.O., Bolaños, J., Chapman, S.C., Lafitte, H.R., Bänziger, M., 1999. Selection improves drought tolerance in tropical maize populations: I. Gains in biomass, grain yield, and harvest index. *Crop Sci.* 39, 1306–1315.
- FAOSTAT 2003. Statistical Database of the Food and Agriculture Organization of the United Nations. http://www.fao.org/waicent/portal/statistics_en.asp
- FAOSTAT 2005. FAO Statistical Databases. Available online at <http://faostat.fao.org/>
- Fischer, R.A., 2011. Wheat physiology: a review of recent developments. *Crop Past. Sci.* 62, 95–114.
- Forkman, J., 2013. The use of a reference variety for comparisons in incomplete series of crop variety trials. *J. Appl. Stat.* 40, 2681–2698.
- Fox, P.N., Rosielle, A.A., 1982. Reference sets of genotypes and selection for yield in unpredictable environments. *Crop Sci.* 22, 1171–1175.
- Furbank, R.T., Tester, M., 2011. Phenomics – technologies to relieve the phenotyping bottleneck. *Trends Plant Sci.* 16, 635–644.
- Ghaderi, A., Everson, E.H., Cress, C.E., 1980. Classification of environments and genotypes in wheat. *Crop Sci.* 20, 707–710.
- Gilmour, A.R., Cullis, B.R., Verbyla, A.P., Gleeson, A.C., 1997. Accounting for natural and extraneous variation in the analysis of field experiments. *J. Agric. Biol. Environ. Stat.* 2, 269–293.
- Grafius, J.E., Kiesling, R.L., 1960. Prediction of relative yields of different oat varieties based on known environmental variables. *Agron. J.* 52, 396–399.
- Granier, C., Aguirrezabal, L., Chenu, K., et al., 2006. PHENOPSIS, an automated platform for reproducible phenotyping of plant responses to soil water deficit in *Arabidopsis thaliana* permitted the identification of an accession with low sensitivity to soil water deficit. *New Phytol.* 169, 623–635.
- Graybosch, R.A., Peterson, C.J., 2010. Genetic improvement in winter wheat yields in the Great Plains of North America, 1959–2008. *Crop Sci.* 50, 1882–1890.
- Guitard, A.A., 1960. The use of diallel correlations for determining the relative locational performance of varieties of barley. *Can. J. Plant Sci.* 40, 645–651.
- Hammer, G.L., Vanderlip, R.L., 1989. Genotype-by-environment interaction in grain-sorghum. 3. Modeling the impact in field environments. *Crop Sci.* 29, 385–391.
- Hammer, G.L., Chapman, S., van Oosterom, E., Podlich, D.W., 2005. Trait physiology and crop modelling as a framework to link phenotypic complexity to underlying genetic systems. *Aust. J. Agric. Res.* 56, 947–960.
- Hammer, G., Cooper, M., Tardieu, F., et al., 2006. Models for navigating biological complexity in breeding improved crop plants. *Trends Plant Sci.* 11, 587–593.

- Hammer, G.L., Jordan, D.R., 2007. An integrated systems approach to crop improvement. In : Spiertz, J.H.J., Struik, P.C., van Laar, H.H., (eds), Scale and complexity in plant systems research: gene-plant-crop relations. pp. 45–61. Springer. Printed in the Netherlands.
- Harrison, M.T., Hammer, G.L., Messina, C.D., Dong, Z., Tardieu, F., 2014. Characterizing drought stress and trait influence on maize yield under current and future conditions. *Glob. Change Biol.* 20, 867–878.
- Heinemann, A.B., Dingkuhn, M., Luquet, D., Combres, J.C., Chapman, S., 2008. Characterization of drought stress environments for upland rice and maize in central Brazil. *Euphytica* 162, 395–410.
- Hernandez-Segundo, E., Capettini, F., Trethowan, R., et al., 2009. Mega-environment identification for barley based on twenty-seven years of global grain yield data. *Crop Sci.* 49, 1705–1718.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. *Internatl. J. Climatol.* 25, 1965–1978.
- Hodson, D.P., Martinez-Romero, E., White, J.W., Corbett, J.D., Bänziger, M., 2002. Africa maize research atlas (v. 3.0). CD-ROM Publication CIMMYT, Mexico, DF, Mexico.
- Hodson, D.P., White, J.W., 2007. Use of spatial analyses for global characterization of wheat-based production systems. *J. Agric. Sci.* 145, 115–125.
- Hoffmann, C.M., Huijbregts, T., van Swaaij, N., Jansen, R., 2009. Impact of different environments in Europe on yield and quality of sugar beet genotypes. *Eur. J. Agronomy* 30, 17–26.
- Horner, T.W., Frey, K.J., 1957. Methods for determining natural areas for oat varietal recommendations. *Agron. J.* 49, 313–315.
- Keating, B.A., Carberry, P.S., Hammer, G.L., et al., 2003. An overview of APSIM, a model designed for farming systems simulation. *Eur. J. Agron.* 18, 267–288.
- Khazaei, H., Street, K., Bari, A., Mackay, M., Stoddard, F.L., 2013. The FIGS (Focused Identification of Germplasm Strategy) approach identifies traits related to drought adaptation in *Vicia faba* genetic resources. *Plos One* 8, e63107–e163107.
- Kholova, J., McLean, G., Vadez, V., Craufurd, P., Hammer, G.L., 2013. Drought stress characterization of post-rainy season (rabi) sorghum in India. *Field Crops Res.* 141, 38–46.
- Kirigwi, F.M., van Ginkel, M., Trethowan, R., Sears, R.G., Rajaram, S., Paulsen, G.M., 2004. Evaluation of selection strategies for wheat adaptation across water regimes. *Euphytica* 135, 361–371.
- Lacaze, X., Roumet, P., 2004. Environment characterisation for the interpretation of environmental effect and genotype \times environment interaction. *Theor. App. Genet.* 109, 1632–1640.
- Lacaze, X., Hayes, P.M., Korol, A., 2009. Genetics of phenotypic plasticity: QTL analysis in barley, *Hordeum vulgare*. *Heredity* 102, 163–173.
- Lobell, D.B., Sibley, A., Ortiz-Monasterio, I., 2012. Extreme heat effects on wheat senescence in India. *Nat. Climate Change* 2, 186–189.
- Löffler, C.M., Wei, J., Fast, T., et al., 2005. Classification of maize environments using crop simulation and geographic information systems. *Crop Sci.* 45, 1708–1716.
- Louarn, G., Chenu, K., Fournier, C., Andrieu, B., Giauffret, C., 2008. Relative contributions of light interception and radiation use efficiency to the reduction of maize productivity under cold temperatures. *Funct. Plant Biol.* 35, 885–899.
- Mackay, M., von Bothmer, R., Skovmand, B., 2005. Conservation and utilization of plant genetic resources – future directions. *Czech J. Genet. Plant Breed.* 41, 335–344.
- Malhotra, R.S., Singh, K.B., 1991. Classification of chickpea growing environments to control genotype by environment interaction. *Euphytica* 58, 5–12.
- Malosetti, M., Voltas, J., Romagosa, I., Ullrich, S.E., van Eeuwijk, F.A., 2004. Mixed models including environmental covariables for studying QTL by environment interaction. *Euphytica* 137, 139–145.
- Manschadi, A.M., Christopher, J., Devoil, P., Hammer, G.L., 2006. The role of root architectural traits in adaptation of wheat to water-limited environments. *Funct. Plant Biol.* 33, 823–837.
- Mathews, K.L., Chapman, S.C., Trethowan, R., et al., 2007. Global adaptation patterns of Australian and CIMMYT spring bread wheat. *Theor. Appl. Genet.* 115, 819–835.
- Mathews, K.L., Trethowan, R., Milgate, A.W., et al., 2011. Indirect selection using reference and probe genotype performance in multi-environment trials. *Crop Past. Sci.* 62, 313–327.
- Muchow, R.C., Hammer, G.L., Carberry, P.S., 1991. Optimising crop and cultivar selection in response to climatic risk. In: Muchow, R.C., Bellamy, J.A. (Eds.), Climatic risk in crop production: models and management for the semiarid tropics and subtropics. CAB International, Wallingford, UK, pp. 235–262.
- Muchow, R.C., Cooper, M., Hammer, G.L., 1996. Characterizing environmental challenges using models. In: Cooper, M., Hammer, G.L. (Eds.), Plant adaptation and crop improvement. CAB International, Wallingford, pp. 349–364.
- Nor, K.M., Cady, F.B., 1979. Methodology for identifying wide adaptability in crops. *Agron. J.* 71, 556–559.
- Palmer, W., 1965. Meteorological drought. US Department of Commerce Weather Bureau Research paper no. 45: 58 pp.
- Pantuwan, G., Fukai, S., Cooper, M., Rajatasareekul, S., O'Toole, J.C., 2002. Yield response of rice (*Oryza sativa* L.) genotypes to different types of drought under rainfed lowlands – Part 1. Grain yield and yield components. *Field Crops Res.* 73, 153–168.

- Passioura, J.B., 2012. Phenotyping for drought tolerance in grain crops: when is it useful to breeders? *Funct. Plant Biol.* 39, 851–859.
- Podlich, D.W., Cooper, M., Basford, K.E., 1999. Computer simulation of a selection strategy to accommodate genotype-by-environment interaction in a wheat recurrent selection program. *Plant Breed.* 118, 17–28.
- Pollak, L.M., Corbett, J.D., 1993. Using GIS datasets to classify maize-growing regions in Mexico and Central America. *Agron. J.* 85, 1133–1139.
- Rathey, A., Shorter, R., 2010. Evaluation of CIMMYT conventional and synthetic spring wheat germplasm in rainfed sub-tropical environments. I. Grain yield. *Field Crops Res.* 118, 273–281.
- Rebetzke, G.J., Chenu, K., Biddulph, B., et al., 2013. A multisite managed environment facility for targeted trait and germplasm phenotyping. *Funct. Plant Biol.* 40, 1–13, <http://www.publish.csiro.au/nid/102/paper/FP12180.htm>.
- Rebetzke, G.J., Fischer, R.A., van Herwaarden, A.F., et al., 2014. Plot size matters: interference from intergenotypic competition in plant phenotyping studies. *Funct. Plant Biol.* 41, 107–118.
- Richards, R., 1996. Increasing the yield potential of wheat: manipulating sources and sinks. In: Rajaram, S., Reynolds, M. (Eds.), *Increasing yield potential in wheat: breaking barriers*. CIMMYT, Mexico, pp. 134–149.
- Richards, R.A., Rebetzke, G.J., Watt, M., Condon, A.G., Spielmeyer, W., Dolferus, R., 2010. Breeding for improved water productivity in temperate cereals: phenotyping, quantitative trait loci, markers and the selection environment. *Funct. Plant Biol.* 37, 85–97.
- Rodriguez, D., Sadras, V.O., 2007. The limit to wheat water-use efficiency in eastern Australia. I. Gradients in the radiation environment and atmospheric demand. *Aust. J. Agric. Res.* 58, 287–302.
- Runge, E.C.A., 1968. Effects of rainfall and temperature interactions during growing season on corn yield. *Agron. J.* 60, 503–507.
- Russell, W.K., Eskridge, K.M., Travnicsek, D.A., Guillen-Portal, F.R., 2003. Clustering environments to minimize change in rank of cultivars. *Crop Sci.* 43, 858–864.
- Sadras, V.O., Denison, R.F., 2009. Do plant parts compete for resources? An evolutionary viewpoint. *New Phytol.* 183, 565–574.
- Sadras, V.O., Lake, L., Chenu, K., McMurray, L.S., Leonforte, A., 2012. Water and thermal regimes for field pea in Australia and their implications for breeding. *Crop Past. Sci.* 63, 33–44, <http://www.publish.csiro.au/nid/40/paper/CP11321.htm>.
- Semenov, M.A., Donatelli, M., Stratonovitch, P., Chatzidaki, E., Baruth, B., 2010. ELPIS: a dataset of local-scale daily climate scenarios for Europe. *Climate Res.* 44, 3–15.
- Setimela, P., Chitalu, Z., Jonazi, J., Mambo, A., Hodson, D., Bänziger, M., 2002. Revision of maize megaenvironments in the Southern African Development Community (SADC) region. Arnel R Hallauer International Symposium on Plant Breeding. CIMMYT Mexico, Mexico, pp. 246–247.
- Siebert, S., Feick, S., Döll, P., Hoogeveen, J., 2005. Global Map of Irrigation Areas Version 3.0. University of Frankfurt (Main) and FAO, Frankfurt and Rome.
- Sinclair, T.R., Hammer, G.L., van Oosterom, E.J., 2005. Potential yield and water-use efficiency benefits in sorghum from limited maximum transpiration rate. *Funct. Plant Biol.* 32, 945–952.
- Skirycz, A., Vandenbroucke, K., Clauw, P., et al., 2011. Survival and growth of *Arabidopsis* plants given limited water are not equal. *Nat. Biotechnol.* 29, 212–214.
- Slafer, G.A., 2003. Genetic basis of yield as viewed from a crop physiologist's perspective. *Ann. Appl. Biol.* 142, 117–128.
- Spitters, C.J.T., Schapendonk, A., 1990. Evaluation of breeding strategies for drought tolerance in potato by means of crop growth simulation. *Plant Soil* 123, 193–203.
- Tardieu, F., 2012. Any trait or trait-related allele can confer drought tolerance: just design the right drought scenario. *J. Exp. Bot.* 63, 25–31.
- Trethowan, R.M., Crossa, J., van Ginkel, M., Rajaram, S., 2001. Relationships among bread wheat international yield testing locations in dry areas. *Crop Sci.* 41, 1461–1469.
- Trethowan, R., Hodson, D.P., Braun, H.J., Pfeiffer, W., van Ginkel, M., 2005a. Wheat breeding environments. In: Lantican, M.A., Dubin, H.J., Morris, M.L. (Eds.), *Impacts of international wheat breeding research in the developing world, 1988–2002*. DF CIMMYT, Mexico, pp. 4–11.
- Trethowan, R.M., Reynolds, M., Sayre, K., Ortiz-Monasterio, I., 2005b. Adapting wheat cultivars to resource conserving farming practices and human nutritional needs. *Ann. Appl. Biol.* 146, 405–413.
- van Eeuwijk, F.A., Bink, M.C.A.M., Chenu, K., Chapman, S.C., 2010. Detection and use of QTL for complex traits in multiple environments. *Curr. Opin. Plant Biol.* 13, 193–205.
- Van Oosterom, E.J., Bidingier, F.R., Weltzien, E.R., 2003. A yield architecture framework to explain adaptation of pearl millet to environmental stress. *Field Crops Res.* 80, 33–56.
- Varshney, R.K., Bansal, K.C., Aggarwal, P.K., Datta, S.K., Craufurd, P.Q., 2011. Agricultural biotechnology for crop improvement in a variable climate: hope or hype? *Trends Plant Sci.* 16, 363–371.
- Veyradier, M., Christopher, J., Chenu, K., 2013. Quantifying the potential yield benefit of root traits. In: Sievänen, R., Nikinmaa, E., Godin, C., Lintunen, A., Nygre, P. (Eds.), *7th International Conference on Functional-Structural Plant Models*. Saarisekä, Finland. pp. 317–319.

- Yang, R.-C., Blade, S.F., Crossa, J., Stanton, D., Bandara, M.S., 2005. Identifying isoyield environments for field pea production. *Crop Sci.* 45, 106–113.
- Yates, F., Cochran, W.G., 1938. The analysis of groups of experiments. *J. Agric. Sci.* 28, 556–580.
- Zheng, B., Chenu, K., Dreccer, M.F., Chapman, S.C., 2012. Breeding for the future: what are the potential impacts of future frost and heat events on sowing and flowering time requirements for Australian bread wheat (*Triticum aestivum*) varieties? *Glob. Change Biol.* 18, 2899–2914.
- Zheng, B., Biddulph, B., Li, D., Kuchel, H., Chapman, S., 2013. Quantification of the effects of VRN1 and Ppd-D1 to predict spring wheat (*Triticum aestivum*) heading time across diverse environments. *J. Exp. Bot.* doi:10.1093/jxb/ert209. <http://jxb.oxfordjournals.org/content/early/2013/07/17/jxb.ert209.full.pdf+html>