

When is breeding for drought tolerance optimal if drought is random?

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Summary

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- Increasing climatic unpredictability associated with characteristics of some species makes plant drought-tolerance an important drought-adaptation strategy. Using norm-of-reaction functions, or empirically determined functions that enable us to predict the state of a trait given the state of an environmental variable, allows modelling of plant performance when water availability varies randomly.
- A mathematical model is proposed to evaluate drought-tolerance and growth strategies given a set of environmental parameters: the frequency of rainy days, the soil water-storage capacity, plant water use and plant growth rates. This model compares the performance of genotypes that differ in drought tolerance expressed as the ability to grow in drier soils, and assumes a general trade-off function between drought tolerance and maximum plant growth rate.
- It is worth selecting plants with a greater degree of drought tolerance, expressed by the ability to grow in drier soils whenever the frequency of rains is smaller than the rate of soil water depletion. Otherwise, maximizing growth rate at the expense of drought tolerance is the best strategy. The nature of the trade-off between drought tolerance and plant growth rate also constrains the selection for optimal drought-adapted genotypes.
- Breeders will have to consider these aspects of plant–environment interactions before establishing selection programs for drought adaptation.

Key words: drought adaptation, drought tolerance, global warming, norms of reaction, plant growth rate, plant responses, random environment.

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Introduction

The high costs of irrigation, the necessity of cultivating in drier areas and the uncertainties posed by world climate change have increasingly required breeders to create drought-adapted cultivars. However, plant drought adaptation is a very complex problem that involves not only aspects of the plant, but also the interaction between these aspects and the environment to which they are adapted (Porporato *et al.*, 2001; Tardieu, 2005). Drought is sometimes predictable, and breeding strategies to cope with dry and predictable environments are becoming well known. Successful cases involve the

enhancement of plant water-use efficiency (Tardieu, 2005), as with wheat in Australia (Rebetzke *et al.*, 2002).

Another example is wheat grown in the Californian mediterranean climate. There, wheat takes advantage of the water stored in the soil after winter rains, and maturation must be as early as possible to avoid an inevitable and predictable drought during the late summer. Thus selecting for early maturation also results in selection for drought-stress avoidance. But drought can occur in humid areas as well, at a frequency that can cause production losses. This can be caused by characteristics of either the climate or the crop. From a climatic perspective, one of the expected consequences of global

warming is an increase in the variance of climatic parameters (Arnell & Liu, 2001), thereby increasing the intensity and unpredictability of drought in many agricultural systems. From a crop perspective, crops such as sugarcane – which is a semiperennial crop – are particularly susceptible to temporal variation in water availability because their lifespans extend for more than a year. In this case, the adoption of drought-avoidance strategies may be limited, and drought-tolerance strategies may be the only alternative. Even annual cultures, when planted in humid areas, may need to cope with eventual unpredictable drought. Dealing with the effects of the interaction between an increasingly unpredictable climate and the particularities of some crops requires a more general understanding of drought adaptation. This problem leads to many practical concerns that breeders will inevitably face. When is it worthwhile to create drought-adapted cultivars? What strategies should be used to improve cultivar drought adaptation? How does the environment interact with plant traits to produce optimally drought-adapted cultivars?

An important aspect of adaptation in general, and drought-adaptation in particular, is the high probability that ecological, morphological and physiological trade-offs will exist that make the adoption of any breeding strategy an exercise in cost–benefit evaluation (Tardieu, 2005). Genotypes adapted to particular conditions usually perform poorly when these conditions are absent. Therefore it is expected that the adoption of a single drought-adaptation strategy will not be adequate for all environments. For example, the trade-off between increased water-use efficiency (caused by reduced stomatal conductance) and biomass accumulation (Condon & Hall, 1997) would certainly lead to losses in production in humid areas if increasing water-use efficiency is chosen as the only drought-adaptation strategy. In the case of selection for reduced stomatal conductance, for example, although plants will avoid drought by saving water when it is scarce, when water is available growth will be limited by the same mechanism that allows drought avoidance: reduced stomatal conductance will also limit CO₂ uptake. It is likely that trade-offs associated with drought-tolerance traits exist as well.

Another crucial concern for understanding drought adaptation is how plants respond to varying levels of water availability. Trait responses or norms of reaction (Schmalhausen, 1949) are known to vary within species in nature as well as in crop species, are usually measured as genotype × environment interaction terms in ANOVAs, and are considered heritable traits themselves subject to natural or artificial selection (Via & Lande, 1985). It has been shown that it is possible empirically to establish functional relations between plant and environmental variables. Recent advances in this field were made for maize leaf extension rate (LER) as a function of the environmental water status. LER is a global trait that can, to a certain extent, be used as a surrogate for plant performance and is affected by changing environmental water availability (Inman-Bamber, 1995; Ben Haj Salah & Tardieu, 1997).

Holding temperature constant, maize LER is regulated by the additive effects of soil water potential when air evaporative demand is zero (measured at night) and air evaporative demand (vapour pressure deficit or VPD) when soil is well watered (measured during the day) (Ben Haj Salah & Tardieu, 1997). The response of maize LER to both effects is linear and heritable, and the parameters of the regression lines of LER on soil water potential or VPD have significant effects on quantitative trait loci, providing empirical evidence that norm-of-reaction functions are also traits themselves (Reymond *et al.*, 2003, 2004). The LER seems to respond to the soil water potential through root-to-shoot signals mediated by abscisic acid (Ben Haj Salah & Tardieu, 1997; Sauter *et al.*, 2001; Holbrook *et al.*, 2002). In fact, it has recently been shown that plant growth can be actively modulated by an intricate network of phytohormonal signals, and not necessarily as a by-product of the stress (Archard *et al.*, 2006). The major contribution of this series of studies is its finding that norms of reactions can be expressed not as discrete character states as usual, but rather as functions of an environmental variable (cf. Stratton, 1998). With this, one can predict the performance of a genotype (again expressed as LER) given a value of VPD or soil water potential.

The possibility of predicting plant performance in a range of environmental scenarios opens up great possibilities for modelling plant performance when the environment is seen as a random variable (Rodriguez-Iturbe *et al.*, 1999; Laio *et al.*, 2001). The purpose of this study is to develop a mathematical framework that evaluates plant performance with a randomly varying soil-water status, bearing in mind what is known about maize LER. The analysis focuses on whole-plant growth-rate responses to soil water potential. Thus the main assumption of the modelling approach presented here is that observed responses of LER (a linear function of soil water potential) can be translated into the whole-plant growth rate. In other words, the plant growth rate is also a linear function of the soil water potential. We are interested in whole-plant growth rate because plant biomass is an important criterion for assessing drought tolerance in plant breeding (Morgan *et al.*, 1993; Sivamani *et al.*, 2000). Small differences in whole-plant growth rate caused by variation in water availability can compound in time, and result in plants with significantly different biomass. The model also compares the performance of genotypes that differ in drought tolerance, expressed as the ability to grow in drier soils, and assumes a general trade-off function between drought tolerance and plant performance. It has been hypothesized that plants that acquire resource efficiently when they are abundant will show a reduced capacity to tolerate shortages of these resources (Chapin, 1980; Turner, 1986; Bazzaz, 1996; Sandquist & Ehleringer, 1998, but cf. Fernández & Reynolds, 2000).

The objectives were: to provide a general heuristic understanding of plant drought-tolerance strategies when norms of reaction are subject to selection; to capture a limited number

of relevant plant and environmental parameters that should be taken into account when optimizing performance in different environmental conditions; and to provide some general guidelines that breeders need to observe when implementing selection for drought-adaptation programmes.

Description

Our model relates the frequency of storm arrivals to the mean growth rate of crops through a trade-off function that describes the dependence of maximum growth rate on drought tolerance. We characterize the availability of soil moisture in terms of the relative plant-available soil moisture, s , which is simply the volumetric soil moisture content ($\text{m}^3 \text{m}^{-3}$) normalized by the field capacity, which is defined as the soil moisture content at which the flux of soil moisture driven by vertical gravity-driven drainage approaches zero. In this framework, we neglect the role of vertical drainage for values above field capacity, which is based on the assumption that at the daily time scale we are considering, many agricultural soils will rarely exceed soil water contents in excess of field capacity. Therefore relative soil moisture is allowed to vary between 1 (field capacity) and 0 (complete soil-moisture depletion). The dynamics of soil moisture are driven by the frequency of stochastic rainfall events and the intensity of water use by plants. Rainfall events occur at a rate of p (d^{-1}), so that the distribution of times t between rainfall events is given as:

$$f_1(t) = pe^{-pt} \quad \text{Eqn 1}$$

In this simple approach, we assume the rainfall events replenish the soil moisture to its maximum value (field capacity), and that any excess rainfall is routed away from the soil surface or is lost vertically below the rooting zone, so that immediately after rainfall events the relative soil moisture value returns to 1. Following a rainfall event, we consider the change in relative soil moisture (Fig. 1), s , to be governed by the crop's characteristic water use, λ (s d^{-1}), so that soil moisture content at time t after a prior rainfall event varies according to:

$$s(t) = e^{-\lambda t} \quad \text{Eqn 2}$$

The parameter λ includes information about both the plant root extent and plant water-uptake rates, which we do not resolve independently. Conceptually, increasing the value of λ suggests either a greater characteristic uptake rate per unit root length, or a greater characteristic total root length (or some combination of both). Conversely, smaller λ values indicate a more conservative rooting strategy or reduced water use per unit root length (or both). Combining the distribution of storm arrivals and the functional dependence of $s(t)$ on λ allows us to derive the probability distribution of relative soil moisture values, given by:

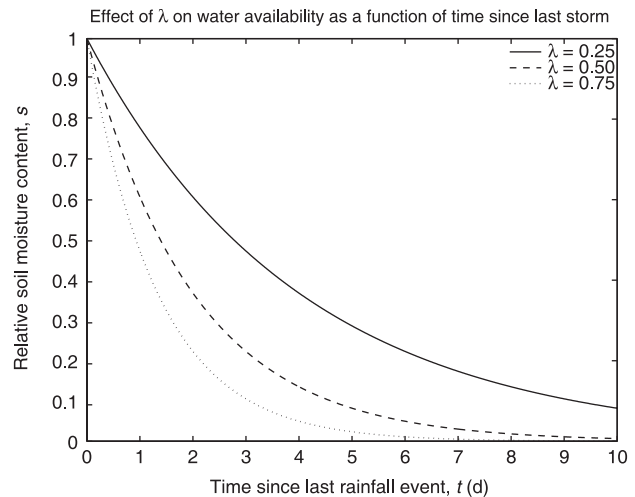


Fig. 1 Rate of decay in soil water content when there is no rain. The vertical axis has an arbitrary scale. The curve obeys an exponential decay according to equation 2.

$$f_s(s) = \frac{\lambda + p}{\lambda} s^{p/\lambda} \quad \text{Eqn 3}$$

In crop systems, plant-available soil moisture is usually characterized by predawn water potential (Ψ) measured in MPa. To determine the empirical functional relationship between soil water potential and soil water content, we use data collected from sugarcane (*Saccharum officinarum*) grown in PVC cylinders measuring 20 cm in diameter and 39 cm in length. These growth containers were placed on a double glasshouse plastic layer and filled with a 2 : 1 mixture of sand and soil ferralitic; 25 l of mixture per pot. Thirty-nine plants were sampled. Irrigation of these plants was stopped, and predawn water potential measurements were taken with a pressure chamber (PMS Instruments, Corvallis, OR, USA) from a subsample of the 39 plants at different times after irrigation ceased. The soil water content was measured with a TDR probe (CS616 Soil Moisture Sensor, Campbell Scientific, Loughborough, UK) in the evening before pressure chamber measurements were performed. Plants were not used twice for predawn water potential measurements. These observations yield a relationship between Ψ (MPa) and relative soil moisture (Fig. 2), s , which is well approximated by:

$$\Psi(s) = 1 - (1/s) \quad \text{Eqn 4}$$

In this simple model we have chosen to express plant growth rate in relative units. Following the discussion in the Introduction, we assume that the plant relative growth rate, r , is correlated to leaf extension rate, LER, and likewise the value of r responds linearly to water potential when temperature is held constant (Ben Haj Salah & Tardieu, 1997; Reymond *et al.*, 2003; Reymond *et al.*, 2004). Therefore we assume that

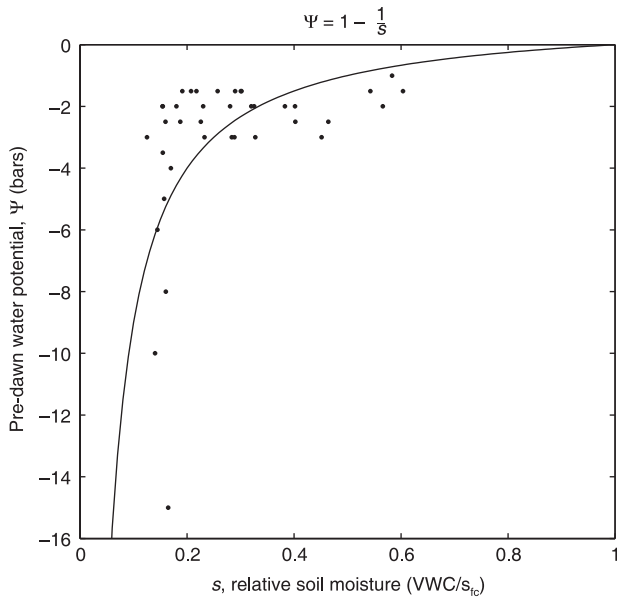


Fig. 2 Empirical fit between observed values of predawn water potential and relative soil moisture for soils. Volumetric water content (VWC) values obtained with a time-domain reflectometry probe were converted to relative soil moisture by normalizing each value by the soil field capacity, s_{fc} , so that $s = VWC/s_{fc}$. Here we use $s_{fc} = 0.35$, which corresponds to a value that minimizes the residual error between s and Ψ .

the plant relative growth rate, r , responds linearly to water potential according to:

$$r = r_{max} + \alpha\Psi \quad \text{Eqn 5}$$

where r is bounded between 0 and r_{max} , which represents a cultivar-specific maximum extension rate under completely moist conditions. In this presentation, we assume that r and therefore r_{max} varies from 0 to 1. The value of α is a measure of the reduction in relative growth rate per unit decrease in Ψ or $d r/d\Psi$ (Fig. 3). The values of r_{max} and α uniquely determine the critical value of soil water potential at which plant growth rate drops to zero, which we define as Ψ_{wp} , given as:

$$\Psi_{wp} = (-r_{max}/\alpha) \quad \text{Eqn 6}$$

In the following section we explain how the values of r_{max} and α are related according to functional trade-offs between drought tolerance, water-use efficiency and maximum plant growth rate.

Plant growth trade-offs

Within our simple model of plant growth and soil moisture variability, we define two distinct but related trade-offs: a trade-off between maximum relative growth rate and drought tolerance; and a trade-off between maximum relative growth

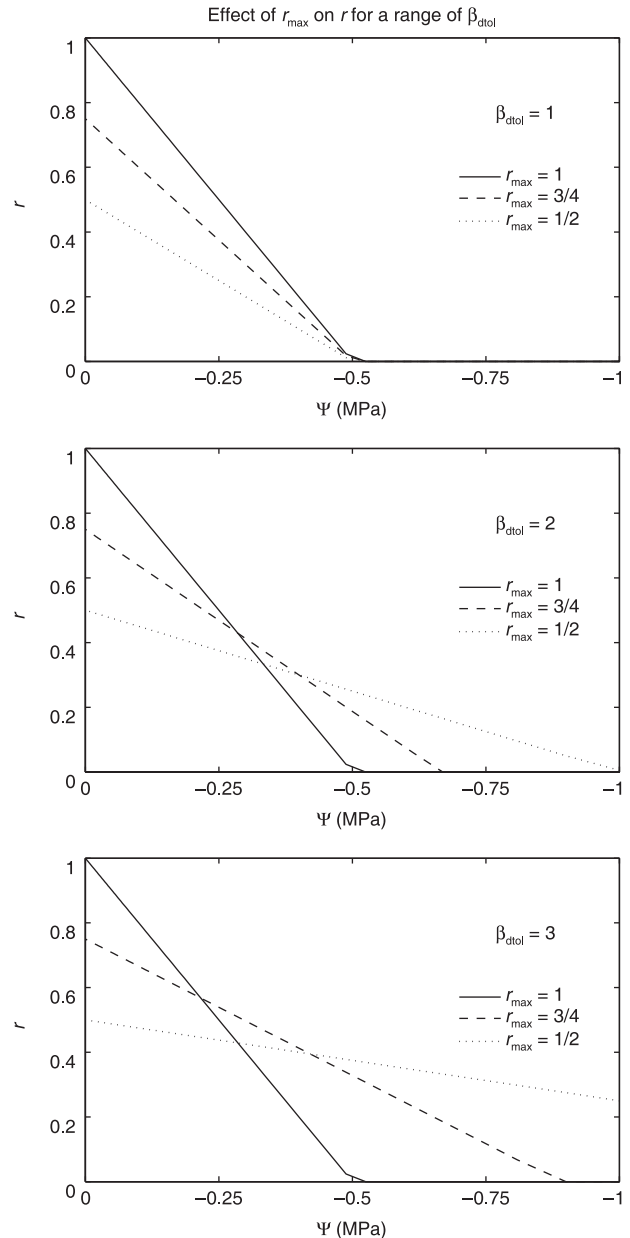


Fig. 3 Relationship between growth rate (r) and soil water potential (Ψ) for a range of potential β_{dtol} values. Three potential genotypes are shown in each graph. The slopes of these lines are represented in the model by the parameter α . The y -intercepts of the response curves represent the growth rate when there is no water limitation, r_{max} . The x -intercept indicates the value of soil water content when plants stop growing, which we specify as Ψ_{wp} . As β_{dtol} increases, the strength of the trade-off between drought tolerance and maximum growth rate (r_{max}) decreases. When $\beta_{dtol} > 1$, cultivars with reduced maximum growth rates are able to maintain positive growth at more negative soil water potentials.

rate and plant water use. The first trade-off establishes the form and intensity of the functional relationship whereby increasing drought tolerance (the ability to grow in drier environments) corresponds with decreased maximum growth

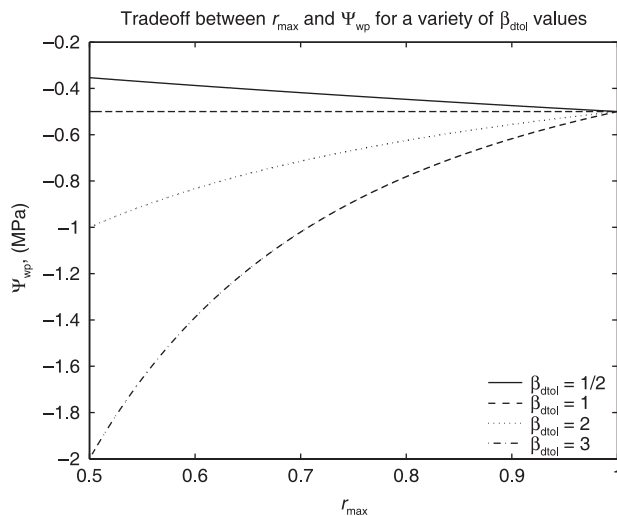


Fig. 4 Relationship between maximum possible growth rate (r_{\max}) and drought tolerance expressed as the soil water potential at which plants stop growing (Ψ_{wp}) for a range of possible β_{dtol} values. More negative values of Ψ_{wp} indicate greater drought tolerance. When $\beta_{\text{dtol}} > 1$, reductions in r_{\max} lead to increased drought tolerance (a more negative value of Ψ_{wp}). However, when $\beta_{\text{dtol}} < 1$, decreases in r_{\max} lead to reduced drought tolerance (an inverse trade-off). Thus we are not considering this case in subsequent analyses. In the special case that $\beta_{\text{dtol}} = 1$, there is no trade-off between growth rate and drought tolerance.

rates when water is abundant (or *vice versa*). This trade-off can be also interpreted as a 'cost' in maximum growth rate that arises when drought tolerance is selected for in a particular cultivar. We define this 'drought-tolerance' trade-off between the maximum possible growth rate, r_{\max} , and α so that as r_{\max} increases, α also increases, according to:

$$\alpha = \frac{(r_{\max})^{\beta_{\text{dtol}}}}{\Psi_0} \quad \text{Eqn 7}$$

where the coefficient β_{dtol} determines the degree to which r_{\max} and α are nonlinearly related, and Ψ_0 is the absolute value of negative water potential that corresponds to the point at which a plant with no adaptation for drought tolerance stops growing. Here we assume the value of Ψ_0 to be 0.5 MPa, which is a typical value for maize and sugarcane (Reymond *et al.*, 2003, 2004; J.S., personal observation). Figure 4 depicts the effect of varying β_{dtol} on the functional trade-off between r_{\max} and α .

The second trade-off defines the expected relationship between maximum growth rate, r_{\max} , and characteristic plant water-use intensity, which we previously defined as λ . We specify this second trade-off based on the fact that, for a given soil type, plants that grow more quickly are those that acquire CO_2 at a higher rate and, consequently, are also likely to extract soil water more rapidly (or more extensively) than plants with smaller maximum growth rates (Condon & Hall,

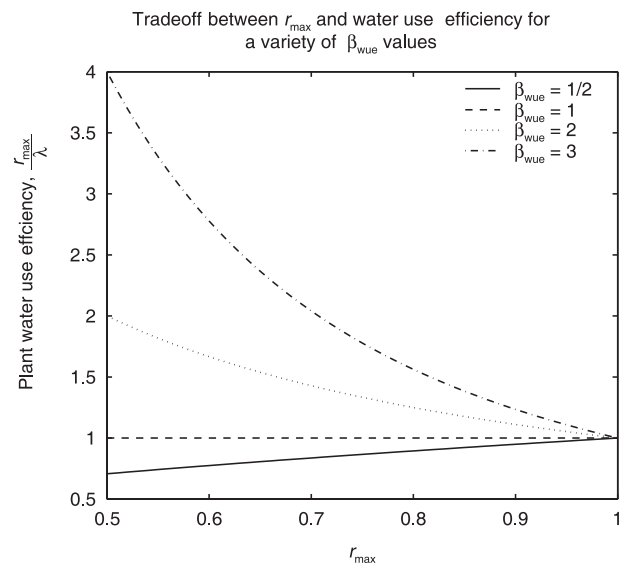


Fig. 5 Relationship between maximum possible growth rate (r_{\max}) and plant water-use efficiency for a range of possible β_{wue} values. Here we take water-use efficiency to be the ratio of maximum plant growth, r_{\max} , and the ratio of maximum plant growth rate and plant water uptake rate (λ). Smaller values of λ indicate greater water-use efficiency. When $\beta_{\text{wue}} > 1$, reductions in r_{\max} lead to greatly reduced plant water uptake rate (a smaller value of λ). However, when $\beta_{\text{wue}} < 1$, decreases in r_{\max} lead to only minor reductions in plant water uptake rate. In the special case that $\beta_{\text{wue}} = 1$, the value of r_{\max} is exactly the same as λ , and there is no trade-off between growth rate and water uptake.

1997). We propose a specific functional relationship that is similar to the first trade-off, so that:

$$\lambda = (r_{\max})^{\beta_{\text{wue}}} \quad \text{Eqn 8}$$

As in the case of the first trade-off, the value of β_{wue} specifies the degree to which changes in maximum growth rate lead to impacts on the characteristic rate of plant water uptake. A larger value of β_{wue} suggests a greater amount of water use for a given value of r_{\max} , while smaller values of β_{wue} are associated with water-conserving strategies, particularly at intermediate values of r_{\max} . An expression of water-use efficiency can be defined as the ratio of maximum plant growth to characteristic plant water use, or r_{\max}/λ . Figure 5 depicts the role that β_{wue} plays in determining the strength of the trade-off between r_{\max} and water-use efficiency r_{\max}/λ . Values of $\beta_{\text{wue}} > 1$ lead to high water-use efficiencies at low r_{\max} , but increasingly lower water-use efficiencies when maximum growth rate is increased. The larger the value of β_{wue} , the stronger the trade-off effect between growth rate and water-use efficiency. When β_{wue} is exactly 1, then changes in r_{\max} do not affect water-use efficiency. Finally, β_{wue} values < 1 lead to the unrealistic case whereby greater r_{\max} values lead to greater water-use efficiencies (an inverse trade-off).

Seasonally averaged expected growth rate

Through substitution of equation 4 into equation 5, we derive a single relationship between relative soil moisture, s , and relative plant growth rate, r , which is expressed as:

$$r = r_{\max} + \alpha \left(1 - \frac{1}{s} \right) \quad \text{Eqn 9}$$

Solving equation 9 for s yields:

$$s = \frac{\alpha}{\alpha + r_{\max} - r} \quad \text{Eqn 10}$$

A couple of critical values arise from our model. The first is the critical value of soil moisture, s_0 , that corresponds to the condition that $r=0$, which is given by:

$$s_0 = s(r=0) = \frac{\alpha}{\alpha + r_{\max}} \quad \text{Eqn 11}$$

A second important (and highly related) parameter is the critical time between storms, t_0 , that corresponds to a time when the soil dries to the value of s_0 , the time between storms at which a plant stops growing. The value of t_0 is given by:

$$t_0 = \frac{-\ln\left(\frac{\alpha}{\alpha + r_{\max}}\right)}{\lambda} = \frac{-\ln(s_0)}{\lambda} \quad \text{Eqn 12}$$

Notice that an implicit assumption of this model is that a plant that stops vegetative growth because of a lack of water will immediately re-establish growth once water becomes available again. There is empirical evidence that this assumption holds for short periods of time (Ben Haj Salah & Tardieu, 1997).

The probability distribution of plant growth rate can be determined by substitution of equation 10 into equation 3, which yields:

$$p_R(r) = C_1 \left(\frac{\alpha}{\alpha + r_{\max} - r} \right)^{p/\lambda} \quad \text{Eqn 13}$$

where C_1 is a normalization constant. The value of this normalization constant can be determined by recognizing that (1) the growth rate of vegetation can vary only between r_{\max} (the maximum rate) and 0; and (2) the integral of the probability distribution for all possible growth rates must be equal to 1. From equation 11 we have already determined that plant growth will occur only when the soil moisture is above the critical value s_0 , which specifies the point at which plants cannot continue to grow because of soil moisture limitation. Furthermore, we can state that the probability of obtaining values of s below s_0 is the same as the probability of time between storms being greater than t_0 , which is noted as $P(t \geq t_0)$ and given by:

$$P(t \geq t_0) = 1 - \int_0^{t_0} p_T(t) dt = 1 - e^{-\lambda t_0} \quad \text{Eqn 14}$$

Using equations 14 and 13, and condition (2) from the previous paragraph, we can now express the total probability distribution of r as:

$$C_1 \int_0^{r_{\max}} p_R(r) dr = 1 - e^{-\lambda t_0} \quad \text{Eqn 15}$$

and solving Eqn 15 for C_1 yields:

$$C_1 = \frac{p - \lambda}{\left(\alpha + r_{\max} + \frac{r_{\max}}{s_0^{p/\lambda} - 1} \right) \lambda} \quad \text{Eqn 16}$$

So the final expression for the probability distribution of r is given as:

$$p_R(r) = \frac{(p - \lambda)}{\lambda} \frac{\left(\frac{\alpha}{\alpha + r_{\max} - r} \right)^{p/\lambda}}{\left(\alpha + r_{\max} + \frac{r_{\max}}{s_0^{p/\lambda} - 1} \right)} \quad \text{Eqn 17}$$

Having obtained the analytical solution to the probability distribution of r in equation 17, it is possible to determine the mean growth rate, $E(r)$, which is given by:

$$E(r) = \int_0^{r_{\max}} r p(r) dr \quad \text{Eqn 18}$$

The resulting analytical expression for the solution of equation 18 is:

$$E[r] = \frac{(\alpha r_{\max} p + s_0^{p/\lambda} (\alpha + r_{\max})^2 \lambda - \alpha \lambda (\alpha + 2r_{\max}))}{\left(\alpha + r_{\max} + \frac{r_{\max}}{s_0^{p/\lambda} - 1} \right) (p - 2\lambda)} \quad \text{Eqn 19}$$

In the following section we use the value of mean growth rate, $E(r)$, as a diagnostic parameter that integrates the action of drought adaptation, functional trade-offs and random climatic variation on plant growth rate. Characteristic values for all necessary parameters, as well as their range of values and units, are provided in Table 1.

Results

Our model describes plant growth when water availability is determined by a combination of a random variable, the frequency of rains that replenish the soil water, and the rate at which plants extract this water. Plants respond to this variation in water availability with more or less growth depending on the genotype and an intrinsic parameter that quantifies the trade-off between being able to grow in more negative soil water potentials and to grow at its maximum

Table 1 Parameters used in the ecohydrological crop-growth model

Parameter	Description	Range	Units
Ψ	Soil water potential	$\Psi \leq 0$	MPa
s	Relative soil water content	(0–1)	–
r	Relative plant growth rate	(0–1)	–
ρ	Rate of rainfall occurrence	(0–1)	d ⁻¹
λ	Characteristic rate of water extraction by vegetation	(0–1)	d ⁻¹
r_{\max}	Maximum relative growth rate that occurs in the absence of soil water deficit (when $s = 1$)	(0–1)	–
α	Slope of growth response to water deficit ($dr/d\Psi$)	$\alpha \geq 0$	MPa ⁻¹
Ψ_0	Characteristic wilting point for a cultivar with no specific drought adaptations expressed in absolute magnitude	$\Psi_{\text{pwp}} \geq 0$	Abs(MPa)
Ψ_{wp}	Critical value soil water potential at which the plant growth rate is zero (cf. Fig 3)	$\Psi_{\text{wp}} \leq 0$	MPa
β_{wue}	Parameter that quantifies the trade-off between increasing maximum growth rate and water use	1	–
β_{dtol}	Parameter that quantifies the trade-off between increasing maximum growth rate and drought tolerance	(0–1)	–
s_0	Characteristic relative soil water content when plant growth rate is zero	(0–1)	–
t_0	Characteristic time between storms at which soil dries below the value of s_0	$t_0 \geq 0$	d

capacity when water is fully available, β_{dtol} . One can use the ratio between the variation in r_{\max} (y -axis in Fig. 3) and the variation in Ψ_{wp} (x -axis in Fig. 3) to quantify this trade-off. In Fig. 3, $\beta_{\text{dtol}} = 3$ is the case with the lowest trade-off because it has the lowest ratio. This means that one can select for greater drought tolerance (a greater ability to grow in drier soils) and expect a relatively low reduction in r_{\max} when compared with the case when $\beta_{\text{dtol}} = 2$. As β_{dtol} decreases, the reduction in r_{\max} as a result of selection for greater drought tolerance, or a more negative Ψ_{wp} , is expected to be greater. When $\beta_{\text{dtol}} = 1$, r_{\max} becomes independent of the x -intercept. When $\beta_{\text{dtol}} < 1$, selection for greater drought tolerance leads to larger r_{\max} . We consider this case a very unlikely scenario, and will not consider it further. Figure 4 describes the relationship between r_{\max} and α , and r_{\max} and Ψ_{wp} for several β_{dtol} values. For the same r_{\max} , α and Ψ_{wp} are negatively correlated. Any two of these parameters define the norm-of-reaction function: the plant growth rate as a function of soil water potential.

The expected value of the growth rate in a random environment, $E(r)$, increases as a function of r_{\max} until a maximum and then decreases (Fig. 6). This maximum can be changed with ρ , the frequency of rains. The larger the ρ , the larger is $E(r)$ maximum. On average, plants grow more quickly when there is more rain, or when the soil is kept wet more frequently. β_{dtol} can also change this maximum. Larger values of β_{dtol} , or reduced trade-off costs in growth rate caused by selection for drought tolerance, produce larger maxima points (Fig. 7). When analysed together, both a greater ρ and a greater β_{dtol} increase $E(r)$ (Fig. 8).

Figure 9 summarizes $E(r)$ as a function of r_{\max} and ρ for a given β_{dtol} with a contour plot where isoclines show different parameter combinations resulting in the same $E(r)$. For a given ρ , $E(r)$ increases until a maximum with increasing r_{\max} and then declines. It is noteworthy that increasing ρ affects $E(r)$ only when r_{\max} , the maximum growth rate, is greater than $\rho^{1/\beta_{\text{wue}}}$. When $r_{\max} < \rho^{1/\beta_{\text{wue}}}$, isoclines are vertical. The effect of increasing ρ on $E(r)$ is much more pronounced when ρ is low

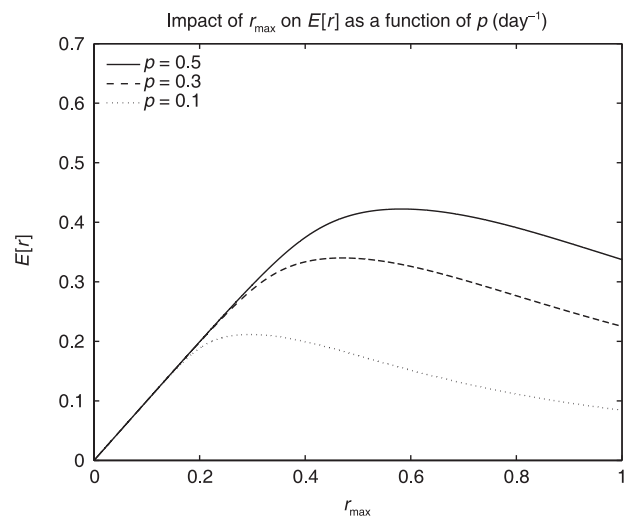


Fig. 6 Relationship between maximum possible growth rate (r_{\max}) and seasonally averaged growth rate ($E(r)$) for a range of rainfall rates (ρ). For all three curves the values of both β_{dtol} and β_{wue} are assumed = 2. As the frequency of rainfall rates increases, both the optimal maximum growth rate and the maximum possible seasonal average growth rate increase. However, for all three rainfall rates there is a clear preference for cultivars with reduced maximum growth (some level of drought adaptation).

and $r_{\max} < \rho^{1/\beta_{\text{wue}}}$. The $E(r)$ increases monotonically with ρ but levels off as ρ increases. As a result, $E(r)$ increases linearly until $r_{\max} < \rho^{1/\beta_{\text{wue}}}$, but after the maxima $E(r)$ decreases nonlinearly (cf. Figs 6, 7). When ρ and r_{\max} increase together, the contribution of r_{\max} to $E(r)$ becomes reduced as these parameters become larger; $E(r)$ changes very little with r_{\max} when both ρ and r_{\max} are large.

Discussion

Plant breeders have increasingly been attempting to create drought-adapted cultivars (Edmeades *et al.*, 1999; Sivamani

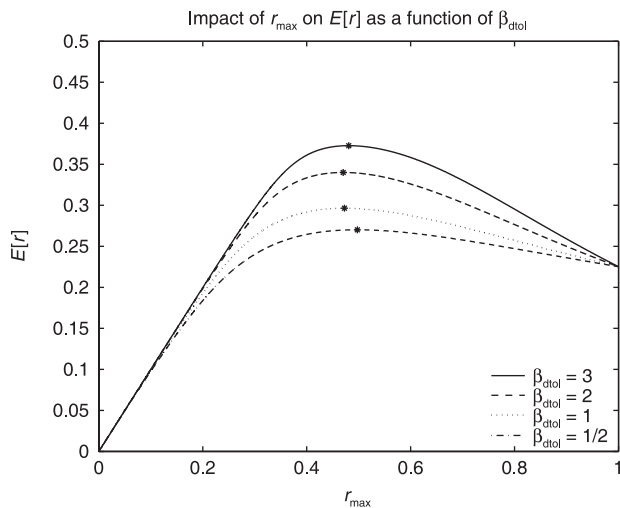


Fig. 7 Relationship between maximum plant growth rate (r_{\max}), and the average seasonal growth rate ($E(r)$) for a range of possible β_{dtol} values, assuming $\beta_{\text{wue}} = 2$. For all four curves, the value of storm frequency (p) is assumed to be 0.3. As β_{dtol} increases, the selection of r_{\max} demonstrates greater sensitivity in determining the value of $E(r)$. Maximum values of $E(r)$ are noted with asterisks for each curve, and they demonstrate that the value of r_{\max} corresponding to the maximum $E(r)$ also increases with increasing β_{dtol} values.

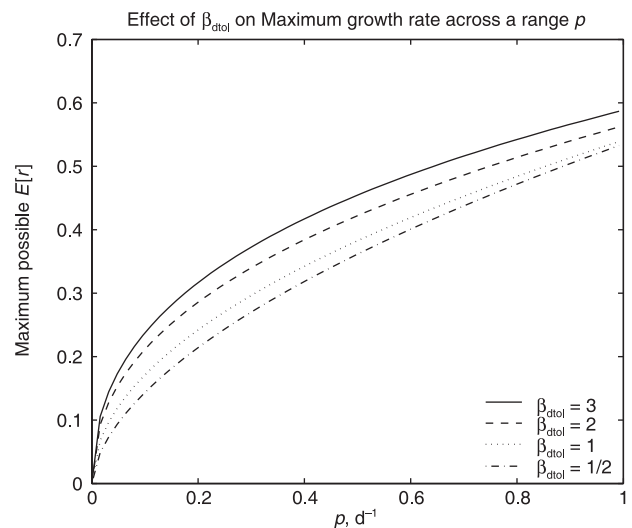


Fig. 8 Relationship between climate (expressed as rainfall frequency, p) and maximum possible seasonal average growth rate. Each curve represents a different value of β_{dtol} , assuming $\beta_{\text{wue}} = 2$. More positive values of β_{dtol} lead to greater possible growth rates for all but the lowest values of rainfall frequency, indicating that stronger trade-offs between growth rate and drought tolerance lead to increased average seasonal plant growth rates when storm arrivals are treated as a random variable.

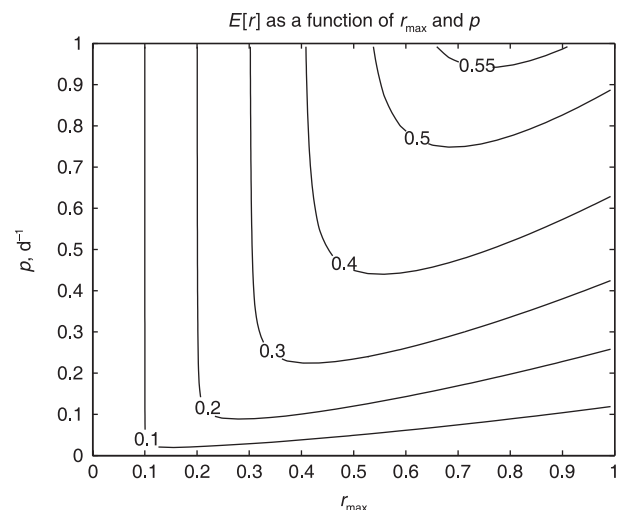


Fig. 9 Summary of how seasonal average growth rate ($E(r)$, contour lines) varies according to maximum plant growth rate (r_{\max}) and rainfall frequency (p). In this plot the value of β_{dtol} is taken to be 2. For all possible rainfall rates, maximum seasonal average growth rates occur when $r_{\max} < 1$, demonstrating the importance of drought tolerance selection when attempting to maximize cultivar growth rate in a stochastic environment.

et al., 2000; Araus *et al.*, 2002; Bruce *et al.*, 2002; Rebetzke *et al.*, 2002). While successful cases are known, drought adaptation when drought is random within a plant's lifetime still lacks a theoretical treatment. This is particularly concerning when the incorporation of drought-avoidance strategies in some species is limited, as is the case for some perennial and

semiperennial species. Moreover, if global warming increases the variance in climatic parameters, then a species that would usually count on drought-avoidance strategies may actually have to cope with drought. We propose here a theoretical model to be used as a framework for breeders to decide whether or not creating drought-tolerant cultivars is worthwhile in a random environment. We use norm-of-reaction functions relating plant growth rate and soil water availability in a random environment to address some aspects of the problem: which environmental variables are relevant, and how these variables interact with plant parameters in maximizing plant growth rate. We are using plant growth rate as a measure of performance because plants that grow more quickly end up showing greater biomass, resulting in more harvestable products.

As expected, the frequency of rains will always be a limiting factor for plant biomass because it regulates the soil mean water potential. However, in the presence of a trade-off between being able to grow in drier soils and the maximum growth rate when water is fully available, there will always be an optimal maximum growth rate for a given climatic condition (a given p). This optimal value can be changed by the climate and/or by the strength of the trade-off. In drier environments, the mean soil water potential will be naturally reduced. In these drier conditions, the mean growth rate will be more sensitive to the growth rate at more negative soil water potentials than the growth rate when water is fully available. Thus, in this case, selecting for rapid growth will compensate the existence of a potential cost to be paid in maximum growth rate. β_{dtol} is the parameter that quantifies this

cost. One can think of β_{dtol} as a property of a trait in a genotype. As a greater β_{dtol} suggests a reduced cost of selection for drought tolerance; and the smaller this cost, the larger the expected growth rate in random environment; the assessment of which trait to select for breeding an optimal drought-adapted cultivar must be evaluated based on its effect on the maximum growth rate. We can determine empirically which is the best drought-tolerance trait to be targeted by using a segregating F_2 population to regress the maximum growth rate when water is available on several candidate traits. Presumably, the most suitable traits are those with a larger β_{dtol} : those that will have the lowest impact on growth rate while maintaining high growth rates when water is available.

We define the characteristic water use of vegetation as a function of r_{max} so that λ is equal to $(r_{\text{max}})^{1/\beta_{\text{wuc}}}$. In our approach, r_{max} is a measure of the potential maximum growth rate of a genotype and λ measures the speed at which a plant depletes the soil water. Everything else being equal, the plant growth rate is proportional to the use of water because of the trade-off between CO_2 acquisition and water loss through the stomata (Condon & Hall, 1997). Thus assuming that these parameters are completely correlated is reasonable for our modelling purposes. From the relationship between r_{max} and λ , we can define a critical point where $\lambda = p$, or more generally, $r_{\text{max}} = p^{1/\beta_{\text{wuc}}}$. This critical point defines completely different optimization strategies. When $\lambda < p$ ($r_{\text{max}} < p^{1/\beta_{\text{wuc}}}$), the best strategy is to increase the water use by selecting genotypes with greater r_{max} . This is so because, on average, a new storm replenishes the soil water before the plants have had time to consume this water. Increasing the rate of water use will confer additional biomass in the same mean time between storms. However, when $\lambda > p$ ($r_{\text{max}} > p^{1/\beta_{\text{wuc}}}$), the soil is more likely to show a more negative water potential, on average. In this case, Fig. 8 suggests that the best strategy is to reduce r_{max} . This can be done in two ways. The first strategy would be directly to select for a cultivar with a reduced r_{max} , but without selecting for greater drought tolerance. This is probably the strategy used to increase water-use efficiency in wheat (Rebetzke *et al.*, 2002). In this case, increasing water-use efficiency by selecting for lower stomatal conductance potentially can limit the photosynthetic rate, resulting in a lower r_{max} . However, without increasing the plant drought tolerance, altering plant water use alone will probably have a very small impact on the seasonally averaged growth rate under drier climates. In our model, the geometrical interpretation of a norm of reaction of a more water-use-efficient genotype is a line the y -intercept of which is a smaller r_{max} , but that maintains the same Ψ_{wp} as before selection for water-use efficiency (cf. Fig. 3a). On the other hand, we can select for greater drought tolerance (a more negative Ψ_{wp}). When $\beta_{\text{dtol}} > 1$, there is a trade-off between drought tolerance and maximum growth rate, therefore r_{max} will be reduced indirectly as a result of selection for increasing drought tolerance. The geometrical interpretation of selecting for a greater drought tolerance is a flatter line with

a more negative Ψ_{wp} and a smaller r_{max} than the nonselected genotype (cf. Fig. 3b,c). Thus the disadvantage of directly focusing on r_{max} is that the norm of reaction is not necessarily optimal, and there may be room for improvement through plant breeding.

Our results suggest an explanation for why selecting for yield in optimal conditions may also produce genotypes adapted to some drier environments (Richards, 1996; Araus *et al.*, 2002, cf. Caruso *et al.*, 2006). It is possible to imagine in Fig. 9 cultivar that can grow optimally at an expected rate of $E(r) = 0.55$ if conditions are $p = 0.9$ and $r_{\text{max}} = 0.8$. If the climate becomes relatively drier with $p = 0.5$, $E(r)$ will still be high between 0.45 and 0.5; not too different from 0.55. Another genotype grows optimally at a rate of 0.35, with $p = 0.15$ and $r_{\text{max}} = 0.4$. If the climate becomes relatively wetter, also with $p = 0.5$, its growth will be limited at a rate of 0.35. Thus the genotype selected in an optimal condition will perform better than the genotype selected for drought adaptation if the climate does not become dry enough. However, this does not mean that the performance of the best cultivar is optimal in this new climate. In this new climate, the optimal cultivar would have an r_{max} closer to 0.4.

An important assumption of our model is that plants resume growth after a period with low soil water potentials. While this may be reasonable when plants are not exposed to severe drought for long periods (Ben Haj Salah & Tardieu, 1997), drought potentially can affect plants in ways that may limit future growth after a severe drought. A drought-tolerant plant may also be defined as one that survives through a long and intense drought period. Looking at plant drought tolerance from different perspectives can yield a more thorough understanding of this complex problem. For example, in a tropical area where the rain distribution is erratic, if water is abundant most of the time, the model presented here suggests that it is reasonable (from a productivity perspective) to maximize the plant growth rate at the expense of drought-tolerance strategies (the ability to grow in drier soils). But there will be years with longer drought periods that may affect plant performance and result in economic impact on crops. A possible alternative to minimize deleterious effects of these rare longer droughts is to select traits that allow plants to survive and maintain their physiological functioning during a drought period such that they would start growing again as soon as water becomes available. The ideal traits under these circumstances are those expressed only in response to drier conditions (when soil water potential is more negative than Ψ_{wp}) and are hopefully independent of performance traits that operate above Ψ_{wp} . Recent studies have revealed physiological mechanisms and gene-expression patterns that seem to operate only in drier conditions (Ramanjulu & Bartels, 2002; for review see Zhu, 2002; Chaves *et al.*, 2003). Selection programmes could simply assess the survivorship rates of different genotypes when soil water content is smaller than Ψ_{wp} . The performance of these cultivars without water limitation

could be compared in an F_2 population, and the costs of surviving for a longer period in drought conditions evaluated.

A drought-tolerance trait that may start operating at the stage when soil water potential is lower than the minimum required for plant growth is the plant's osmotic potential (Inman-Bamber & Smith, 2005). In nature, leaf shedding in perennial trees is a trait expressed only when drought is established, without posing any performance costs when water is available. Although the physiology of some of these traits is becoming increasingly understood, such specific plant environmental responses have not yet been fully explored in breeding programmes.

We have developed a simplified theory to describe optimal norms of reaction under a varying soil moisture regime that is governed by the interaction of random rainfall occurrences and plant water-use/growth trade-offs. The resulting theory provides breeders with some quantifiable parameters that can be used to determine the conditions when selecting for water tolerance is desirable in a breeding programme, and suggests an empirical methodology to determine what traits in general to target to achieve optimally adapted genotypes for a given environment. The applicability of this theory depends, of course, on particularities of each species. Nonetheless, theories are also valuable to indicate the important quantities that should be measured to solve a problem. In addition to measuring norms of reaction, we have also shown that measuring the trade-off functions between drought tolerance, water-use efficiency and plant growth rate are very important empirical steps that govern the resulting optimization of these norms of reaction. We hope that our findings stimulate further empirical and theoretical work.

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