Climate change threatens endangered plant species by stronger and interacting water-related stresses

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[1]   Atmospheric CO_2-concentration, temperature and rainfall variability are all expected to increase in the near future. The resulting increased dynamics of soil moisture contents, together with increased plant physiological demands for both oxygen and water, will lead to an increased occurrence of wet and dry extremes of plant stresses, i.e., of oxygen and drought stress, respectively, alone and in interaction. The use of indirect environmental variables in previous studies and a focus on individual stresses rather than their combined effects has hampered understanding of the causal impact of climate change on plant species composition through changes in abiotic site conditions. Here, we use process-based simulations of oxygen and drought stresses in conjunction with a downscaled national version of IPCC scenarios in order to show that these stresses will increase (on average by ~20% at sites where both stresses occur) in a warmer and more variable future (2050) climate. These two types of stresses will increasingly coincide, i.e. both stresses will occur more often (but not at the same time) within a single vegetation plot. We further show that this increased coincidence of water-related stresses will negatively affect the future occurrence of currently endangered plant species (causing a reduction of ~16%), while apparently no such decrease will occur among common species. Individual stresses did not appear to affect the occurrence of endangered plant species. Consequently, our study demonstrates that species that are already threatened under the current climate will suffer most from the effects of climate change.

1.   Introduction

[2]   With recent climate change, extremes in meteorological conditions are forecast and observed to increase globally [*Karl et al.*, 1995; *Dai et al.*, 1998; *Easterling et al.*, 2000; *Weltzin et al.*, 2003; *Solomon et al.*, 2007; *Knapp et al.*, 2008]. More prolonged dry periods will alternate with more intensive rainfall events, both within and between years, which will change soil moisture dynamics [*Weltzin et al.*, 2003; *Porporato et al.*, 2004; *Fay et al.*, 2008; *Knapp et al.*, 2008]. Soil moisture, in concert with nutrient availability and soil acidity, is the most important environmental filter in determining local plant species composition [*Easterling et al.*, 2000; *Weltzin et al.*, 2003; *Porporato et al.*, 2004; *Witte et al.*, 2007; *Knapp et al.*, 2008; *Levine*

et al., 2008], as it determines the availability of both oxygen and water to plant roots [*Knapp et al.*, 2008].

[3]   When the availability of oxygen or water is insufficient to meet the metabolic demands of plants for these resources, the plant suffers from oxygen and drought stress, respectively [*Knapp et al.*, 2008]. The first physiological process inhibited at oxygen stress (resulting from high soil moisture contents) is plant root respiration, i.e., oxygen consumption in the roots, a process that increases with rising temperatures [*Lloyd and Taylor*, 1994; *Amthor*, 2000]. High soil moisture contents hamper oxygen transport from the atmosphere through the soil, where part of the oxygen is additionally consumed by soil microorganisms, to the root cells [*Bartholomeus et al.*, 2008b]. Reduced respiration negatively affects the energy supply to plant metabolism. Drought stress as a result of low soil moisture content inhibits plant transpiration, a process that also responds to increased temperatures and atmospheric CO_2 concentrations [*Porporato et al.*, 2004]. As a result of increased stomatal closure, which reduces water loss by transpiration, both photosynthesis and cooling are negatively affected [*Lambers et al.*, 2006].

[4]   A large number of physiological adaptations have evolved to minimize oxygen and water deficits and to enable

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survival at specific soil moisture conditions. Generally, species that grow on a specific site are somehow adapted to the prevailing moisture conditions. For instance, species may be able to grow on very dry sites because they have either a succulent structure or hairy leaves that reduce transpirational water loss. Other species, able to grow on very wet, anoxic sites, have adapted, e.g., by developing aerenchyma [*Jackson and Armstrong*, 1999], which provides their roots with oxygen, or by rooting only superficially or by lacking root-like organs.

[5] The occurrence of both excessive dry and wet moisture conditions at a particular site has strong implications for the survival of species, because they must possess traits that allow them to respond to such counteracting conditions [*Sun et al.*, 1995; *Bakker et al.*, 2007; *Suralta and Yamauchi*, 2008]. Adapting to one stress, however, may come at the cost of the other, i.e., there exists a trade-off in the tolerance for wet conditions and the tolerance for dry conditions [*Niinemets and Valladares*, 2006]. *Suralta and Yamauchi* [2008], for instance, showed that plants that have been waterlogged may be more susceptible to drought conditions than plants that have not been waterlogged and vice versa. Although temporal variation in resource availability may reduce the effects of competitive exclusion, allowing more species to coexist [*Ricklefs*, 1977; *Knapp et al.*, 2002], the trade-off among the tolerances for contrasting moisture regimes hampers niche differentiation [*Niinemets and Valladares*, 2006]. It is to be expected that large temporal heterogeneity in soil moisture conditions may be especially harmful for endangered plant species, as these species generally show strong specializations and have narrow physiological tolerance ranges [*Schemske et al.*, 1994; *Lawler et al.*, 2002] and are poor competitors [*Liu et al.*, 2008].

[6] Until now, both large-scale (global) and plot-scale effects of climate change on plant species composition have mostly been investigated through indirect environmental measures [*Easterling et al.*, 2000; *McCarty*, 2001; *Levine et al.*, 2008] such as mean winter and summer precipitation [*Bakkenes et al.*, 2002; *Thuiller et al.*, 2005], neglecting simultaneous changes in plant oxygen and water demands. Since relationships based on such indirect measures do not include the key soil physical and plant physiological processes in the soil-plant-atmosphere system [*Easterling et al.*, 2000; *Parmesan et al.*, 2000; *McCarty*, 2001], they are likely to result in biased predictions [*Botkin et al.*, 2007]. Moreover, researchers only determined effects of one of the water-related stresses, i.e., either oxygen or drought stress. The neglect of causal relationships between climate change and simultaneous increased temporal variation in oxygen and drought stress, may explain the contradictory findings regarding the effects of soil moisture dynamics on species composition described so far [*Knapp et al.*, 2002; *Drake and Lodge*, 2004; *Adler and Drake*, 2008]. Here, we have overcome these limitations using a process-based modeling approach to quantify both oxygen and drought stress in a future climate (2050) and to predict, based upon relationships between these stresses and species composition, the occurrence of endangered and common species.

[7] Applying this approach, we show that the predicted climate change-induced increased variability in soil moisture contents [*Fay et al.*, 2008; *Knapp et al.*, 2008], together with increased physiological demands for both oxygen

and water [*Drew*, 1983; *Dai et al.*, 1998], will lead to an increased variability in plant stresses and will especially affect endangered plant species.

2. Material and Methods

2.1. General Approach

[8] Groundwater levels alone do insufficiently account for the moisture conditions, and thus oxygen and drought stress, in the root zone. Therefore, following a recently proposed conceptual framework on the effects of increased rainfall variability on water-related plant stresses [*Knapp et al.*, 2008], we calculated process-based oxygen and drought stress for terrestrial vegetation plots from a variety of natural habitats, ranging from dry to wet, in a temperate climate, i.e., the Netherlands. We use the reductions in respiration and transpiration due to low oxygen and water availability, respectively, to characterize these stresses. Respiration reduction accounts for the effects of both extreme rainfall events and high temperatures, known to affect vegetation composition [*Sojka et al.*, 1972; *Drew*, 1983]. Transpiration reduction accounts for the effects of both prolonged dry periods and high atmospheric demand for plant transpiration, i.e., factors that determine drought stress in plants [*Porporato et al.*, 2004].

[9] In order to make an unbiased comparison of the occurrence of oxygen and drought stress among sites, and following *Dyer* [2009], we simulated the daily respiration and transpiration reduction for a hypothetical reference grassland instead of the actual vegetation. By doing so, we obtained stress measures that reflect the moisture and oxygen status of the soil, independent of the actual vegetation (by adaptations, the natural vegetation reduces stress, hence poor relations between the actual stress and vegetation characteristics are expected). Our reference vegetation is defined as a temperate natural grassland not adapted to oxygen and drought stress, i.e., a grassland as defined by *van Dam* [2000] and *Bartholomeus et al.* [2008b]. The use of a reference vegetation improves the applicability of models in which stress measures are implemented, especially in predicting climate change effects [*Dyer*, 2009]. The use of a reference vegetation allows defining a reference stress, as a habitat characteristic, instead of having to deal with the various ways in which the actual vegetation could acclimate, among those plasticity in rooting, physiology and morphology. This actual stress level is not needed when inferring vegetation responses to the habitat stresses (which is a strength of our approach). Knowing and quantifying the actual stress would be useful when aiming to calculate fluxes of e.g., moisture and water vapor and the dynamic responses of vegetation.

[10] We assessed reference oxygen and drought stress for 185 vegetation plots by a dynamic process-based modeling procedure. With this procedure, we computed stresses for both the present and the future (2050) climate as predicted by *van den Hurk et al.* [2006] (see section 2.3 and Table 1). To quantify reference oxygen and drought stress, we focused on interacting meteorological, soil physical, microbial, and plant physiological processes in the soil-plant-atmosphere system. As both the supply and demand of oxygen and water depend strongly on the prevailing meteorological conditions, both reference oxygen and drought stress were calculated dynamically in time to capture climate change effects (Figure 1):

Table 1. Quantification of the W[+] Climate Scenario[a]

Variable	Summer (June–July–August)	Winter (December–January–February)
mean temperature (K)	+2.8	+2.3
mean precipitation (%)	−19.0	+14.2
wet day frequency (%)	−19.3	+1.9
precipitation on wet day (%)	+0.3	+12.1
reference evapotranspiration (%)	+15.2	

[a]Quantification of the effects of the W[+] climate scenario in the Netherlands [*van den Hurk et al.*, 2006] on temperature, precipitation and evapotranspiration.

[11] First, we used the hydrological model Menyanthes [*von Asmuth et al.*, 2002] to determine daily groundwater levels (Figure 1, see A) from biweekly measurements. Second, daily soil moisture (Figure 1, see C) and temperature (Figure 1, see D) were simulated with the widely applied dynamic Soil-Water-Atmosphere-Plant (SWAP) model [*van Dam et al.*, 2008] for the unsaturated zone, which also gives the daily transpiration reduction (Figure 1, see B). Third, daily respiration reduction (Figure 1, see E) was simulated with a recently developed model for oxygen stress to plant roots [*Bartholomeus et al.*, 2008b], which involves macro- and micro-scale diffusion, as well as the plants' physiological demand for oxygen. Further details are explained in section 2.2.

[12] Our modeling approach was used to analyze (1) whether climate change actually leads to an increased variability in water-related plant stress, and (2) if these changes particularly affect currently endangered plant species. For the latter, we related the number of endangered species within each vegetation plot (independent variable) to current reference oxygen and drought stress (predicting variables) using quantile regression [*Koenker and Basset*, 1978; *Cade et al.*, 1999]. On the basis of this relationship, we predicted the

effect of future reference oxygen and drought stress on the future potential number of endangered species within each vegetation plot.

2.2. Simulation of Reference Oxygen and Drought Stress

2.2.1. Data

[13] We used 185 vegetation plots [*Runhaar*, 1989; *de Jong*, 1997; *Jansen et al.*, 2000; *Beets et al.*, 2003; *Jansen and Runhaar*, 2005] distributed across the Netherlands, that originate from a wide range of terrestrial vegetation types differing in succession stages, soil type (sandy, clayey, loamy), soil moisture regime, nutrient availability and soil pH. None of the investigated plots had been under the influence of a structural change in water management conditions in the last decades. All vegetation plots were representative of (semi-) natural habitats. For groundwater-dependent sites, biweekly measurements of groundwater level data were available in or immediately next to each vegetation plot, but only for specific periods and for a limited number of years (min 3 years, max 8 years). The groundwater level series were extended to the period 1971–2000, and interpolated to daily values with the Menyanthes model [*von Asmuth et al.*,
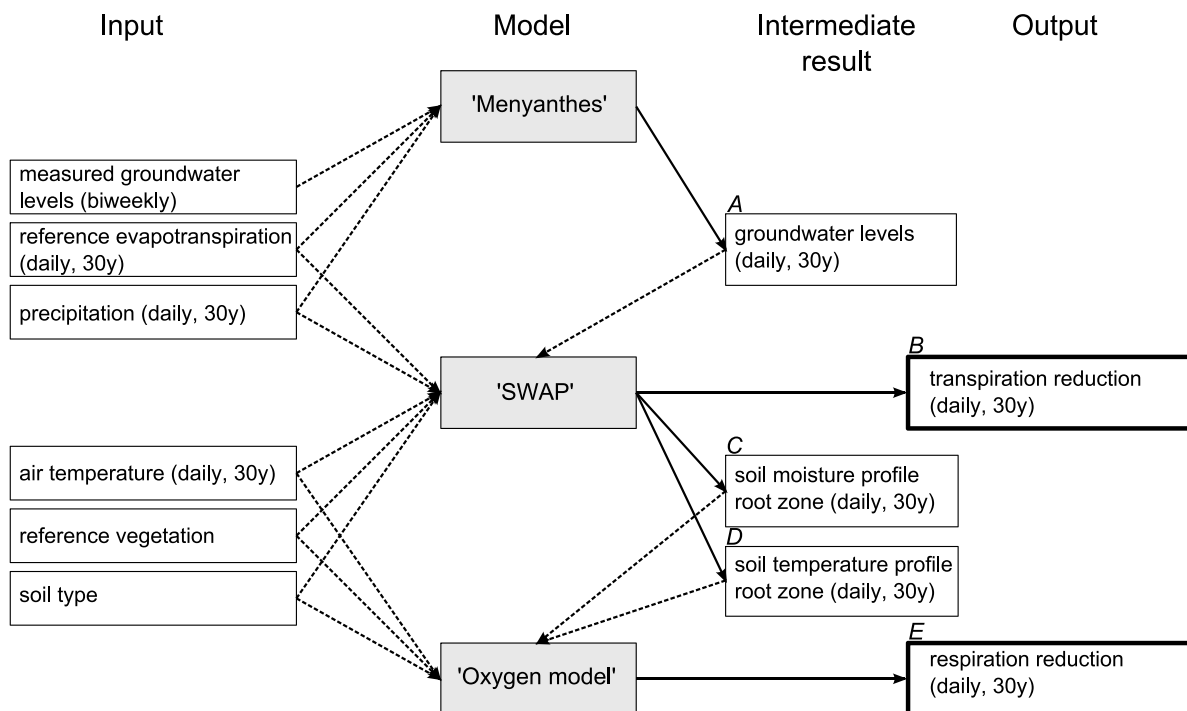
Figure 1. Modeling procedure for both daily respiration and transpiration reduction.
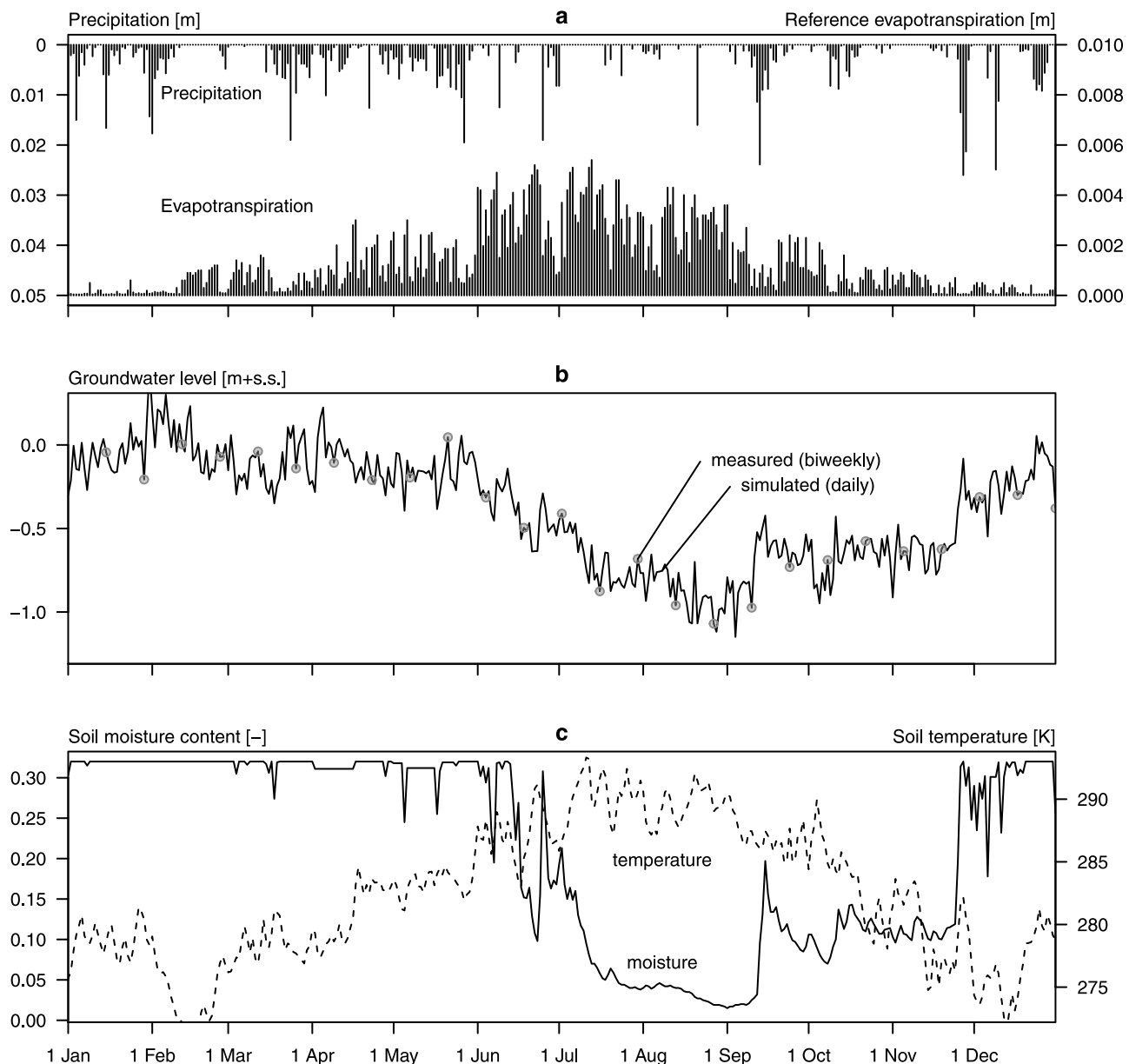
Figure 2. Example of hydrological simulations. Measured groundwater levels (b) are interpolated to daily values (b) on the basis of precipitation and evapotranspiration data (a). Daily soil moisture and soil temperature (c) are simulated on the basis of precipitation and evapotranspiration data (a), air temperature, and groundwater level data (b) (except for groundwater independent sites).

2002] (Figure 1, see A), to characterize temporal deviations in meteorological conditions and to show long-term average conditions [*Bartholomeus et al.*, 2008a]. Menyanthes transforms precipitation and evapotranspiration series (impulse) into groundwater level series (response) [*Bartholomeus et al.*, 2008a] (Figures 2a–2b). Daily local meteorological data on precipitation and reference evapotranspiration (according to *Makkink* [1957]) were available from neighboring weather stations of the Royal Netherlands Meteorological Institute (KNMI) from 1970 onwards.

2.2.2. Soil Moisture and Soil Temperature Profiles

[14] For each plot, soil moisture and soil temperature profiles in the root zone (consisting of 16 layers to allow for layer-specific soil physical properties) were simulated on a

daily basis for the period 1971–2000 with SWAP (*van Dam et al.*, 2008]) (Figure 1, see C and D; Figure 2c). We improved SWAP for nearly saturated conditions using the method of *Schaap and van Genuchten* [2006] [*Cirkel et al.*, 2010]. Daily groundwater levels taken from the Menyanthes model (Figure 1, see A) served as the bottom boundary conditions. For the groundwater independent sites, constant deep groundwater levels were used as bottom boundary condition. The meteorological input for the SWAP simulations consisted of daily precipitation and reference evapotranspiration data (as used for simulating groundwater levels (Figure 1, see A)) and daily temperature. Daily local air temperature was available from the KNMI from 1970 onward. For each plot, soil physical parameters according to

Table 2. Detailed Plot Information[a]

	Endangered Species	Common Species	Fraction of Sites With Endangered Species
Single stress	79	92	0.86
Coinciding stress	59	93	0.63
Total	138	185	0.75

[a]Breakdown of the total number of sites (185) into the number of sites with endangered species and common species and into the number of sites with single stress and coinciding stress. The fraction of sites with endangered species is higher for sites with a single stress than for sites with coinciding stress.

van Genuchten [1980] were derived from a national soil database [*Wösten et al.*, 2001].

2.2.3. Reference Drought and Oxygen Stress

[15] Plants transpire at a potential rate under nonlimiting water availability. This potential transpiration depends on the atmospheric demand (global radiation, air humidity, wind speed, air temperature and atmospheric CO_2 concentration) [*Monteith and Unsworth*, 1990]. When water becomes limiting, however, the water uptake by plant roots and herewith plant transpiration is reduced. SWAP [*van Dam et al.*, 2008] uses the water-limited side of the Feddes function for root water uptake [*Feddes et al.*, 1978], based on soil water potential h (for the reference vegetation, reduction starts at $h = -800$ cm and decreases linearly to zero at $h = -10000$ cm), to describe this reduction. Daily transpiration reduction, i.e., the difference between the potential and the actual transpiration, was output from the SWAP-model (Figure 1, see B). Plant characteristics of the reference grassland (of which the root density decreases exponentially with depth), actual soil type, and daily groundwater level, precipitation, air temperature and reference evapotranspiration were model input.

[16] Root respiration is determined by interacting respiratory (i.e., oxygen consuming) and diffusive (i.e., oxygen providing) processes in and to the soil. Plant roots respire at a potential rate under optimal soil aeration and thus nonlimiting oxygen availability. This potential root respiration is in equilibrium with the oxygen demand of plant roots, which is determined by plant characteristics and soil temperature [*Amthor*, 2000] (as simulated with SWAP) only. Upon increasingly wetter conditions, however, the gas-filled porosity of the soil decreases and oxygen availability becomes insufficient for potential root respiration. Daily respiration reduction (i.e., potential minus actual respiration) was calculated with a novel model for oxygen transport and consumption, which uses generally applied physiological and physical relationships to calculate both the oxygen demand of, and the oxygen supply to plant roots. For details we refer to *Bartholomeus et al.* [2008b].

[17] Simulation of the actual root respiration for the reference grassland requires actual data on soil type, daily soil temperature and daily gas-filled porosity in each soil layer. The latter two variables were output from the SWAP simulations (Figure 1, see C and D). We applied the model of *Bartholomeus et al.* [2008b] to the 16 soil layers of SWAP, to account for layer-specific soil physical properties, moisture contents and temperatures. The difference between potential and actual root respiration for each plot was calculated for each soil layer separately and then summed.

[18] Suboptimal moisture conditions do not necessarily directly affect the vegetation, because normal metabolism of plants is flexible, responding to moderate fluctuations in environmental changes [*Gaspar et al.*, 2002; *Körner*, 2003]. Therefore, the events that deviate most from the average conditions, i.e., the extremes, will have most impact on the vegetation [*Chapin et al.*, 1993; *Knapp et al.*, 2002; *Weltzin et al.*, 2003; *van Peer et al.*, 2004; *Bokhorst et al.*, 2007]. To take account of the amplitude of stress [*Knapp et al.*, 2008], we selected for each simulation year, and for each stress, the 10-day period with highest reduction in plant metabolic functioning, i.e., in respiration reduction or transpiration reduction for oxygen and drought stress, respectively. A 10-day period was chosen, because a period of 10 days of either oxygen or drought stress has been shown to hamper the plant metabolism already [*Huang et al.*, 1998; *Volaire et al.*, 1998; *Poulson et al.*, 2002]. These yearly maximum reductions in transpiration or root respiration for a 10-day period were averaged over 30 years to represent drought and oxygen stress, respectively.

2.3. Future (2050) Temperature and Moisture Regime

[19] For the calculations of future oxygen and drought stress, we considered the W^+ climate scenario [*van den Hurk et al.*, 2006] for the year 2050 (Table 1). This scenario is based on general circulation model simulations published in the *Fourth Assessment Report* of the IPCC [*Solomon et al.*, 2007] and includes changes in temperature, precipitation and reference evapotranspiration. The scenario is related to the IPCC A_2 and A_1B scenarios and comprises a +2°C global temperature increase, with changed air circulation patterns in summer and winter [*van den Hurk et al.*, 2006]; it also represents the increase in both prolonged dry periods and more intense rainfall events. The W^+ scenario accounts in detail for the interacting effects of altered temperature, CO_2 concentration and rainfall [*Weltzin et al.*, 2003]. Hence, in contrast to the global IPCC scenarios, the W^+ scenario allows to investigate the effect of climate change for the Netherlands, as done in this study.

[20] For each plot, we projected temperature, precipitation and reference evapotranspiration daily time series from 1971 to 2000 to the 2050 climate, applying the software supplied by the KNMI [*Bakker and Bessembinder*, 2007]. This software represents the W^+ scenario as presented by *van den Hurk et al.* [2006] (Table 1). Complementary to this climate scenario, we corrected for a higher water use efficiency of plants at increased CO_2 levels in 2050 by decreasing reference evapotranspiration values by 2% [*Kruijt et al.*, 2008].

[21] Future precipitation and evapotranspiration were used to simulate future groundwater levels in Menyanthes. Subsequently, future soil moisture and soil temperature profiles were created with SWAP. Future drought stress was derived from the SWAP output. Future oxygen stress was simulated on the basis of the future soil moisture and soil temperature profiles.

[22] Dealing with the various ways in which the actual vegetation could acclimate to climate change to some extents, and particularly quantifying the extent to which genetic adaptation (in contrast to phenotypic plasticity) may occur, was currently not feasible due to a lack of data. However, neglecting adaptation will hardly affect our results, as the rate
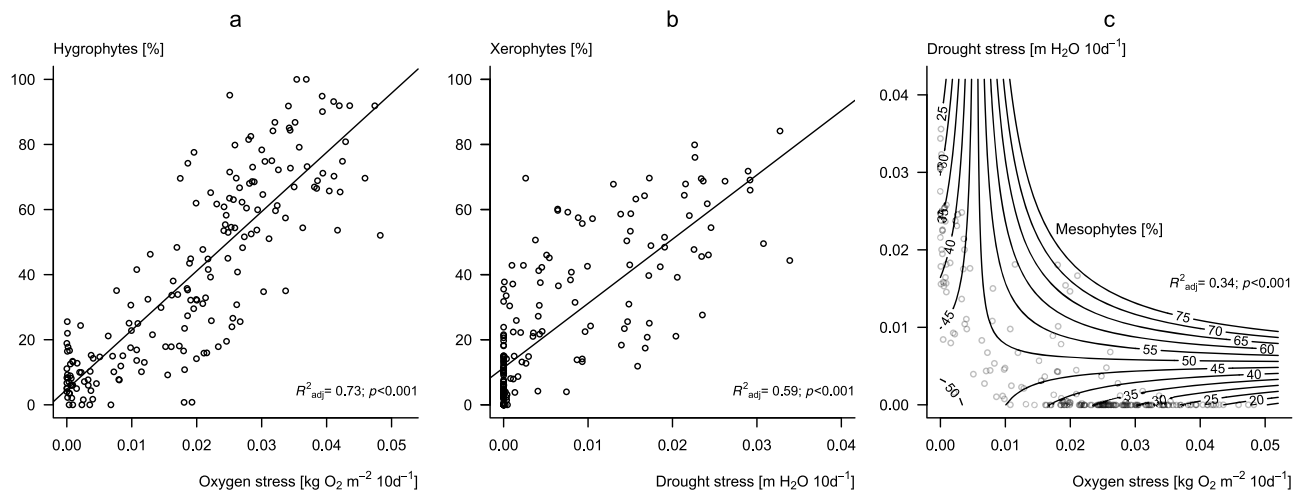
Figure 3. (a) Percentage of hygrophytes and (b) percentage of xerophytes as a function of oxygen stress and drought stress, respectively, and (c) percentage of mesophytes (the isolines represent the percentage of mesophytes) as a function of both oxygen and drought stress.

of natural adaptation will be slower than the rate of climate change [*Fischlin et al.*, 2007].

2.4. Vegetation Characteristics

2.4.1. Fraction Hygrophytes, Xerophytes and Mesophytes

[23] Hygrophytes, mesophytes and xerophytes can be considered to reflect generic functional (direct) responses of vegetation to soil moisture conditions. Hygrophytes form a functional species group with reported preference for wet sites, mesophytes for moist sites, and xerophytes for dry sites [*Runhaar et al.*, 1997]. Some species may occur at both wet and moist sites, others at moist and dry sites, or at sites ranging from dry to wet. Such species are defined accordingly e.g., as 80% hygrophyte and 20% mesophyte. This fractional division is used in the calculation of the fraction of hygrophytes, mesophytes and xerophytes of each vegetation plot (*Runhaar et al.*, 2004; *Witte et al.*, 2007). In order to test the validity of our simulations of reference oxygen and drought stress, we related these stresses to the percentage of hygrophytes and of xerophytes (as defined by *Runhaar et al.* [2004] and *Witte et al.* [2007]) in each plot. These percentages may be considered as measures of vegetation adaptation to wet and dry extremes, respectively [*Runhaar et al.*, 1997]. Additionally, we related the percentage of xerophytes, hygrophytes and mesophytes (i.e., species occurring at intermediate moisture conditions) to the co-occurrence of oxygen and drought stress by least squares regression. Doing so, we analyzed (1) the need of considering wet and dry extremes simultaneously in relation to vegetation characteristics, and (2) the effect of co-occurring stresses on the percentage of nonspecialists (i.e., mesophytes) within a vegetation plot.

2.4.2. Endangered and Common Species

[24] We determined the number of endangered (Red List) species for the Netherlands [*Van der Meijden et al.*, 2000] within each vegetation plot. The relationship between this number and oxygen and drought stress was described by the 95% regression quantile [*Koenker and Basset*, 1978]. Unlike conventional regression, which considers solely changes in the mean of the response variable, quantile regression excludes the effect of unmeasured limiting factors [*Cade et al.*, 1999] and is therefore a powerful method for analyzing the change in the potential number of endangered species as a function of the limiting factors oxygen and drought stress only. Using the 95% quantile enabled us to determine the potential number of endangered species that could occur under specific stress conditions. In total, our data set included 97 endangered species, of which 64 species occurred at coinciding oxygen and drought stress. A total of 138 sites (75%) in our data set contained endangered species. This fraction was higher (86%) at sites with only oxygen or drought stress and lower (63%) at sites with both oxygen and drought stress (Table 2). Also the relationship between the number of common species and oxygen and drought stress was described by the 95% regression quantile.

[25] Additionally, we tested whether the endangered species in our data set occur at narrower ranges of oxygen and drought stress than common species, i.e., whether endangered species actually have smaller physiological tolerance ranges. A Mann-Whitney Test tested whether the standard deviations of oxygen and drought stress at which

Table 3. Least Squares Regression Statistics[a]

	a_1	a_2	a_3	a_4
Percentage hygrophytes	$1.67 \ 10^3 \ (p < 1 \ 10^{-3})$	$-1.42 \ 10^2 \ (p = 0.39)$	$-1.23 \ 10^5 \ (p < 1 \ 10^{-3})$	$1.19 \ 10^1 \ (p < 1 \ 10^{-3})$
Percentage xerophytes	$-9.22 \ 10^2 \ (p < 1 \ 10^{-3})$	$9.02 \ 10^2 \ (p < 1 \ 10^{-3})$	$-1.65 \ 10^4 \ (p = 0.30)$	$3.56 \ 10^1 \ (p < 1 \ 10^{-3})$
Percentage mesophytes	$-7.45 \ 10^2 \ (p < 1 \ 10^{-3})$	$-7.61 \ 10^2 \ (p < 1 \ 10^{-3})$	$1.39 \ 10^5 \ (p < 1 \ 10^{-3})$	$5.25 \ 10^1 \ (p < 1 \ 10^{-3})$

[a]Parameter values of the relationships between oxygen and drought stress (explaining variables) and percentages of hygrophytes, xerophytes or mesophytes. Percentage = a_1*oxygen stress + a_2*drought stress + a_3*oxygen stress*drought stress + a_4.
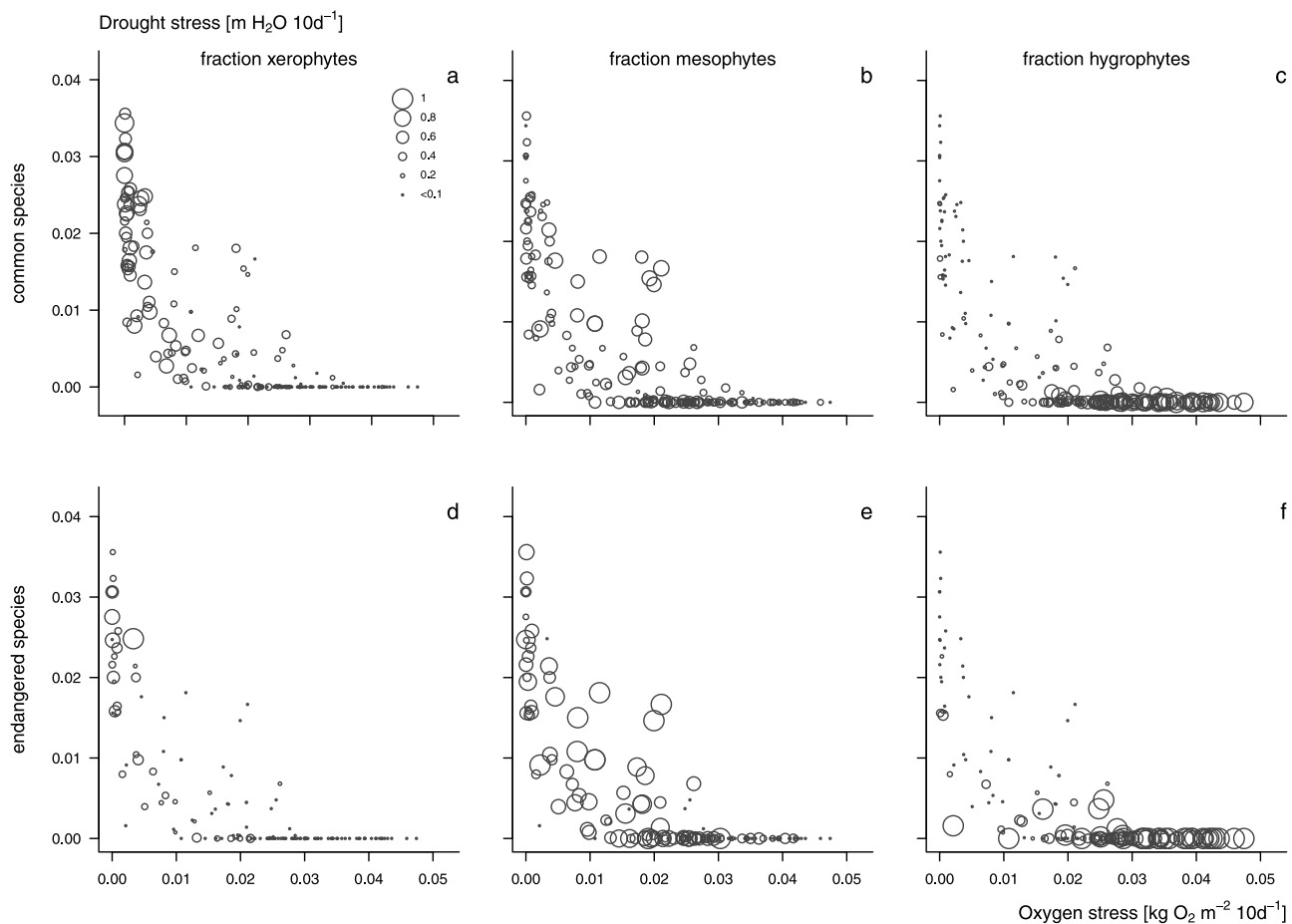
Figure 4. Observed fractions of xerophytes, mesophytes and hygrophytes for common and endangered species, for specific combinations of oxygen and drought stress.

endangered species and at which common species occur differed significantly.

2.5. Nutrient Availability

[26] Besides soil moisture, nutrient availability also potentially affects the occurrence of endangered species. To account for additional variation caused by nutrient availability, instead of oxygen and drought stress, we included a measure for nutrient availability, i.e., nutrient indicator values [*Witte et al.*, 2007], as covariate in the 95% regression quantile that relates the number of endangered species to oxygen and drought stress. If effects attributed to oxygen and drought stress are caused by (correlations with) nutrient availability, then the power of the relationships between the number of endangered species and these stresses would decrease (or would be eliminated) when including this covariate.

[27] A list of nutrient indicator values for plant species tailored to the Netherlands [*Witte et al.*, 2007] was used to compute the arithmetic mean indicator value for nutrient availability for each plot. Following the findings of *Käfer and Witte* [2004], no weight was given to species abundance.

3. Results

[28] Both reference oxygen stress and drought stress were a good predictor of vegetation characteristics related to moisture availability, i.e., the percentage of hygrophytes

and xerophytes, respectively (Figures 3a–3b). In the current climate of the Netherlands, potential transpiration ranges from about 0.001 m H_2O d^{-1} in spring up to 0.004 m H_2O d^{-1} in summer. The uppermost drought stress of 0.04 m H_2O 10 d^{-1} (Figure 3b) thus indicates that during high water demand for transpiration, i.e., the summer period, the availability of water was close to zero. Potential respiration ranges from about 0.002 kg O_2 m^{-2} d^{-1} in spring up to 0.006 kg O_2 m^{-2} d^{-1} in summer. The uppermost oxygen stress of 0.05 kg O_2 m^{-2} 10 d^{-1} (Figure 3a) is thus obtained under extremely wet conditions together with a high respiratory oxygen demand.

[29] Considering oxygen and drought stress, and their interactions, led to significantly stronger ($p < 0.001$) relationships with water-related vegetation characteristics than when considering only one stress (Table 3). The explained variance in the prediction of hygrophytes increased by considering both stresses and their interactions with 6% to R^2_{adj} = 79%, while the prediction of xerophytes increased with 14% to R^2_{adj} = 73%. For the hygrophytes, particularly the interactions between oxygen and drought stress allowed for better predictions, whereas for xerophytes the main effects of oxygen stress added to the predictive power (Table 3).

[30] Co-occurrence of oxygen and drought stress (i.e., at the same plot, but not at the same time) reduces the
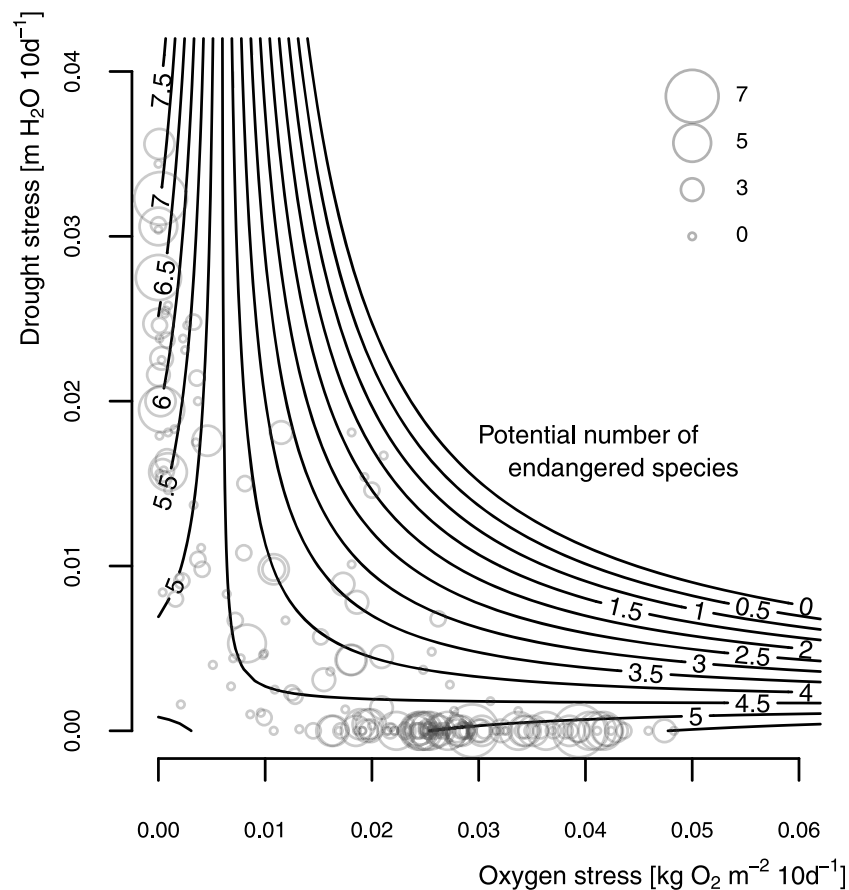
Figure 5. Ninety-five percent regression quantile contour plot [*Koenker and Basset*, 1978; *Cade et al.*, 1999] showing the potential number of currently endangered species within vegetation plots of 4 m^2 as a function of oxygen and drought stress. The circles represent the observed number of endangered species, which is highest on sites with only oxygen or drought stress.

percentage of specialists within a vegetation plot, i.e., either hygrophytes or xerophytes, while increasing the occurrence of mesophytes (Figure 3c). As Figure 3c also shows, the percentage of mesophytes within a vegetation plot (i.e., the percentage of nonspecialists) decreases significantly with increasing stress as long as only one of the stresses prevails (i.e., negative regression terms for both oxygen and drought stress, Table 3).

[31] Figure 4 shows the fraction of xerophytes, mesophytes and hygrophytes as a function of a combination of oxygen and drought stress, for both common and endangered species. Both for common (Figures 4a–4c) and endangered species (Figures 4d–4f), the fractions of specialists are highest at sites with either oxygen or drought stress, and the fraction of mesophytes is highest at sites with both stresses prevailing. The graphs further show that sites with endangered species cover the whole range of stresses, i.e., the occurrence of these species is not confined to plots with specific hydrological conditions.

[32] Further analyses showed that a combination of oxygen and drought stress not only decreases the occurrence of hygrophytes and xerophytes, but may also hamper the occurrence of endangered species. We first analyzed the ranges, given by mean standard deviations, of oxygen and drought stress at which endangered and common species

occurred. The stress ranges at which endangered species persist were $6.0 \ 10^{-3}$ kg O_2 m^{-2} 10 d^{-1} and $3.5 \ 10^{-3}$ m H_2O m^{-2} 10 d^{-1} for oxygen stress and drought stress, respectively. For common species, the ranges were significantly higher ($7.4 \ 10^{-3}$ kg O_2 m^{-2} 10 d^{-1}, $p = 0.01$; and $5.3 \ 10^{-3}$ m H_2O m^{-2} 10 d^{-1}, $p < 0.001$, respectively). Thus, endangered species are associated with smaller tolerance ranges of oxygen and drought stress than common species. Moreover, sites with coinciding oxygen and drought stress more often lack endangered species than sites with only one stress (Table 2).

[33] Additionally, we found that under the current climate, the coincidence of oxygen and drought stress is coupled to a significantly lower potential number of endangered plant species (Figure 5). This was indicated by the highly significant interaction for the combination of oxygen and drought stress for the 95% regression quantile that described the potential number of endangered species as a function of oxygen and drought stress (Table 4). A significant interaction term is not apparent for the number of common species (Table 4). Thus, unlike endangered species, the number of common species is not affected by coinciding oxygen and drought stress. When using nutrient availability as covariate, the interaction term in the regression quantile for the number of endangered species as function of oxygen and drought

Table 4. Quantile Regression Statistics[a]

	a_1	a_2	a_3	a_4
Number of endangered species without nutrient availability	$2.24\ 10^1$ ($p = 0.66$)	$8.22\ 10^1$ ($p = 0.14$)	$-1.40\ 10^4$ ($p < 1\ 10^{-3}$)	$0.44\ 10^1$ ($p < 1\ 10^{-3}$)
Number of endangered species with nutrient availability as covariate	$3.38\ 10^1$ ($p = 0.40$)	$9.62\ 10^1$ ($p = 0.03$)	$-1.55\ 10^4$ ($p < 1\ 10^{-3}$)	$0.41\ 10^1$ ($p < 1\ 10^{-3}$)
Number of common species within a vegetation plot	$1.68\ 10^2$ ($p = 0.12$)	$7.12\ 10^2$ ($p = 1\ 10^{-3}$)	$-2.17\ 10^4$ ($p = 0.15$)	$2.62\ 10^1$ ($p < 1\ 10^{-3}$)

[a]Parameter values of the 95% regression quantiles, describing the inhibiting effect of oxygen and drought stress on (1) the number of endangered plant species within a vegetation plot without nutrient availability as covariate, (2) the number of endangered plant species within a vegetation plot with nutrient availability as covariate, and (3) the number of common species within a vegetation plot. Number of species = a_1*oxygen stress + a_2*drought stress + a_3*oxygen stress*drought stress + a_4.

stress remained highly significant (Table 4), and the predictive power increased (t-value for the interaction term was −4.8 and −5.3 for the model with and without nutrient availability, respectively). Nutrient availability thus decreased some of the residual variation in the regression and thereby strengthens the relationship, but this is an additional effect on top of the predominant effect of oxygen and drought stress.

[34] Figure 6 shows the simulated oxygen and drought stress for the vegetation plots in both the current and the future (2050) climate. For clarity, we included a polygon that envelopes 90% of the data points. In the current climate (Figure 6a) 50% of the vegetation plots had both oxygen and drought stress larger than zero, i.e., coinciding oxygen and drought stress. Model results show that there is a shift in habitat conditions toward more extreme coincidence of plant

oxygen and drought stress under future climatic conditions (Figure 6b). Information about the intermediate results on groundwater levels, soil moisture and soil temperature for both the current and future climatic conditions is provided in Appendix A.

[35] In vegetation plots with either oxygen or drought stress under the current conditions, the degree of stress was projected to increase under the future climate. Compared to the current average stresses at these plots, oxygen and drought stress will increase with 21% and 22%, respectively. At the plots where only one stress prevails, the increase in stress is projected to cause an average 4% shift in favor of the specialists (i.e., hygrophytes or xerophytes), ranging up to shifts of 9%. In vegetation plots where the stresses currently coincide, both stresses will intensify simultaneously in the
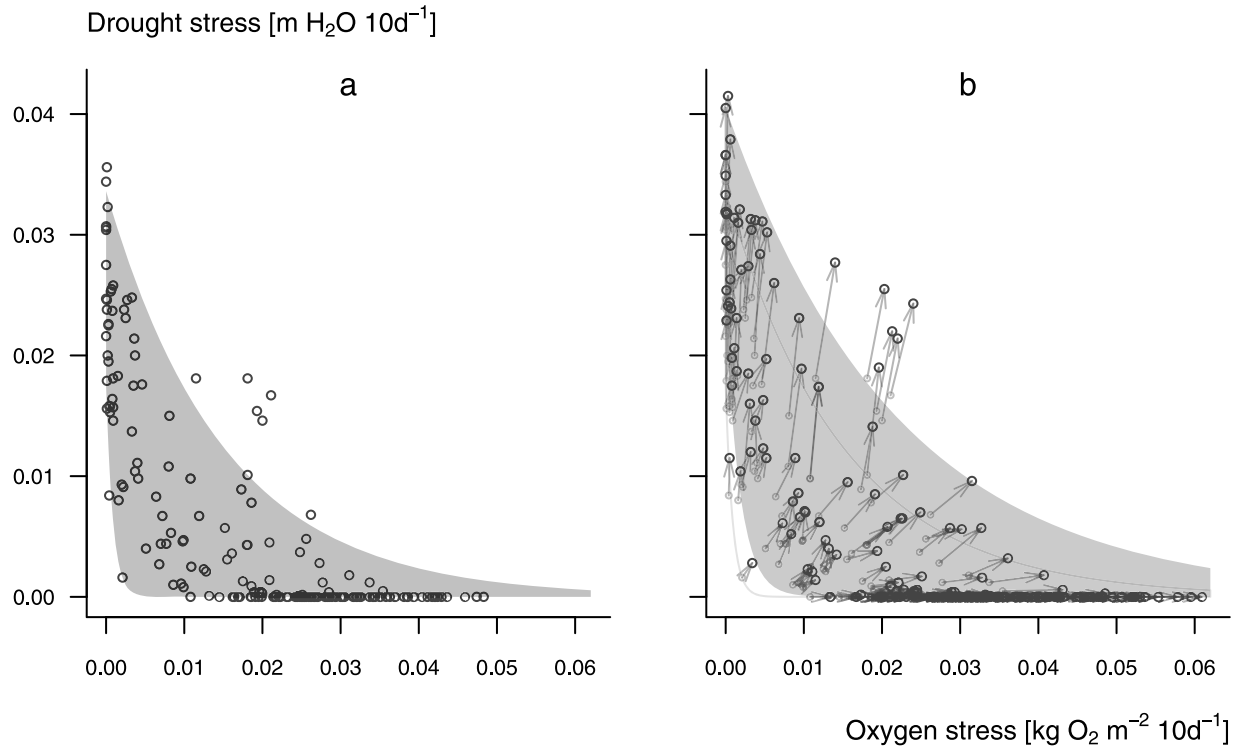

Figure 6. Oxygen stress and drought stress for 185 vegetation plots for the current (a) and future climate (b). Arrows indicate the direction of climate-induced shift for each plot. The polygons show the area enclosed by the 5% and 95% regression quantiles [*Koenker and Basset*, 1978], thus encompassing 90% of the data points. Under the future climate, this area represents both an increased coincidence and intensification of oxygen and drought stress.

future climate (the arrows in Figure 6b that move away from both axes). Compared to the current average stresses at these plots, oxygen and drought stress will increase with 20% and 35%, respectively. The simultaneous increase of both stresses may lead to a proportional shift toward mesophytes of on average 5%, but up to even 24%. This goes at the cost of the fraction of specialists at these plots.

[36] Similarly, projecting Figure 6b onto the relationship between oxygen and drought stress and the number of endangered species (Figure 5), shows that a shift toward a lower number of endangered species within a vegetation plot will occur under the future (2050) compared to the current moisture conditions. The statistically significant negative interaction term in the relationship between oxygen and drought stress, and the number of endangered species leads to a reduction of 16% in the potential number of endangered species per vegetation plot in 2050. Climate change thus threatens the future occurrence of currently endangered species. On the other hand, as long as only one of the stresses prevails (47% of our data set in the future climate), climate change does not significantly affect endangered species. For those plots, the potential number of endangered species will remain high, but do not increase (approximately >5 endangered species within a plot of 4 m^2).

4. Discussion

4.1. Co-occurring Environmental Stresses Negatively Affect Endangered Species

[37] To the best of our knowledge, this study is the first that addresses the negative effect of co-occurring wet and dry extremes in moisture conditions on the occurrence of currently endangered plant species. Additionally, explicit process-based simulations of amplifying stresses due to climate change have not been done so far. Given the negative interactions between wetness and drought tolerance of plant species found by *Niinemets and Valladares* [2006] for their global data set, the relationships between oxygen and drought stress and vegetation characteristics we found, are likely to exist globally.

[38] We analyzed the effect of variation in water-related stresses, i.e., oxygen and drought stress, on vegetation characteristics, for both the current and future climatic conditions. *Knapp et al.* [2008] hypothesized that climate change could amplify the wet and dry extremes in plant stresses simultaneously. Our model simulations show that under the W$^+$ scenario of the Royal Dutch Meteorological Institute for 2050, indeed more severe wet and dry extremes in plant stresses will co-occur over time within the same vegetation plot.

[39] Due to the more severe wet and dry hydrological extremes, an increased co-occurrence of oxygen and drought stress, both becoming moreover more intense, is predicted (Figure 6b). The significant interaction for the combination of oxygen and drought stress (Figure 5) on the habitat suitability of endangered species underpins the critical influence of this combination. The significant negative interaction we found was obtained by using regression quantiles, thus isolating the limiting effects of oxygen and drought stress. This interaction was not an artifact caused by a correlation between nutrient availability and water-related stresses. So, although other factors, like soil fertility, may decrease the

number of endangered species in the future climate too, we illustrated that the increased co-occurrence of water-related stresses alone will already result in less favorable conditions for currently endangered plant species.

[40] It has already been shown before that increased variability and more extremes in resource availability can be highly detrimental to plant species ("you can only die once"). *Drake and Lodge* [2004] used a meta-analysis to identify the negative effect of variable availability of resources for the survival of plant species. They found that high variability in the availability of resources increases the probability of both extinction and establishment. Here, we show that particularly the combination of stresses is detrimental to endangered species.

[41] In contrast to endangered species, the number of common species (i.e., non-Red List species) within a vegetation plot did not decline with increasing co-occurrence and intensification of oxygen and drought stress as a significant interaction term was not apparent for the number of common species. The different pattern for the number of common and of endangered species will be caused by the different abilities of species to adapt to variable moisture conditions. Our results showing the significantly smaller tolerance ranges for oxygen and drought stress at which endangered species persist reflect these different abilities. Variability in the availability of resources is especially detrimental to species with narrow physiological tolerance ranges [*Parmesan et al.*, 2000].

[42] A physiological explanation for this has been provided by *Smith and Huston* [1989], *Silvertown et al.* [1999] and *Niinemets and Valladares* [2006], who argued that variable stress conditions require a trade-off among plant traits for species to survive. Such a trade-off determines the ability of a species to tolerate each stressor [*Vinebrooke et al.*, 2004]. The high number of specialists prevailing at one dominant stress, together with the significant increase in mesophytes with increased coincidence of oxygen and drought stress we found, confirms the suggestion of *Niinemets and Valladares* [2006] that species that are simultaneously tolerant to multiple stresses, lack full adaptation to each potential stress. Specific adaptations to either oxygen or drought stress thus reduce the adaptive ability to the other stress and increases the impact of the other stress. Additionally, differences in the species' ability to adjust to the increased variability in water and oxygen availability will alter competitive interactions [*Knapp et al.*, 2008] and, therewith, the species' composition of the vegetation. Species with small physiological tolerance ranges for soil moisture conditions (i.e., xerophytes, hygrophytes and endangered species as demonstrated by us) will have a lower competitive ability at co-occurring stresses than species that have traits to adapt to both wet and dry conditions. Overall, specialists will be less abundant at coinciding stresses. However, variation in resource availability can also reduce the effects of competitive exclusion, thus allowing more species to coexist [*Ricklefs*, 1977; *Knapp et al.*, 2002]. Variation in the availability of soil moisture, for example, has been found to increase species diversity for sites where only drought stress occurs [e.g., *Knapp et al.*, 2002]. Our data did not show an increased number of species with increased co-occurring oxygen and drought stress. On the basis of our results and the findings of *Niinemets and Valladares* [2006], we argue that variation in
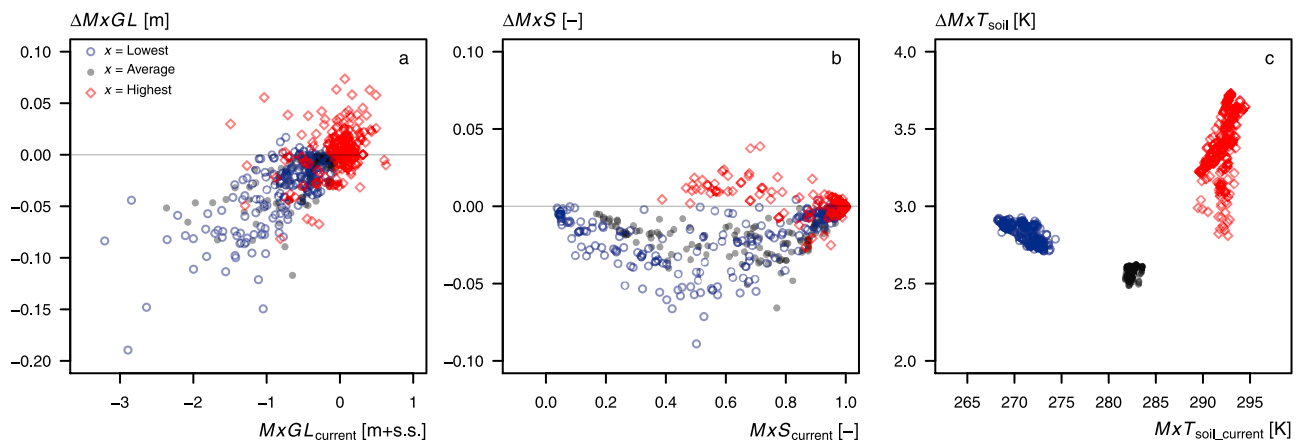
Figure A1. Climate-induced change (vertical axes) in (a) minimum, average and maximum groundwater level, (b) root zone saturation and (c) root zone temperature relative to these characteristics for the current climate (horizontal axes).

moisture conditions may only increase species diversity if a single stress (i.e., either oxygen or drought stress) is involved. The trade-off among the tolerances for contrasting moisture regimes may thus even hamper species coexistence.

4.2. Toward Applications to Identify Regional Species Loss

[43] We based reference oxygen and drought stress on the reductions in physiological processes, i.e., respiration and transpiration respectively. By considering the relevant physical and physiological processes that determine both the supply and demand of resources, our stress measures have a direct relationship with vegetation characteristics that are related to soil moisture availability [*Schimper*, 1903; *Knapp et al.*, 2008]. The ecological relevance of this approach is supported by the strong relationships between reference oxygen and drought stress with the percentages of xerophytes and hygrophytes, i.e., vegetation characteristics that have a causal connection to these dry and wet extremes in moisture conditions. On the basis of these process-based simulations, we show that the future existence of species with small physiological tolerance ranges (a common characteristic of endangered species) is at risk as a result of ongoing climate change, since the natural moisture conditions may become increasingly unsuitable for these species. Increased dynamics in habitat factors other than soil moisture may further decrease the future occurrence of endangered species. An increase in abundance of endangered species, by invading new habitats upon the development of no-analog habitats, is unlikely, as invasive species commonly have wide physiological ranges [*Funk et al.*, 2008; *Hellmann et al.*, 2008] and are consequently seldom endangered. Thus, our results have direct implications for policies to protect endangered species, as formulated by national and international nature conservation organizations (e.g., IUCN). For nature management, process-based habitat suitability models provide valuable tools for identifying sites and regions where endangered species are at risk.

[44] We argue that our ecologically relevant stress measures considering both the wet and dry extremes in plant stresses could improve predictions of species losses due to climate change. First of all, because they allow relationships derived from process-based predictive variables to describe biotic responses to climate projections [*Guisan and Zimmermann*, 2000; *Botkin et al.*, 2007]. Second, because we have shown that the interaction between oxygen and drought stress is particularly detrimental to the survival of endangered plants. Intensification of co-occurring stresses should thus be considered explicitly to capture climate change effects on species survival. For large-scale (e.g., global) analysis, the approach of *Dai et al.* [1998] to the variations in meteorological droughts and wet spells, which uses the Palmer Drought Severity Index as a proxy for soil moisture content, might be a starting point for improving the predictions of ecosystem responses to future climate projections. For identifying threats to species diversity on a local scale, we advocate our detailed approach, as plants are sensitive to fine-scale moisture conditions [*Silvertown et al.*, 1999].

Appendix A: Results of Hydrological Simulations

[45] Hydrological simulations of groundwater levels, soil moisture and soil temperature (Figure 2) form the basis for the calculation of oxygen stress and drought stress. These stresses are based on interacting processes in the soil-plant-atmosphere system. Because of these interactions, the climate-induced increase in both oxygen and drought stress (Figure 6) should not be attributed to a single environmental factor. In this appendix, we provide insight into the effects of climate change on mean minimum, average and maximum groundwater level, root zone saturation, root zone temperature, and how these wet and dry extremes in soil conditions contribute to increased oxygen and drought stress.

[46] For each year, we derived the minimum, average and maximum groundwater level (only for groundwater dependent sites), saturation and temperature, and averaged it over 30 years. This resulted in mean lowest, average and highest groundwater levels ($MLGL$, MGL and $MHGL$, respectively), saturation rates (MLS, MS and MHS), and soil temperatures (MLT, MT and MHT). Saturation rates are defined as the ratio between volumetric water content and porosity, thus ranging from zero (dry) to 1 (saturated). Both saturation rates and soil temperature are root zone averages.
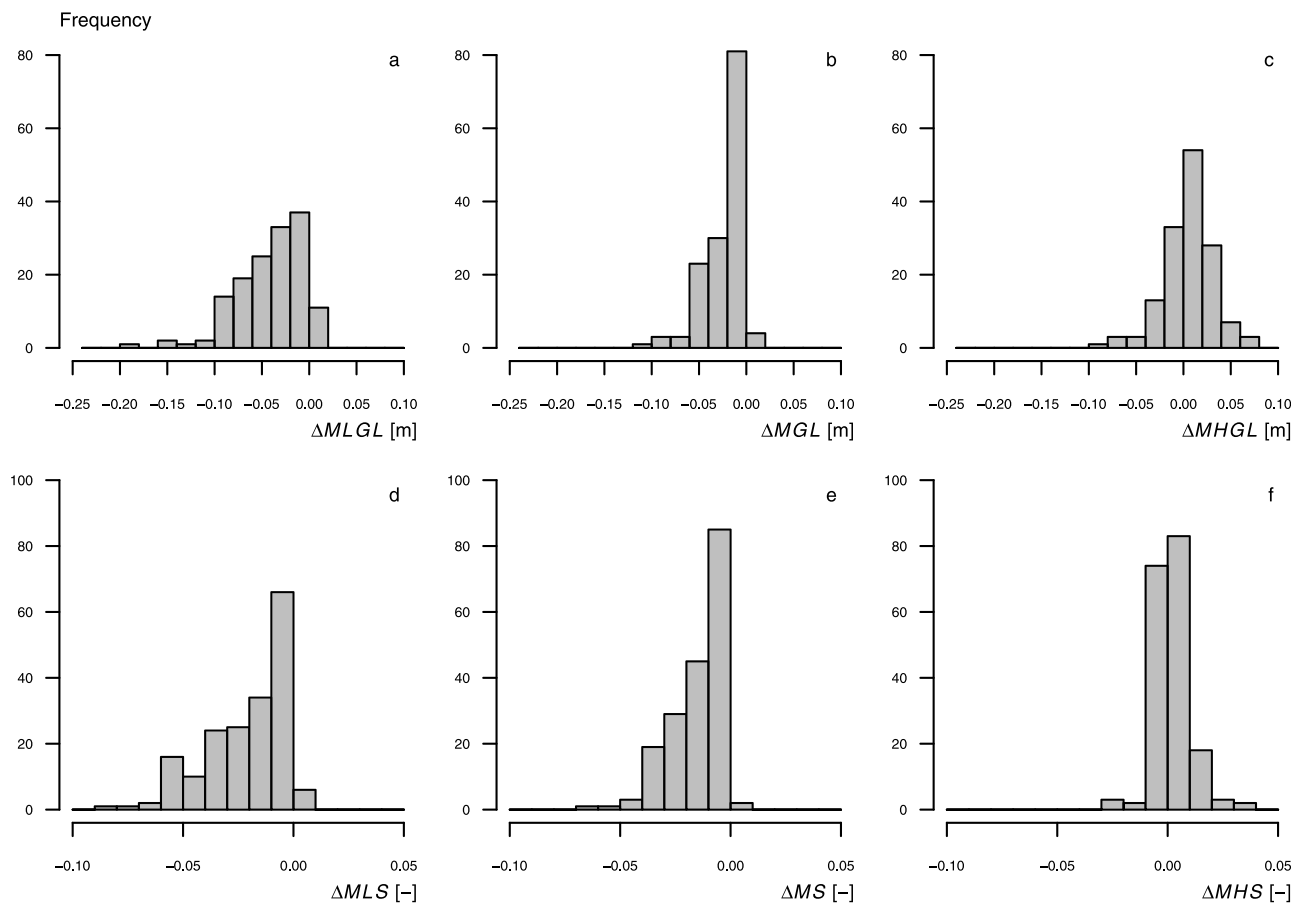
Figure A2. Frequency histograms for the climate-induced changes in (a–c) minimum, average and maximum groundwater level and (d–f) root zone saturation.

[47] Figure A1a shows that both *MGL* and *MLGL* will decrease (i.e., deeper groundwater levels) due to climate change. The decrease is largest for sites with relatively deep *MGL* and *MLGL* under the current climate. *MHGL*, however, does not show a shift toward either lower or higher values. The frequency histograms of Figures A2a–A2c provide additional insight into the generality of the shifts shown in Figure A1a: *MLGL*s will generally decrease, while $\Delta MHGL$ does not show a general shift.

[48] However, it is the soil moisture conditions in the root zone rather than groundwater levels that determine plant performance, either due to dry (low saturation) or wet (high saturation) conditions. Figure A1b illustrates that *MLS* and *MS* will decrease, with relatively small changes for sites at both the wet and dry extremes. The decrease in *MLS* is largest at sites with $MLS_{current}$ of about 0.5, while especially at these sites *MHS* will increase. Together with the frequency histograms of Figures A2d–A2f, these results demonstrate that climate change amplifies the saturation rates.

[49] It can be concluded that the increased drought stress we found (Figure 6) originates both from an increased evaporative demand for water (Table 1) and decreased water availability (Figures A1a–A1b and Figures A2a and A2d). The plants' demand for oxygen also depends on soil temperature. Soil temperature will increase for all sites (Figure A1c), and will therefore contribute to the increase in oxygen stress we

found (Figure 6). Differences between sites are relatively small for ΔMLT and ΔMT compared to ΔMHT. The variation in ΔMHT will originate from differences in soil type and soil moisture conditions, which are more pronounced for high temperatures.

[50] As soil temperature will increase for all sites, this variable will have a major impact on the general increase in oxygen stress we found (Figure 6), especially because *MHS* will not increase for all sites (Figure A2b). However, for the sites with high oxygen stress for the current climate, saturation rates are already high and could therefore hardly increase.

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