*New Idea***Conservatives and Gamblers: Interpreting plant functional response to water stress in terms of a single indicator****Martin Kazmierczak, Karin Johst, and Andreas Huth***Martin Kazmierczak, Helmholtz Centre for Environmental Research—UFZ, Department of Ecological Modelling, Permoserstrasse 15, 04318 Leipzig, Germany**Karin Johst (karin.johst@ufz.de), Helmholtz Centre for Environmental Research—UFZ, Department of Ecological Modelling, Permoserstrasse 15, 04318 Leipzig, Germany**Andreas Huth, Helmholtz Centre for Environmental Research—UFZ, Department of Ecological Modelling, Permoserstrasse 15, 04318 Leipzig, Germany***Abstract**

Water availability has a decisive impact on plant growth, survival and distribution. Climate change is expected to alter both the amount and variability of precipitation. To predict and understand plant responses to water stress, efficient and robust mechanisms for describing their functional responses to water availability are needed. However, most ecohydrological processes and models which take into account these responses are inherently complex, difficult to understand and require large amounts of data. We develop a novel straightforward approach and hypothesize that: (1) Plants exhibit two archetypical response patterns under water stress, one typical to slow-growing plants and one typical to fast-growing ones, with most plants being situated between these two; (2) Differences within and between these functional types can be adequately described by a single parameter—the threshold of relative soil water content—at which plants reduce their transpiration in response to water stress. This indicator is straightforward and relies on data which is relatively easy to measure. Its effect has been previously described and it is already used in several models to simulate the effect of water stress on plants. In our approach, we combine this indicator with a description of reactions patterns. This combination provides a general and efficient way of classifying plant responses and allows the assessment of the impact of water stress on a wide

variety of plants. Due to its simplicity, our approach offers the opportunity to include water relations of plants in a larger set of models and descriptions than it is possible with more complex ecohydrological descriptions. It also can be used to explain biodiversity in fluctuating environments.

Keywords: water stress, soil water threshold, relative extractable water, plant functional types, coexistence.

Introduction

Water availability is considered one of the main factors influencing the growth, survival and distribution of plants both globally and locally (Breckle 2002, Kreft and Jetz 2007). Nearly all ecosystems are afflicted by periods of low water supply either occasionally or periodically and plants need to be able to cope with these periods to survive. Changes in climatic conditions lead to changes in patterns of plant survival and distribution both on longer temporal scales (e.g. Lotter 1999, Hessler et al. 2010, Igarashi and Zharov 2011) and shorter ones (e.g. Feeley et al. 2011).

Therefore, if we are to understand the dynamics of vegetation ecosystems, we must understand their response to climate and precipitation patterns. However, the

complexity of plant responses to varying climatic parameters as well as the complexity of ecohydrological processes make this a challenging task.

In this paper, we argue that differential responses of plants to water stress can largely be described by a single, specific parameter which is relatively easy to measure, and that differences in this parameter lead to characteristic and predictable patterns of plant behaviour which are widely described for a large number of different plants and plant types.

Existing hydrological models often require not only extensive knowledge about thermodynamics, soil characteristics and plant physiology, but also large amounts of detailed data which often is not available. Our approach is no substitute for these models. Instead, it offers a simple yet reasonably accurate description of plant behaviour under water stress in cases where either a detailed physiological description is not possible or not needed. In light of changing climate and weather patterns, robust and easily applicable models of plants reactions to water stress will become vital to our ability to understand and predict ecosystem functioning (Wiegand and Jeltsch 2000).

Our approach is not based on a mechanistic explanation. We see it as an analogon to methods like Holling's functional response curves or Lotka-Volterra-equations—these too, do not describe mechanics but only results. Its simplicity allows the description of functional responses for widely different plant types as African xerophytes and Sphagnum mosses within the same framework.

We also suggest that the differential response of plants based on this parameter can be used to describe coexistence mechanisms based on fluctuating environments which are important to explain biodiversity (Chesson and Huntly 1997).

Plant responses to declining soil water

Although plants need water for cell enlargement, cooling and as an electron and proton source for photosynthesis, most of the water use of plants is an

accidental 'by-product' of them opening their stomata to gain access to carbon dioxide which in turn is necessary for biomass production. Under optimal water supply, the amount of transpiration is largely a function of leaf area, air temperature and plant type where plants adapted to humid environments generally transpire higher amounts of water than those adapted to arid environments (Sitte et al. 2002).

Plants derive their water from the soil. The maximal amount of water plants can extract from a given soil volume (PAW: plant available water; see Box 1 for summary of abbreviations) depends on two parameters: the field capacity (FC), which is the maximal amount of water a given soil volume can contain, and the permanent wilting point (PWP), which is the lower limit of soil water still extractable by plants. PAW is the difference between FC and PWP: $PAW = FC - PWP$. Relative extractable water (REW) is defined as the relation between the current volumetric soil water content (SWC) and PAW:

$$REW = \frac{SWC}{PAW} \quad \text{eqn. 1}$$

Thus, REW is a relative quantity and has values between 1 (water saturated soil) and 0 (no water available for transpiration). Generally, PAW is higher for soils containing moderate amounts of clay and lower for sandy soils (Scheffer and Schachtschabel 2009).

Under abundant water supply, plants transpire a fraction of the potential evapotranspiration (PET) which is defined as the evapotranspiration of an area of short grass under current weather conditions. Calculating PET can be complicated but it is often included in meteorological datasets and, if not, a wide array of formulas exists for calculating it for different combinations of available data (Borman 2010).

Relative transpiration (RT) refers to the amount of transpiration of a plant or stand and is expressed as a fraction of the PET. RT is largely a function of the leaf area index (Granier et al. 1999).

When soil water becomes limited, plants decrease their transpiration and therefore their ability to assimilate carbon dioxide through stomatal closure, leading to reduced growth. Under severe water stress, some further responses are wilting, leaf abscission and, ultimately, mortality.

This reduction in transpiration occurs at a specific threshold called critical relative extractable water (REWC) (see Figure 1a). At this point, RT begins to decline until it becomes zero when REW becomes zero. This is described by:

$$RT = \begin{cases} REW/REWC & REW < REWC \\ 1 & REW \geq REWC \end{cases} \quad \text{eqn. 2}$$

Box 1. Abbreviation quick reference guide.

Abbreviation	Full term
FC	Field capacity
PAW	Plant available water
PET	Potential evapotranspiration
PWP	Permanent wilting point
REW	Relative extractable water
REWC	Critical threshold for REW
RT	Relative transpiration
SWC	Volumetric soil water content

Figure 1. Conceptual scheme showing the REWC-dependent reduction of transpiration (a) and the use of soil-water over time (b) for ‘gamblers’ and ‘conservatives’. ‘Conservatives’ reduce their transpiration at high soil water content (REW_c) while ‘gamblers’ only reduce transpiration once soil water content reaches REW_g. In (b), the situation where soil water declines steadily is shown: the late reduction of transpiration in ‘gamblers’ leads to an early depletion of soil water at time t_g while the ‘conservatives’ can transpire water till t_c . If no precipitation occurs after the ‘gamblers’ reach point t_g , they will suffer from severe water stress while the ‘conservatives’ still have sufficient water for transpiration till t_c . On the other hand, if precipitation occurs between the point where ‘conservatives’ reduced their transpiration and the point where ‘gamblers’ would start to suffer from water stress, the ‘conservatives’ would have reduced their transpiration and therefore growth unnecessarily.

The value for REWC differs from species to species and is influenced by stand characteristics but the general pattern of transpiration reduction based on this threshold has been shown for a large number of plants (see Table 1).

REWC values have been widely used in agricultural settings to describe plant responses to water stress. However, in ecology, the use of water potentials, often defined as vapour pressure differences between soils, plants and the atmosphere, was and is dominant,

Table 1. REWC values determined for different plant species sorted by increasing REWC

Species	REWC	Source
<i>Acer rubrum</i>	0.233	Sinclair et al. (2005)
<i>Gossypium spec.</i>	0.25	Ritchie et al. (1972)
<i>Vigna unguiculata</i>	0.26	Sinclair and Ludlow (1986)
<i>Sorghum spec.</i>	0.28	Rosenthal et al. (1987)
<i>Pseudostuga mensiezii</i>	0.3	Granier (1987)
<i>Triticum spec</i>	0.3	Meyer and Green (1980)
<i>Robinia pseudoacacia</i>	0.322	Sinclair et al. (2005)
<i>Glycine max</i>	0.33	Sinclair and Ludlow (1986)
<i>Pisum sativum</i>	0.4	Lecoeur and Sinclair (1996)
<i>Eucalyptus spec.</i>	0.4	Dunin and Aston (1984)
<i>Picea abies</i>	0.4	Biron (1994)
<i>Pinus halepensis</i>	0.4	Maseyk (2008)
<i>Quercus petraea</i>	0.4	Bréda (1994)
<i>Cicer arietinum</i>	0.48	Soltani et al. (2000)
<i>Helianthus annuus</i>	0.7	Dubbelde et al. (1982)

possibly due to them being more mechanistic than the empirical dependence of transpiration and growth on REW according to equation 2. A summary of the use of REWC in agricultural settings can be found in Sadras and Milroy (1996). A detailed study of the impact of different soil types and rooting patterns for Sorghum can be found in Robertson et al. (1993) and a comparison of different water-extraction models based on REW in Robertson and Fukai (1994).

Two examples of the use of REWC in ecological modelling are Granier et al. (1999) and Wagner et al. (2011). Granier et al. used a model centred on the REWC-dependent reduction of transpiration according to equation 2 to calculate the drought intensity in *Quercus* and *Picea* stands in Europe. The same approach was used by Bauwe et al. (2012) for stands of *Pinus* in Germany.

Usefulness of REWCs and possible objections against their use

In this section, we discuss the pros and cons of the use of REWCs as descriptors of plant behavior. We will argue that, due to their simplicity and flexibility,

REWCs are useful and powerful tools for the description of functional responses of plants to water stress.

Possible objections against the use of REWC as an important plant parameter are:

1. Soil water contents are generally not low enough for this mechanism to have much effect.
2. REWC might be largely dependent on variable parameters like vapour pressure deficit or stand-specific soil characteristics.
3. The effects of different REWCs are not large enough to significantly influence plant growth.
4. The strong influence of soil depth, rooting depth and soil texture is not taken into account.

However, arguments against these objections exist as well:

1. Low soil water contents are common in most ecosystems.

Soil water contents lower than the REWCs of most plants are common in many ecosystems. In a grassland ecosystem in Kansas, Nippert and Knapp (2007) reported soil water content (SWC) to be below 30% for about half of the vegetation period. An article by Bréda et al. (2006) about the 2003 drought in Europe showed that REW was below 0.4 for about 12 weeks in nemoral and for about 16 weeks in Mediterranean forests. In a dry forest in Hawaii, the annual maximum SWC was 33% and the minimum 18% (Stratton et al. 2000). These examples show that soil water contents low enough to trigger a reduction in transpiration are widespread and frequent in many ecosystems.

2. Even small differences in REWCs have large impacts.

Simulation experiments conducted by Soltani et al. (2000) for chickpea calculated that the expected difference in biomass production between plants with higher and lower REWCs was 5%, depending on climate. They therefore concluded that the impact of REWC on yield is low. In agricultural settings, this difference may not be important. However, under the assumption that fecundity is proportional to biomass production, 5 % increase *per vegetation period* would make an important difference in terms of abundance after only a few generations.

Jørgensen et al. (2010) reported that two varieties of *Vigna subterranea* with different REWCs showed differences in biomass of 4% after only 13 days of water stress.

It should also be noted that not only transpiration is decreased after reaching a certain threshold REWC but also other important physiological processes like leaf- and stem extension and photosynthesis (Braatne et al. 1992, Sadras and Milroy 1996). Thus, even slightly

different REWC values may have a strong impact on plant growth.

3. Although REWC is dependent on other parameters, it is still useful.

For stands of *Pinus* and *Picea*, Lundblad and Lindroth (2002) reported that they had great difficulty determining one single REWC where transpiration begins to decline due to the influence of different soil types and microclimate although they were still able to derive a REWC of 0.3. They speculate that their difficulties might have been caused by infrequent measurements of soil water.

Sadras and Milroy (1996) investigated the dependence of REWC on soil type, evaporative demand and root architecture. While they found that REWC is indeed influenced by these parameters, they still conclude that it is a simple and attractive measure of plant responses to water supply which is 'sufficiently' sensitive and appropriate for many modeling purposes.

The articles by Braatne et al. (1992), Granier et al. (1999), and Jørgensen et al. (2010) show figures similar to Figure 1a plotted against actual transpiration measurements. These graphs show that the dependence of RT on REW and REWC can indeed be represented by simple approximations.

Typical values for the PAW of different soil types are well known (Scheffer and Schachtschabel 2009) and although the exact value might vary between different stands, good estimates can be made. PET is often available or can be calculated. Other parameters, like microclimate or the rooting depth of individual plants, are very hard to measure on the level of individual plants—let alone for stands or ecotones—and are therefore usually not available and even if they were, only very detailed models would be able to include them.

The effects of different soil textures along with different soil water capacities, rooting depths and soil depths have an impact on the growth of plants and their water-related strategies (February et al. 2007) and comparing the effects of different soils is a problem encountered by all hydrological models. Due to the simplicity of using the relative extractable soil water, these factors can all be accounted for by changing the absolute amount of extractable water available for a plant.

We therefore think that—despite its dependence on plant and stand characteristics—REWC is a very useful parameter. REWC is similar to water use efficiencies: while it is known, that these are imperfect representations of actual processes, they are still widely used because of their simplicity and applicability and because we often lack the knowledge and data to describe the underlying processes in more detail. Each of these four arguments support our hypothesis that considering

REWC values is highly relevant for vegetation growth under water stress.

A paper by Moreno-Gutierrez et al. (2012) compared the water-use strategies of 10 coexisting plant species of different life forms and taxonomic units in a semiarid area of Spain using extensive measurements of stomatal conductance, water-use efficiency and isotope discrimination ratios for ^{13}C and ^{18}O . While they did not measure soil water contents, they did describe exactly the same patterns of water use and choice of habitats as predicted by these plants having different REWCs. They also situated plants along an axis of opportunistic vs. conservative water use. This shows that our two response types can describe the same types of behaviour as derived from extensive and highly detailed measurements.

Derivation of two archetypical responses to declining soil water

In this section, we argue that plants exhibit two basically different response patterns when faced with declining soil water and that these two functional types can be attributed to the plants REWC being higher or lower.

We are aware that this is a strong simplification and that in reality plants exhibit a whole spectrum of possible responses between these two extremes. Nonetheless, we will show that these two basic functional types can be used to describe a wide range of plants in different environments.

Braatne et al. (1992) measured the responses of *Populus trichocarpa* (T), *P. deltoides* (D) and their F1-hybrids (H) to a soil drying cycle in a greenhouse experiment. The different plants reduced transpiration at REWCs of 0.35, 0.45, and 0.6 respectively. Experiments began when the soil was water-saturated and ended when the plants had only one living leaf left, with no intermittent irrigation. The different plants showed a clear gradient of drought-resistance with T being the least resistant, H being the most resistant and D being an intermediate. This hierarchy of resistance showed itself consistently in all measured traits (Figure 2). Under drought stress, the plants showed distinct responses. The parents T and D transpired large amounts of water until soil water content became highly critical, which is especially true for T which endures low leaf water potentials before stomata closure occurs. H used water conservatively and used most of it in later stages of drought. Although all plants started with similar leaf areas, H was not only able to maintain its leaf area under drought but actually increased it slightly although the new leaves were much smaller than the original ones. In contrast, the parents T and D suffered leaf loss and newly formed leaves differed less in size from previous ones. H survived longer during drought and

Figure 2. Reactions of three different species of poplar to soil drying. The RWC values of T (*Populus Trichocarpa*), D (*Populus deltoids*) and H (hybrid poplars) are 0.35, 0.45 and 0.60 respectively (data from: Braatne et al. (1992). For H, the arithmetic means for male and female hybrids are shown). All measurements show a strong relation between drought-induced reactions and the RWC: (a) survival time in days after soil water content reaches zero, (b) amount of embolisms measured after drought, (c) number of days until plants began to reduce their transpiration due to low soil water and (d) change of leaf area between the points where plants reduced their transpiration due to low soil water and the point where stomatal control was no longer able to compensate for water loss. In all measured reactions, the ability to withstand and survive drought increases with an increasing RWC value.

maintained its functioning even under severe water stress. It is interesting to note that under a complete drying cycle, the absolute amount of water transpired was very similar for all plants (maximal difference: 8%). But the same amount of transpired water was used quite differently which surprised the authors as H had higher hydraulic conductivity and eventually a larger leaf area. Also, plants started with similar leaf areas. Braatne et al. (1992) noted that in the hybrids responses to drought stress began earlier but were more gradual.

Five other articles comparing the responses of different poplars from different environments, life stages and species (Dickmann et al. 1996, Tschaplinsky et al. 1998, Marron et al. 2003, Coccozza et al. 2010, Henderson and Jose 2010) showed the same, consistent pattern of two typical, basically different responses to drought.

Jørgensen et al. (2010) investigated the response of two varieties of *Vigna subterranea*, an annual grain

legume from sub-Saharan Africa. One variety, S19-3, had an RWC of 0.50, the other, Uniswa Red, had an RWC of 0.69. The plants showed the same response patterns as described above for poplars: Uniswa Red decreased transpiration when soil water was still high, S19-3 transpired freely until soil water became relatively low. Uniswa Red maintained its leaf water status under drought and even initiated new leaves while leaves of S19-3 dried out. The experiment was stopped when both varieties were still transpiring, therefore the authors did not report upon mortality. Compared with well watered plants, water stress decreased biomass production more strongly in S19-3 than in Uniswa Red (-42% vs. -38% during 13 days without irrigation). In the water-stressed treatment, Uniswa Red increased its biomass more strongly than S19-3 (+122% vs. +89%).

From these examples, we derive two functional plant types characterised by the following strategies:

1. Plant Type A:

- Grows more vigorously under sufficient water supply;
- During droughts, leaf area is lower and leaf-loss is severe;
- Mortality during drought is higher.

2. Plant Type B:

- Grows slower but more steadily even when water-supply is low;
- Leaf area is often higher and always more stable under drought than in plant A;
- Mortality during drought is lower.

These strategies are descriptions of general reaction patterns and actual plants are situated along an axis between these extremes. In the rest of this section, we will show how this pattern can be applied to diverse plants from trees to mosses. We will also show that these differences are not only visible when comparing different types of plants but can also describe different reactions to water stress between closely related ones. For example, all *Sphagnum* mosses are adapted to a very humid environment but even within this genus, one can distinguish the two reaction patterns.

These two types of responses have been described for a wide variety of other plants. In the following, we give some further examples to illustrate the applicability of our approach to a wide range of plants and situations. All examples show that plants face a trade-off between using the available soil water freely and conserving it and that this trade-off is associated with other plant traits as described by our characterization of plant types A and B.

A comparison of two *Glycine max* (soybean) varieties under drought by Sadok and Sinclair (2010) showed that one species wilted more slowly under water stress due to its lower maximum transpiration and its restricted water use and the resulting soil water conservation. For two wheat species, Kholodova et al. (2007) reported that one of the species reduced its transpiration rate more strongly and therefore conserved more water compared to the other species. This resulted in lower stress and a higher recovery potential after the drought.

An investigation of the growth-mortality trade-off as related to soil resources and soil water for 960 tree species in a Bornean rain forest showed that the trade-off is influenced to a large degree by underground resources including water (Russo et al. 2008). Fast-growing species were efficiently eliminated from soils with low underground resources while slow-growing species were less competitive on richer soils. Slow-growing trees are described as having traits that promote resource conservation but lacking traits that enable them to respond plastically to increased resource availability.

Engelbrecht and Kursar (2003) described the responses of seedlings in a tropical forest in Panama and found that the seedlings of some species are well adapted to drought and maintain their leaf area under water stress while others show high mortality due to high production until soil water is very low. The authors described the former as adapted to drought and the latter as “taking a gamble” as severe droughts lead to very high mortality in these seedlings. They also reported an intermediate strategy by facultatively deciduous seedlings—these plants drop their leaves under drought which enables them to survive longer than the ‘gamblers’.

Exactly the same type of graphic as Figure 1a is shown in Proctor (2008) for two mosses—*Tortula ruralis* (a bryopsida) and *Conocephalum conicum* (a liverwort)—the only difference being that relative transpiration is shown as a function of relative water content of the mosses. Here too, one species (the liverwort) reduces its relative transpiration earlier but more slowly while the other one transpires freely larger amounts of water for longer and then decreases transpiration faster.

Titus et al. (1983) investigated the photosynthesis of two *Sphagnum* mosses, one found mainly in drier areas, the other in more humid ones. To their surprise they found that the species occurring in drier areas (hummocks higher above the water table) fixed less carbon when its water content was low than the species growing nearer the water table and called this a paradox—with little water, plants from drier areas are expected to grow better than plants from more humid habitats. They published a figure showing the photosynthesis over the water content of the mosses (*Sphagnum* does not grow in soil in the strict meaning of the sense) which shows the same two response patterns as seen in Figure 1a. The species from drier areas reduced its transpiration when its water content is still relatively high while the species from moist areas continues until its water contents are lower. In a later paper (Titus and Wagner 1984), they described the two species and their behaviour in very similar terms as we do in this paper and also called one of the plants “conservative” regarding its water use. This shows that our two response types can describe the behaviour of plants even if they grow in extreme environments and even if they lack such common features as a mineral soil or stomata.

Link between reaction patterns and the REWC

All these examples suggest that there are two archetypical patterns of response to water stress. As a novel approach to classify these patterns, we suggest relating them to high versus low REWC values: One—

with a relatively low REWC—is characterised by high growth potential and inflexible responses to declining soil water, the other—with a relatively high REWC—by lower growth potential but more flexible responses to water stress. Engelbrecht and Kursar (2003) described the former as “taking a gamble,” referring to their high growth until soil water was very low, while Larchevêque et al. (2011) called this a “risky strategy”. We are going to refer to these two reaction types as ‘conservatives’ and ‘gamblers’:

1. Conservatives (refers to Plant type B): higher REWC
2. Gamblers (refers to Plant type A): lower REWC

These two functional types are situated along a trade-off exemplified in Figure 1a and 1b. When soil water is consistently high or periods of low soil water are short, the ‘gamblers’ with their low REWC are favoured because they maintain a higher transpiration and therefore growth rate when soil water begins to decline (Figure 1a). But during longer periods of low soil water, the ‘conservatives’ are favoured as they use the same amount of water over a longer time span ($t_c > t_g$ in Figure 1b). Note that they can show further adaptations which enable them to withstand the effects of drought, e.g. their ability to maintain their leaf area even under severe water stress.

The existence of different strategies for coping with environmental fluctuations has been described extensively and the categorization proposed within this article is similar: the ‘gamblers’ and ‘conservatives’ could be classified as C- and S-strategists according to Grimes’ CSR classification (Grime 2001). The latter also fit well into the ‘stress resistance syndrome’ described by Chapin et al. (1993) who postulated response curves of growth upon resource supply similar to the ones described in this paper for transpiration. However, our categorization according to high versus low REWC is a novel approach which can also facilitate the explanation and understanding of species coexistence.

Which strategy is optimal depends on climate: when Jørgensen et al. (2010) compared the two varieties of *Vigna subterranea*, they used descriptions which nearly were the opposites of the ones used in this paper: they named the variety which we would describe as being a ‘gambler’ (S19-3) as “conservative” and the variety which we would describe as ‘conservative’ (Uniswa Red) as an “optimistic” plant. These names were chosen because Uniswa Red maintains its leaf water status under drought which it does because it ‘expects’ rainfall in the future and because S19-3 is ‘pessimistic’ about rainfall and does not maintain its leaf water status.

These differences in interpreting the same reaction patterns can be ascribed to the fact that Jørgensen et al. investigated plants from Africa which they describe as

being highly adapted to droughts which is reflected in their high REWCs (0.5 and 0.69). S19-3 occurs mainly on sandy soils in dry environments while Uniswa Red occurs on clay soils and under high precipitation. Also, the growing period of Uniswa Red is about twice as long as the one of S19-3. Therefore, S19-3 follows a strategy which was described by Turner (1979) as ‘drought escape’: in environments where water availability is low and unreliable, plants maximize their fitness by completing their life cycle during periods of high water availability in the shortest amount of time possible. Under these circumstances, a low REWC is advantageous because it allows high transpiration during the time when water is available. This shows that care must be taken when comparing plants from very different environments but it also shows that our approach is able to describe the responses of plants even in extreme environments. We still feel that our description of the two response types is valid as ‘conservatives’ conserve soil water and ‘gamblers’ are less well adapted to droughts—the S19-3 described by Jørgensen et al. transpires high amounts of water and completes its life cycle in a short time exactly because it is not adapted to droughts and could not survive them.

An interesting side note is that REWC is very often at or near 0.4 for quite distinct species in both herbaceous plants and trees although the range of values is much greater for the former. This could be due to the fact that the measurements for trees have been performed on fewer species and individuals or there could be an underlying pattern under which a REWC is optimal for a given climate and plant type. Also, trees do not grow in areas with low or very unpredictable precipitation and extremely high or low REWC values are probably not a viable strategy for long-lived perennials.

Plant coexistence under varying water stress explained by high versus low REWC values

The differential response of plants to water availability has been postulated as one possible mechanism allowing species coexistence. As Silvertown et al. (1999) said: “The hitherto largely vain search for plant niches in the established phase of the plant life cycle has been confined mainly to axes of nutrients and light availability, but our findings suggest that investigations of variation in soil hydrology at a fine spatial scale and over longer time-spans might well reveal a potent force that structures many types of plant community”.

In the following we argue that the different thresholds for transpiration reduction (REWCs) could act as a mechanism for coexistence by providing temporal niches under fluctuating environments. The ‘gamblers’ with their low REWC should be favoured when water supply is sufficient throughout the vegetation period (e.g. in generally humid environments or where

precipitation is strongly predictable). Under these conditions, they will outcompete the ‘conservatives’ with their high REWCs due to greater resource usage in shorter time. In environments where water is generally scarce or precipitation is unpredictable, the ‘conservative’ strategy should be favoured. Coexistence would occur in intermediate environments where periods of sufficient water alternate with occasional droughts. While plants following the ‘gambler’ strategy would be favoured during periods of sufficient water supply, every severe drought would cause high mortality in these plants and support the ‘conservative’ plants. These conditions are very common: e.g. in Europe with droughts in 2003 and 2007, in tropical seasonal forests outside the equatorial zone (Condit et al. 2000, Feeley et al. 2011) and even in tropical forests usually considered perhumid, longer periods of relatively low water supply are common and frequent (Borchert 1994).

Pineda-Garcia et al. (2011) investigated tree seedlings from a seasonally dry forest in Mexico with a rainy season of five months where plants shed their leaves during the dry season. Although they expected to find plants with characteristics promoting conservative water use in the drier habitat and plants spending water more freely in the wetter habitats, they were surprised to find both strategies present in both kinds of habitat, although the general pattern still holds. This again could be explained by the plants with different strategies having different REWCs: as both the length of the rainy season as well as the amount of precipitation varies—especially as Mexico is strongly influenced by the El Niño Southern Oscillation (Badan 2003)—different years favour different plants, leading to an equilibrium of strategies.

A similar description of different plant strategies concerning water use was done by Schwinning and Sala (2004) although their focus was on the short-term use of water pulses in an arid environment. They differentiated between “optimists” who make better use of relatively large pulses of water and “pessimists” which are better at exploiting small pulses.

The two functional types can also be seen as an example of coexistence through ‘relative non-linearity’ (Chesson et al. 2004). Chesson et al. described different responses of plants to water pulses in arid environments. They also compared different curves of water uptake functions for drought-adapted and non-adapted plants and see this as a possible mechanism for species coexistence (relative non-linearity). Like Jørgensen et al. (2010), they see lower leaf area as a sign of adaptation to drought which too can be attributed to the fact that they investigated plants in arid environments. In contrast, we think that maintaining higher leaf areas during drought is an attribute of the drought-adapted conservative plant functional type (see also character-

istics of the two functional types) as it increases its long-term fitness and spares it the cost of constructing new leaves when water supply is sufficient again.

Chesson (2000) describes two mechanisms for coexistence: equalizing mechanisms which minimize average fitness differences between species and stabilizing mechanisms which support coexistence by making intraspecific competition stronger compared with interspecific competition. Trade-offs like the one between fast resource use and increased risk of mortality as described in this article can act as either kind or simultaneously and disentangling these different mechanisms can be difficult. Factors like different rooting depths, variability of climate and differences in the length of the life-cycle of different plants all provide additional temporal and spatial niches which can be included in our approach and which have the potential to promote coexistence.

Also, root competition for water occurs where two root systems meet, which typically happens on the borders of root systems. In dry soils, water flow is severely limited which means that plants have to rely on water in their immediate vicinity (Ritchie et al. 1972, Scheffer and Schachtschabel 2009) which would mean that direct competition for water would decrease with decreasing soil water, further complicating the issue.

Different REWCs and plant productivity

The different patterns of soil water uptake and the resulting patterns of transpiration based on different REWCs (equation 2) may also partly explain why mixtures of species often show higher productivity than monocultures (complementarity effect): stands of fast-growing plants would produce high amounts of biomass when and only when water supply is sufficient while stands of slow-growing plants have generally low productivity—but a mixture of them would extract more water from the soil over longer time spans and therefore potentially increase productivity (Ewel and Bigelow 2011). In experimental grasslands, De Boeck et al. (2006) found that mixtures extract more water from the soil than monocultures, and that mixtures also show higher productivity.

Novoplansky and Goldberg (2011) took three different perennial grass species from a semi-arid grassland in New Mexico and investigated their growth and their relative competitive ability depending on the total amount of irrigation and its variability. These three species occur in habitats which differ in productivity due to a spatial gradient of water availability. The fastest growing species occurs in relatively humid environments while the slowest growing species occurs in the most arid environments. Under sufficient water supply, competitive ability was proportional to productivity. However, under infrequent water supply, the slowest

growing species was the better competitor. In monocultures, all plants increased growth with increased water supply although the fastest growing species benefited the most from high amounts of water. They also reported that, in mixed stands, the variability of the water supply was more important for the relative competitive ability than the amount of water. The authors concluded that, for them, the shift in competitive ability was not explainable. Although the authors of this study did not measure REWCs for these plants, these differential responses could be explainable by the plants having different REWCs.

Conclusions

We argue that using REWC values to describe the differential response of plants to water stress provides a novel method for describing and modelling the influence of water availability on plant growth both on short and long time scales. Due to its simplicity, this method is applicable to a large number and variety of plants both in situ for measurements on actual plants and in silicio for modelling. It is suitable both for environments with water pulses and environments in which soil water declines relatively steadily during the vegetation period (e.g. nemoral habitats).

Although, the ‘gamblers’ (with their low REWC) and the ‘conservatives’ (with their high REWC) describe the extremes of a wide spectrum, REWC can also be used to describe intermediate strategies—like the facultatively deciduous seedlings described by Engelbrecht and Kursar (2003) or *Populus deltoides* described by Braatne et al. (1992). REWCs can be measured with commonly used field equipment and our approach can be used to produce testable hypotheses.

It cannot and does not try to include and explain every detailed aspect of plant behaviour under drought—which no theory or model can. Instead, by establishing a mental framework for differential plant reactions to water stress and linking them to a single indicator, we provide a way to describe these reactions in a simple and elegant way when the use of a fully-fledged hydrological model is not possible or necessary. We argue that the extensive examples cited in this article present strong support for our approach. In our opinion, the use of REWC as a central parameter for describing plant responses to water stress provides a robust and straightforward way to model and possibly understand contrasting functional responses - a problem which will become more pressing in the future due to climate change.

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Referees

Steven Higgins – steven.higgins@otago.ac.nz
University of Otago

Florian Jeltsch – jeltsch@uni-potsdam.de
University of Potsdam

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