Quantifying the functional responses of vegetation to drought and oxygen stress in temperate ecosystems

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Summary

1. Our understanding of the generality of plant functional responses to water availability is limited; current field studies use either very rough approximations of water and oxygen availability or only focus on water-stressed ecosystems. Studies that relate species' responses to a surplus of water are limited to controlled experiments.

2. The aim of this study was to investigate how traits are selected along a gradient of soil moisture, ranging from oxygen-stressed to drought-stressed. We tested 15 traits: eight leaf traits, two root traits, two seed traits and three allometry traits and related their community means to process-based measures of drought stress and oxygen stress for 171 plots in the Netherlands. Because the trait values had been taken from a large database, an independent field survey was carried out to validate the relationships thus derived.

3. We show that root porosity and seed floating capacity are mostly strongly related, although still moderately, to oxygen and drought stress ($R^2 = 27\%$ and 42%, respectively). Leaf traits responded weakly to either of the stressors. The field survey yielded similar relationships. Trait combinations were much more closely related to oxygen or drought stress than individual traits, suggesting that there are multiple trait solutions at a given level of water and oxygen stress.

4. The relatively weak relationships found between traits and water-related stressors contrast with the strong control of other environmental drivers (disturbance, nutrients) on traits and suggest that these strong constraints imposed by other environmental drivers necessitate varied solutions to cope with water availability.

Key-words: allometry traits, co-occurring stress, drought stress, leaf traits, oxygen stress, root porosity, seed buoyancy, temperate climate

Introduction

A central goal of community ecology is to understand patterns of plant species distribution. Research of the past decade shows that this can successfully be done by studying species' traits that reflect how species are adapted to their environment. These successes were mainly obtained by linking soil nutrients and light availability to suites of traits (Falster & Westoby 2005; Ordoñez *et al.* 2009), but less so for water-related stressors. Yet, it is particularly important to understand the response of plants to water availability, as climate change is expected to strongly affect precipitation (both intensity and frequency) and evapotranspiration (via changes in temperature and atmospheric CO_2 concentration) and hence species distributions.

The importance of water in shaping plant communities is emphasized by several recent global analyses showing the effect of water availability on distributions of plant traits. These studies reveal that, across large water availability gradients, species in dry environments have deep roots (Schenk & Jackson 2002), slightly denser stems (Swenson & Enquist 2007), thick and dense leaves and comparatively more nitrogen per leaf area (Wright *et al.* 2005) to optimize water use efficiency (Song *et al.* 2008), all of which are adaptations to increase water uptake and/or to reduce water use. Although these studies provide insight into the role of water in shaping species traits, these studies suffer from two main limitations. Firstly, water availability is

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estimated only approximately, for example, by mean annual precipitation or potential/actual evapotranspiration or combinations of these, neglecting local hydrology and other factors such as soil water-holding capacity (Schenk & Jackson 2002; Wright *et al.* 2005; Moles *et al.* 2009 among others). Secondly, these global studies mainly show the effects of drought on species traits because wetlands and wetland species are absent in these analyses. Regional-level studies tend to apply more accurate measures of soil moisture (such as soil water content), but have mostly been carried out in ecosystems with a (severe) drought period, see, for example, Cornwell & Ackerly (2009), with a notable exception of Ordoñez *et al.* (2010a,b).

At the other end of the water availability gradient, that is, where there is a surplus of water, plants have to deal with a shortage of oxygen in the soil, which requires a rather different set of adaptations (known as aeration stress or oxygen stress, hereafter called oxygen stress, Voesenek *et al.* 2006; Niinemets & Valladares 2006). As a consequence, niche segregation takes place because different adaptations are needed for oxygen stress and drought stress (Silvertown *et al.* 1999). Important adaptations to cope with oxygen stress are the formation of aerenchyma (both in shoots and roots, Jackson & Armstrong 1999), enhanced shoot elongation (Voesenek *et al.* 2004) and increased anaerobic metabolism. Most studies investigating the effect of oxygen stress on plant traits focus on the physiological mechanisms of adaptation (Engelaar *et al.* 1993; Blom & Voesenek 1996 among others) and use controlled experiments to test species response to flooding (Visser, Blom & Voesenek 1996; Visser *et al.* 2000; Mommer, Pons & Visser 2006). In contrast, the number of ecological field studies on trait responses is highly limited (but see van Eck *et al.* 2004). As a result, the responses of plant traits to field gradients of water availability remain unclear.

The aim of this study is to investigate how plants respond along a gradient of soil water availability ranging from oxygen-stressed (waterlogged) to drought-stressed (groundwater independent) through a suite of commonly measured plant traits. To separate those effects, direct measures of both oxygen and drought stress were used as explanatory variables in this study. The response of species to soil water and soil oxygen availability is tested on ecosystems within the temperate biome because in this climatic zone a broad gradient from drought-stressed to water-stressed can be found.

Materials and methods

GENERAL APPROACH

We combined species composition data from plots distributed across a broad water availability gradient with a species–trait database to calculate community-level trait means for a variety of traits. We then constructed a (linear) regression model relating these traits (singly and in combination) to site-level measures of drought and oxygen stress. Finally, to independently validate the

modelled relationships, we conducted a field survey of community trait means across a water availability gradient within a single dune–valley complex.

PLOT SELECTION

To test the effect of water availability on the functional composition of species assemblages, one needs combined measurements of water availability and species composition across the water gradient. The only data set available that spanned this whole range is from Bartholomeus *et al.* 2011a; who simulated oxygen and drought stress for the data of Runhaar (1989), De Jong (1997), Jansen *et al.* (2000), Jansen & Runhaar (2005), Hommel *et al.* (2007). Altogether, the data set contained information about species composition, soil physical properties and water supply in 171 plots from natural ecosystems throughout the Netherlands. The mean summer temperature in the Netherlands is 16·4 °C, the mean winter temperature is 3·2 °C, the mean annual precipitation is 754 mm (locally varying from 831 to 712 mm) and the precipitation surplus is 191 mm (locally varying from 125 to 250 mm). The precipitation deficit during the growing season (April–August) is 122 mm (Royal Netherlands Meteorological Institute (KNMI); www.knmi.nl). Together, the plots covered a range from dry to wet, nutrient-poor to nutrient-rich and frequently disturbed to undisturbed ecosystems. None of the plots had had experienced any major changes in hydrological conditions in the years before the plots were sampled.

ESTIMATES OF WATER AVAILABILITY: OXYGEN STRESS AND DROUGHT STRESS

Although water is essential for plant growth, a shortage will limit photosynthesis and plant transpiration, while a surplus limits diffusion of oxygen to roots and hence limits respiration and the metabolic activity of plants. Groundwater levels alone do not fully represent the moisture conditions, and consequently, oxygen and drought stress, in the root zone. Therefore, to test the effects of each component, individual measures of oxygen and drought stressors were applied. We calculated process-based oxygen and drought stress for terrestrial vegetation plots from a variety of natural habitats. We used the reductions in respiration and transpiration because of low oxygen and water availability, respectively, to characterize these stresses. As a result, respiration reduction includes effects of both extreme rainfall events and high temperatures, known to affect vegetation composition (Sojka, Joseph & Stolzy 1972; Drew 1983). Transpiration reduction accounts for the effects of both prolonged dry periods and high atmospheric demand for plant transpiration, that is, factors that determine drought stress of plants (Porporato, Daly & Rodriguez-Iturbe 2004).

For an unbiased comparison of oxygen and drought stress between sites, and following Dyer (2009), we simulated the daily respiration and transpiration reduction for a hypothetical reference vegetation instead of the actual vegetation. By doing so, we obtained stress measures that reflect the soil moisture and oxygen status, independent of the actual vegetation. The use of a reference vegetation improves the applicability of models in which stress measures are implemented (Dyer 2009). By adaptation, the natural vegetation reduces stress. Hence, poor relations between the actual stress and vegetation characteristics are expected, although quantifying actual stress would be useful when aiming at calculating fluxes of, for example, water and carbon. Our reference vegetation is defined as a temperate natural grassland not adapted to oxygen and drought stress, that is, a grassland as defined by Van Dam (2000) and Bartholomeus *et al.* (2008b).

Oxygen stress, defined as the reduction in root respiration relative to respiration under optimal soil aeration, is a function of soil

texture, soil organic matter content, gas-filled porosity and soil temperature (Bartholomeus *et al.* 2008b, 2011b). In the Netherlands, with its rather shallow groundwater tables, these variables greatly depend on the groundwater table depth, soil type and soil temperature. Daily groundwater levels were calculated from fortnightly series of groundwater levels measured with piezometers located in or closely to the plots (www.dinoloket.nl). These observed groundwater levels were first interpolated to daily values and then extrapolated to a 30-year period (1971–2000) with the help of the impulse–response (impulse = precipitation and reference evapotranspiration and response = groundwater levels; climate data were taken from the KNMI) software Menyanthes (Von Asmuth, Bierkens & Maas 2002). As is shown by Bartholomeus *et al.* (2008a), a 30-year time frame of daily values is needed to obtain a robust estimate of the moisture conditions of a particular plot. These daily values were subsequently used in a detailed soil–water–atmosphere–plant model (SWAP, Van Dam *et al.* 2008) together with soil texture, air temperature, rainfall and evapotranspiration data to calculate gas-filled porosity and soil temperature for different layers in the soil profile. These variables were used in an additional model to calculate actual and potential root respiration (Bartholomeus *et al.* 2008b). A difference between potential and actual root respiration under the influence of an oxygen deficiency in the root zone indicates the potential oxygen stress experienced by a plant. The yearly maximum respiration reduction in a 10-day period averaged across 30 years was taken as a measure of oxygen stress (OS–kg O_2 m^{-2} 10 day^{-1}). For a detailed description and justification of this procedure, see Bartholomeus *et al.* (2011a,b)

Drought stress was calculated as the reduction in potential plant transpiration relative to conditions where they transpire at potential rate (sufficient supply of water to meet the demands), as determined by global radiation, air humidity, wind speed, air temperature and atmospheric CO_2 concentration. The transpiration is reduced when water becomes limited. This reduction in transpiration was calculated for the same reference vegetation as used for the OS calculations. Analogous to the OS measure, drought stress was defined as the yearly maximum reduction in a 10-day period averaged across 30 years (DS–m 10 day^{-1}). For a detailed description and justification of this procedure, see Bartholomeus *et al.* (2011a).

Our measures of oxygen and drought stress have been shown to be strongly related to the fractions of xerophytes and hygrophytes in a vegetation plot (Bartholomeus *et al.* 2011a) and have been used with success in a vegetation model to predict vegetation distribution (Douma *et al.* (2012c).

TRAIT SELECTION

A vascular plant species–trait database was compiled for species in the Netherlands, taken from Douma *et al.* (2012a) and BioBase (2003), LEDA-traitbase (Kleyer *et al.* 2008, www.leda-traibase. org), Hodgson *et al.* 2011 and (P.M. van Bodegom, T.D. Colmer, B.K. Sorrell, E.J.W. Visser, P. Adam, W. Armstrong *et al.* unpublished data). Compiled trait information of wetland species around the globe and included approximately 200 studies and 1200 species (see http://www.vegfunction.net). We selected 15 plant traits which (i) together reflect how species disperse, establish and persist, (ii) can reasonably be assumed to be under selective pressure of water-related stressors, based on ecological theory and previous regional and global analyses (see Introduction) and (iii) are commonly measured and available for many species. These 15 traits included eight leaf traits: specific leaf area (SLA in mm^2 mg^{-1}), leaf nitrogen content (LNC mg g^{-1}), leaf nitrogen per area (Narea, mg mm^{-2}), leaf density (LD, mg mm^{-3}), leaf volume (LV, mm^3), leaf thickness (LT, mm), leaf phosphorus content (LPC in mg g^{-1}) and leaf size (LS, mm^2); two root traits: rooting depth (RD in m) and root porosity (RP in%); two seed traits: seed mass of the germinule (SM_g in mg; seed without fruits or detachable appendages) and seed buoyancy (BYC; floating capacity defined as percentage seeds floating after 1 week; see details of this measure in Knevel *et al.* 2005; and three allometry traits: seedling maximum relative growth rate (RGR in day^{-1}), maximum canopy height (maxCH in m) and specific stem density (SSD in g cm^{-3}). The number of species for which trait data were available is shown in Table 1. Leaf traits based on leaf size or leaf thickness (LS, LT, SLA, Narea, LV and LD) of species with cylindrical leaves were omitted from the analysis. Leaf area measurements of species are mostly estimated by the projected area (Cornelissen *et al.* 2003), but these estimates may be problematic for species with cylindrical leaves as it does not reflect to the total surface area of that leaf, which is important when related to water availability. Four traits were log10-transformed prior to analysis because their geometrical mean is more closely related to their ecosystem functioning: maxCH, LS, RD and SM_g (Leps *et al.* 2006). We coupled the species–trait database to the plot–species database to construct a plot–trait database. Plot mean trait values indicate the average response

Table 1. Traits used for the analyses, the number of vascular plant species involved (in total 386) and its sources

Types	Trait	Scale and units	Total number of species	Sources
Leaf traits	Leaf nitrogen content (LNC)	Continuous (mg g^{-1})	208	1,2
	Leaf nitrogen per area (Narea)	Continuous (g m^{-2})	177	1,2
	Leaf phosphorus content (LPC)	Continuous (mg g^{-1})	198	1,2
	Specific leaf area (SLA)	Continuous (mm^2 mg^{-1})	325	1,2
	Leaf size (LS)	Continuous (mm^2)	211	1
	Leaf thickness (LT)	Continuous (mm)	328	3
	Leaf density (LD)	Continuous (mg mm^{-3})	197	1,2,3
	Leaf volume (LV)	Continuous (mm^3)	108	1,2,3
Structural traits	Relative growth rate (RGR)	Continuous (day^{-1})	130	1
	Stem specific density (SSD)	Continuous (g cm^{-3})	90	1
	Max. canopy height (maxCH)	Continuous (m)	380	1
Root traits	Rooting depth (RD)	Continuous (m)	229	1, 2
	Root porosity (RP)	Continuous (%)	93	2
Reproduction traits	Seed mass of the germinule (SM_g)	Continuous (mg)	359	1
	Seed buoyancy (BYC, proportion of seeds floating after 1 week)	Continuous (%)	91	4

1) Douma *et al.* 2012a; 2) van Bodegom *et al.* (unpublished data), 3) Hodgson *et al.* 2011, 4) Kleyer *et al.* 2008; LEDA-traitbase (www. leda-traitbase.org).

of species to environmental drivers, given that species filtering takes place at the community level (Ackerly & Cornwell 2007). Therefore, plot mean traits were regressed against water and oxygen stress in separate single regressions and their combined effect, including interactions, in a multiple regression. Only those plots that had trait information for at least five species were selected. To obtain reliable parameter estimates, a weighted regression was applied (Quinn & Keough 2002), weighing each plot by the fraction of species that had a trait value.

VALIDATION OF TRAIT–WATER RELATIONSHIPS BY A FIELD SURVEY

To test the generality of the relationships between *OS, DS* and trait values and to evaluate potential biases because of the use of trait values from databases (not accounting for trait plasticity or missing trait information for particular species), a field survey was carried out at 10 sites along a water gradient from wet to dry. To avoid other confounding factors such as soil type and soil nutrient status, the validation was carried out within one ecosystem. Dune slack valleys are very suitable for this validation as the water-table varies by almost 2 m (from + 0·3 m + s.s. to −1·7 m + s.s.) within a distance of 25–50 m. They are nutrient poor, and the parent material (sand) does not change along this gradient. In total, two dune–valleys were sampled with five plots per valley that were equally distributed over the water gradient. Within each plot (approximately 1–4 m²), the five most dominant species were selected, assuming these species represent the local conditions best. In total, 48 species samples from 23 different species and 10 different sites were taken.

When available, five individuals of each dominant species were selected for each site. For these species, a selected set of traits was measured: specific leaf area (SLA; m² kg⁻¹), leaf nitrogen concentration (LNC; mg g⁻¹), leaf size (LS, mm²; including petiole), leaf thickness (mm) and stem specific density (SSD; mg mm⁻³) were determined at peak biomass (from mid-July until the end of August) and measured following standardized protocols from Cornelissen *et al.* (2003). In addition, root porosity (RP;%) was determined. For this, non-woody roots attached to the stem of the selected individual were dug up and removed. Samples, including adherent soil particles, were packed in a moist paper bag and inserted in a sealed plastic bag. Samples were transported in moist paper and stored under cooled conditions. After collection, the roots were washed and root porosity was determined on 1–3 g of root material using the pycnometer procedure, as described by Burdick (1989).

Groundwater levels were measured directly adjacent to the plots at three occasions during the growing season. Two nearby located piezometers were used, after accounting for the differences in soil surface height, as reference for the long term groundwater dynamics in that plot. Drought stress and oxygen stress were calculated following the same procedure as described in the section '*Estimates of water availability: Oxygen stress and drought stress*'. Nutrient availability, as approximated by C : N ratio, was homogeneous across the plots (results not shown).

We tested to what extent the slopes and intercepts of the regressions derived from the database and the *in situ* trait validation differed. This was tested as follows: a dummy variable (0 and 1 for the two data sets, respectively) was included in the regression: $Y = a*X + b + c*\text{group} + d*\text{group}*X$. If the slope of the subset is significantly different from the full set, then the parameter d will be significantly different from zero. Likewise, significant differences in the intercept are shown by c being significantly different from zero. Also here, plots were weighted by the fraction of species that had a trait value. The plots from the field survey were assigned maximal weights (1) because *in situ* measurements were used. The dummy regression was only performed for oxygen stress as drought stress did not vary sufficiently among the plots for a

meaningful analysis. Note that neither the sites, nor the *in situ* trait measurements were used for the database predictions and therefore the validation is strictly independent of the database predictions.

Finally, to test whether oxygen stress and drought stress lead to the selection of a suite of traits, a multiple regression was run on the database observations with oxygen stress or drought stress as dependent and the traits as predictor. A backward stepwise regression was run to obtain a minimal model with high predictive power (of the models with lowest AIC, the model with highest adjusted R^2 was selected). As LNC and LPC were highly correlated ($r = 0.87$), LPC was omitted in this analysis.

Results

Root porosity showed the strongest correlation of all traits to oxygen stress ($R^2 = 0.24$), followed by seed buoyancy ($R^2 = 0.22$, Fig. 1a, Table 2; for full details see Appendix S1, Tables 1 and 2 in the Supporting Information). The response of both traits to drought stress was even stronger ($R^2 = 0.25$ and 0·45, respectively, Fig. 1b, Table 2); root porosity and seed buoyancy increased with increasing oxygen stress and decreased with increasing drought stress. Note that the results for seed buoyancy need to be interpreted with care; see Appendix S2, Supporting information. In addition, rooting depth, relative growth rate and stem specific density consistently showed a significant negative response to oxygen and a positive response to drought stress. Leaf traits showed a much weaker response to both of the stressors. Leaf nitrogen, both on a mass and area basis, showed a negative response to oxygen stress and positive to drought stress (Table 2 and Fig. 1a,b). In contrast, SLA did not respond significantly to oxygen stress and had a weak response to drought stress (marginally significant, $P = 0.04$). Leaf size was consistently lower at dry sites compared with wet sites, although this relationship was rather weak for oxygen stress and not significant for drought stress. Leaf thickness was positively related to drought stress (a quadratic relationship between leaf thickness and oxygen stress did not perform better than a linear one). Leaf density did not respond significantly to either stressor. Leaf volume showed a weak positive relationship with oxygen stress. Maximum canopy height was not related to either oxygen or drought stress. Seed mass showed a negative, although weak, response to oxygen stress (and the reverse relationship with drought stress).

The combination of the single effects of oxygen stress and water stress were significant for only two traits: relative growth rate and root porosity. (Appendix S1, Table 3, Supporting information). In contrast, the interaction between oxygen stress and drought stress was significant for many more traits: LNC, LPC, SM_g, RD and LT. This shows that although water and oxygen stress are highly correlated (−0·75), their curvilinear relationship (Appendix S3, Fig. 1, Supporting information) means that the degree of response of species to drought stress depends on the level of oxygen stress, and *vice versa*. The results suggest that at a given level of one stressor, the response of species from sites with high co-occurring stress, the traits are modified in the direction of

Table 2. Results of regression analysis of traits compiled in our database with oxygen stress and drought stress showing the standardized regression coefficient of the relationship (correlation, the change in SD units of a trait by a change of one SD in the predictor), the explained variance and its significance (See Table 1 for abbreviations of traits and main text for definition of oxygen and drought stress)

Trait	Oxygen stress			Drought stress			
	Standardized slope	R^2	P	Standardized slope	R^2	P	d.f.
LNC	−0·33	0·11	<0·0001	0·33	0·09	<0·0001	159
SLA	−0·07	0·00	0·401	0·17	0·03	0·037	165
LPC	−0·24	0·06	0·002	0·33	0·09	<0·0001	161
LS	0·23	0·05	0·005	−0·11	0·01	0·184	162
maxCH	−0·06	0·00	0·453	−0·03	0·00	0·719	166
SM_g	−0·35	0·12	<0·0001	0·33	0·11	<0·0001	162
BYC	0·46	0·22	<0·0001	−0·73	0·45	<0·0001	117
RGR	−0·24	0·06	0·004	0·47	0·20	<0·0001	142
SSD	0·42	0·13	<0·0001	0·26	0·05	0·007	141
RD	−0·36	0·13	<0·0001	0·41	0·17	<0·0001	146
RP	0·49	0·24	<0·0001	−0·55	0·25	<0·0001	126
Narea	−0·28	0·07	0·000	0·28	0·07	0·001	159
LD	0·05	0·00	0·572	−0·10	0·01	0·283	143
LV	0·33	0·10	0·000	−0·22	0·05	0·012	137
LT	−0·16	0·03	0·045	0·28	0·08	0·000	144

the response of the other stressor. For example, a high level of oxygen stress and a co-occurring high level of drought stress lead to higher leaf nitrogen and phosphorus content, heavier seeds, thicker leaves and deeper roots than when examined for oxygen stress alone.

The regression analysis of the *in situ* trait validation measurements had a much smaller power (because of lower number of observations) and was significant only for the two traits most strongly related to oxygen stress in the database analysis (i.e. root porosity and stem specific density, Table 3). However, in these cases the R^2-values of the regression were much higher compared with the R^2-values of the database analysis, showing a tight relationship when accounting for potentially confounding factors.

Comparing the slopes of the regression equations for both datasets showed that the relationships derived from the validation set were not significantly different from the database derived relationships, except for Narea and leaf density (both slope and intercept) and SLA and leaf volume (intercept only), see Appendix S1, Table 4, Supporting information for details. All traits that had been more strongly coupled to oxygen and drought stress (LNC, RP, SSD) showed no significant differences.

A multiple regression to test how traits are collectively selected by oxygen or drought stress showed that a combination of traits can explain the impacts of water and oxygen availability well. The best model (AIC = −647·94, d. f. = 87), consisted of seven traits SSD, LNC, LD, RGR, LS, RP and BYC and explained up to 67% of the variation in oxygen stress (Table 4), compared with 24% for the single trait with the highest predictive power RP. In contrast to what would be expected from the single regressions, not RP but SSD, BYC and LNC were the most important in explaining the variation in oxygen stress. A model without BYC resulted in similar standardized coefficients for the other traits (Appendix S2, Table 1, Support-

ing information). The variation in drought stress (64%, Table 5) was best explained by BYC, RP, Narea, RD, SLA, SSD, LD and LT and was again much higher than the predictive power of the best single trait (43%, AIC = −1101·79, d.f. = 102). Here, BYC and RP were the most important in explaining drought stress as they were in the single regressions. A model without BYC resulted in similar standardized coefficients for the other traits (Appendix S2, Table 2, Supporting information).

As the predictors were measured at different scales, for all regressions standardized regression coefficients were calculated to assess the relative effects (effect sizes) of the different predictors on the response variable (Quinn & Keough 2002). All analyses were performed in R (R Development Core Team 2009).

Discussion

To our knowledge, this is the first field study that simultaneously quantifies the role of oxygen and drought stress on trait selection in species assemblages along a gradient of dry to wet ecosystems. Both the database analysis and the field survey validation consistently showed that across a range of dry to wet ecosystems within the temperate biome the functional characteristics of species assemblages can partly be explained by the combined action of water and oxygen stress. Root porosity and seed buoyancy appeared to be particularly affected by differences in water availability, while leaf traits responded only weakly to either stress measure.

CONSISTENT BUT WEAK RESPONSE OF INDIVIDUAL TRAITS TO WATER AND OXYGEN STRESS

Individual traits showed only a moderately strong response to water and oxygen stress: none of the traits exceeded an
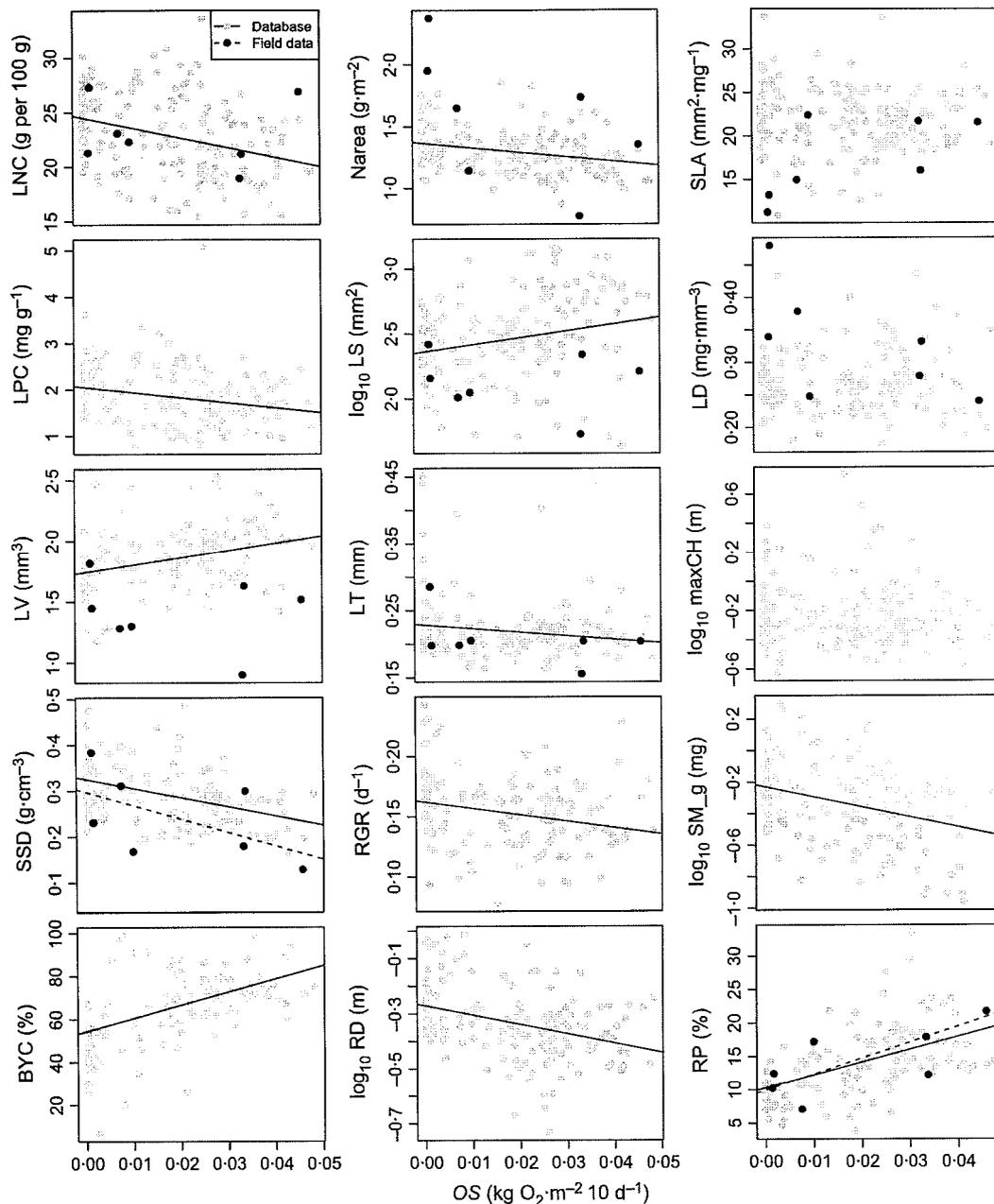
Fig. 1. Relationships between traits and oxygen stress (a) or drought stress (b) from database predictions (grey dots) and independently measured field data as black dots. Significant relationships between the drivers are shown with the estimated regression line for both the traits derived from the database (solid line) as the fieldwork (dashed line). See Table 1 for abbreviations of traits and main text for definition of oxygen and drought stress.

explained variance of 45%. Traits that were best explained by water and oxygen stress were traits that are not part of the commonly accepted plant strategy schemes (Westoby 1998; Weiher *et al.* 1999; Diaz *et al.* 2004), which mainly reflect adaptations to light, nutrients and disturbance. This shows that coping with water availability requires a specific set of adaptations both during the persistence and dispersal phase (*sensu* Weiher *et al.* 1999). Root porosity (one of the traits most strongly related to oxygen stress) is an important adaptation to cope with waterlogged conditions as it enables oxygen transport to the roots. In dry sites,

porous roots may be disadvantageous as porous roots are more vulnerable to external compressive soil forces (Striker *et al.* 2007). Seed buoyancy (adj. R^2 42% from the multiple regression) is a specific adaptation to disperse seeds via water to new sites and was found to be higher in wet environments than in dry environments [in concert with findings of van den Broek, Diggelen & Bobbink (2005)]. Paradoxically, species that rely on buoyant seeds as a dispersal mechanism are as a consequence also limited to those locations that are inundated more or less frequently. This may explain the strong relationship between water
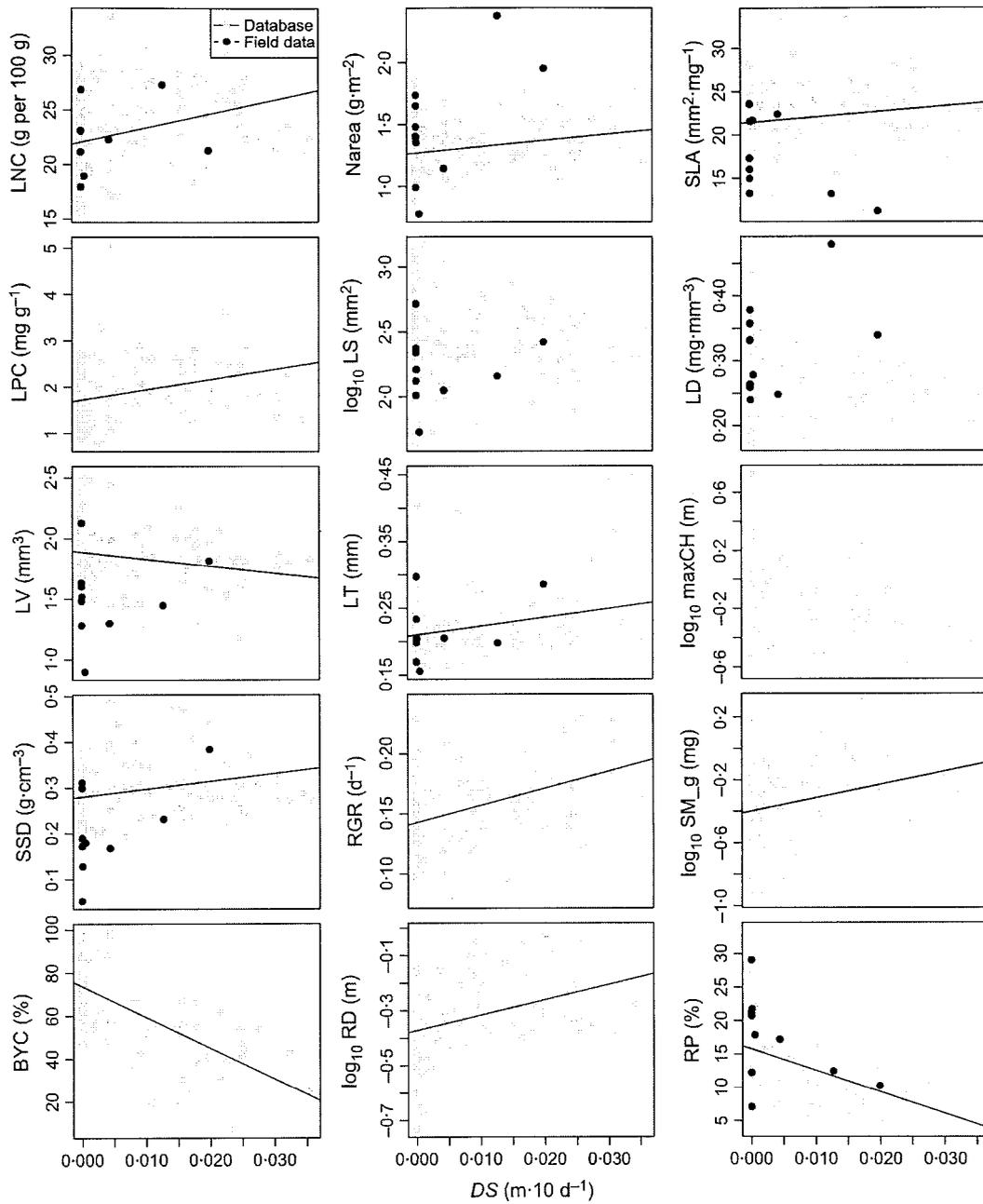
Fig. 1. (Continued).

stress with seed buoyancy and oxygen stress with seed buoyancy, although inundation frequency would be have been a more direct measure for this trait. The increase in buoyancy along the water gradient may also explain the decrease in seed mass with increasing oxygen stress, because seed mass was negatively correlated with seed buoyancy (Pearson correlation = −0·50). The relationships derived from the database were not significantly different from the response found in the field survey (except for Narea and LD). The congruence between the results of the database and the field survey gives confidence in the reliability of database predictions and suggest that they could be safely used to interpret water availability trait relationships.

In general, leaf traits responded weakly to both measures of water supply, which contrasts with the relatively strong relation between the approximate measures of water availability (through precipitation and evapotranspiration) and traits found in global analyses. Still, supporting earlier findings of Wright *et al.* (2005) on a global scale, our analyses also indicate that species growing under dry conditions generally have a higher leaf nitrogen content (both on an area and mass basis), most likely to optimize their water use efficiency and reduce transpiration (Wright, Reich & Westoby 2003). Previous regional studies (Ackerly 2004; chaparral vegetation and Ordoñez *et al.* 2010b; temperate vegetation) did not find a relationship between

Table 3. Results of regression analysis (standardized regression coefficient, explained variance and significance respectively) of traits that have been measured in the field and oxygen and drought stress (See Table 1 for abbreviations of traits, Table 2 for explanation of standardized regression coefficient and main text for definition of oxygen and drought stress)

| Trait | Oxygen stress | | | |
	Standardized slope	R^2	P	d.f.
LNC	−0·28	0·08	0·47	7
SLA	0·40	0·16	0·25	8
LS	0·29	0·08	0·42	8
SSD	−0·67	0·44	0·04	8
RP	0·81	0·65	0·01	8
LT	0·00	0·00	0·99	8
Narea	−0·55	0·31	0·10	8
LD	−0·54	0·29	0·11	8
LV	0·26	0·07	0·47	8

Table 4. Best multiple trait model to predict oxygen stress (see Table 1 for abbreviations of traits). Stepwise backward selection. R^2 adj = 0·67, AIC = −647·94, d.f. = 87. Standardized regression coefficients and standardized standard errors are shown (see Table 2 for full explanation of standardized regression coefficient)

Trait	Standardized slope	St. Std. Error	P
SSD	−0·47	0·08	<0·0001
LNC	−0·35	0·09	<0·001
LD	−0·12	0·08	0·13
RGR	0·11	0·07	0·13
LS	0·14	0·07	0·04
RP	0·17	0·09	0·06
BYC	0·45	0·08	<0·0001

Table 5. Best multiple trait model to predict drought stress (see Table 1 for abbreviations of traits). Stepwise backward selection. R^2 adj = 0·64, AIC = −705·97, d.f. = 86. Standardized regression coefficients and standardized standard errors are shown (see Table 2 for full explanation)

Trait	Standardized slope	St. Std. Error	P
BYC	−0·60	0·08	<0·0001
RP	−0·29	0·09	<0·01
Narea	−0·09	0·08	0·24
RD	0·10	0·07	0·18
SLA	0·14	0·11	0·20
SSD	0·23	0·08	0·01
LD	0·25	0·11	0·02
LT	0·26	0·08	<0·01

the same growing season. Interestingly, the effect of oxygen stress on trait responses is dampened by co-occurring high drought stress. In those cases, plants generally have higher leaf nitrogen and phosphorus contents, heavier seeds, thicker leaves and surprisingly deeper roots than without co-occurring stress. This effect becomes stronger upon rising levels of co-occurring stressors. Consequently, species at sites with co-occurring stresses lack full adaptation to either of the stresses, which may hamper species performance relative to their performance on sites without co-occurring stress (Silvertown *et al.* 1999; Niinemets & Valladares 2006; Bartholomeus *et al.* 2011a).

ARE WE MEASURING THE WRONG TRAITS?

This study tested, as a first step, the relationships of commonly measured traits to water and oxygen stress. A surprising result was that most commonly measured plant traits do not appear to be strongly constrained by water and oxygen stress. There may be two explanations for the relatively low explained variance of individual traits by oxygen and drought stress. Firstly, as water availability varies strongly in space and time, species have to adapt on both short [e.g. closing of the stomata (seconds–hours) and long time-scales (e.g. avoiding unfavourable periods (months–years)]. Plants with different life-history strategies may respond differently to variation in soil moisture within a site (Blom & Voesenek 1996; Grubb 1998). As a result, the community mean trait may be only weakly affected by either of the stressors (van Ommen Kloeke *et al.* 2011). Secondly, we may have measured the wrong traits. Other traits, which are currently not available in databases and which were not measured in the field because of time constraints, are probably more directly related to optimizing water supply and transpiration and oxygen stress and respiration. For example, leaf size/twig size ratio and its whole plant analogue leaf area/sapwood area ratio (Westoby *et al.* 2002; Martinez-Vilalta *et al.* 2009) may be a better indicator of transpirational demand and water supply. In addition to traits that are related to root oxygen supply, such as root porosity, traits related to oxygen demand in

LNC and water availability, probably because their water gradient was narrower. SLA seems to have a more varied response to differences in water availability. In our data set, we did not find a significant relationship, and neither did Ackerly (2004) for chaparral species, while Wright *et al.* (2005) and Ordoñez *et al.* (2010b) did find a positive relationship between water availability and SLA. The differential response of SLA to water availability is perhaps because SLA is additionally dependent on other factors, such as soil nutrients (Ordoñez *et al.* 2009), disturbance (Douma *et al.* 2012b) and growth form (Ordoñez *et al.* 2010a). Despite the absence of a relationship between SLA, leaf density and water availability, species at dry sites had smaller but thicker leaves and therefore less voluminous leaves than at sites with higher water availability, but again this effect was only moderate.

The average trait response of plant communities to oxygen and drought stress displayed an inverse relationship, for example, an increase in oxygen stress leads to a decrease in LNC, and an increase in drought stress leads to an increase in LNC. This is probably because both stressors are naturally correlated; sites with a high level of oxygen stress are not likely to suffer from drought stress in

the root zone may also be strongly constrained by oxygen stress. For example, root respiration is largely determined by root nitrogen (Reich *et al.* 2008) and lowering root nitrogen may provide an alternative way to deal with reduced levels of oxygen in the soil.

Alternatively, traits relevant for coping with unfavourable periods probably would have been strongly related to water and oxygen stress. For example, Raunkaier (Raunkiaer 1934) showed that the position of the growth bud is a trait demonstrating an adaptation to unfavourable conditions, and as such, it could be an important trait to classify both species and communities.. This view is supported by regressing the percentage of helophytes in a community (flowering parts above water and growth buds submerged) against oxygen stress and therophytes (annuals, surviving the critical period via seeds) against drought stress. This analysis revealed that 51% and 20% of the variation in the helophytes and therophytes could be explained by the level of oxygen stress or drought stress. (for details see Appendix S4, Supporting information).

ARE THERE MULTIPLE TRAIT SOLUTIONS TO COPE WITH WATER SHORTAGE OR SURPLUS?

There is a large difference between the rather low explained variance of the single regressions and the high explained variance of the two multiple regressions that predicted oxygen and drought stress by a combination of traits (67% and 64%, respectively). A combination of several traits [BYC and SSD combined with one or two leaf traits (and RP for oxygen stress)] contributed significantly to explaining oxygen and drought stress. This shows that at a given level of oxygen or drought stress, multiple functional solutions seem to prevail across species assemblages. These differences may be caused by differences in other environmental drivers, for example, nutrients or disturbance that also co-determine trait composition of species assemblages. Compared with water, disturbance and nutrient availability have a relatively strong constraining effect on traits. For example, Douma *et al.* (2012c) have shown for the same temperate climate that the explained variance of SSD by time since disturbance and LPC by soil C/P ratio is 78% and 44%, respectively. In the case of SSD, this implies that, assuming that disturbance and water availability can vary independently, only 22% of the variance remains to be explained by water. Therefore, we hypothesize that because of this strong coordination of traits by disturbance and nutrients (Westoby *et al.* 2002; Wright *et al.* 2004), multiple solutions for these traits are needed to cope with a level of oxygen and drought stress. In conclusion, the extent to which multiple solutions are indeed a common way to deal with water availability, or whether these results were because of the type of traits selected during this study, remains to be seen. Future studies would benefit from estimating the relative effects of different environmental drivers on traits to further test this hypothesis.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Details of regression analyses of traits and oxygen and drought stress.

Appendix S2. Interpretation of seed buoyancy impacts.

Appendix S3. Relationship between oxygen stress and drought stress.

Appendix S4. Relationship between oxygen and drought stress and the percentage helophytes and therophytes in a community.

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