



Review article

Review: An integrated framework for crop adaptation to dry environments: Responses to transient and terminal drought

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ARTICLE INFO

Article history:

Received 23 June 2016

Received in revised form

16 September 2016

Accepted 20 September 2016

Available online 23 September 2016

Keywords:

Crop adaptation

Transient and terminal water deficits

Trade-offs

Drought escape/postponement/tolerance

ABSTRACT

As the incidence of water deficit and heat stress increases in many production regions there is an increasing requirement for crops adapted to these stresses. Thus it is essential to match water supply and demand, particularly during grain-filling. Here we integrate Grime's ecological strategies approach with traditional drought resistance/yield component frameworks describing plant responses to water deficit. We demonstrate that water use is a function of both short and longer term trade-offs between competing demands for carbon. Agricultural crop adaptation is based on escape. Rapid growth rates and high reproductive investment maximize yield, and stress is avoided through a closely regulated, climate-appropriate annual phenology. Crops have neither the resources nor morphological capacity to withstand long periods of intense water deficit. Thus, under terminal drought, yield potential is traded off against drought escape, such that drought postponing and/or tolerance traits which extend the growing season and/or divert source from reproductive sinks are maladaptive. However, these traits do play a supporting role against transient water deficits, allowing longer season cultivars to survive by mining water through deeper roots, or restricting transpiration. Recognizing these trade-offs made within escape-strategy limits will allow breeders to integrate complementary adaptive traits to transient and terminal water deficits.

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1. Introduction

The incidence of transient water deficit and/or heat stress is predicted to increase in many crop production regions as a result of

climate change [3]. Water-limited, terminal drought-prone environments in the semi-arid tropics and the Mediterranean climatic zone are predicted to get drier, while some higher rainfall regions will experience increasing transient drought and heat stress. Future annual warming is predicted to be 0.2–0.5 °C per decade for Asia, and 1.6 °C in the Sahara and semi-arid regions of southern Africa [4,5]. The number of reliable crop growing days is expected to reduce from >90 to <90 days by 2050 throughout much of sub-Saharan Africa [6]. Since 1950, Australia has become warmer, with less rainfall in the south and east, and the frequency of extremely

Abbreviations: CAM, crassulacean acid metabolism; $\delta^{13}\text{C}$, carbon isotope discrimination.

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hot years is expected to increase to once every one to two years [7]. These climatic changes are driving changes in land-use. In south west Australia, which has experienced a step change reduction in annual rainfall in the last 4 decades, the cropping zone is migrating up the rainfall gradient, at the expense of intensive animal production [8]. In India, chickpea production has moved southwards, where the increasingly early onset of high summer temperatures is forcing breeding programs to either use shorter season, earlier lines and select for heat tolerance [9].

The combination of changing temperature and rainfall patterns is driving the development of drought-adapted crops through conventional breeding, genetic modification, and marker-assisted selection. Commonly this problem is addressed as a numbers game, where proponents hope that by widening the size or more rarely the genetic diversity of their screening pool, the likelihood of successfully identifying tolerance is increased. In this review we argue that to adopt this approach blindly is to engage in magical thinking based more on faith than understanding. We contend that plant water use is a function of both short and longer term trade-offs between competing demands for carbon. These are defined by life histories, traits and behaviours, integrated into adaptive strategies shaped by selection pressures imposed by the environment in which the species evolved. Understanding these selection pressures and the adaptive strategies they shape simplifies crop improvement by allowing breeders to introgress new traits that complement existing adaptation to transient or longer term water deficits.

To this end we will provide a cohesive understanding of plant adaptation to transient and terminal drought stress (Box 1) by integrating previously disparate frameworks that have been used to understand plant responses to water deficit. These include drought

resistance [10], yield component [11] and ecological frameworks such as Grime's triangle [12] which emphasises trade-offs among adaptive traits according to the intensity of disturbance, stress and competition imposed by the environment. We will review annual plant adaptation to transient and longer term drought stress in the context of this new integrated framework, and discuss its implementation in crop improvement. Long term water deficit stress tolerance adaptation in perennial plants is discussed briefly in order to explain why these are inappropriate in an annual crop life cycle. The point of this exercise is to provide a holistic conceptual framework for crop adaptation to transient and terminal drought stress, highlighting the inherent trade-offs. Some will argue that this is only feasible with quantitative, process-based simulation models. While these are indeed valuable, they have their limitations, and do not reach all practitioners. Here our aim is to provide a broad, qualitative context that the exponents of crop improvement can use to consider the wider ramifications of the adaptive traits they are intending to introduce to their crop of interest.

1.1. Drought resistance and yield components: traditional frameworks for understanding adaptation to drought stress

Perhaps the most widely adopted framework in discussing plant responses to water deficit is the drought resistance framework, where plants are grouped by their capacity to either: (a) escape, (b) avoid/postpone or (c) tolerate drought [10]. Drought escape is based on phenology as defined by germination, the onset and termination of the reproductive phase, such that the life cycle is completed before a severe water deficit develops. In natural ecosystems, germination is controlled by environmentally-regulated dormancy mechanisms responding to changes to water, temperature, light, nitrate and smoke that facilitate seasonally and spatially appropriate germination [13]. In agricultural crops seed dormancy was lost during domestication, and germination is regulated by sowing at the appropriate time, typically as early as seasonally-possible in water limited environments. The reproductive phase of annual plants is particularly sensitive to water deficit stress, evident in reduced pollen viability, stigma/style function, flower and seed set, and seed size [14]. Accordingly the discussion of phenology in the drought escape literature (Table 1) is dominated by the onset of flowering. This is appropriate, all the more so because flowering defines the division of the vegetative and reproductive phases. Moreover, the onset of flowering tends to be correlated to later events such as the start of seed production, end of flowering, and physiological maturity, even in indeterminate plants. (Although the correlation between flowering and maturity date is reduced by high temperature and water deficit, later flowering plants invariably mature later as well). Thus, plants flowering before the onset of terminal water deficit 'escape' drought in time. Finally, the remobilization of previously fixed C and N into grain is also a form of rarely recognized drought escape because these represent resources acquired before the onset of water deficit (Table 1). Drought escape is a widespread adaptive strategy in low rainfall environments imposing predictable late season water deficits, such as the terminally drought-prone Mediterranean or semi-arid tropics.

Conversely, drought postponing mechanisms can have a role throughout the growing season (Table 1). (Note that while Levitt [10] uses the term 'avoidance' for this category, we prefer 'postponement' to prevent confusion between 'avoidance' and 'escape', and because in the annual plant lifecycle these mechanisms do indeed only postpone, rather than avoid drought stress). Indeed, in annual plants they are arguably more effective against transient water deficit than terminal drought because there is little to be gained by postponing maturity date under climatic conditions from which there can be no growth recovery. Drought

Box 1: Definitions of drought

Drought is a climatic term, often used as a convenient shorthand for plant water deficit stress, describing the interaction of low precipitation with manifold environmental processes. Accordingly, climatic classification systems such as the Palmer drought index or Thornwaite's moisture index (TMI) are based on water budgets that account for precipitation, temperature, soil water storage capacity/loss, runoff and potential evapotranspiration [1]. In the dry subhumid and semi-arid cropping environments discussed in the present review, potential evapotranspiration exceeds precipitation annually, as indicated by Thornwaite's moisture index:

Climate Category	TMI	Distribution
Dry subhumid	–20 to 0	Central Africa, N & S America, E Europe, N Mediterranean, Siberia, S Asia (NE) coastal Australia & S Africa
Semi-arid	–40 to –20	Mediterranean climates globally, Sahel, S Africa, S America, Siberia, S Asia. Fringing core arid regions in Central Asia, N America & Australia
Arid	–60 to –40	Global deserts, Antarctica and Greenland

Within these broad categories there is considerable spatial and temporal variation in the seasonal water supply/demand ratio (where <0.7 is indicative of plant stress) [2]. For the purposes of this review we define terminal drought as being an unrelieved water deficit that terminates the reproductive phase. Terminal drought is common in Mediterranean climates and stored soil moisture systems of the semi-arid tropics such as winter (rabi) cropping in South Asia. Conversely, transient drought is relieved by precipitation within the growing season to allow ongoing growth. While transient drought can occur at any stage in the growing season, grower practices and low water use when plants are small tend to defer the onset of transient stress to the late vegetative phase [2].

Table 1
Agricultural examples of the drought resistance framework, where crops are categorized by their capacity to either escape, postpone (avoid) or tolerate drought [10].

Drought Escape		
Early phenology: escapes terminal drought in canola [82], chickpea [37], lupin spp. [40,83], wheat [84], lentil [85]		
Dry matter remobilization: remobilization of non-structural carbohydrates fixed during the vegetative phase ameliorates yield loss under terminal drought in wheat [86,87] and rice [88]		
Drought Postponement		
Transpiration rates: reduced vegetative transpiration increases yield under terminal drought in chickpea [16]. In soybean [89], pearl millet [50], sorghum [90] and peanut [91] there are genotypic differences in the capacity to adjust transpiration rate in response to increasing vapour pressure deficit (the difference between actual and saturated vapour pressure in the air surrounding the plant). Drought sensitivity positively correlated to well-watered transpiration rate in pearl millet & chickpea [92,93]		
Epidermal conductance (g e): negatively correlated between species with terminal drought survival (pigeonpea > cowpea > mungbean > soybean) [94] & within species in soybean [95]		
Short term management of leaf area: paraheliotropic leaf movement (sunflower, cowpea, lupin spp.) [96]. Leaf rolling (yellow lupin, pigeonpea [97])		
Long term management of leaf area: water deficit induced leaf senescence reduces reproductive water use in sunflower [98], soybean, lupin spp.		
Hydraulic conductivity of roots: limiting vegetative water use in wheat by constraining hydraulic conductivity of seminal (but not nodal) roots [18]. Crops that have a high proportion of symplastic or trans-cellular water flow (e.g. wheat) can regulate transpiration via aquaporin control [99].		
Increasing water uptake: deep roots in chickpea [100]. Osmotic adjustment facilitates deep water extraction in wheat [101]. Increased root:shoot ratio in wheat by tillering inhibition increases plant available water [78]		
Drought Tolerance		
Osmotic adjustment (OA): correlated with survival in soybean [95] pigeonpea [102], terminal drought yield in pea [103], chickpea [104] and wheat [101]. See other references in [11,20]		
Climate Category	TMI	Distribution
Dry subhumid	–20 to 0	Central Africa, N & S America, E Europe, N Mediterranean, Siberia, S Asia (NE) coastal Australia & S Africa
Semi-arid	–40 to –20	Mediterranean climates globally, Sahel, S Africa, S America, Siberia, S Asia. Fringing core arid regions in Central Asia, N America & Australia
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postponement is achieved by maximizing water uptake (e.g. by deep rooting) and/or minimizing water loss (e.g. sensitive stomatal control, low epidermal loss, paraheliotropic leaf movement, leaf area reduction, temporary wilting [10,15]). When these mechanisms are invoked early enough in soils that retain water they may be adaptive even under terminal drought. For example, in the high water holding capacity clay soils of central and southern India, reproductive water deficits in chickpea are postponed by limiting vegetative phase transpiration by constraining leaf area and stomatal control (Table 1), setting aside water that becomes more valuable during grain filling, promoting high transpiration efficiency [16]. Similar arguments have been proposed for wheat grown in low rainfall environments on stored soil moisture [17,18]. This adaptive strategy is appropriate in crops (as opposed to wild plants) where parsimonious water use does not advantage competing neighbours, and where a high water holding capacity makes it feasible to delay water-use without the risk of losing this precious resource. However, as pointed out previously [19,20], these postponing mechanisms limit yield potential because of the link between photosynthesis and transpiration, and may be maladaptive in higher rainfall environments. Furthermore in plants growing on in-season rainfall in low water holding capacity soils, or in competition with neighbours, drought postponement is also expected to be maladaptive in this ‘use it or lose it’ situation.

Finally drought tolerance is the specific adaptation to water deficit through organs or processes that facilitate tolerance. Levitt [10] argues that only those processes that are independent of drought escape or avoidance (postponement) can be considered as tolerance traits, because by definition if the stress is escaped or avoided, it is not encountered by the plant. While this is logically correct, it is problematic because the broad range of metabolic adjustments plants make to ameliorate the effects of water stress tend to fall in either the avoidance or tolerance category (or occasionally both), depending on the degree of rigour applied to the definition, as illustrated by the following examples. Turgor is maintained through adjustment of cell wall elasticity and/or osmotic potential through solute accumulation and molecular chaperone production. These processes facilitate water retention, protein and membrane stability, maintaining metabolic activity and cellular

integrity under increasing water deficit [11,21]. Aquaporins regulate transmembrane water transport, impacting root and leaf hydraulic activity, and cell turgor and volume [22]. Late embryogenesis abundant proteins direct intracellular water distribution and bind inorganic ions, protecting cells from damage caused by high ion accumulation during water stress events [23]. Enzymatic and non-enzymatic antioxidant defence mechanisms protect against damage caused by the accumulation of reactive oxygen species under water stress [23]. More important than semantic distinctions between tolerance and avoidance is the ubiquity of these processes. Because these metabolic responses to water deficit and other stresses are widespread in the plant world, they are not an effective criterion for the definition of drought tolerance. This is highlighted in crop classifications based on the drought resistance framework, where species may occur in multiple categories (Table 1). Chickpea, for example appears to be a drought escaper, postponder and tolerator (Table 1). This begs the question of which is its primary adaptive strategy, and under what circumstances, highlighting the need for a more holistic approach to put these various adaptive strategies into context.

The yield component framework is based on the partitioning of plant growth and/or resource acquisition to separate complex processes underlying yield into fewer, readily understood parameters [11]. Thus yield is divided into biomass and harvest index; and biomass further subdivided into: growth rate and duration, water-use/water-use efficiency, transpiration/transpiration efficiency, radiation interception/radiation use efficiency etc. [24]. This is not a trivial exercise: measuring the components to define this framework is difficult to implement in breeding programs, even given recent advances in phenotyping [25]. Moreover, it should not be assumed that the components of this framework have fixed values linked by stable linear relationships [26,27]. The value of transpiration varies over time, such that water transpired during grain filling has a much larger bearing on yield than earlier transpired water [16,28]. Therefore the assumption that production is a linear function of both source capacity (e.g. biomass, water uptake etc.) and its partitioning into seed (sink strength), and can be improved by manipulating either of these levers, must be modified by considering the timing, value or cost of these pro-

cesses. Otherwise the yield component frameworks do little to improve our understanding of plant adaption because the inherent trade-offs between source and sink are not addressed, and the circumstances where maximizing either source capacity, or partitioning are expected to be adaptive, remain unclear.

These shortcomings are exacerbated by the tendency for both yield and drought frameworks to ignore the role of environmental selection pressure in shaping plant responses to water deficit. As a result the distinctions between the adaptive strategies discussed above become obscure, particularly when some species such as chickpea appear to meet the criteria of multiple categories, or when partitioning measures such as harvest index vary within and between genotypes and environments. To integrate traits into an adaptive strategy that explains how species address stresses along their distribution ranges requires a more holistic approach that also considers environmental selection pressures.

1.2. Grime's triangle: an ecological framework for understanding adaptation to drought stress

In contrast to the two frameworks introduced previously, environmental selection pressure is uppermost in Grime's triangle [12], which defines environments by the intensity of stress and disturbance, and summarizes plant adaptive strategies in light of these pressures. Plant stress is caused by those factors that restrict plant growth, such as shortages of water, light, sub- or supra-optimal temperatures, and poor soil fertility. Disturbance is defined as events that suddenly curtail growth or destroy biomass, such as fire, herbivory, disease, agricultural practices such as ploughing or harvesting, but also extreme climatic events such as frost or terminal drought [12]. In the context of this review, the onset of water deficit can be defined either as a stress or a disturbance, depending on intensity, duration and plant response. According to Grime [12] only 3 of the 4 factorial combinations of stress and disturbance are viable plant habitats, hence the use of the triangle to define 3 distinct environment types selecting for contrasting adaptive strategies (Fig. 1).

1.2.1. Low stress/low disturbance habitats: competition (C)

Productive low stress/low disturbance habitats (Fig. 1, Apex C) such as nutrient-rich alluvial basins or fertile high rainfall regions select for a competitive adaptive strategy that maximises resource capture. Rapid growth rates and phenotypic plasticity produce spatially dynamic, dense leaf canopies and large root systems (typically in perennial herbs, shrubs or trees) that can monopolize resources such as light, water and soil nutrients. This is important because competition generates strong spatial resource gradients, selecting genotypes with the morphological plasticity to grow out of depletion zones, sustaining resource capture and maximizing fitness [29]. As a result, competitive plants tend to invest dry matter vegetatively, facilitating resource acquisition above and below ground, such that their reproductive effort is relatively low.

1.2.2. Low stress/high disturbance habitats: escape (R)

Low stress/high disturbance habitats such as grasslands and agricultural fields (Apex R) select for escape-based strategies facilitating the exploitation of intermittently favourable environments, typically by annual and more rarely perennial herbs. These were termed 'ruderal' by Grime [12] because of their prevalence in weedy colonizing plants (ruderals), but are referred to as 'escaper' in this review for the sake of clarity. Escaper growth rates are rapid [15] and life cycles short to facilitate avoidance of disturbance in time, as outlined in the earlier discussion of drought escape. Escapers are characterized by high reproductive investment (harvest index), which reduces the opportunity cost of time-limited terminal reproduction because seeds represent a high proportion of plant biomass.

Consequently escapers have neither the time nor the excess dry matter to invest in specialized organs that acquire resources (e.g. deep roots, large canopies) or resist drought stress (e.g. sclerophyllous leaves). Moreover, because escaper phenology matches plant water requirements to supply by completing the life cycle before the onset of terminal drought, there is little selection pressure for postponing or tolerance adaptations.

1.2.3. High stress/low disturbance habitats: tolerance (S)

High stress/low disturbance, resource-poor habitats such as tundra, extreme arid zones or deep shade select for stress tolerators (typically evergreen perennials) that can conserve captured resources and resist stresses imposed by such habitats (Apex S, Fig. 1). Consequently, inherent growth and tissue turnover rates are low [15] and tend not to increase under more favourable conditions, leading to long-lived plant organs that can store excess photosynthate and mineral nutrients. Opportunities for seedling establishment are limited due to chronic stress, and therefore annual reproductive efforts are low. By combining Levitt's [10] 'tolerance' and 'avoidance' (postponement) into a single workable adaptive strategy, Grime's classification of stress tolerators is intuitively attractive. Clearly, stress tolerant xerophytes do have specialized organs and metabolic adaptations to water deficit that fall into both categories. Examples include small waxy, sclerophyllous leaves with thick cuticles and sunken stomata that resist water loss [30] and can tolerate low water potentials (<-4 MPa in some eucalypts [31]). Leaves may also be highly reflective, or orientated at steep angles to minimize radiation interception [15] and channel rainfall to the base of the stem, while water may be stored in the fleshy storage organs of cacti and succulents. In the latter these adaptations are augmented by crassulacean acid metabolism (CAM) that separates gas exchange and decarboxylation by night and day, maximizing transpiration efficiency at the cost of growth rate [32,33]. Inducible CAM succulents such as agaves have some competitive capacity under favourable circumstances, producing rapidly expanding, short lived superficial roots within 5 h after rainfall to capture rarely available soil water [34]. However, even facultative C3/CAM plants under plentiful water supply tend to retain their more conservative CAM for the bulk of photosynthesis [35], maintaining a stress tolerant strategy even under favourable conditions. *Mesembryanthemum crystallinum*, an inducible CAM succulent from strongly seasonal Mediterranean climates is an exception, alternating between C3 metabolism in the cool wet winter and CAM in the hot dry summer [36]. This is a fascinating example of selection for both competitive and stress tolerating strategies in a single species that appears to be driven by the interaction of phenology and environment. As a perennial, *M. crystallinum* cannot escape summer drought, hence the induction of CAM to minimize water loss, while winter C3 metabolism facilitates biomass production during the wetter months.

The 4th factorial combination: high stress/high disturbance habitats such as wind-blown desert dune landscapes are not viable for plant growth [12].

2. An integrated framework for crop responses to drought

For the purposes of this review, Grime's triangle [12] can readily be modified to represent the impact of drought in 2 dimensions. Drought that terminates the annual growing season in Mediterranean and semi-arid tropical climates is captured by the disturbance gradient. In this context, very short growing seasons such as the southern Indian winter (rabi) season that is almost completely supplied by stored soil moisture, and where late season water deficits are inevitable as a result of rising temperatures, are considered to be 'highly disturbed'. Conversely, transient

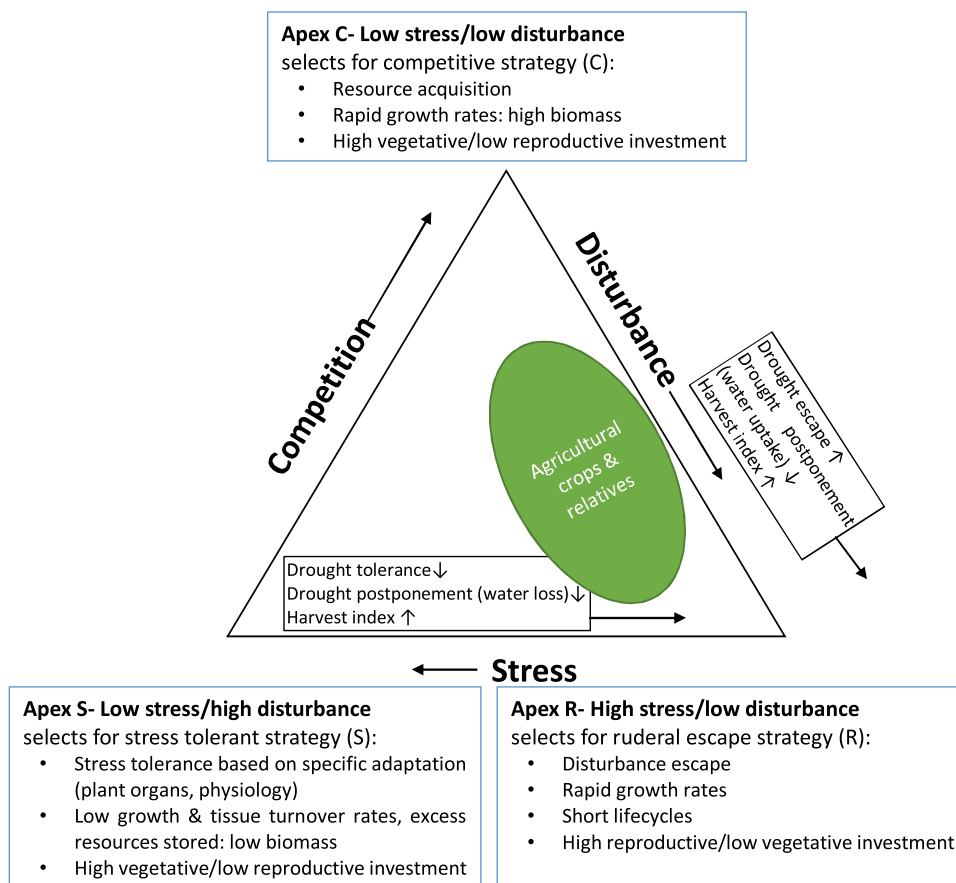


Fig. 1. An integrated framework for crop responses to drought formed by superimposing the drought resistance [10] and yield component frameworks [11] on a modified Grime's triangle [12] where plant habitats are defined by the intensity of stress (in this case imposed by transient water deficits) and disturbance (in this case imposed by terminal drought).

water deficits throughout the growing season are captured by the horizontal stress gradient in Fig. 1. Moreover, both the drought resistance and yield frameworks introduced previously are readily accommodated in this scheme, highlighting their inherent trade-offs. Agricultural crops and their wild relatives occupy the middle to lower right of Fig. 1, where disturbance is defined by growing season length. Short season environments are 'disturbed' by terminal drought as a result of high temperatures, and low, uncertain rainfall select escaper cultivars (Fig. 1, Apex R). These 'escape' terminal drought through rapid growth rates, short life cycles, and typically have a high harvest index. Conversely, cooler, longer season environments with high, consistent rainfall (Fig. 1, Apex C) select cultivars with longer life cycles supporting the development of competitive traits that facilitate resource capture. These include a greater investment in leaf area, root and shoot biomass, leading to higher seed yield, albeit at a lower harvest index. Accordingly, over-use of the drought escape strategy can constrain yield potential of crops in higher rainfall environments [37,38].

The contrast between Apex C and R type agricultural environments outlined above is analogous to the yield potential-drought postponement trade off introduced previously [19,20]. However, drought postponement can also be visualized in 2 different dimensions of Grime's triangle [12]: competition and stress. Increasing water uptake through deeper, longer roots diverts source from reproductive sinks and requires time, and is therefore consistent with the competitive, resource acquisition strategy selected in low disturbance habitats, rather than time-limited terminal drought-prone environments. Conversely, drought postponement through minimizing water loss, or tolerance adaptations such as the capac-

ity for osmotic adjustment extend the life cycle and reduce growth rates, and are consistent with lower disturbance/higher stress environments. Indeed, traits that minimize water loss are only expected to be adaptive in habitats where competition between plants is not a major selection pressure. This is because individuals that minimize water use make this resource available to competitors and reduce their acquisition of biomass. Agricultural crops meet this criterion because plant breeding selects cultivars on the basis of population yield rather than individual fitness [39].

These concepts work both within and between species. There is a wide range of Mediterranean pasture legumes, crops and their wild relatives where intra-specific variation in phenology is explained by collection site rainfall [40]. In the 4–6 studies that measured productivity, germplasm from low rainfall habitats also accumulated less biomass with a higher reproductive index than that from high rainfall habitats. Similarly, Indian pearl millet hybrids selected in low rainfall environments have a smaller leaf canopy than those bred for high rainfall zones [25]. Recent work in *Lupinus luteus* L. demonstrates how a wide range of adaptive traits are integrated differently in wild ecotypes from low and high rainfall areas [40], aligning closely with Fig. 1. High rainfall ecotypes were characterized by later phenology, supporting higher above- and below-ground biomass production, leaf area, seed yield, and seed number, albeit at a lower harvest index than in low rainfall ecotypes. This greater productivity came at the cost of higher water-use, and the earlier onset of terminal drought stress. Interestingly, there were no ecotypic differences in the regulation of transpiration as leaf water potential declined [40]. However, high rainfall ecotypes maintained higher relative leaf water content at

lower critical potentials, a tolerance capacity that mitigated self-imposed deficits driven by high transpiration rates during a long growing season in low water holding capacity sands. This capacity is not found in low rainfall ecotypes that escape this terminal drought stress through earlier phenology and lower transpiration rates [40]. Thus it appears that *L. luteus* mitigates the impact of profligate water use by combining tolerance and competitive traits only in high rainfall ecotypes. These examples highlight the value of a holistic approach to investigating adaptation by characterizing both environment and a wide range of plant traits by demonstrating adaptive trade-offs along the R- and C-apices of their distribution ranges.

Note that the same environment may select for different R- and C-type trade-offs between species, indicating that different complementary trait combinations may be adaptive. Among Mediterranean annuals, notwithstanding a trend to earliness with increasing aridity, flowering time variation is larger within than that between rainfall zones [41]. This is elegantly demonstrated by contrasting lentil with chickpea, in both wild and domesticated forms. Throughout SE Anatolia, *Lens orientalis* L. flowers and matures up to a month earlier than sympatric *Cicer reticulatum* L. and *C. echinospermum* L., and appears to produce less biomass. These differences are reflected in their domesticated counterparts. Chickpea has a later phenology, is deeper rooting, using more water and accumulating biomass and seed yield at lower water-use efficiency than lentil [42]. This contrast between the escaper lentil, and the drought postponing chickpea shapes their preferred production regions. In the Mediterranean, lentil is grown in regions receiving 300–400 mm rainfall annually, whereas chickpea is restricted to regions >400 mm/yr [42]. In India chickpea production has moved S to drier and hotter production environments, a transition made possible by the selection of increasingly early phenology [9].

The scheme proposed in Fig. 1 also explains the apparently contradictory trends arising in the carbon isotope discrimination ($\delta^{13}\text{C}$) literature. $\delta^{13}\text{C}$ is an integrator of leaf conductance [43], where high values indicate open stomata, while low values are associated with closed stomata and higher transpiration efficiency. Surprisingly, $\delta^{13}\text{C}$ is negatively correlated with flowering time in many domesticated crops (e.g. barley [44], wheat [45], cowpea [46]) and wild annuals (e.g. *Polygonum arenastrum* [47], *Triticum dicoccoides* [48], *Xanthium strumarium* L. [49]). This has been confirmed by more direct studies of plant water relations. Transpiration rates of Rajasthani dry-zone pearl millet (e.g. H77/833-2) are higher than those bred for higher rainfall areas (PRLT 2/89-33), and do not reduce as vapour pressure deficit increases [50]. Conversely, high rainfall PRLT 2/89-33 transpiration rates are lower than H77/833-2, and sensitive to increasing vapour pressure deficit, indicative of greater transpiration efficiency. These examples lead to the seemingly counter-intuitive conclusion that low transpiration efficiency is advantageous in water limited conditions, but is well explained by the importance of escape. Fig. 1 suggests that escapers avoiding terminal drought must maximize growth rates for an early completion of their life cycle. This is facilitated by maximizing photosynthesis at the expense of instantaneous transpiration efficiency [51], and also ensures that the water is used while it is available, before being lost to evaporation, drainage or competitors. Moreover, in Mediterranean and semi-arid climates the opportunity cost of maintaining photosynthesis is likely to be lower in early than in late season genotypes. Assuming that $\delta^{13}\text{C}$ is largely driven by differences in stomatal conductance, early varieties probably assimilate (and possibly also remobilize) a greater proportion of their grain C relatively early, when higher plant available water levels allow stomata to stay open. Conversely, later genotypes may be obliged to close their stomata more often during grain fill because of their relatively greater exposure to terminal drought at that time. Like the earlier *L. luteus* example, it appears that the later flowering

annuals listed above have some tolerance traits (in this case postponement mechanisms) that support a longer life cycle, trading off a temporary reduction in growth rates against a longer growing season.

If annual plants trade off transpiration efficiency to maximize growth rates and escape drought, the opposite is the case among perennial stress tolerators that cannot escape water deficit. Here transpiration efficiency increases with increasing aridity [33], reaching an apex in facultatively 'idling' CAM plants that can refix internally generated CO_2 , almost completely eliminating water loss [15]. By trading-off growth to maximize transpiration efficiency, this adaptive response is the basis for stress tolerance that facilitates long term survival in temperate succulents and desert perennials. As such it is completely inappropriate for a time-limited annual life cycle where selection pressure for reproduction within the growing season is paramount.

3. Application of the integrated framework to transient and terminal drought stress

The principal value of the integrated framework (Fig. 1) to crop improvement is to provide context to plant adaptation to transient and terminal drought deficits. Crop adaptation to these stresses is based on an integrated group of complementary traits operating within the limits of an escape-based adaptive strategy. Annual agricultural crops are characterized by rapid growth rates and high reproductive investment that maximises yield, and avoid stress through a closely regulated, climate-appropriate phenology. This is well illustrated by chickpea which becomes increasingly early, regulated by an increasingly sensitive temperature response as mean vegetative phase temperatures rise from the Mediterranean, through northern, central and southern India [52]. As a result the sensitive reproductive phase of chickpea is timed to avoid winter frosts, spring chilling temperatures and summer terminal drought throughout its distribution range. (While low temperature stresses are more common in northerly latitudes of the chickpea distribution, terminal drought is a widespread stress for the crop). Similar examples of regionally-appropriate phenology regulation by differential responses to vernalization, daylength and temperature exist in lentil [53] and wheat [54].

Consequently the adaptive trade-offs made by crops must be viewed within this escaper context: everything happens within a limited time frame, and annuals have neither the resources nor the morphological capacity to develop the suite of traits that enable stress-tolerant perennials to withstand long periods of intense water deficit. Instead, specific adaptation to low or high rainfall environments in annual crops largely represent trade-offs between the C- and R-apices of Fig. 1. Under terminal drought, yield potential is traded off against drought escape, such that drought postponing and/or tolerance traits which extend the growing season, and/or divert source from reproductive sinks will generally be maladaptive. Conversely, these traits do have a supporting role in the adaptation to transient water deficits, facilitating the survival of longer season cultivars by mining water through deeper roots, or restricting transpiration when demand for water temporarily exceeds supply, as outlined previously. However as outlined earlier, the full complement of stress tolerating 'survival' traits found in perennial xerophytes necessarily leads to very low productivity, and has little relevance for annual agriculture crops.

Recognizing these trade-offs made within escaper limits will expedite crop improvement under both transient and terminal water deficit by promoting understanding. Rather than unravelling natural selection [19], it behoves breeders to integrate complementary adaptive traits as outlined above. This applies equally to proponents of transgenic or conventional approaches to improving

adaptation to drought, as demonstrated by the examples outlined below.

The last decade has seen a plethora of molecular approaches to improving adaptation to water stress [21,23,55,56]. The most common transgenic modification has been indirect: overexpression of drought inducible transcription factors and other regulators of downstream genes, rather than targeting the effector genes directly (Supplemental Table 2). They include the DREB series transcription factors, interacting with CRT/DRE promoter elements [21], NAC-type transcription factors, Arabidopsis homodomain-leucine zipper transcription factor (Enhanced Drought Tolerance/HOMEODOMAIN GLABROUS11 (EDT1/HDG11)) among others. Calcium sensors such as the Ca^{2+} -dependent protein kinases (CPKs or CDPKs) [57] and elements influencing abscisic acid biosynthesis (e.g. AtLOS5) [58] are also upstream regulators effected by water deficits that have been subject to transgenic overexpression. In contrast there has been relatively little published literature describing transgenic events targeting downstream effector drought tolerance directly through the production of LEA proteins, protein chaperones or osmolites such as proline and trehalose (Supplemental Table 2). Although the molecular engineering of yield improvement under water stress has been comprehensively reviewed recently [21,23,55,56,59], it is useful to distil the common elements of this work that pertains to plant adaptation.

While these diverse transgenic approaches are usually reported to increase the drought tolerance of their respective hosts, their most common mode of action is a reduction in transpiration (Supplemental Table 2). Interestingly, this appears to be the case across the range of upstream regulators targeted to date (Supplemental Table 2), but also in events targeting seemingly unrelated downstream effectors such as bacterial cold shock protein B (CspB) expression as in DroughtGard™ maize [60,61]. Water deficit responses are overwhelmingly evaluated in small pot experiments favouring water savers. Plants that are reported as being drought tolerant are actually reducing their water use, delaying the onset of stress symptoms such as leaf rolling, wilting and death. In addition, associated metabolic stress indicators such as leaf water content, malondialdehyde concentration, electrolyte leakage and photosystem II efficiency are also delayed. Occasionally, improved recovery after stress, increased biomass, seed set and yield are also reported (Supplemental Table 2).

These changes can be attributed to the reduced water use that is entirely consistent with the water saving component of the drought postponement strategy. As such we expect these transgenic interventions to be most efficacious under transient drought in stored soil moisture situations where water competition is minimized, and water saved is likely to still be available during the reproductive phase. This bodes well for their application in paddy rice and South Asian rabi crop production if weed competition can be effectively managed, while their utility in in-season rainfall systems will depend on seasonal weather and soil moisture holding capacity. In contrast, these transgenic interventions are unlikely to improve yield in poor water holding capacity soils, especially where terminal drought is commonly encountered. Drought postponement strategies are ineffective under these circumstances for the reasons outlined in the previous discussion of the carbon isotope discrimination ($\delta^{13}\text{C}$) literature. Under these conditions water saved is water lost, and sacrificing instantaneous transpiration efficiency to maximize growth rates [51] and facilitate drought escape by an early completion of the lifecycle is the preferred strategy.

Two other common themes emerge from the recent transgenic work on improving adaptation to drought stress. Firstly, there is considerable variation in water deficit responses between transgenic events within families, irrespective of whether these are upstream or downstream interventions (Supplemental Table 2). For

example, DREB1A transgenesis in wheat improved either water use efficiency or survival, but not both, and there were significant differences between events in either group, such that differences between the null-event control were not always realized [62]. Similar trends emerge in closer examination of the downstream chaperone work [63] and other listed examples (Supplemental Table 2), demonstrating the complexity of molecular approaches that generate a range of outcomes, presumably reflecting positional variation of the transgene insertion point. The second common theme that emerges is that there is relatively little realistic field evaluation of the transgenic material. While this is understandable, given constraints in seed and space availability in rainout shelters used for drought evaluation, both issues are limiting our understanding of the potential of this technology. This constraint will be overcome by more thorough, carefully controlled research of what the technology can deliver, and where it will fit.

There are important outstanding questions in both categories. The transgenic work gives tantalizing glimpses that drought postponement and tolerance are linked on a molecular level. For example, while over expression of upstream transcription factors largely targets transpiration, there are many reports that osmolyte production is also increased [58,64–68]. Surprisingly, the reverse situation also seems to apply; as suggested by the reduction in transpiration in events overexpressing tolerance effectors such as bacterial cold shock proteins [61]. These observations indicate that it is important to make a broad range of observations to realize the impact of transgenic intervention because many traits may be influenced in the plant. This is underlined by studies indicating that stomatal density and aperture as well as root biomass can be effected by overexpression of upstream transcription factors [61]. The same applies to the physiological studies of plant responses to water deficit. There are many examples of drought postponement where crops adjust their transpiration rate in response to increasing vapour pressure deficit (Table 1). Given the results from the transgenic literature this begs the question of whether these crops may also be simultaneously modifying their osmotic potential to better tolerate water deficit stress. Furthermore, this is an excellent opportunity to unite the 2 disciplines. Gene expression studies of genotypes modifying transpiration in response to vapour pressure deficit offer a reverse engineering opportunity to further investigate the molecular mechanisms regulating these processes. It will be fascinating to discover whether nature has selected for overexpression of the same transcription factors currently favoured by molecular biologists, or whether there are other levers that can be modified to regulate water use.

Much more widespread, rigorous field testing is required to understand where this technology (or indeed any other form of drought postponement) will fit. This is a current weakness of the transgenic work, which largely relies on small pot studies, or small unrealistic field experiments, and where relatively large percentage yield differences may not be significant at even $P < 0.2$ (e.g. [63]). The limited published field testing demonstrates that transgenic drought postponement has inconsistent effects on yield. For example wheat genotypes overexpressing DREB1A show clear differences in WUE that do not translate into yield gains under stress [62]. Conversely, drought postponement in DroughtGard™ maize led to small, but significant yield and harvest index gains in 2 of 3 trial years [61]. These inconsistent results are the expression of G \times E interaction, indicating that, as expected, transgenic drought postponement is not universally applicable [19,69]. This is not a criticism of this technology, as this pertains to any trait that is bred into a crop, regardless of the methodology used. Rather it is a salutary reminder that it is important to test widely and rigorously to understand the best application of our innovations. This is particularly pertinent to drought postponement strategies that rely on saved water being subsequently available. Accordingly it

is essential to test across a range of agronomy (sowing time, row spacing, density, weed burden), soil types and seasonal climates to effectively evaluate their potential.

Contrary to the drought postponing examples cited above, there are also transgenic approaches that increase plant growth under mild water deficit. Peanut was transformed with the isopentenyl-transferase gene, an enzyme in the cytokinin biosynthesis pathway whose overexpression delays plant-induced senescence [70]. As a result, under mild water deficit the transgene maintained higher rates of stomatal conductance, transpiration and photosynthetic than the wild type, leading to larger above- and below-ground biomass and seed yield [70]. In the long season Valencia-type cultivar background, this combination of competitive traits was complementary in the irrigated low stress/low disturbance target environment of Lubbock, Texas.

Finally, attempts to engineer drought tolerance into crops by inserting genes from resurrection plants (*Xerophyta viscosa* Baker) [71] and other stress tolerators [72], or the opposite idea of basing dryland agriculture on CAM metabolism [73] are unlikely to be sufficiently productive for the reasons outlined previously. These genes come from plants that have evolved at the very extreme of the S apex (low disturbance/high stress), where productivity is traded off against survival. Even if modified annual crops had the morphological capacity to develop these specialized stress tolerating organs/mechanisms, which is unlikely, their productivity would necessarily be low.

The hope that unexploited, minor 'orphan' crops may harbour a magic bullet solution to water deficit adaptation is equally misplaced. Relatively unimproved crops such as tef can capture public imagination because they are grown across a wide rainfall range, and exhibit characteristics consistent with water deficit adaptation such as deep root systems, osmotic adjustment and sensitive stomatal regulation [74,75]. However, the same argument applies: variation must be understood to allow complementary traits to make best use of the water resources of the target environment. Orphan crops are at a disadvantage here because by definition, as under researched species, less is known about their adaptive potential. This shortcoming can be allayed by applying the integrated framework to select orphan crops from similar habitats to the target environment. For example, a recent comparison of peanut and cowpea (from Sahel, Africa) in central India demonstrated that the latter used less water under deficit, producing a more stable, higher yield as a result of increased transpiration efficiency and harvest index [76]. In this case the water demands of low biomass, early flowering, short-season cowpea was well-matched with water availability in central India. In tef, the establishment of a wide Ethiopian germplasm collection offers similar opportunities to study material adapted to contrasting drought stress environments [74,75].

However, from a grower perspective orphan crops face an additional hurdle: the produce must be sold, and there is little incentive to grow even a perfectly adapted crop if there is no market for it. While cowpea may be a good fit in post rainy season India, demand must be generated by developing attractive, preferably human end-uses. There are precedents for this. The common bean has become completely integrated into South Asian, Middle Eastern and European diets since its introduction from the New World, while soybean and canola have both become very widely adopted multifunction oil seed crops. Other species have been less successful. The narrow-leaved lupin is well adapted to acid sandy soils in Mediterranean climates and produces nutritious high protein grain that is predominantly used as animal feed, which does not attract the price premiums of the human consumption market [77]. As a result, narrow-leaved lupin is struggling to hold its place against higher value alternatives in the Western Australian farming system. This is an important lesson for proponents of putatively drought

adapted orphan crops with limited markets, such as grass pea or tef (which has a high market value in Ethiopia, but is limited in size).

This is not to argue against innovation. Indeed, plant breeders have the freedom to assemble complementary combinations unlikely to have evolved outside of agriculture. Unlike most wild species, crop cultivars are selected on a communal basis, whereby the ideotype is a weaker competitor than that arising when genotypes are selected on an individual basis [39]. This allows breeders to disassemble Grime's triangle [12] for specific systems because they can disregard the ramifications of competition because neighbouring crop plants are poor competitors and weeds are excluded. For example, limiting vegetative transpiration in stored soil moisture environments sets aside water for grain filling [16,17]. This is a novel way of marginally postponing terminal drought in this special case, and is complementary in these examples: set in an early flowering background, improving grain fill, without extending the maturity date. Similarly, manipulation of *tin* genes in wheat can increase water uptake, and decrease transpiration by increasing root to shoot ratios by influencing both above- and below-ground biomass, again setting aside water for grain filling [78]. This blend of resource acquisition (deep, high biomass roots) and escaper parsimony (low above ground biomass/transpiration) is unlikely to exist in the natural world, and will be fascinating to evaluate in contrasting environments. However, in both these chickpea and wheat examples, yield is likely to be limited when grown under higher rainfall [19,20]. By contrast, the introgression of high rainfall ecotype drought tolerance into escaper-type European and Australian yellow lupin cultivars [40] may improve pod-fill on later-set lateral branches with positive ramifications in both low and high rainfall.

Finally, the sensible application of integrated frameworks requires an equally good understanding of the target environment. As pointed out previously, almost any trait combination can be either adaptive, or maladaptive depending on the stress scenario [19]. The application of climate and crop simulation models provides a probabilistic understanding of the likelihood and types of water deficit that are experienced in target environments [2,79], and should be used to drive the assembly and evaluation of appropriate complementary adaptive traits. This will facilitate matching water supply to crop water demand, especially during the grain filling period, and is achieved by assembling a complementary suite of traits within an appropriate phenology window [80,81].

Acknowledgments

The authors would like to acknowledge generous research funding support from the Commonwealth Scientific and Industrial Research Organization (CSIRO), the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), the CGIAR Research Programs on Dryland Cereals and Grain Legumes, and the Australian Grains Research and Development Corporation (GRDC).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.plantsci.2016.09.007>.

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