Moisture Matters

Climate-proof and process-based relationships between water, oxygen and vegetation

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Klimaatbestendige en op processen gebaseerde relaties tussen water, zuurstof en vegetatie

The research in thesis was carried out at VU University Amsterdam and at KWR Watercycle Research Institute. The research was carried out in the framework of both Project A1 'Biodiversity in a changing environment: predicting spatio-temporal dynamics of vegetation' of the Dutch national research program Climate Change and Spatial planning (www.klimaatvoorruimte.nl) and the joint research program of the Dutch Water Utility sector.

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Summary

&

Nederlandse samenvatting

Summary

Climate change has been forecast and has been observed worldwide. This change could have substantial effects on natural ecosystems. As a consequence, it is questionable whether current nature targets, partly obligatory through law, may still be obtained in a future climate.

To assess the impact of environmental changes on terrestrial vegetation, scientists apply habitat distribution models, i.e. models that are capable of predicting the future spatial distribution of habitats. These habitat suitability predictions can be converted into maps of potential vegetation. Current models, however, generally use indirect and simple site factors to characterize habitats, resulting in a highly correlative relationship with the vegetation. Consequently, these models are likely to be inapplicable under changing climatic conditions.

In order to improve vegetation predictions for the future climate, process-based and climate-proof relationships between site factors and vegetation are needed. This thesis addresses the development of climate-proof relationships between soil moisture conditions and vegetation. Soil moisture is one of the main site factors that determine terrestrial vegetation composition.

Groundwater levels, and the related soil moisture conditions, vary in time due to temporal variations in meteorological conditions, both within and between years. Due to these temporal variations, systematic differences in the relationships between soil moisture conditions and vegetation are found when the relationships are based on too short measurement periods. Chapter 2 shows that data harmonization removes such differences and increases the general applicability of empirically derived relationships.

In order to capture the climate effects on oxygen stress to plant roots, caused by a surplus of soil moisture, a process-based model was developed. This model involves the relevant interacting soil physical, soil microbial and plant physiological processes in the soil-plant-atmosphere system. Chapter 3 demonstrates that constant soil moisture thresholds for the occurrence of oxygen stress are insufficient in the face of climate change, as these thresholds depend strongly on soil temperature, among other things. The new model takes relevant processes in the soil-plant-atmosphere system into account, and allows for the calculation of oxygen stress thresholds, also under changing climatic conditions.

The oxygen stress model was applied to derive a site factor for oxygen stress, i.e. a measure for the wetness of the soil to which the actual vegetation may be adapted, defined as root respiration stress (Chapter 4). Respiration stress enables to account for the effects of extreme rainfall events and high temperatures; it is especially the combination of these conditions that affects vegetation. Moreover, this combination is expected to increase in the near future. Indirect measures of oxygen stress that are currently used – i.e. the mean spring groundwater level and the sum exceedence values of groundwater level thresholds – underestimate the future occurrence of oxygen stress to plant roots because they do not include essential climate variables like temperature and extreme rainfall events. Consequently, these indirect measures result in predicted future vegetations that are systematically too dry.

Besides oxygen stress, water stress (in terms of transpiration stress) also increases under changing climatic conditions. Increased rainfall variability in interaction with predicted changes in temperature and CO_2, appeared to affect soil moisture conditions and plant oxygen and water demands such, that both oxygen stress and water stress will intensify due to climate change (Chapter 5). Moreover, these stresses will increasingly coincide, causing variable stress conditions. These variable stress conditions were found to decrease future habitat suitability, especially for plant species that are presently endangered. The future existence of such species is thus at risk by climate change.

This thesis shows that the use of correlative, indirect relationships between site factors and vegetation in habitat distribution models should be discouraged. Predictions made with currently used correlative models should therefore be interpreted cautiously. The effect of climate change on moisture-related plant stresses is complex; both wet and dry extremes may be affected, and conditions that are not present under the current climatic conditions could occur in the future. In order to capture such effects, climate-dependent processes that directly affect vegetation should be analysed. By providing such analysis, this research contributes to one of the required improvements of habitat distribution models.

Nederlandse samenvatting

Zowel waarnemingen als modelvoorspellingen tonen aan dat het klimaat wereldwijd verandert. De effecten daarvan op natuurlijke ecosystemen zouden weleens aanzienlijk kunnen zijn. Hierdoor is het de vraag of de huidige natuurdoelen, die voor een deel wettelijk vastgelegd zijn, in het toekomstige klimaat nog wel gehaald kunnen worden.

Om de invloed van milieuveranderingen op de terrestrische vegetatie te voorspellen worden meestal habitatmodellen gebruikt. Met deze modellen kan de toekomstige ruimtelijke verspreiding van de standplaats (habitat) van plantensoorten en vegetatietypen voorspeld worden, welke vervolgens vertaald kunnen worden in kaarten van de potentiële vegetatie. De standplaatsfactoren om habitats te karakteriseren zijn in de huidige modellen echter vaak dusdanig indirect en eenvoudig, dat de relatie met de vegetatie een hoog correlatief gehalte heeft. Hierdoor zijn habitatmodellen waarschijnlijk niet toepasbaar om de effecten van klimaatverandering te voorspellen.

Om dat wel te kunnen doen, moeten we gebruik maken van op processen gebaseerde en klimaatbestendige relaties tussen standplaatsfactoren en vegetatie. Dit proefschrift richt zich op de ontwikkeling van klimaatbestendige relaties tussen bodemvocht en vegetatie. Bodemvocht is één van de belangrijkste standplaatsfactoren die de vegetatiesamenstelling in terrestrische systemen bepalen.

Grondwaterstanden en de hieraan gekoppelde bodemvochtcondities, variëren in de tijd door temporele variaties in meteorologische condities, zowel binnen als tussen jaren. We hebben aangetoond dat te korte meetreeksen resulteren in systematische fouten in de relatie tussen bodemvocht en vegetatie. Hoofdstuk 2 laat zien dat door het harmoniseren van meetreeksen systematische verschillen tussen relaties verdwijnen. De algemene toepasbaarheid van de empirische relaties neemt daardoor toe.

Een overschot aan bodemvocht kan leiden tot zuurstofstress van plantenwortels. Om de invloed van het klimaat op zuurstofstress van plantenwortels te onderzoeken, is een op processen gebaseerd model ontwikkeld. Dit model beschouwt de samenhangende bodemfysische, bodemmicrobiologische en plantfysiologische processen in het bodem-plant-atmosfeer systeem die zuurstofstress bepalen. Hoofdstuk 3 toont aan dat constante grenswaarden van de bodemvochtcondities voor het inschatten van zuurstofstress ongeschikt zijn onder een veranderend klimaat, onder andere omdat het optreden van zuurstofstress sterk afhangt van de bodemtemperatuur. Het nieuwe model kan toegepast worden om grenswaarden voor het optreden van zuurstofstress te berekenen, ook voor toekomstige klimatologische omstandigheden.

Het zuurstofstressmodel is toegepast om een standplaatsfactor voor zuurstofstress te bepalen (Hoofdstuk 4). Deze standplaatsfactor, gedefinieerd als respiratiestress, is een maat voor de natheid van de bodem waaraan de vegetatie is aangepast. Respiratiestress maakt het mogelijk zowel de effecten van extreme neerslag, als van hoge temperaturen te onderzoeken. Het tegelijkertijd optreden van deze condities, wat vaker zal gebeuren onder het toekomstige klimaat, heeft grote invloed op de vegetatie. Huidige maten voor zuurstofstress, namelijk de gemiddelde voorjaarsgrondwaterstand en cumulatieve overschrijdingswaarden van kritische grondwaterstanden, onderschatten de toekomstige zuurstofstress van plantenwortels. Deze maten houden namelijk geen rekening met cruciale klimaatvariabelen, zoals temperatuur en extreme neerslag. Hierdoor worden op basis van deze indirecte maten systematisch te droge toekomstige vegetaties voorspeld.

Behalve zuurstofstress neemt ook waterstress, gedefinieerd als transpiratiestress, toe onder het veranderende klimaat. Veranderende neerslagpatronen, samen met de voorspelde toenames in temperatuur en CO_2, blijken de bodemvochtcondities en de vraag van planten naar zuurstof en water dusdanig te beïnvloeden, dat zowel zuurstof- als waterstress heviger worden (Hoofdstuk 5). Bovendien zullen deze stressen vaker beide voorkomen op eenzelfde plaats, wat variabele stresscondities veroorzaakt. Juist deze variabele stresscondities blijken nadelig te zijn voor plantensoorten die momenteel al bedreigd worden. Dit betekent dat door klimaatverandering de toekomst van deze soorten onder druk komt te staan.

Dit proefschrift toont aan dat het gebruik van correlatieve, indirecte relaties tussen standplaatsfactoren en vegetatie in habitatmodellen, afgeraden moet worden. Voorspellingen op basis van zulke modellen moeten op zijn minst zorgvuldig worden geïnterpreteerd. Het effect van klimaatverandering op plantstressen is complex; zowel natte als droge extremen zullen beïnvloed worden en condities die onder het huidige klimaat niet voorkomen, zullen in de toekomst wel optreden. Om deze effecten met habitatmodellen goed te kunnen voorspellen, dienen we kennis te hebben van klimaatafhankelijke processen die de vegetatie direct beïnvloeden. Dit onderzoek draagt bij aan de ontwikkeling van deze kennis.

CONTENTS

CHAPTER

1

Introduction

Setting the scene

The climate is forecast to change globally, and can be observed to change globally as expressed by the increase in three main climate variables: atmospheric temperature, atmospheric CO_2 concentration and rainfall variability (Solomon et al. 2007). This climate change could have substantial effects on natural ecosystems, because climate plays a dominant role in the natural distribution of species (Pearson & Dawson 2003) and the functioning of ecosystems. Many consequences of climate change on ecosystems have already been observed or have been predicted, such as shifts in geographic range, changes in the species composition of plant communities (McCarty 2001) and species extinction (Easterling et al. 2000; Thuiller et al. 2005).

Within global change research, much attention is being paid to our ability, or inability, to predict the effect of climate change on the occurrence of species, species groups and ecosystems (e.g. Pearson & Dawson 2003; Guisan & Thuiller 2005; Botkin et al. 2007). This thesis contributes to the prediction of climate change effects on the species composition of terrestrial ecosystems.

Clarification of some of the terminology used will facilitate the understanding of this thesis. Every plant species has specific demands concerning its environment, e.g. regarding temperature, light, and the availability of nutrients and water. The common demands of individuals belonging to a certain species is called the 'habitat' of that species, but for the environment of a plant, the term 'site' is often used (Witte 1998). In this study, the term 'site' will also be applied to the environment of a 'vegetation', i.e. a community of plant species. Moreover, the term 'site' will be applied in a concrete sense, i.e. to a specific geographical location of a vegetation. The species composition of the vegetation at a site is called the 'vegetation composition'. It includes species with specific 'plant traits': distinguishable characteristics that are related to the demands of the plant. For example, *Hieracium pilosella* can survive at dry sites due to hairy leaves that reduce the transpirational water loss. 'Vegetation characteristics' denote the average plant traits within a vegetation plot.

Habitat distribution models (see next section) play an important role in evaluating the effects of climate change on the vegetation composition (Guisan & Zimmermann 2000; Botkin et al. 2007). Such models produce habitat suitability maps, which can be converted into maps of the potential vegetation. Habitat distribution models can be used to analyse the response of terrestrial vegetation to (man induced) changes in the environment. On the basis of these results, measures can be taken to maintain or develop nature reserves, to define areas where nature development has the highest potential to succeed, or to formulate new nature targets. The need for reliable predictive habitat distribution models is widely recognized (e.g. Guisan & Zimmermann 2000; Parmesan et al. 2000; Botkin et al. 2007), but unfortunately, as I will discuss below, current methods are likely to be inadequate under the changing climatic conditions.

Problem definition

Habitat distribution models

The vegetation of terrestrial ecosystems depends on a variety of site factors. Besides factors like dispersal capacity and biotic interactions that determine plant species distribution, abiotic factors like soil moisture, acidity and nutrient availability are important. Quantitative knowledge of the demands of plant species is required in order to analyse the vegetation response to changes in site conditions as induced by climate change (Ertsen 1998). Habitat distribution models (Botkin et al. 2007) provide such a quantitative basis.

Habitat distribution models are based on the principle that species or species groups can be viewed as an integrated measure of a set of site factors. Habitat distribution models, however, have a number of limitations (Pearson & Dawson 2003; Guisan & Thuiller 2005; Botkin et al. 2007). Firstly, the relationships between the site factors and vegetation composition in such models are generally correlative by nature (Guisan & Zimmermann 2000). The relationships are usually empirical relationships between occurrences of plant species and their site, which do not necessarily have a causal meaning. Secondly, observed species distributions may not be in equilibrium with the observed site conditions, as these are sampled during a limited period of time. Moreover, it is generally unknown how long it would take to reach a new equilibrium after a change in site conditions. For example, it is unknown how a year with extreme climatic conditions will propagate in the vegetation composition, because the vegetation responses likely lag behind environmental changes. Thirdly, habitat distribution models are difficult to validate, because sufficient data are usually lacking. Fourthly, most models do not consider dispersal and migration rates and biotic interactions like competition. Because of biotic interactions, the observed distribution of a species reflects the realized range of site conditions, not necessarily the range of site conditions where the species could potentially occur (i.e. physiological range). The physiological ranges include the total ranges of site conditions that are suitable for existence without biotic interactions, but the realized ranges reduce the physiological ranges to those that are actually occupied by the species. As future biotic interactions change, the future distributions of species may occur under different ranges of site conditions. Such biotic interactions should therefore be considered explicitly. Fifthly, models generally do not include variations in genotypes and phenotypes across a species' range, and evolutionary change, slow or rapid, is thus not considered.

To enhance reliable predictions of the future vegetation composition, all these problems require attention. With the research presented in this thesis, I will contribute to a solution of the first problem through the development of causal relationships between site and vegetation, in order to replace the currently used indirect relationships.

Causal relationships

Current habitat distribution models describe the site conditions of plant species by statistically derived (e.g. by generalized regression, environmental envelopes or Bayesian modelling) response curves of a set of site factors (e.g. Guisan & Zimmermann 2000; Bakkenes et al. 2002; Thomas et al. 2004; Guisan & Thuiller 2005; Botkin et al. 2007). Various explanatory site factors have been proposed (Palo et al. 2005), ranging from elevation, slope and geology (e.g. Davis & Goetz 1990; Ostendorf & Reynolds 1998), to soil moisture content (e.g. Sykes et al. 2001) and air temperature (e.g. Ashcroft 2006). However, the ecological relevance of these explanatory site factors is often indirect and simple (Botkin et al. 2007), so that the relationships with the vegetation composition have a highly correlative character (Guisan & Zimmermann 2000).

Causal relationships are especially necessary for forecasting the vegetation composition under site conditions that differ strongly from those under which these relationships were derived (Guisan & Zimmermann 2000). Therefore, the development of generally applicable, causal relationships has been identified as one of the main objectives in ecological modelling (Franklin 1995; Guisan & Zimmermann 2000). To reliably predict the effects of climate change, process-based and climate-proof relationships (i.e. relationships that are applicable under changing climatic conditions) between site conditions and vegetation composition are even a prerequisite. In contrast to indirect and correlative relationships, they do not have to be calibrated for future periods or other regions.

Researchers from the VU University Amsterdam and the KWR Watercycle Research Institute are collaborating on the BSIK-project 'Biodiversity in a changing environment: predicting spatio-temporal dynamics of vegetation'. The main objective of the project is to predict the effects of climate change on the spatial distribution of ecosystems, especially in the Netherlands. In order to do so, a robust habitat distribution model will be developed based on climate-proof relationships. It will not only be able to predict the impact of climate change on vegetation composition, but also the impact of water management, for example. The model output is intended to supply organizations that are responsible for the conservation of nature (e.g. drinking water companies and governmental bodies) with spatial information to evaluate, conserve and create biodiversity.

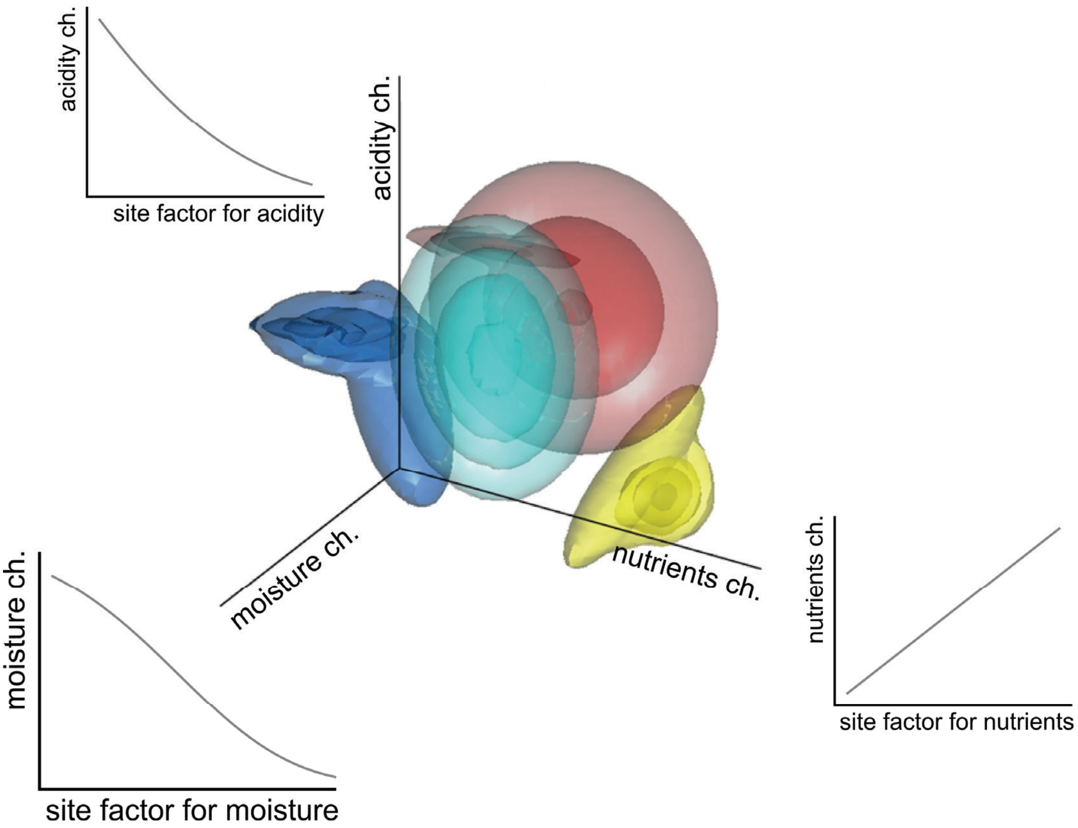

Figure 1.1: Illustration of how different vegetation types (coloured surfaces) fit within a multidimensional space of vegetation characteristics (ch.) that determine terrestrial vegetation composition (after Witte et al. 2007). Site factors should be coupled to vegetation characteristics through causal relationships.

One of the key components of this project is the coupling of site factors to vegetation characteristics through causal relationships (Witte et al. 2004). Once these vegetation characteristics are known, they can be converted into the vegetation composition. This approach is illustrated in Fig. 1.1, which shows how different vegetation types are located within a multidimensional space described by characteristics for nutrients, acidity and soil moisture. Nutrient availability, acidity and soil moisture are important site factors that determine vegetation composition (Witte et al. 2007). Each of the site factors should thus be described in detail, in order to accurately predict future vegetation composition. With the research presented in this thesis, I will contribute to a robust relationship between the site factors for soil moisture conditions and vegetation characteristics, i.e. the relationship on the bottom left in Fig. 1.1.

General approach and theoretical background

Plant traits in relation to soil moisture

The existence of relationships between soil moisture and vegetation has been recognized for a long time. In Biblical times, the prophet Isaiah related rainfall and groundwater to plant species occurrence (Ross 2007; Batelaan & Witte 2008). The Roman architect and engineer Vitruvius, also wrote about plants and groundwater. He related specific plant species to the occurrence of groundwater. Systematic research on the relationship between groundwater and vegetation started at the end of the 19th century. Schimper (1898) *fide* Batelaan & Witte (2008) divided plant species into different groups regarding their preference for water, based on their morphology; Meinzer (1927) introduced phreatophytes as plants that obtain their water supply from saturated soil, while Tüxen (1954) *fide* Wierda et al. (1997) related the vegetation composition to a certain groundwater regime. The long history of research led to an increased understanding of the mechanisms behind the interaction between soil moisture and vegetation, with a clear movement from direct observations to a more process-based understanding. The research in this thesis further contributes to an increasing mechanistic understanding of soil moisture-vegetation relationships.

The direct influence of the availability of soil moisture on plant species is twofold: a surplus of water and herewith a shortage of soil oxygen causes oxygen stress and reduces plant respiration, negatively affecting the energy supply for plant metabolism. Plants respire to obtain energy for growth and maintenance. Plant roots usually obtain a sufficient amount of oxygen for their respiration directly from gas-filled pores in the soil. If the soil becomes too wet, however, air in the soil pores will be replaced by water. Subsequently, the availability of oxygen may become limiting for root respiration and plants may suffer from oxygen stress. Root respiration is the first physiological process in plants that is restricted by oxygen deficiency. Many secondary responses of the vital functions of plants have also been reported, such as growth and water and nutrient uptake. Reductions in these processes, however, are the consequence of a restricted root respiration rate (Glínski & Stępniewksi 1985).

A shortage of water, on the other hand, causes water stress and reduces plant transpiration, negatively affecting both photosynthesis and cooling. Plants need water for biochemical reactions and to maintain turgor, but most of the water taken up by the roots is transpired to the atmosphere through the stomata (Jackson et al. 2000). This transpirational water loss, which prevents the occurrence of heat stress, coincides with the plant's uptake of CO_2 from the atmosphere, which is needed for photosynthesis. If the soil becomes too dry, however, the transpirational water loss is regulated by the stomata to avoid plant damage due to low xylem pressure and low tissue water status (Jackson et al. 2000). While transpiration is the first process to be limited by moisture deficiency or so-called water stress, photosynthesis will be limited indirectly (Kruijt et al. 2008).

Many different physiological adaptations exist for individual plant species to survive at specific soil moisture conditions. These adaptations are most directly represented by functional plant traits, which depict process-based characteristics of plants (Suding et al. 2008). For instance, some species are able to grow on very dry sites due to internal water storage by means of a succulent structure (such as *Sedum acre*) or by reducing the transpirational water loss by having hairy leaves (such as *Hieracium pilosella*). Other species are able to grow on very wet, anoxic sites; they are adapted e.g. by having aerenchyma, which provide their roots with oxygen (e.g. *Phragmites sp.*), by rooting only superficially (e.g. *Drosera sp.*) or by the absence of root-like organs (e.g. *Sphagnum sp.*). Species that grow on a specific site are all somehow adapted to the prevailing site conditions.

The use of plant traits that link directly to the most important drivers of vegetation responses would be ideal to causally relate vegetation to soil moisture. However, because there are many physiological responses to oxygen stress and water stress, it is difficult to combine all possible adaptations into a single variable. In addition, information on physiological adaptations to oxygen or water stress for all representative plant species is lacking. Because such information is difficult and laborious to obtain, it is unlikely that it will become available in the near future.

Nevertheless, an alternative approach to identify plant traits is available in the concept of species indicator values. The principle behind species indicator values is that plant species can be used as indicators of site conditions, because specific plant species may be regarded to have different requirements for natural resources. Indicator values have been compiled by experts based on literature, measurements and expert judgement about the site requirements of plant species. The lists of species indicator values for moisture, for example, provide a quantification of the preferred soil wetness of individual plant species, e.g. on a 1 to 12 scale *sensu* Ellenberg (1992) or 1 to 4 scale *sensu* Runhaar (Witte et al. 2007). By definition, indicator values represent the realized ranges of site conditions of plant species, which do not necessarily represent their physiological preferences. Additionally, as indicator values are derived under the current climatic conditions, it is unsure whether the future realized ranges will still be the same as the current ones (Diekmann 2002). By definition, indicator values are indirect parameter values that reflect adaptive plant traits, which is a disadvantage. On the other hand, the species indicator values from Ellenberg (1992), for example, are meant for the western part of Middle Europe, but have also been successfully applied in other climates, ranging from the north of Sweden (Hannerz & Hånell 1997) to Italy and Spain (Testi et al. 2007). This suggests that indicator values are rather robust to characterize plant traits under different climatic conditions with different biotic interactions. Moreover, the realized ranges of site conditions, as implicitly incorporated in the concept of indicator values, can be altered to more physiological ranges on the basis of theoretical and physiological principles, as demonstrated by Malanson et al. (1992) (Guisan & Zimmermann 2000). Applying this method goes beyond the scope of this thesis, but it allows the application of indicator values as response variables, also under future climatic conditions.

From the indicator value for each plant species in a vegetation plot, the average indicator value of the plot can be calculated. This value gives a non-discrete quantification of the average actual plant traits at a site. An important advantage of the mean indicator value is that it implicitly integrates the many different physiological adaptations of plant species into a single value.

In this thesis, the mean indicator value for moisture will act as the dependent variable in the relationship with soil moisture conditions.

Soil moisture, plant and atmosphere

Plant survival is primarily affected by soil moisture through deficiencies of oxygen and water. Hence, climate-robust relationships between soil moisture and vegetation should have oxygen and water stress as dependent variables. Some hydrological background information on the processes that determine the availability of oxygen and water in the root zone is given below.

Plants usually obtain sufficient oxygen and water from the soil. If the availability of oxygen or water in the root zone is insufficient to meet the plants' requirements (for respiration and transpiration, respectively), plant species that have no physiological adaptations to these conditions will suffer from oxygen stress or water stress.

The subsurface of the soil can be divided in two main zones: the water-saturated zone, which includes the zone below the groundwater table and the capillary fringe (i.e. the part of the saturated zone directly above the groundwater table), and the unsaturated zone, which is the zone above the capillary fringe (Fig. 1.2). Plant roots generally prevail in the unsaturated zone. In contrast to the saturated zone, the soil pores in the unsaturated zone contain both air and water, supplying both oxygen and water to the plant roots. The moisture content and herewith the gas filled porosity of the unsaturated zone strongly depend on the groundwater table, soil type, root water uptake, precipitation and soil evaporation, and are strongly variable in both time and space. The groundwater table indirectly influences the amount of oxygen and water in the unsaturated zone, namely by capillary rise. The amount of capillary rise strongly depends on soil texture and organic matter content.

Groundwater recharge (i.e. the process of water percolating through the soil and to the groundwater table) and therewith the variation of the groundwater table, mainly depends on the precipitation surplus, and thus on climate. The precipitation surplus is defined as the difference between precipitation and actual evapotranspiration (the water loss to the atmosphere through both soil evaporation and plant transpiration), and varies within and between years. Consequently, the prevailing meteorological conditions in a period are reflected in the course of the groundwater table and the soil moisture content in the root zone. Temporal fluctuations of meteorological conditions might affect relationships between soil moisture and vegetation if these relationships are based on too short measurement periods.

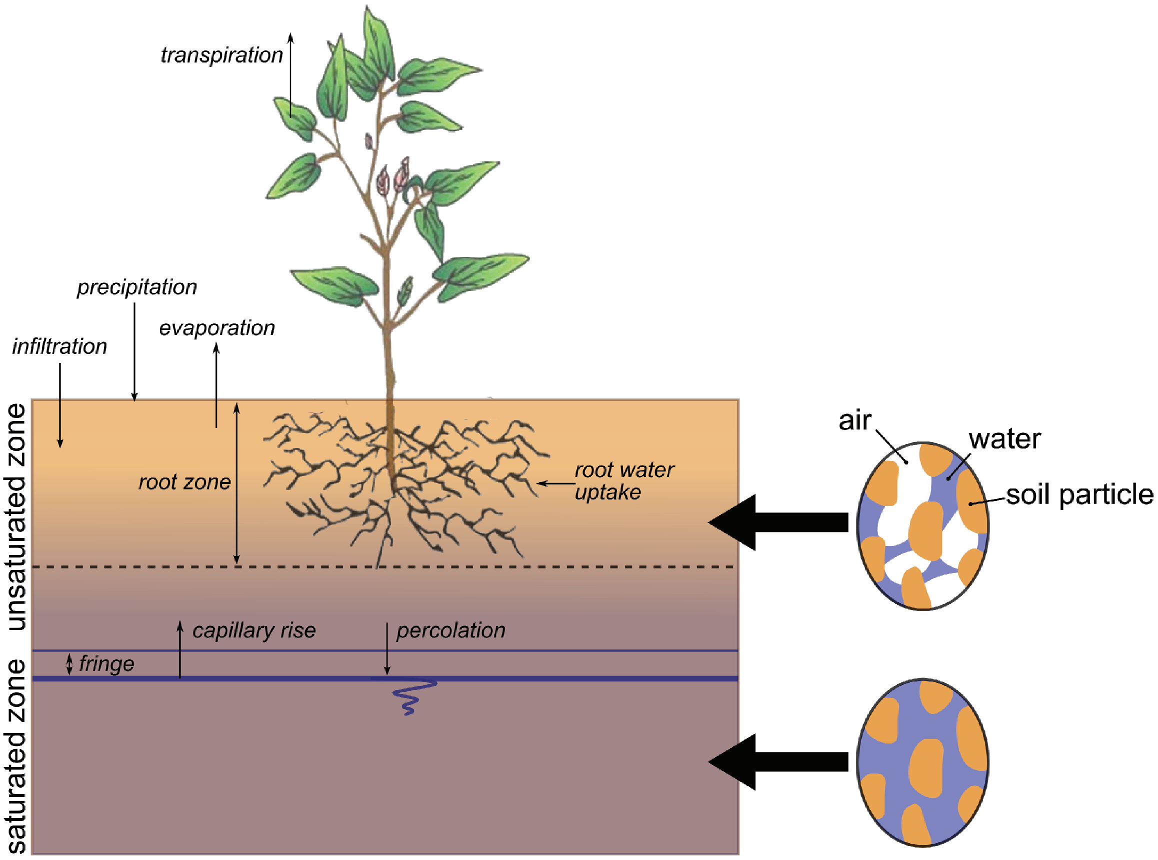

Figure 1.2: The division of the soil subsurface into the saturated and unsaturated zone, with hydrological processes that determine the moisture conditions in the root zone.

Climate-proof site factors

Apart from the availability of water and oxygen, climate also determines the plant requirements for these resources, since potential transpiration depends on global radiation, humidity, wind speed, temperature and atmospheric CO_2 concentration; potential respiration is temperature dependent. Hence, in order to define climate-proof relationships between soil moisture and vegetation, relevant interacting processes of the soil-plant-atmosphere system should be considered. In this research, the site factors oxygen and water stress will be based on modelling procedures that include these processes.

In a natural vegetation, plants are normally adapted to oxygen and water stress. In this way, the actual stress experienced by plants is reduced. Consequently, minimal relationships between this actual stress and the realized plant traits are to be expected. To avoid such poor relationships, both potential oxygen and water stress will be computed in this thesis instead. This will be done by applying a hypothetical reference vegetation, instead of the actual vegetation. This reference vegetation is defined as a temperate natural grassland not adapted to oxygen or water stress. The site factors thus obtained reflect the oxygen and water status of the soil, independent of the actual (adapted) vegetation. So, I will compute process-based measures for the soil moisture status in terms of the potential oxygen and water stress to which the actual vegetation is adapted.

Additionally, using a reference vegetation improves the applicability of habitat distribution models. Note that the alternative, i.e. using the actual vegetation to simulate future site conditions, would require a dynamic modelling approach in which vegetation feedbacks are accounted for.

Aims and outline of the thesis

Based on the above arguments, the general aim of this thesis is to develop robust, generally applicable and climate-proof relationships between soil moisture conditions and vegetation characteristics, and as such, to contribute to the applicability of habitat distribution models under changing climatic conditions. More specifically, I will:

- optimize the predictive power and general applicability of soil moisture-vegetation relationships by filtering out systematic errors due to climatic noise;
- develop a process-based procedure for the calculation of oxygen stress to plant roots;
- define process-based and climate-proof site factors for oxygen and water stress, replacing currently used correlative site factors;
- predict the effect of climate change on both future oxygen and water stress, and relate this to the impact of climate change on the future species diversity.

To this end, I will use a dataset consisting of several subsets of vegetation recordings taken in different years in the Netherlands, together with groundwater level time series with different lengths and time intervals. In order to obtain relationships that are generally applicable and that are not biased by temporal deviations in meteorological conditions, the effect of these temporal deviations should be filtered out. Chapter 2 illustrates the need of data harmonization to derive robust and non-biased relationships.

Chapter 3 presents a process-based model for the calculation of oxygen stress to plant roots, to replace currently used constant thresholds for oxygen stress. This model provides insight into the relevant, indispensable variables in the soil-plant-atmosphere system that need to be considered when evaluating the effect of climate change on oxygen stress to plant roots. The oxygen stress model is compared to the frequently used Feddes-function for the reduction of root water uptake, which is a result of root oxygen stress.

In Chapter 4, the oxygen stress model is subsequently used to derive a site factor for oxygen stress. This site factor, Respiration Stress, is related to the mean moisture indicator value of the vegetation. Future oxygen stress and corresponding future indicator values are predicted for four climate scenarios for the year 2050. The results are compared to two currently used indirect, correlative measures of oxygen stress.

In Chapter 5, the effect of climate change on both oxygen and water stress is presented, with a focus on the future variability in stress and the coincidence of both stresses. Moreover, the impact of climate-induced alterations in these stresses on the future habitat suitability of currently endangered plant species is demonstrated.

A synthesis of the research presented in this thesis is given in Chapter 6. Additionally, implications and applications of the results for ecological modelling and perspectives for further research regarding optimization of climate-proof relationships between soil moisture and vegetation are discussed.

CHAPTER

2

The need of data harmonization to derive robust empirical relationships between soil conditions and vegetation

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Abstract

Question: Is it possible to improve the general applicability and significance of empirical relationships between abiotic conditions and vegetation by harmonization of temporal data?

Location: the Netherlands.

Methods: Three datasets of vegetation, recorded after periods with different meteorological conditions, were used to analyse relationships between soil moisture regime (expressed by the mean spring groundwater level – MSL_t calculated for different periods) and vegetation (expressed by the mean indicator value for moisture regime F_m). For each relevé, measured groundwater levels were interpolated and extrapolated to daily values for the period 1970-2000 by means of an impulse-response model. Sigmoid regression lines between MSL_t and F_m were determined for each of the three datasets and for the combined dataset.

Results: A measurement period of three years resulted in significantly different relationships between F_m and MSL_t for the three datasets (F-test, $p < 0.05$). The three regression lines only coincided for the mean spring groundwater level computed over the period 1970-2000 ($MSL_{climate}$) and thus provided a general applicable relationship. Precipitation surplus prior to vegetation recordings strongly affected the relationships.

Conclusions: Harmonization of time series data (1) eliminates biased measurements, (2) results in generally applicable relationships between abiotic and vegetation characteristics and (3) increases the goodness of fit of these relationships. The presented harmonization procedure can be used to optimize many relationships between soil and vegetation characteristics.

Introduction

A central question in ecology is how species and communities respond to variation in environmental conditions. In plant ecology, most studies focus on relationships between vegetation and measured site factors such as temperature, soil acidity, soil nutrient availability and groundwater level. These site factors act as drivers in selecting species with different physiological characteristics. Only plant species with the appropriate physiological characteristics can survive in specific environmental conditions. Numerous studies exist in which field measurements of soil and groundwater are used to define relationships between vegetation and site characteristics. Several researchers have focused on the response of plant species or vegetation types (Allen-Diaz 1991; Dzwonko 2001; Schröder et al. 2005), while others, in pursuit of relationships that are generally applicable, used plant traits (Kennedy et al. 2003; Cousins & Lindborg 2004; McGill et al. 2006) or indicator values (Diekmann 1995; Ertsen et al. 1998; Schaffers & Sýkora 2000) as response variables of vegetation. Empirical relationships derived from such studies have been applied for predictions (Guisan & Zimmermann 2000), for instance, to assess the effects on vegetation of water management (e.g. Witte et al. 1992), of vegetation management (e.g. Jansen & Roelofs 1996), of climate change (e.g. Thomas et al. 2004) and of air pollution (e.g. Van Dobben & Ter Braak 1999).

However, because of temporal fluctuations in site conditions in combination with delayed vegetation responses, the general applicability of these empirical relationships cannot be taken for granted. Usually, the implicit assumption of these studies is that plant species composition reflects site conditions over many years. Such equilibrium is assumed as sufficient knowledge on the temporal dynamics of plant species composition on changes in site conditions is lacking. Moreover, since there is no unambiguous rule for length and frequency of a measuring program needed to calculate representative site conditions, and since the time and money to perform a research are usually limited, researchers often base their relationships on short time series or even to single measurements.

There is much evidence that site factors that are important to plant performance (e.g. soil water content, nitrate, phosphate, total organic carbon) may vary considerably in time (between days as well as years) (Kieft et al. 1998; Cain et al. 1999; Farley & Fitter 1999). Single or short-term (both months and years) measurements, therefore, probably deviate from the site conditions that the species composition of the vegetation is assumed to reflect. As a consequence of this temporal variability in site factors, it is likely that differences occur among empirical relationships with the same scope, but based on different measurement periods.

In this paper, we will analyse differences between empirical relationships, caused by temporal variation in site conditions between measurement periods. We will discuss the effect of time series length, i.e. the number of years in which a site factor has been measured, on the general applicability and on the goodness of fit of relationships between site factors and vegetation characteristics.

As a case study, we will analyse empirical relationships between groundwater level, relative to soil surface, and moisture indicator values *sensu* Runhaar (Witte et al. 2007). Empirical relationships between the mean groundwater level in spring (*MSL*) and moisture indicator values (F_m) are commonly used in ecological modelling. Therefore, we decided to use *MSL* as the variable to be correlated with F_m.

Groundwater levels vary within and between years through variability in meteorological conditions and particularly through variability in precipitation surplus. Therefore, it is hypothesized that empirical relationships between *MSL* and moisture indicator values as determined for short time series depend on the prevailing meteorological conditions. We will investigate whether it is possible to minimize systematic differences between the empirical relationships, caused by temporal variation in meteorological conditions, by harmonization of groundwater level series measured in different periods. Harmonization is the minimization of systematic differences between different sources of environmental measures (Keune et al. 1991). Thus, the effect of temporal meteorological variation will be filtered out, improving the significance and general applicability of the relationships.

Methods

General approach

We used three datasets of vegetation relevés and observed groundwater levels in, or immediately next to, each relevé. Each dataset contained vegetation relevés taken in the same year, but different from the other two datasets. Groundwater levels were measured fortnightly and for a limited number of years (see below). To be able to analyse soil moisture conditions over long time series, the groundwater level time series were extended to the period 1970-2000, as well as interpolated to daily values.

For each relevé we calculated a mean indicator value for moisture regime, F_m, based on the indicator values of the individual plant species (see below). Then, for each dataset, F_m was regressed on MSL_t computed over a period of t years, preceding the vegetation record. We validated the statistical differences between the relationships for each of the datasets with emphasis on how the differences were influenced by time series length t. We quantified the need for data harmonization by cross-prediction. Additionally, we studied changes in the relationship between MSL_t and F_m with increasing t for all datasets merged into one database.

Data

The three datasets considered are: (A) the dataset of Runhaar (1989), with 188 relevés taken in 1987 and groundwater levels observed from 1980-1987; (B) the dataset of Ertsen (1999) with 56 relevés from 1991 and groundwater levels observed from 1991-1993 and (C) the dataset of the Dutch State Forest Service (Beets et al. 2003) with 63 relevés from 2002 and observed groundwater levels with starting dates ranging from 1974 to 1998 and end date 2002.

The relevés refer to vegetation types from different succession stages, on various soils (with sandy soils dominating), ranging from dry to very wet, from nutrient-poor to nutrient-rich and from acid to alkaline. Five phytosociological alliances are dominant in the datasets. Descriptions of these alliances are found in parts 2 and 3 of the vegetation description of the Netherlands (Schaminée et al. 1995; Schaminée et al. 1996). ^{2} and ^{3} added to the names in the following list refer to the respective references: *Nardo-Galion saxatilis*^{3}, *Calthion palustris*^{3}, *Ericion tetralicis*^{2}, *Caricion nigrae*^{2} and *Caricion davallianae*^{2}. Besides these types, that make up ca. 50% of the datasets, the relevés mainly belong to: *Lolio-Potentillion anserinae*^{3} and *Junco Molinion*^{3} (dataset A), *Empetrion nigri*^{3} and *Hydrocotylo-Baldellion*^{2} (B), *Empetrion nigri*^{3} and *Oxycocco-Ericion*^{2} (C).

Some terrestrial plant communities are characterized by groundwater levels close to, or even above, the soil surface in wet periods. None of the investigated plots had been under influence of a major change in hydrological conditions.

All vegetation relevés were recorded in the Netherlands, a small and flat country with a temperate climate that has small spatial differences in meteorological conditions. The spatial deviations in mean annual precipitation and reference evapotranspiration (the evapotranspiration of grassland under optimal water supply, according to Makkink (1957)), are within 20% and 10% of the overall mean, respectively (Sluijter & Nellestijn 2002). The temporal variation in precipitation surplus (precipitation minus reference evapotranspiration) for the Netherlands is given in Fig. 2.1a and b.

The relevés of datasets A and B were distributed across the whole country and the relevés of dataset C were located mainly in the dune areas of the western and northern parts of the Netherlands. Because the spatial meteorological differences are small and because sandy soils dominate each dataset, systematic deviations in the relationships caused by the spatial prevalence of relevés within a dataset are not to be expected (see also the Discussion section).

The species composition of each dataset was recorded after periods with different meteorological conditions, as characterized by the precipitation surplus: dataset A follows a relatively average, B a dry and C a wet period, respectively (Fig. 2.1a). Differences in mean precipitation surplus were apparent over long periods of time: mean precipitation surplus of datasets A and B coincided when calculated over four years, but dataset C showed a consistently higher precipitation surplus for the whole time period of 30 years considered (Fig. 2.1b).

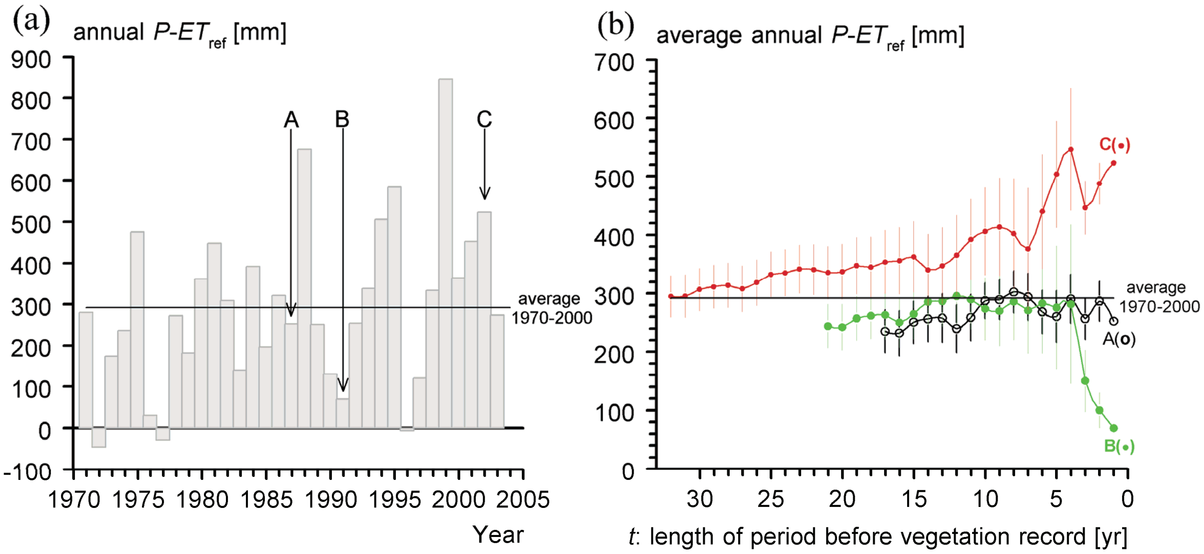

Figure 2.1: Precipitation surplus data (difference between precipitation and reference evapotranspiration $P\text{-}ET_{ref}$) for De Bilt, the weather station in the centre of the Netherlands. (**a**) Annual $P\text{-}ET_{ref}$. Each bar represents the cumulative difference between precipitation and reference evapotranspiration for a hydrological year (e.g.: 2000 = 1 April 1999 - 31 March 2000). A, B, C: year of vegetation recording of the three datasets. (**b**) Average annual $P\text{-}ET_{ref}$, with standard errors, derived from (a), across t years preceding the vegetation recording, indicating deviations between datasets A, B and C and the long-term average. $t = 1$ year corresponds to the year of the vegetation recording for each dataset: 1987 for dataset A, 1991 for B and 2002 for C.

Extension and interpolation of groundwater level series

Fortnightly measurements of groundwater level data were available for each relevé, but only for a limited number of years. To analyse long time series of daily groundwater level data, the groundwater level series were extended to the period 1970-2000 and interpolated to daily values with Menyanthes (Von Asmuth et al. 2002). The interpolation was needed to calculate *MSL* values accurately. Menyanthes is an impulse-response model, which transforms precipitation and evapotranspiration series (impulse) into groundwater level series (response). Local meteorological data on precipitation and reference evapotranspiration were available from the Royal Netherlands Meteorological Institute on a daily basis from 1970 onwards for stations with a maximum of 30 km (precipitation data) and 70 km (evapotranspiration data) from any relevé.

For each time series measured at a relevé, a Menyanthes-model was created that links the local precipitation surplus series, as input to the hydrological system, to groundwater level series. Then, groundwater levels were simulated over the period 1970-2000 by feeding the fitted Menyanthes-models with the same local precipitation surplus series of daily values of the period 1970-2000.

Menyanthes presents the quality of a model in terms of the explained variance. We omitted relevés from the analysis with groundwater level series that could not be modelled in a reliable manner (explained variance < 70%; Von Asmuth et al. 2006).

Calculation of MSL_t and F_m

At groundwater independent sites, vegetation composition has no causal relationship with groundwater level (Witte & Von Asmuth 2003). Consequently, relevés coinciding with deep groundwater levels (*MSL* calculated from 1970-2000 data deeper than 1.3 m below soil surface) were omitted. Overall, 133, 45 and 54 relevés could be used for further analysis of dataset A, B and C, respectively.

For each relevé, harmonization of groundwater levels was achieved by computing MSL_t as the mean of the groundwater level at the first of April (Van der Sluijs 1990) for t years preceding the vegetation recording:

$$MSL_t = \tfrac{1}{t} \sum_{t^*=1,t} gwl_{(1\mathrm{April})_{t^*}} \tag{2.1}$$

MSL_t was calculated for minimal $t = 1$ year and maximal $t = 18$ years (dataset A), 22 years (B) and 33 years (C). These maxima equal the period from 1970 to the year of the vegetation record (1987, 1991 and 2002, respectively). To avoid groundwater level fluctuation data biased by overly wet or dry years, three years is the minimum measuring period that should be considered (Mew Jr. et al. 1997; Wamelink et al. 2002). According to Knotters & van Walsum (1997), a period of at least $t = 30$ yr is needed to calculate a reliable mean groundwater level, representative of climatic conditions. Therefore, we also computed the *MSL* from simulated groundwater levels over the period 1970-2000. This *MSL* is referred to as MSL_{climate}.

A list of moisture indicator values for plant species tailored to the Netherlands based on expert judgement and national and international literature (e.g. Londo 1975; Ellenberg 1992), was used to compute the arithmetic mean moisture indicator value F_m for each relevé. Witte et al. (2007) compiled this list of indicator values from published ecological groups for vascular plants (Witte 2002; Runhaar et al. 2004), mosses and liverworts (Dirkse & Kruijsen 1993) and *Characeae* (Van Raam & Maier 1993). The consistency of the division into ecological groups has been tested on a set of ca. 50 000 relevés from all over the Netherlands (Runhaar 1989). Indicator values were derived directly from the division of plant species into ecological groups, without the use of physical habitat factors such as groundwater level. All plant species present in each relevé were used to calculate the vegetation characteristics of each relevé in terms of mean indicator values. Following the findings of Käfer & Witte (2004), no weight was given to species abundance. The indicator values range from one, for species from aquatic systems, to four, for species from extremely dry systems.

Statistical analysis

Theoretically, the relationship between MSL_t and F_m is confined by the two boundaries of the F_m-scale: $F_m = 1$ (aquatic) and $F_m = 4$ (dry). In practice, the range of F_m-values is smaller because of ecological reasons. Hence, the data points level off towards both ends of the indicator value scale (Witte & Von Asmuth 2003). Relationships of this form can be described by sigmoid functions.

Sigmoid regression lines between MSL_t (independent) and mean indicator value for moisture (F_m) (dependent) were fitted to each dataset, using the least square method. Because of the asymptotes, sigmoids were physically more correct than linear regression lines for the considered ranges of *MSL*s. Furthermore, sigmoids were statistically better (the correlation coefficient r between predicted vs observed values is generally 0.02 higher). Residuals of the sigmoid relationships were normally distributed and not affected by the spatial configuration of the data.

Statistical differences between the shapes -in parts- of the empirical relationships based on dataset A, B and C were tested through an F-test (Motulsky & Christopoulos 2003).

To quantify the mean error in the prediction of F_m and the differences in the mean error when relationships are based on different periods t, cross-prediction was performed for MSL_3 and $MSL_{climate}$ data. For the cross-prediction, the relationships for $t = 3$ yr and t = climate from A, B and C were fed with MSL_3 and $MSL_{climate}$ values, respectively, of the other datasets and the root mean squared errors (*RMSE*s) of the predictions were calculated. The *RMSE* represents the mean error that is made in F_m across the range of *MSL*s. Additionally, the Pearson correlation coefficients r between predicted and observed values of the cross-prediction were calculated.

Empirical relationships between MSL_t and F_m were also calculated for all datasets together (i.e. datasets A, B and C were merged) for an increasing number of contributing years t. The effect of t on the predictive value of this empirical relationship was tested by determining the significance of differences between Pearson's correlation coefficient r between predicted vs observed values for $t = 1$ to 18 yr (r_t) vs r_{climate} using the method of Meng et al. (1992). This method compares two different correlation coefficients while taking account of dependencies between explanatory variables.

As multiple significance tests were executed on the same datasets, significant differences were corrected by False Discovery Rate (Benjamini & Hochberg 1995).

Results

The sigmoid relationship between F_{m} and MSL_3 was significantly different for dataset B compared to the other two datasets (Fig. 2.2a, Table 2.1). At F_{m} = 2-3, for instance, sigmoids B and C deviate 20-30 cm. The 95% confidence intervals show, that especially in this sloped part of the sigmoids, the sigmoids were statistically different.

The differences between the relationships coincided with differences in meteorological conditions during the measurement period. The dry years before the vegetation record of dataset B (Fig. 2.1a) resulted in relatively low MSL_3 values. Wetter conditions (as in dataset C) resulted in a shift of the sigmoid curve to the right, i.e. towards higher groundwater levels, although sigmoid C did not differ significantly from sigmoid A (Table 2.1).

When considering a period of 4 years or more, the difference between sigmoids A and B became insignificant (Table 2.1). Again, this insignificant difference coincided with an insignificant difference in mean precipitation surplus from $t = 4$ years onwards (Fig. 2.1b). The very wet year of 1988 apparently compensated the dry period of 1989-1991. The differences in both precipitation surplus and sigmoid B and C remained significant for all t's observed (Table 2.1, Fig. 2.1b). Only in the case of MSL_{climate} did the three regression lines coincide and the (visibly small) differences became insignificant (Fig. 2.2b, Table 2.1).

The cross-prediction showed that only the *RMSE*s and the correlation coefficient r between predicted and observed values of cross-prediction of the *MSL*-data of dataset A on the regression lines of dataset C were not influenced by a different period t (Table 2.2). The decreases in *RMSE*s of the other cross-predictions of MSL_{climate} vs MSL_3 were 20 to 30%. This indicates that data harmonization (Table 2.1) substantially decreased prediction errors.

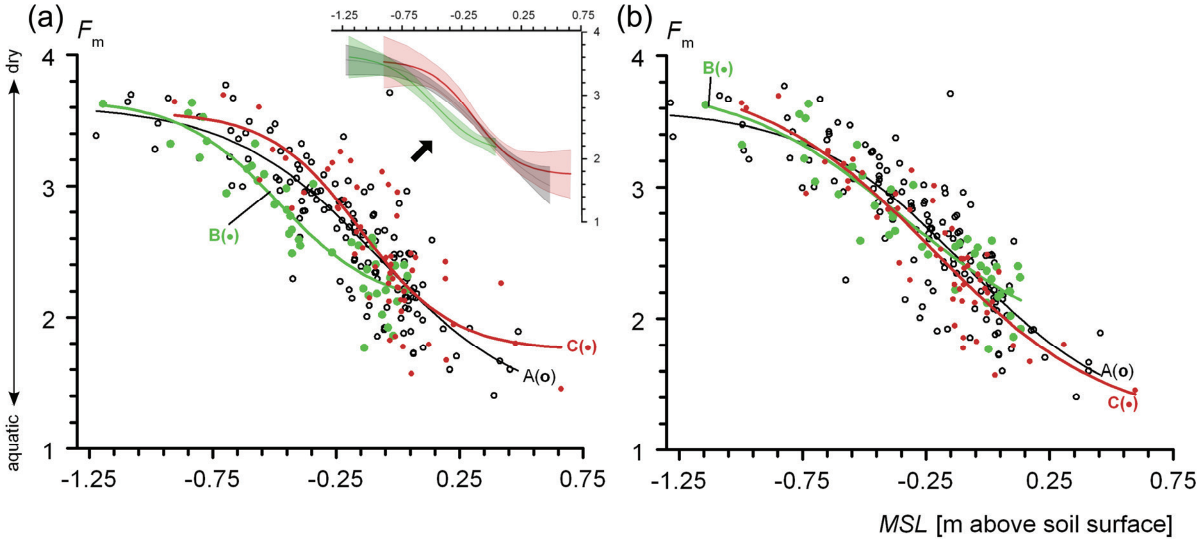

Figure 2.2: Mean moisture indicator values of the vegetation (F_m) for datasets A, B and C, in relation to the mean spring groundwater level calculated (a) over three years (MSL_3) and (b) for average climatic conditions (1970-2000; MSL_{climate}). Each point represents a relevé. The insert in (a) shows the 95% confidence intervals for the relationships. Equations and correlation coefficients can be found in Table 2.3.

Table 2.1: Results of *F*-tests to compare sigmoid regression lines between MSL_t and F_m for t different periods. Significant differences ($p < 0.05$, corrected by False Discovery Rate; Benjamini & Hochberg 1995) are marked by *. Climate = 1970-2000.

	Comparison of datasets:					
	A and B		A and C		B and C	
t (yr)	*F*	*p*	*F*	*p*	*F*	*p*
1	9.79	3.77E-07*	1.12	0.350	5.85	3.09E-04*
2	9.27	8.44E-07*	1.01	0.403	6.50	1.20E-04*
3	4.91	9.00E-04*	0.87	0.486	5.84	3.13E-04*
4	0.97	0.426	1.21	0.306	3.00	0.023
5	1.17	0.328	1.09	0.363	3.79	0.007*
6	1.12	0.348	1.25	0.290	3.97	0.005*
7	1.17	0.328	2.10	0.083	4.07	0.004*
8	1.12	0.347	1.73	0.146	4.45	0.002*
9	0.91	0.462	1.72	0.148	4.72	0.002*
10	0.78	0.541	2.07	0.087	4.63	0.002*
11	0.91	0.458	1.94	0.105	4.94	0.001*
12	1.09	0.363	1.90	0.113	5.00	0.001*
13	0.97	0.426	2.02	0.093	4.80	0.001*
14	1.00	0.410	1.81	0.129	4.83	0.001*
15	0.89	0.472	1.55	0.190	4.53	0.002*
16	0.88	0.475	1.43	0.226	4.33	0.003*
17	0.98	0.422	1.36	0.248	4.34	0.003*
18	0.84	0.501	1.40	0.235	4.25	0.003*
19	-	-	-	-	4.04	0.005*
20	-	-	-	-	3.85	0.006*
21	-	-	-	-	3.61	0.009*
22	-	-	-	-	3.66	0.008*
Climate	0.65	0.628	1.43	0.226	1.96	0.107

Table 2.2: Results of cross-prediction indicating the change in predictive error (*RMSE*) and the change in correlation coefficient between predicted and observed values (r) of F_m based on *MSL*-values calculated over t = 3 yr and over t = climate. F_m-values were predicted with the regression parameters of one dataset and the *MSL*-values of another dataset. Climate = 1970-2000.

		RMSE			*r*	
MSL data	regression line	*t* = 3 years	*t* = climate	change %	*t* = 3 years	*t* = climate
A	B	0.36	0.30	18.2	0.79	0.84
B	A	0.29	0.21	26.3	0.89	0.91
A	C	0.30	0.30	-0.6	0.85	0.85
C	A	0.32	0.26	18.8	0.82	0.90
B	C	0.36	0.24	34.9	0.86	0.91
C	B	0.40	0.27	33.1	0.76	0.90

The increasing resemblance of the regression lines was associated with the number of years contributing to *MSL* and with differences in precipitation surplus in the sampling year compared to the mean precipitation surplus. For the same reason, there was an increasing resemblance of data points with increasing t in the combined datasets A, B and C, reflected by increased values for the Pearson's correlation coefficients r (Fig. 2.3). Conversely, r_1–r_3 were significantly different from r_{climate}. A peak in r occurred in the period that the meteorological conditions for datasets A and B were similar (Fig. 2.1b): r_4–r_8 were not significantly different ($p > 0.10$) from r_{climate}. For t = 9-18 year, r fluctuated around 0.856 (SD = 0.003). The small fluctuations in r and the low p-values (r_9–r_{16}: $p < 0.05$; r_{17}–r_{18}: $p < 0.10$) indicate that temporal deviations in meteorological conditions with respect to the climate conditions were still apparent in the defined relationship between *MSL* and F_m.

The relationships between *MSL* and F_m, based on harmonized data as well as the combined datasets, are described in Table 2.3.

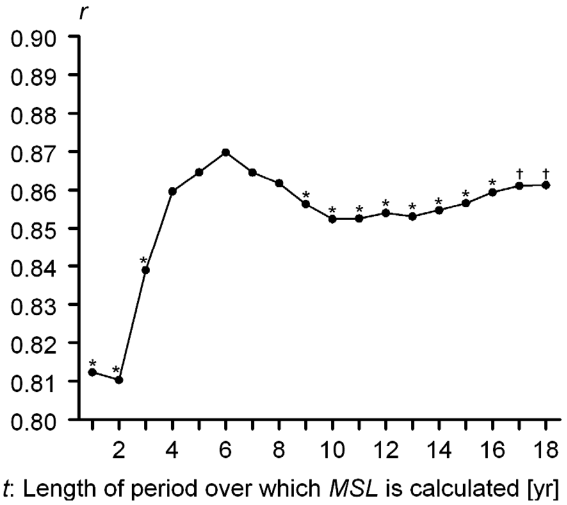

Figure 2.3: Pearson's correlation coefficient r between observed and predicted values for relationships between MSL_t and F_m as a function of t. Significant differences (corrected by False Discovery Rate; Benjamini & Hochberg 1995) between r_t and r_{climate} (0.87) are indicated by * ($p < 0.05$) and † ($p < 0.10$).

Discussion

Deriving relationships between environmental conditions and vegetation

Our analysis clearly shows that abiotic variables, including meteorological conditions, may need to be measured for long periods to remove systematic differences between empirical relationships and thus to derive general relationships between environmental conditions and vegetation characteristics. Some of the relationships found in literature are only valid for specific meteorological conditions, for instance after a number of very dry years and are thus not generally applicable.

We showed that basing relationships on short time series of abiotic measurements resulted in biased relationships and that harmonization of abiotic data in time removed the bias and led to relationships that are generally applicable. Furthermore, we showed that merging data from different sources without harmonization of data in time, resulted in large variation and thus low goodness of fit of the defined relationships. This fact was already brought to attention by Witte & Von Asmuth (2003), but it was only hypothetical until now. This paper confirms the hypotheses of Witte & Von Asmuth (2003) that: (1) fitting a model through data from different datasets will yield a poor fit and (2) that describing the moisture indicator value of the vegetation as a function of the climatologically averaged *MSL* produces a higher explained variance.

The relevés of dataset C were mainly confined to the dune area in the western and northern parts of the Netherlands. This confinement might have caused a systematically different relationship between *MSL* and F_m for datasets A and B. We checked if specific soil types (clay, loam, peat and sand) caused extra noise in the harmonized relationship. The *RMSE*s of relationships of each soil type were larger than the *RMSE* of all soil types together. This indicates that soil type did not cause systematic differences between the relationships. If soil type would have mattered, the three datasets would not have coincided when data were harmonized.

Table 2.3: Values for coefficients that describe the sigmoid regression lines between MSL_t and F_m for t = 3 years and t = climate (1970-2000). ABC represents the combined datasets and ABC with t = climate represents the relationship between *MSL* and F_m based on harmonized data and the combined datasets. Sigmoid regression lines are described by:

$F_m = a + \frac{b}{\left(1 + \exp\left(c + d \cdot MSL_t\right)\right)}$. Last column: r correlation coefficient between predicted and observed values.

	t	*a*	*b*	*c*	*d*	*r*
A	3 years	1.29	2.32	0.26	3.39	0.85
	climate	1.21	2.39	0.29	3.17	0.85
B	3 years	2.09	1.57	2.41	5.00	0.91
	climate	1.73	2.06	1.01	2.96	0.91
C	3 years	1.75	1.82	0.81	5.43	0.90
	climate	1.18	2.67	0.62	2.84	0.83
ABC	3 years	1.41	2.23	0.44	3.25	0.84
	climate	1.19	2.51	0.36	2.84	0.87

The harmonization of data in time includes two important aspects: (1) definition of an appropriate estimator of abiotic conditions and (2) quantification of historical relationships between vegetation and abiotic conditions, reflected by a certain present-day vegetation characteristic. Both aspects have to be, and implicitly were, considered simultaneously to come to unbiased relationships. In this paper, we used simple arithmetic means to harmonize groundwater levels. At the same time, we are aware that the abiotic conditions of 30 years ago will only have a minor contribution to the actual species composition. We therefore think that harmonization based on time-weighted means will increase the statistical significance of the relationships even more. Unfortunately, more process based functions weighing the abiotic history of sites are presently unavailable. Nevertheless, our results show that a limited period of abiotic measurements should be avoided, as there is a fair chance that it biases the derived relationships (Table 2.1). Even the maximum measurement period of 22 years for dataset B was still too short to make the regression line coincide with dataset C. Only a MSL_{climate} based on 30 years of measurements was sufficient to create one uniform relationship. So, arithmetic means over long periods of time (up to 30 years) improved the robustness of the relationships. Presumably, if weighted means would have been used, the abiotic conditions of 30 years ago would still have had a significant weight. This indicates that the mean vegetation composition of the relevés from each of the three datasets reflect the relationships between vegetation and abiotic conditions over a long period in the past and thus that generally the relevés have a large delayed response. If one of the three datasets would have been dominated by relevés with a small delayed response, the regression lines would never have coincided when considering the same period preceding the vegetation recordings for each comparison. We hypothesize that incorporation of formulations on the delayed response of functional species groups (like annual and perennial species), as a further refinement of deriving relationships between environmental conditions and vegetation, might result in an even higher predictive value of relationships.

Extrapolation to other relations between vegetation and abiotic conditions

As well as the relationship between soil moisture regime, described by *MSL*, and vegetation characteristics, the problem outlined here also applies to relationships of vegetation characteristics to other soil parameters such as soil nitrogen content, soil phosphate content and soil pH or climatic variables such as temperature, that vary stochastically in time (Kieft et al. 1998; Cain et al. 1999; Farley & Fitter 1999). For three reasons, the time period to be considered for these relationships will be different from the one identified here. Firstly because each abiotic process has its own specific characteristic time constant, which quantifies the long-term fluctuations of the entity (e.g. pH or concentration of soil chemical parameters). This characteristic time will vary from weeks to centuries, depending on the time scale of the dominant process (e.g. adsorption, erosion or precipitation surplus, as in this study). Secondly, the characteristic time of the vegetation is important. In this paper we used mean indicator value, a constant, which by definition has a large characteristic time as indicator values are representative for equilibrium conditions. Other vegetation characteristics, e.g. the formation of aerenchyma (also related to soil moisture conditions) or specific leaf area may have shorter time constants, since these also vary within species. Thirdly, the considered time period depends on the relationships between plant species and abiotic parameters. Particularly disturbances causing e.g. nutrient pulses through vegetation die-back (e.g. Van Bodegom et al. 2006) and feedbacks, e.g. those controlling nutrient losses (e.g. Knops et al. 2002), are important in this respect.

All these factors are known qualitatively, but quantitative knowledge is lacking. This implies that the optimal period over which data have to be harmonized should be determined empirically. The data harmonization procedure, outlined and exemplified in this paper, can be used for this in combination with existing process-based models on the abiotic conditions of consideration like nitrogen dynamics (e.g. Rastetter et al. 1997), available phosphorus (e.g. Grant & Heaney 1997) or acidity (e.g. Wade et al. 1999). Through these models, error propagation, inherent to interpolation and extrapolation involved in data harmonization procedures, can be minimized. With time series of abiotic conditions thus derived, an analysis similar as to ours can be used to obtain generally applicable relationships.

Conclusion

Single and short term field measurements of abiotic conditions are likely to deviate from the mean conditions reflected by vegetation characteristics. Without data harmonization, relationships among these variables are only valid for environmental conditions resembling those during the collection of field data. Application to other conditions leads to systematic prediction errors and is dissuaded. This problem can be overcome by harmonization of abiotic data in time as this (1) eliminates biased measurements, (2) results in general applicable relationships between abiotic and vegetation characteristics and (3) increases the goodness of fit of these relationships. The presented harmonization procedure can be used to optimize many relationships between abiotic conditions and vegetation characteristics by generating time series through process-based models.

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CHAPTER

3

Critical soil conditions for oxygen stress to plant roots: Substituting the Feddes-function by a process-based model

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Abstract

Effects of insufficient soil aeration on the functioning of plants form an important field of research. A well-known and frequently used utility to express oxygen stress experienced by plants is the Feddes-function. This function reduces root water uptake linearly between two constant pressure heads, representing threshold values for minimum and maximum oxygen deficiency. However, the correctness of this expression has never been evaluated and constant critical values for oxygen stress are likely to be inappropriate. On theoretical grounds it is expected that oxygen stress depends on various abiotic and biotic factors. In this paper, we propose a fundamentally different approach to assess oxygen stress: we built a plant physiological and soil physical process-based model to calculate the minimum gas filled porosity of the soil ($\phi_{\mathrm{gas\_min}}$) at which oxygen stress occurs.

First, we calculated the minimum oxygen concentration in the gas phase of the soil needed to sustain the roots through (micro-scale) diffusion with just enough oxygen to respire. Subsequently, $\phi_{\mathrm{gas\_min}}$ that corresponds to this minimum oxygen concentration was calculated from diffusion from the atmosphere through the soil (macro-scale).

We analysed the validity of constant critical values to represent oxygen stress in terms of $\phi_{\mathrm{gas\_min}}$, based on model simulations in which we distinguished different soil types and in which we varied temperature, organic matter content, soil depth and plant characteristics. Furthermore, in order to compare our model results with the Feddes-function, we linked root oxygen stress to root water uptake (through the sink term variable *F*, which is the ratio of actual and potential uptake).

The simulations showed that $\phi_{\mathrm{gas\_min}}$ is especially sensitive to soil temperature, plant characteristics (root dry weight and maintenance respiration coefficient) and soil depth but hardly to soil organic matter content. Moreover, $\phi_{\mathrm{gas\_min}}$ varied considerably between soil types and was larger in sandy soils than in clayey soils. We demonstrated that *F* of the Feddes-function indeed decreases approximately linearly, but that actual oxygen stress already starts at drier conditions than according to the Feddes-function. How much drier is depended on the factors indicated above. Thus, the Feddes-function might cause large errors in the prediction of transpiration reduction and growth reduction through oxygen stress.

We made our method easily accessible to others by implementing it in SWAP, a user-friendly soil water model that is coupled to plant growth. Since constant values for $\phi_{\mathrm{gas\_min}}$ in plant and hydrological modeling appeared to be inappropriate, an integrated approach, including both physiological and physical processes, should be used instead. Therefore, we advocate using our method in all situations where oxygen stress could occur.

Introduction

Plants need soil oxygen to keep their root metabolism running. Consequently, in water saturated soil conditions, where oxygen diffusion is limited, most terrestrial plants suffer from a lack of oxygen. The effect of insufficient soil aeration on the functioning of plants has been an important field of research for a long time, e.g. in: (1) agriculture, as oxygen stress reduces yields (Dasberg & Bakker 1970), (2) ecology, since water logging affects plant species composition (Chapter 2; Burdick & Mendelssohn 1987; Runhaar et al. 1997; Niinemets & Valladares 2006), and (3) hydrological modeling, as water logging reduces root water uptake (Feddes et al. 1978).

In reference to the latter field of research, current hydrological models for the unsaturated zone describe soil water flow by solving the Richards' equation, which includes a sink term that represents water uptake by plant roots. Different procedures for the simulation of root water uptake exist (e.g. Doussan et al. 1998; Van den Berg & Driessen 2002; Roose & Fowler 2004). A well-known and frequently used procedure to simulate root water uptake, is the reduction function of Feddes et al. (1978). Current hydrological models that include the Feddes-function, such as SWAP (Kroes et al. 2008) and HYDRUS (Šimůnek et al. 2005), compute root water uptake by multiplying potential transpiration (which is determined by meteorological conditions and crop type) with a sink term variable F (Fig. 3.1). Depending on soil water pressure head h, F corrects for conditions that are either too dry, or too wet. Root water uptake decreases linearly between pressure head h_2 and the anaerobiosis point h_1 due to oxygen stress in wet situations. However, a detailed analysis of this wet side of the function has never been performed, in contrast to the dry side of the Feddes-function (the part between h_3 and h_4) (Metselaar & de Jong van Lier 2007). None of the procedures for root water uptake, including the Feddes-function, combine both plant physiological and soil physical processes to predict the reduction of root water uptake at insufficient soil aeration.

Feddes et al. (1978) already indicated that a fixed anaerobiosis point h_2, identical for all

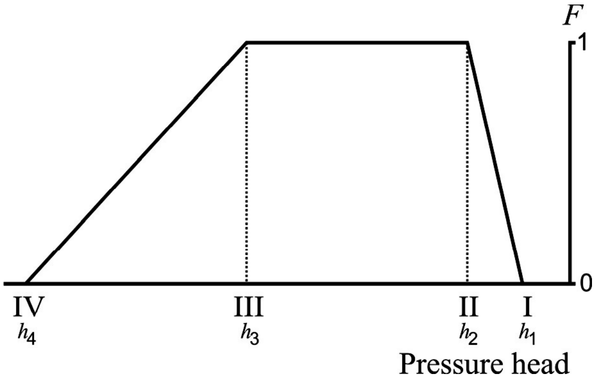

Figure 3.1: Sink term variable F as function of pressure head h according to Feddes et al. (1978). Root water uptake reduces linearly from III (h_3) to IV (h_4) due to moisture stress, as well as from the critical values II (h_2) and I (h_1), due to oxygen stress. In between II and III, root water uptake is optimal ($F = 1$).

environmental conditions, may be inappropriate, because pressure heads do not provide direct information on the aeration status of the soil. Alternative approximations of oxygen stress have been defined, like the gas filled porosity of the soil, ϕ_{gas} (Wesseling & van Wijk 1957). This proxy might provide a better relationship between soil aeration and root oxygen stress, as soil aeration substantially depends on ϕ_{gas} (Hillel 1980) and plant functioning appears to be well-correlated to this proxy (Dasberg & Bakker 1970). Constant critical values for ϕ_{gas} have frequently been applied to represent oxygen stress (Barber et al. 2004; Leao et al. 2006), but constants are unlikely to be sufficient for any proxy. In fact, oxygen consumption of, and oxygen transport to plant roots depend on soil temperature, growth stage, soil texture and microbial activity (Hillel 1980). Each of these variables should be considered simultaneously to determine the degree of oxygen stress accurately, but an accurate procedure does not seem to exist up to now. Such a procedure should combine two very different types of equations: (1) Oxygen consumption of plant roots described by plant physiological processes, focusing on the energy demand of plants (Cannell & Thornley 2000), and (2) Oxygen transport to plant roots described by physical laws, focusing on the diffusion of oxygen through different media (e.g. Glínski & Stępniewksi 1985). These plant physiological and soil physical processes have to be considered simultaneously, as the oxygen transport (ad 1) is determined by oxygen consumption (ad 2) and vice versa.

In this paper we introduce such a procedure: we propose a model to compute plant oxygen stress based on the above mentioned processes. Through this model, we quantified the sensitivity of oxygen stress to various model parameters. Moreover, we calculated root water uptake reduction under the influence of oxygen stress. Finally, we argue why our model will lead to better predictions of root water uptake under oxygen stress than the Feddes-function.

Model description

General setup

The general model setup is visualized by Fig. 3.2. The main output parameter of our model is the minimum gas filled porosity of the soil $\phi_{\text{gas\_min}}$ at which oxygen stress occurs (Fig. 3.2C). To calculate this parameter, we need to model the diffusion-driven transport of oxygen from the gas phase of the soil to root cells (oxygen diffusion at the micro-scale; Figs. 3.2A and B) and from the atmosphere to the gas phase of the soil (oxygen diffusion at the macro-scale; Figs. 3.2C and D) (De Willigen & Van Noordwijk 1987). Diffusion fluxes, described by Fick's law, are determined by: (a) oxygen consuming processes, (b) diffusivity, which depends on the medium through which diffusion takes place, (c) the concentration gradient, which depends on (d) the distance over which diffusion takes place. These aspects are different for diffusion at the micro-scale and macro-scale (Table 3.1) and will be discussed in detail in Sections "Calculation of C_{min} (diffusion at the micro-scale)" and "Calculation of C (diffusion at the macro-scale)", respectively.

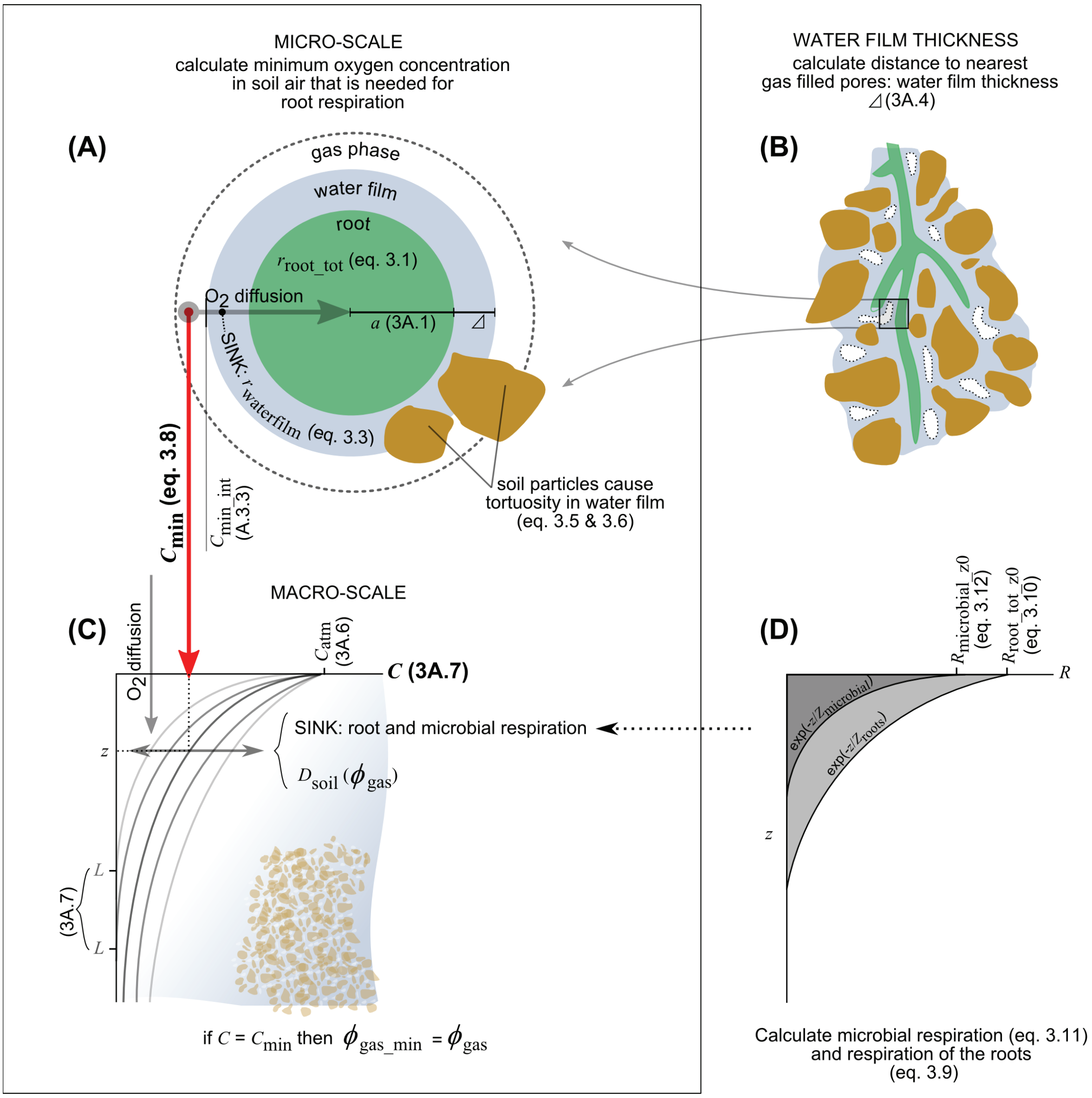

Figure 3.2: Scheme for the calculation of critical values for oxygen stress, based on both physiological and physical processes.

Table 3.1: Parameters that are involved in the diffusion processes for oxygen supply to plant roots.

	Micro-scale (Figs. 3.2A and B)	Macro-scale (Figs. 3.2C and D)
Oxygen consuming processes	root respiration ($r_{\text{root\_tot}}$) microbial respiration ($r_{\text{waterfilm}}$)	root respiration ($R_{\text{root\_tot}}$) microbial respiration ($R_{\text{microbial}}$)
Diffusivity	water-film ($D_{\text{waterfilm}}$) root tissue (D_{root})	soil (D_{soil})
Gradient	[O_2] gas phase soil (C_{min}) – [O_2] center of root (0)	[O_2] atmosphere (C_{atm}) – [O_2] gas phase soil (C)
Distance	thickness water-film (Δ) + root radius (a)	soil surface to certain depth (z)

Diffusion at the micro-scale (Figs. 3.2A and B) focuses on the minimum oxygen concentration in the gas phase of the soil (C_{min}), needed to meet the oxygen requirements of roots. We schematized roots as cylinders and assumed that the root zone has a uniform soil texture and temperature. Subsequently, C_{min} was calculated based on oxygen consumption and diffusion pathway through a root cross-section (Fig. 3.2A). Two temperature dependent oxygen consuming processes occur in the root zone: respiration of roots (needed for both maintenance and root growth) and microbial respiration in the water-film surrounding the roots. The water-film is a thin layer of soil moisture that covers soil particles and plant roots (Fig. 3.2B). Oxygen that diffuses from the gas phase of the soil to the root passes this water-film. Because the diffusivity of oxygen in water is 10^4 times lower than that in free air (Stumm & Morgan 1996), this water layer can be a serious barrier for oxygen diffusion to plant roots (De Willigen & Van Noordwijk 1984; Armstrong & Beckett 1985).

Diffusion at the macro-scale (Figs. 3.2C and D) focuses on oxygen transport from the atmosphere through the soil to the gas phase surrounding the roots. Root respiration and microbial respiration are sink terms, eliminating oxygen from the gas phase of the soil. We assumed that both volumetric root density and microbial respiration rate decrease exponentially with depth (Campbell 1985 *fide* Cook 1995). As a result, oxygen concentration C decreases with depth z in the soil profile. The diffusivity of the soil typically controls soil aeration and varies with soil type and gas filled porosity ϕ_{gas} (Buckingham 1904; Moldrup et al. 2000).

In our model, both scales of diffusion were linked by iteratively adjusting ϕ_{gas} until C (macro-scale) equaled C_{min}. This resulted in the minimum gas filled porosity of the soil, $\phi_{\mathrm{gas\_min}}$, needed to meet the oxygen requirements of plant roots at soil depth z. $\phi_{\mathrm{gas\_min}}$ is a threshold for oxygen stress and depends on both abiotic and biotic conditions, like soil texture, soil temperature, growth stage and microbial activity.

Parameterization

All model parameters are given in Table 3.2. We used the model to calculate $\phi_{\mathrm{gas\_min}}$ for different soil physical properties derived for sandy, loamy and clayey soils (Table 3.3, Fig. 3.3). All plant characteristics used for calculating $\phi_{\mathrm{gas\_min}}$ (see also Appendix 3A.1) were mean values, taken from literature, for a temperate terrestrial natural grassland. All parameter values were derived from independent sources, and thus were not optimized to improve model results. Other parameter values than chosen here, e.g. for other vegetations, may be used to calculate $\phi_{\mathrm{gas\_min}}$.

Table 3.2: Input parameters and calculated parameters (including standard deviations) used in the model.

Symbol	Unit	Description	
Input parameters			Value
k_m	-	maintenance coefficient	0.016 ± 0.008 (Kroes et al. 2008)
M	-	Van Genuchten parameter M	Table 3.3
M_{O_2}	kg mol^{-1}	Molar mass of dioxygen	0.032
N	-	Van Genuchten parameter N	Table 3.3
p	Pa	atmospheric pressure	1e5
Q_{10_root}	-	relative increase in root respiration rate at a temperature increase of 10 °C	2.0 (Amthor 2000)
$Q_{10\_microbial}$	-	relative increase in microbial respiration rate at a temperature increase of 10 °C	2.8 (Fierer et al. 2006)
R	m^3 Pa K^{-1} mol^{-1}	universal gas constant	8.314427
S	kg root m^{-3} root	specific weight of non-airfilled root tissue	1.0e3 (De Willigen & Van Noordwijk 1987)
SRL	m root kg^{-1} root	Specific Root Length	3.8 ± 1.6e5 (De Willigen & Van Noordwijk 1987)
T_{air}	K	air temperature	273 – 303
T_{soil}	K	soil temperature	273 – 303
T_{ref}	K	reference temperature	298
var(a)	m^2	variance of a	4.175e-10 (De Willigen & Van Noordwijk 1987)
W	kg root m^{-3} soil	dry weight of bulk roots at $z = 0$	0.785 ± 0.385 (Jackson et al. 1996)
Y	-	dry matter content of roots	0.07 (De Willigen & Van Noordwijk 1987)
z	m	depth	0.0 – 0.5
$Z_{microbial}$	m	shape factor for exponential decrease of microbial respiration with depth	0.3 (Campbell 1974 *fide* Cook & Knight 2003)
Z_{root}	m	shape factor for exponential decrease of root respiration with depth	0.127 ± 0.013 (Jackson et al. 1996)
α	1/Pa	Van Genuchten parameter α	Table 3.3
β	kg O_2 kg^{-1} C d^{-1}	vegetation dependent respiration rate	2.258 ± 1.085e-4 (Fierer et al. 2006)
ε_{org}	%	organic matter content of the soil	0.0 – 15.0
η	-	respiration factor	1 – 5 (Penning de Vries et al. 1979)
θ_{res}	-	residual water content	Table 3.3
θ_{sat}	-	saturated water content	Table 3.3
ρ_{soil}	kg soil m^{-3} soil	soil density	Table 3.3
τ_{root}	-	tortuosity of the root tissue	0.4
ϕ_{root}	-	air filled root porosity	0.05 (De Willigen & Van Noordwijk 1987)

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Table continued

Calculated parameters		
a	m	root radius
A	m^2	area of a cross-section of water film
b	-	Campbell soil water retention parameter
C	kg O_2 m^{-3} soil air	oxygen concentration in the gas phase of the soil
C_{atm}	kg O_2 m^{-3} air	oxygen concentration in the atmosphere
C_{min}	kg O_2 m^{-3} root	minimum oxygen concentration in the gas phase of the soil
C_{min_int}	kg O_2 m^{-3} root	minimum oxygen concentration at the interface of the water film and the gas phase of the soil
D_0	m^2d^{-1}	diffusivity of oxygen in free air
D_{root}	m^2d^{-1}	diffusivity of the root
D_{soil}	m^2d^{-1}	mean diffusivity of the soil
D_{water}	m^2d^{-1}	diffusivity of water
$D_{waterfilm}$	m^2d^{-1}	diffusivity of water film
f_{φ}	-	reduction factor for microbial respiration through moisture
F	-	sink term variable
h	cm	soil water pressure head
L	m	depth where $C = 0$
n	m^{-2} soil	length density of gas filled pores
$R_{microbial}$	kg O_2 m^{-3} soil d^{-1}	volumetric microbial respiration of the soil
$R_{microbial\_z0}$	kg O_2 m^{-3} soil d^{-1}	volumetric microbial respiration of the soil at $z = 0$
$r_{root\_m\_ref}$	kg O_2 m^{-1} root d^{-1}	reference maintenance respiration per unit length of root
$R_{root\_m\_z0\_ref}$	kg O_2 m^{-3} soil d^{-1}	volumetric reference root maintenance respiration at $z = 0$
R_{root_tot}	kg O_2 m^{-3} soil d^{-1}	volumetric total root respiration
r_{root_tot}	kg O_2 m^{-1} root d^{-1}	total respiration per unit length of root
$r_{root\_tot\_ref}$	kg O_2 m^{-1} root d^{-1}	reference total respiration per unit length of root
$R_{root\_tot\_z0}$	kg O_2 m^{-3} soil d^{-1}	volumetric total root respiration at $z = 0$
$R_{root\_tot\_z0\_ref}$	kg O_2 m^{-3} soil d^{-1}	volumetric reference total root respiration at $z = 0$
$r_{waterfilm}$	kg O_2 m^{-1} root d^{-1}	microbial respiration rate in water film
$r_{waterfilm\_z0}$	kg O_2 m^{-1} root	microbial respiration in water film at $z = 0$
w	kg root m^{-1} root	specific root mass
α_B	m^3 gas m^{-3} liquid	Bunsen solubility coefficient for oxygen
δ	-	ratio of rhizosphere (water-film) respiration to the total root respiration
Δ	m	thickness of water-film
ε_{sand}	%	sand content of the soil
θ	-	water content
λ	-	ratio of D_{root} and $D_{waterfilm}$
σ	N m^{-1}	surface tension of water
μ	kg C m^{-3} soil	organic carbon content of the soil
ϕ_{gas}	-	gas filled porosity of the soil
ϕ_{gas_min}	-	minimum gas filled porosity that is needed to meet the oxygen requirements of the roots
$\phi_{waterfilm}$	m^3 soil particles m^{-3} water film	porosity of the water film
ϕ_{gas_100}	-	gas filled porosity at $h = 100$ cm
ϕ_{total}	-	total porosity of the soil
φ	Pa	matric potential of soil moisture
φ_{sat}	Pa	saturated matric potential

Calculation of C_{min} (diffusion at the micro-scale)

Oxygen consuming processes at the micro-scale

The calculation of root respiration is based on the growth-and-maintenance-respiration paradigm, which involves both empirical studies and theoretical principles (Amthor 2000). Despite the partly empirical basis of the equations, they are commonly used in plant physiological modeling.

Applying this approach, total respiration of a cylindrical root $r_{\mathrm{root\_tot}}$ [kg O_2 m^{-1} root d^{-1}] was calculated from the root respiration at a reference temperature $r_{\mathrm{root\_tot\_ref}}$ [kg O_2 m^{-1} root d^{-1}] correcting for differences in soil temperature T_{soil} [K] (Amthor 2000):

$$r_{\mathrm{root\_tot}} = r_{\mathrm{root\_tot\_ref}} \cdot Q_{10\_\mathrm{root}}^{(T_{\mathrm{soil}} - T_{\mathrm{ref}})/10} \tag{3.1}$$

where Q_{10_root} is the relative increase in $r_{\mathrm{root\_tot}}$ at a temperature increase of 10 °C [-] (Atlas & Bartha 1987). Q_{10} is a widely accepted empirical measure to describe the sensitivity of plant physiological processes to temperature (Lloyd & Taylor 1994).

$r_{\mathrm{root\_tot\_ref}}$ is the sum of reference maintenance respiration and reference growth respiration. Oxygen is always used first for maintenance, and only if oxygen availability allows, additional oxygen is used for growth respiration. Reference maintenance respiration $r_{\mathrm{root\_m\_ref}}$ [kg O_2 m^{-1} root d^{-1}] is described as (Amthor 2000):

$$r_{\mathrm{root\_m\_ref}} = k_{\mathrm{m}} \cdot w \tag{3.2}$$

where k_{m} is the empirical maintenance coefficient of roots [kg O_2 kg^{-1} root d^{-1}] and w the specific root mass [kg root m^{-1} root]. In our approach, total respiration is taken relative to maintenance respiration. This ratio is depicted as η [-], and it is assumed that $\eta = \eta_{\mathrm{potential}} = 5$ at optimal oxygen availability (Penning de Vries et al. 1979). ϕ_{gas} for $\eta = 1$ and ϕ_{gas} for $\eta = \eta_{\mathrm{potential}}$ correspond to the points I (h_1) and II ($h2$) in the Feddes-function (Fig. 3.1), respectively.

Microbial respiration in the water-film $r_{\mathrm{waterfilm}}$ [kg O_2 m^{-1} root d^{-1}] was assumed to decrease exponentially with depth z [m below soil surface] (Campbell 1985 *fide* Cook 1995):

$$r_{\mathrm{waterfilm}} = r_{\mathrm{waterfilm\_z0}} \cdot \exp\left(-z/Z_{\mathrm{microbial}}\right) \tag{3.3}$$

where $r_{\mathrm{waterfilm\_z0}}$ represents the microbial respiration rate in the water-film [kg O_2 m^{-1} root d^{-1}] at the soil surface. $Z_{\mathrm{microbial}}$ is a shape parameter that empirically describes the decrease of organic resources for microbial respiration with depth z. Microbial respiration was calculated as an empirical function of T_{soil} [K], organic carbon content of the soil μ [kg C m^{-3} soil] (Appendix, 3A.2) and a vegetation dependent respiration rate β [kg O_2 kg^{-1} C d^{-1}] (Arora, 2003):

$$r_{\mathrm{waterfilm\_z0}} = 0.5 \cdot (\mu \cdot A) \cdot \beta \cdot Q_{10\_\mathrm{microbial}}^{(T_{\mathrm{soil}} - T_{\mathrm{ref}})/10} \tag{3.4}$$

with $Q_{10\_microbial}$ the relative increase in $r_{waterfilm\_z0}$ at a temperature increase of 10 °C [-] (Atlas & Bartha 1987). A is the area of a cross-section of the cylindrical water-film [m^2].

Diffusivity at the micro-scale

The diffusivity for oxygen in the water-film $D_{waterfilm}$ [m^2 d^{-1}] was derived from the diffusivity for oxygen in water D_{water} [m^2 d^{-1}] and a correction for the tortuosity of the water-film. As the thickness of the water-film equals the distance from the root surface to the nearest gas filled pores (see Section "Distance at the micro-scale"), the water-film can be regarded as a saturated soil. Therefore, the calculation of the diffusivity for oxygen in the water-film is equivalent to that of the diffusivity in a saturated soil, as described by Millington and Quirk (1961):

$$D_{\text{waterfilm}} = D_{\text{water}} \cdot \phi_{\text{waterfilm}}^{4/3} \tag{3.5}$$

where $\phi_{waterfilm}$ is called the 'porosity of the water-film' [m^3 water m^{-3} water-film] defined as the ratio between the soil water content and the volume of the liquid and solid phase (Currie 1965 *fide* Simojoki 2000):

$$\phi_{\text{waterfilm}} = \left(\phi_{\text{total}} - \phi_{\text{gas}}\right) \Big/ \left(1 - \phi_{\text{gas}}\right) \tag{3.6}$$

with ϕ_{total} the total porosity of the soil and ϕ_{gas} the gas filled porosity of the soil.

The diffusivity for oxygen in the plant root D_{root} was derived from D_{water}, assuming that the sensitivity of D_{root} to temperature equals that of D_{water} (Langø et al. 1996), and a correction for the tortuosity of root tissues τ_{root} [-]:

$$D_{\text{root}} = \tau_{\text{root}} \cdot D_{\text{water}} \tag{3.7}$$

By scaling a published reference value of D_{root} for a terrestrial grassland species at T_{soil} = 293 K (Van Noordwijk & De Willigen 1984) to $D_{water,}$ we obtained $\tau_{root} = 0.4$.

Concentration gradient at the micro-scale

A steady-state equation for the distribution of the concentration of oxygen in the water-film and the root (De Willigen & Van Noordwijk 1984) was used to calculate C_{min_int} (Appendix, 3A.3). C_{min_int} [kg O_2 m^{-3} root] represents the oxygen concentration at the interface of the water-film and the gas phase of the soil, that is required to ensure sufficient oxygen supply for r_{root_tot} to all cells in the root (De Willigen & Van Noordwijk 1987). The oxygen concentration at the outer edge of the water-film C_{min_int} and the gas phase of the soil C_{min} were considered to be in equilibrium, thus:

$$C_{\text{min}} = C_{\text{min\_int}} \big/ \alpha_{\text{B}} \tag{3.8}$$

where α_B is the Bunsen solubility coefficient for oxygen [m^3 gas m^{-3} liquid] (Langø et al. 1996).

Distance at the micro-scale

The thickness of the water-film Δ [m], i.e. the distance from the root surface to the nearest gas filled pores, was calculated according to Simojoki (2000) (Appendix, 3A.4). Root radius a [m] was calculated according to De Willigen & Van Noordwijk (1987) (Appendix, 3A.1).

Calculation of *C* (diffusion at the macro-scale)

Oxygen consuming processes at the macro-scale

The calculation of the total root respiration of the bulk roots at $z = 0$ m $R_{\text{root\_tot\_z0}}$ [kg O_2 m^{-3} soil d^{-1}] was similar to the procedure for a cylindrical root (Eq. 3.1). The only difference is that respiration rates are considered per volume soil [kg O_2 m^{-3} soil d^{-1}], instead of per meter root [kg O_2 m^{-1} root d^{-1}]. $R_{\text{root\_tot}}$ was assumed to decrease exponentially with z, based on the decrease of root dry weight with depth (Campbell 1985 *fide* Cook 1995):

$$R_{\text{root\_tot}} = R_{\text{root\_tot\_z0}} \cdot \exp\left(-z/Z_{\text{root}}\right) \tag{3.9}$$

where Z_{root} is an empirical shape factor and $R_{\text{root\_tot\_z0}}$ is the total root respiration at depth $z = 0$ m [kg O_2 m^{-3} soil d^{-1}]:

$$R_{\text{root\_tot\_z0}} = R_{\text{root\_tot\_z0\_ref}} \cdot Q_{10\_\text{root}}^{\left(T_{\text{soil}}-T_{\text{ref}}\right)/10} \tag{3.10}$$

and the reference total root respiration at $z = 0$ $R_{\text{root\_tot\_z0\_ref}}$ [kg O_2 m^{-3} soil d^{-1}] as defined in Section "Oxygen consuming processes at the micro-scale", but using W (substituting w, Eq. 3.2) as the dry weight of bulk roots at $z = 0$ m [kg root m^{-3} soil].

The calculation of the microbial respiration in the bulk soil $R_{\text{microbial}}$ [kg O_2 m^{-3} soil d^{-1}] was also similar to that of $r_{\text{waterfilm}}$ (Eq. 3.3). The differences are that volumetric respiration rates, i.e. [kg O_2 m^{-3} soil d^{-1}], and unsaturated conditions are considered here:

$$R_{\text{microbial}} = R_{\text{microbial\_z0}} \cdot \exp\left(-z/Z_{\text{microbial}}\right) \tag{3.11}$$

with the microbial respiration at $z = 0$ m $R_{\text{microbial\_z0}}$ [kg O_2 m^{-3} soil d^{-1}]:

$$R_{\text{microbial\_z0}} = f_{\varphi} \cdot \mu \cdot \beta \cdot Q_{10\_\text{microbial}}^{\left(T_{\text{soil}}-T_{\text{ref}}\right)/10} \tag{3.12}$$

with f_{φ} a reduction factor for soil moisture [-] (Appendix, 3A.5).

Diffusivity at the macro-scale

The mean diffusivity of soils D_{soil} [m^2 d^{-1}] was calculated from soil water characteristics, and thus pore size distributions, according to Moldrup et al. (2000):

$$D_{\text{soil}} = D_0 \cdot \left(2 \cdot \phi_{\text{gas\_100}}^3 + 0.04 \cdot \phi_{\text{gas\_100}}\right) \cdot \left(\phi_{\text{gas}}/\phi_{\text{gas\_100}}\right)^{2+3/b} \tag{3.13}$$

where D_0 is the diffusion coefficient for oxygen in free air [m^2 d^{-1}], ϕ_{gas_100} is the gas filled porosity at a soil water pressure head h = -100 cm [-] and b = the Campbell soil water retention parameter (Campbell 1974). The b-value can be determined as the slope of the soil water retention curve in a log-log plot (log[θ] vs log[-h]), which means that the soil water retention characteristics have to be known at least at two h's. Moldrup et al. (2000) propose to take: $b = \left(\log[500]-\log[100]\right)/\left(\theta_{h=-100\mathrm{cm}}-\theta_{h=-500\mathrm{cm}}\right)$. Moldrup et al. (2000) showed that the inclusion of soil water characteristics in the calculation of D_{soil} represents the measured mean D_{soil} much better than previous models that only considered the gas filled porosity (ϕ_{gas}) and the total porosity (ϕ_{total}) of the soil (e.g. Millington & Quirk 1961). Such models highly underestimate D_{soil} for low ϕ_{gas} (Moldrup et al. 2000).

Concentration gradient at the macro-scale

The concentration gradient at the macro-scale was determined by the oxygen concentration in the atmosphere C_{atm} [kg O_2 m^{-3} air] and the oxygen concentration C [kg O_2 m^{-3} soil air] in the soil at a certain depth z. C_{atm} was calculated according the general gas law, assuming 21% of oxygen in the atmosphere (Appendix, 3A.6). An analytical solution for $C(z)$, considering the exponential decrease of both root and microbial respiration with depth, is given by Cook (1995). To increase the flexibility of our model, we considered, unlike Cook (1995), root and microbial respiration as two separate sink terms with specific exponential decreases, leading to slightly adapted equations (Fig. 3.2D and Appendix, 3A.7).

Distance at the macro-scale

The distance over which diffusion takes place equals depth z [m below soil surface] at which the oxygen concentration is calculated.

The relation between oxygen stress and water uptake

Our model computes ϕ_{gas_min} as a function of the oxygen demand of plant roots for root respiration. However, it is also possible to compute root water uptake as function of ϕ_{gas_min}. The latter approach was used to evaluate the relation between oxygen stress and root water uptake. To do so, we assumed that root water uptake is proportional to growth respiration. There are several arguments that support this assumption.

Root water uptake occurs by hydrostatic forces (passive transport) and by the metabolic activity of root cells (active transport). Stomata represent the highest resistance to water flow (Ehlers & Goss 2003; Katul et al. 2003). If stomata are fully opened, root water uptake is optimal (F = 1) and dominated by hydrostatic forces. At fully open stomata, potential photosynthesis is achieved and oxygen is needed for both maintenance and growth respiration. Potential root water uptake is thus only possible as long as there is no oxygen stress. Oxygen stress induces stomatal closure (e.g. Kramer 1951; Glínski & Stępniewksi 1985). At complete stomatal closure, the actual transpiration and photosynthesis approach zero ($F = 0$). In that case, oxygen is solely used for maintenance respiration.

Between the limits $F = 1$ and $F = 0$, we assume the reduction of root water uptake to be directly proportional to the reduction in root respiration: Kamaluddin and Zwiazek (2001) demonstrated, by inhibition of the metabolism of the roots, that there is a positive correlation between root respiration and water uptake. This implies a gradual decrease of root water uptake with increased oxygen stress.

Model Analysis

Sensitivity of ϕ_{gas_min}

ϕ_{gas} was iteratively adjusted between 10^{-8} (~0) and ϕ_{total}, until the convergence criterion abs(C_{min}-C) < 10^{-4} kg m^{-3} was met. This ϕ_{gas} corresponds to $\phi_{\mathrm{gas\_min}}$ (Figs 3.2A and C). Together with adjusting ϕ_{gas}, the parameters depending on ϕ_{gas} (Δ, $R_{\mathrm{microbial\_z0}}$ and D_{soil}, and thus both C_{min} and C), were recalculated.

After numerical verification of our model, we analysed the validity of uniform critical values h_1 and h_2 for oxygen stress (Fig. 3.1). A sensitivity analysis for $\phi_{\mathrm{gas\_min}}$, and herewith

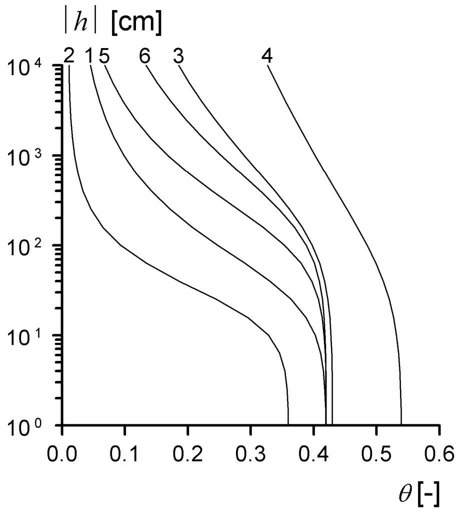

Figure 3.3: Soil water retention curves (Wösten et al. 2001) for the soil types that were used in the calculation of critical values for oxygen stress. The numbers in the retention curves correspond to the soil types and the soil physical characteristics in Table 3.3.

Table 3.3: Soil types and soil physical characteristics (Wösten et al. 2001) that were used in the calculation of critical values for oxygen stress.

Nr.	Soil type	θ_{res} [-]	θ_{sat} [-]	α [1/Pa]	N (M = 1-1/N) [-]
1	moderately loamy, very fine sand	0.02	0.42	2.76e-4	1.491
2	course sand	0.01	0.36	4.52e-4	1.933
3	light clay	0.01	0.43	6.4e-4	1.210
4	heavy clay	0.01	0.54	2.39e-4	1.094
5	sandy loam	0.01	0.42	8.4e-4	1.441
6	silty loam	0.01	0.42	5.1e-4	1.305

h, was performed for different abiotic conditions, relevant for the Netherlands. We distinguished different soil types (Table 3.3, Fig. 3.3), temperatures ($T_{\mathrm{soil}} = T_{\mathrm{air}} = 273 - 303$ K), organic matter contents ($\varepsilon_{\mathrm{org}} = 0.0 - 15.0$ %), depths ($z = 0.0 - 0.5$ m) and oxygen requirements ($1 \leq \eta \leq 5$).

Secondly, we performed a Monte Carlo analysis to study the sensitivity of $\phi_{\mathrm{gas\_min}}$ to plant characteristics. Plant characteristics were randomly extracted from normal distributions, defined by average values and standard deviations (Table 3.2). $\phi_{\mathrm{gas\_min}}$ was calculated for each combination of abiotic conditions (soil type, T_{soil}, $\varepsilon_{\mathrm{org}}$ and z) and for thousands of extractions from the normal distributions of plant characteristics. Monte Carlo analysis was performed both for $\eta = 1$ and $\eta = 5$. $\phi_{\mathrm{gas\_min}}$ values were normalized to the average $\phi_{\mathrm{gas\_min}}$ across all simulations. Linear regression was used to analyse the sensitivity of normalized $\phi_{\mathrm{gas\_min}}$ to each plant characteristic. Variation in the $\phi_{\mathrm{gas\_min}}$ values around each regression line, caused by variation in all parameters other than the plant characteristic on the x-axis, was visualized by regression quantiles (Koenker 2007).

Sensitivity of F

We used the model to calculate F (Fig. 3.1) as function of $\phi_{\mathrm{gas\_min}}$ (see Section "The relation between oxygen stress and water uptake"). η was iteratively adjusted between 10^{-4} (~0) and $\eta_{\mathrm{potential}}$, until abs($C_{\mathrm{min}}$-$C$) < 10^{-4} kg m^{-3}. $\eta = 1$ and $\eta = \eta_{\mathrm{potential}}$ correspond to $F = 0$ and $F = 1$, respectively. Together with adjusting η, the parameters $r_{\mathrm{root\_tot}}$ and $R_{\mathrm{root\_tot\_z0}}$, and thus both C_{min} and C, were recalculated. Since $\phi_{\mathrm{gas\_min}}$ is related to h — via soil porosity and the water retention curve — this enabled us to compare F from our model with F from the reduction function of Feddes et al. (1978).

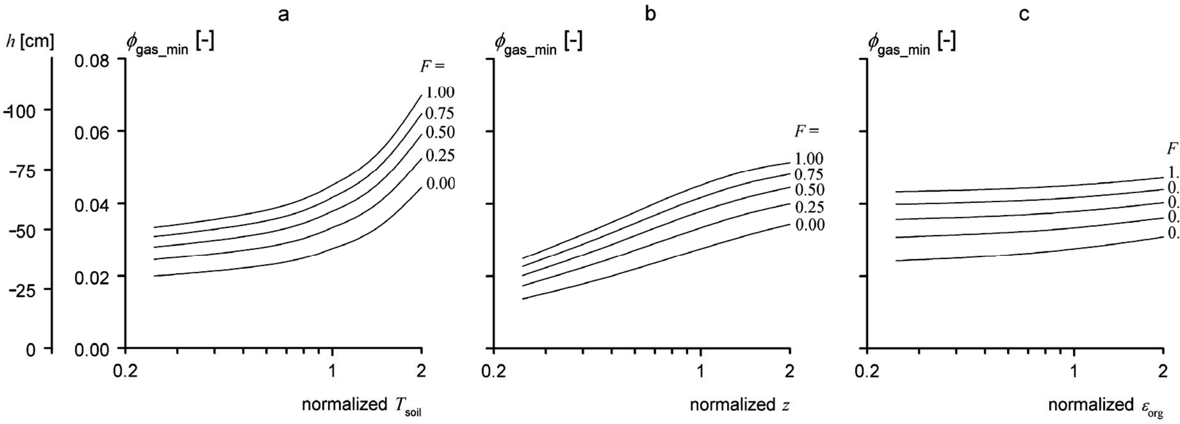

Figure 3.4: Sensitivity of $\phi_{\mathrm{gas\_min}}$ and h to (a) T_{soil}, (b) z and (c) $\varepsilon_{\mathrm{org}}$ at different respiration rates (varying from $\eta = 1$ ($F = 0$), to $\eta = 5$ ($F = 1$)) for a temperate terrestrial grassland (Table 3.2) on sandy loam (soil type = 5, Table 3.3). T_{soil}, $\varepsilon_{\mathrm{org}}$ and z were normalized around the reference values 15 °C (288 K), 7.5 % and 0.25 m, respectively. For each analysis, only one of the abiotic parameters was varied, while keeping the other parameters at their reference values. Other investigated soil types show similar sensitivities.

Results

Sensitivity of ϕ_{gas_min} and F to environmental parameters

The minimum gas filled porosity ϕ_{gas_min}, and herewith the soil water pressure head h corresponding to oxygen stress, was especially sensitive to the abiotic parameters soil temperature T_{soil} and depth z (Fig. 3.4). ϕ_{gas_min} was hardly sensitive to soil organic matter content ε_{org}. This sensitivity pattern held for all investigated six soil types, although ϕ_{gas_min} differed considerably between soil types.

The Feddes-function uses uniform values h_1 and h_2 for a specific crop type or plant species. Values of h_1 = -10 cm and h_2 = -25 cm are commonly used for grasslands (Wesseling 1991; Feddes & Raats 2004; Kroes et al. 2008). In all states tested, oxygen stress started at more negative h (drier) conditions, than these standard values (Fig. 3.4). The differences between the calculated reduction functions are considerable among the various soil types (Fig. 3.5). ϕ_{gas_min} was larger in sandy soils than in soils that contain clay particles, as could be expected (Pierce et al. 1983; Håkansson & Lipiec 2000). Clayey soils are well structured, which provides connected gas filled pores through which diffusion occurs. Sandy soils with high water contents consist of isolated gas filled pores that cannot contribute to the oxygen diffusion pathway (Horn et al. 1994). Especially for clayey and loamy soils, the critical h-values of Wesseling (1991) corresponded to extremely low ϕ_{gas}-values that are unlikely to be sufficient (< 0.01, see Figs. 3.3 and 3.5 and Table 3.3) for the oxygen requirements of roots. Unfortunately, in spite of all our efforts we were unable to discover how Wesseling (1991) derived the h-values.

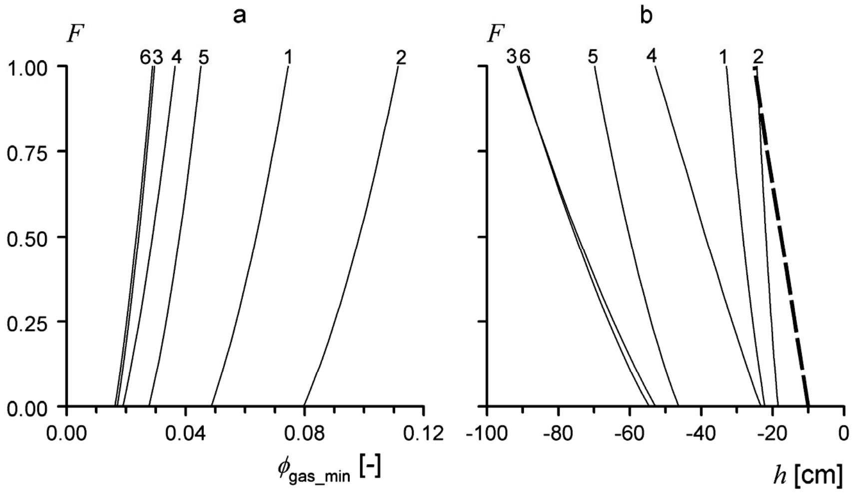

Figure 3.5: Sink term variable F as function of both soil type (Table 3.3) and (a) ϕ_{gas_min} and (b) h. T_{soil} = 288 K, ε_{org} = 7.5 %, z = 0.25 m and average reference vegetation characteristics (Table 3.2). The dotted line in (b) represents the function by Feddes et al. (1978). The reduction functions are only valid for the very specific parameter values chosen here. For each of the soil types, the values for ϕ_{gas_min} and thus h change with e.g. T_{soil} and z.

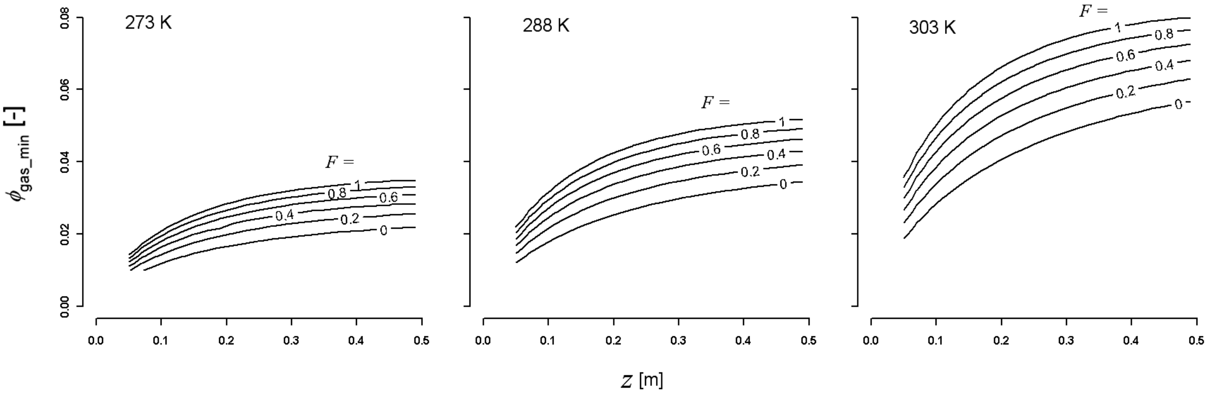

Figure 3.6: Contour plots of F as function of ϕ_{gas} and z for three temperatures (T_{soil} = (a) 273 K, (b) 288 K and (c) 303 K) and ε_{org} = 7.5 %; $T_{soil} = T_{air}$. Only the results for a sandy loam (soil type = 5, Table 3.3) are presented here, but the trend holds for all investigated soil types. The range in F-values corresponds to those of the y-axis in Fig. 3.5a.

Analysis of our model showed that transpiration reduction differed strongly between soil types (Fig. 3.5), but that within a specific soil type, F mainly depends on T_{soil}, z and ϕ_{gas} (Figs. 3.4 and 3.6). The reduction was highly nonlinear with z and the influence of temperature was considerable (Fig. 3.6), which means that F (Fig. 3.5) shifts to a different ϕ_{gas_min} (and h) upon changes in T_{soil} and z. Like the original Feddes function (Feddes et al. 1978), the shape F as function of h (Fig. 3.5b) was close to linear.

Sensitivity of ϕ_{gas_min} to plant characteristics

ϕ_{gas_min} appeared to be especially sensitive to plant characteristics W and k_m and hardly to SRL, β and Z_{root} (Fig. 3.7). The differences in sensitivity to W vs SRL imply that the characteristics of a single cylindrical root (w and a, calculated from SRL, Appendix 3A.1), have less influence on ϕ_{gas_min} than the characteristics of the bulk roots. This indicates that diffusion processes at the micro-scale were less influential than those at the macro-scale. This corresponds to our finding that in the diffusion at the macro-scale, only a small change in ϕ_{gas} is needed to provide a large change in C. The sensitivity of ϕ_{gas_min} to the maintenance coefficient k_m can be problematic for some model applications, because k_m is an empirical parameter that is difficult to acquire accurately (Cannell & Thornley 2000).

Discussion

Progress obtained in the simulation of oxygen stress

In this paper, we introduced a process-based model to simulate the minimum gas filled porosity ϕ_{gas_min}, needed to provide plant roots with just sufficient oxygen for root maintenance and growth respiration. Both the oxygen demand of plant roots and soil microbes and the oxygen transport from the atmosphere, through the soil and to the roots were incorporated. Our model is based on important processes involved in the diffusion processes at the micro-scale (described by e.g. Lemon & Wiegand 1962; De Willigen & Van Noordwijk 1984; Armstrong & Beckett 1985; Glínski & Stępniewksi 1985) and macro-scale (described by e.g. Glínski & Stępniewksi 1985; Cook 1995; Jones & Or 1998; Kalita 1999). So far, only one model considered diffusion at both scales (Cook & Knight 2003). We combined the most appropriate equations involved in each of the diffusion processes, and extended and improved existing calculations where necessary.

Important improvements incorporated in our model are, first of all, to model microbial respiration in dependency of gas filled porosity ϕ_{gas} of the soil, and thus on water content. Overestimation of oxygen concentrations and $\phi_{\mathrm{gas\_min}}$ by too high microbial respiration rates (Kalita 1999; Cook & Knight 2003) is thus avoided. Second, we considered root and microbial respiration as two separate processes, instead of combining them (Glínski & Stępniewksi 1985; Cook 1995; Jones & Or 1998; Kalita 1999). This has the advantage that the model has more flexibility in incorporating differences in depth profiles between root and microbial respiration. Third, the thickness of the water film that covers plant roots

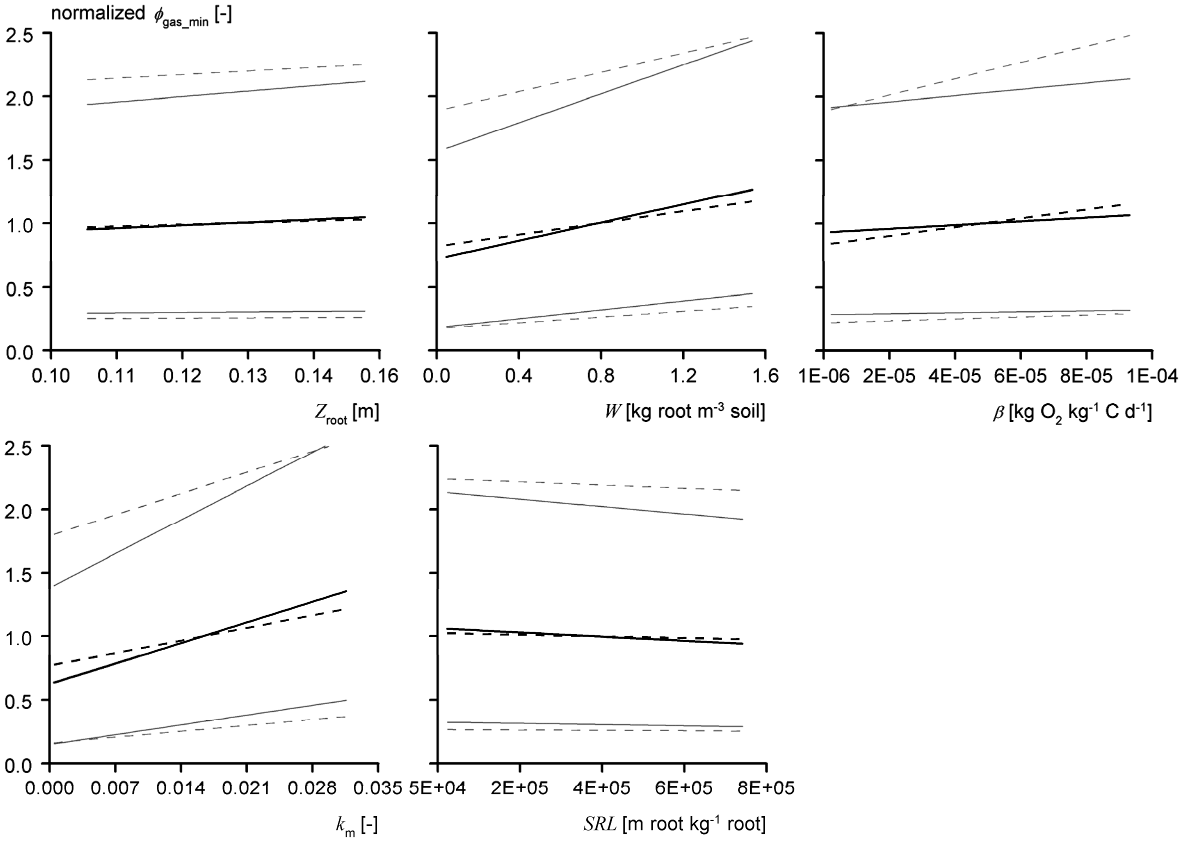

Figure 3.7: Sensitivity of $\phi_{\mathrm{gas\_min}}$ to plant characteristics of the reference plant species (Table 3.2). $\phi_{\mathrm{gas\_min}}$ is normalized around the mean $\phi_{\mathrm{gas\_min}}$ of all model runs. Monte Carlo analysis was performed for $\eta = 1$ (dotted lines) and $\eta = 5$ (solid lines). The slopes of the black lines indicate the effect on $\phi_{\mathrm{gas\_min}}$ of the parameter on the x-axis. The grey lines represent the 10 and 90 % regression quantiles (Koenker 2007). This bandwidth is caused by all varied parameters (abiotic and plant characteristics) other than the parameter on the x-axis.

and through which oxygen diffusion takes place, was calculated as function of ϕ_{gas} and not taken as a fixed value (Armstrong & Beckett 1985; Glínski & Stępniewksi 1985; Cook & Knight 2003). Fourth, the microbial respiration within the water-film was considered instead of ignored (Lemon & Wiegand 1962; Glínski & Stępniewksi 1985; Simojoki 2000; Cook & Knight 2003). Fifth, our calculation of the soil diffusivity D_{soil} on the basis of the soil water retention curve gives a better representation of D_{soil} at low ϕ_{gas} than the method of Millington and Quirk (1961) (Glínski & Stępniewksi 1985; Jones & Or 1998; Cook & Knight 2003). The method of Millington and Quirk (1961) is solely based on ϕ_{gas}, irrespective of soil type, and on total soil porosity ϕ_{total}. Moldrup et al. (2000) proved that the method of Millington and Quirk (1961) underestimates D_{soil} at low ϕ_{gas}, which results in an overestimation of ϕ_{gas_min}.

All in all, we improved the descriptions of relevant processes and parameters and considered them simultaneously to calculate representative values for ϕ_{gas_min} accurately. Thus, we avoided the structural overestimation of ϕ_{gas_min} as happened in Cook & Knight (2003). Our model enabled us to simulate the variation in ϕ_{gas_min} resulting from differences in both abiotic and biotic conditions.

Constant vs process-based critical measures for oxygen stress

In the literature, constant critical values for ϕ_{gas_min} have been applied to represent root oxygen stress (e.g. Barber et al. 2004; Leao et al. 2006). We demonstrated, however, that ϕ_{gas_min} depends on a number of environmental parameters, especially soil type, temperature and depth below soil surface (Figs. 3.4, 3.5 and 3.6).

The low sensitivity of ϕ_{gas_min} to soil organic matter content ε_{org} likely has to do with the reduced microbial activity under the wet conditions at which oxygen stress occurs (through the moisture reduction factor for microbial respiration f_{φ}, Appendix, 3A.5). This will have led to a relatively low microbial contribution to total oxygen consumption. The high sensitivity to temperature T is caused by the strong increase in respiration rate with T (Eqs. 3.1 and 3.10). This sensitivity apparently dominated the sensitivity of diffusivities to T (Eqs. 3.5, 3.7 and 3.13) as the reverse should have led to decreased ϕ_{gas_min} with increased T. The sensitivity to soil depth z is due to depth dependent macro-scale diffusion distances.

All in all, the use of constant critical measures for oxygen stress should be avoided. $\phi_{gas\_min} = 0.10$ is generally (e.g. Engelaar & Yoneyama 2000; Zou et al. 2001; Lipiec & Hatano 2003; Leao et al. 2006) used as a critical value for aeration. However, Wesseling and van Wijk (1957) who introduced this threshold, already warned that $\phi_{gas\_min} = 0.10$ "must be considered as preliminary". Despite this remark, this threshold is still applied in many studies.

Our simulations illustrate that in general, $\phi_{gas\_min} = 0.10$ is too high for the abiotic conditions and plant characteristics considered in our research, except for those at higher temperatures and sandy soils. The real overestimation is even stronger, because Wesseling and van Wijk (1957) applied $\phi_{gas\_min} = 0.10$ to the bottom end of the root zone, where ϕ_{gas_min} is higher than in the upper part of the root zone.

Our simulations were done for a temperate terrestrial grassland, but also characteristics of other crops or vegetation types can be used. ϕ_{gas_min} appeared to be sensitive to some of the plant characteristics, in particular to the respiration maintenance coefficient (k_m). This illustrates the importance of an accurate description of plant characteristics for the calculation of ϕ_{gas_min}. Consequently, ϕ_{gas_min} will be different for other crops and vegetation types.

Fortunately, in many applications exact knowledge on actual plant characteristics is less important. Models like SWAP (Kroes et al. 2008) can be used with plant characteristics of a reference vegetation, instead of the actual vegetation, to assess a potential stress at a site. Such a measure, reflecting the oxygen status of the soil, can be used to predict the suitability of a site for certain natural vegetation types (e.g. Runhaar et al. 1997).

Improving oxygen stress thresholds

We used our model to simulate the reduction of water uptake by plant roots and herewith the sink term *F* that is involved in hydrological models like SWAP (Kroes et al. 2008) and HYDRUS (Šimůnek et al. 2005). Oxygen stress was coupled to *F* under the assumptions that: (i) root water uptake reaches a maximum ($F = 1$) upon obtaining the maximum growth respiration, (ii) root water uptake reaches zero ($F = 0$) when only maintenance respiration is feasible, and (iii) in between these thresholds, reduced root water uptake is directly proportional to reduced growth respiration. A maximum value of $\eta = 5$ was used to calculate the maximum growth respiration (Penning de Vries et al. 1979). This should be considered as an empirical value that seems valid in most cases, but deviations are likely to occur (Amthor 2000). Although potential growth respiration and only maintenance respiration most likely correspond to $F = 1$ and $F = 0$, respectively, further research on the relationship between reduced respiration and reduced root water uptake in between these thresholds is recommended.

Although the linear shape of the Feddes-function seems valid (Fig. 3.5), constant threshold values for the points I and II (Fig. 3.1) are inappropriate for an accurate determination of oxygen stress. Reduction of root water uptake already starts at much drier conditions than according to the Feddes-function and additionally depends strongly on soil type and temperature. For instance, according to our model, oxygen stress on sandy loam (soil 5) occurs at a ca. 40 cm lower groundwater level than according to the Feddes-function (assuming hydrostatic equilibrium) (Fig. 3.5). For sites where the occurrence of oxygen stress could be an issue, i.e. at shallow groundwater levels, such a difference is considerable and cannot be ignored.

Assuming a linear relationship in between the two thresholds I and II (Fig. 3.1), our model can be used to generate repro-functions to assess *F* for a variety of biotic and abiotic conditions (Appendix 3B). The advantage of such functions is that they speed-up the simulations considerably.

Applicability of the oxygen stress model

Our oxygen stress model can be applied to improve the simulation of both root water uptake and root growth in models that consider the soil-plant-atmosphere-continuum, like SWAP (Kroes et al. 2008). In this paper, we used it to substitute the sink term variable F at the wet side of the Feddes-function. However, other models for root water uptake can be improved with our approach as well. In several models (e.g. Molz 1981; Doussan et al. 1998; Roose & Fowler 2004), root water uptake is calculated on the basis of water absorption driven by hydraulic pressure differences between the root rhizosphere and the root xylem (passive transport). These types of models probably work well under conditions with sufficient oxygen supply to plant roots, but not in wetter conditions where water transport to roots is increasingly limited by metabolic processes (active transport) (see Section "The relation between oxygen stress and water uptake"). Our model might be used to improve the pressure driven root water uptake models, by incorporating a root sink term F to adjust the water flux from the rhizosphere to the root xylem.

The simulation of root growth (e.g. WOFOST and SUCROS (Van den Berg et al. 2002)), which is based on the net production of root biomass, can also be improved with the aid of our model. The production of root biomass is determined both by photosynthesis and by respiration (Cannell & Thornley 2000). Our model might contribute to a better description of both processes: Carbon dioxide diffusion from the atmosphere into the plant is only possible when stomata are open. Consequently, photosynthesis is affected by root oxygen stress (Van Bodegom et al. 2008). Therefore, many crop growth models calculate the actual photosynthesis by linking it to potential photosynthesis and the relative transpiration rate (ratio of actual and potential transpiration = F) (Van den Berg et al. 2002). An accurate description of the relative transpiration and thus root water uptake is desired. Part of the carbohydrates produced by photosynthesis is used for respiration. Our model calculates the reduction in respiration rate of the roots due to oxygen stress, as a function of the actual (a)biotic conditions.

Our model is freely available from the internet in SWAP (Kroes et al. 2008). By including our model within SWAP, it has been integrated in a full hydrological modeling environment. Processes that are not directly involved in our model, but that might affect oxygen availability, like swelling and shrinking of soils and macro-pore flow, are accounted for in SWAP. Furthermore, with SWAP, relevant processes like heat flow and plant growth can be simulated.

Conclusions

In this paper, we showed that substantial differences in the minimum gas filled porosity of the soil — $\phi_{\text{gas\_min}}$ — are especially related to soil type, soil temperature and soil depth.

Consequently, constant values for $\phi_{\text{gas\_min}}$ should be avoided, since they may result in large prediction errors of both transpiration and plant growth. The same holds, of course, for the fixed anaerobiosis pressure heads of the frequently used Feddes-function. To determine the oxygen stress experienced by roots accurately, we advocate an approach that takes account of relevant abiotic and biotic factors in an integrative manner.

Acknowledgements

This study was carried out in the framework of both Project A1 'Biodiversity in a changing environment: predicting spatio-temporal dynamics of vegetation' of the Dutch National Research Program Climate Change and Spatial planning (www.klimaatvoorruimte.nl) and the joint research program of the Dutch Water Utility sector. We thank the editor and three anonymous reviewers for their valuable comments on the manuscript.

Appendix 3A: Calculation of model parameters

This appendix presents and justifies a number of equations that are part of our oxygen stress model.

3A.1 Root radius

The root radius a [m] of a cylindrical root was calculated following the method of De Willigen and Van Noordwijk (1987):

$$a = \sqrt{\frac{w}{\pi \cdot Y \cdot \left(1-\phi_{\text{root}}\right) \cdot S} - \text{var}(a)}$$

with w the specific root mass [kg root m^{-1} root], Y the dry matter content of roots [-], ϕ_{root} the air filled root porosity [-], S the specific weight of non-airfilled root tissue [kg root m^{-3} root] and var(a) the variance of a [m^2].

3A.2 Organic carbon content

The organic carbon content of the soil μ [kg C m^3 soil] was calculated from the organic matter content of the soil ε_{org} [%] and the soil density ρ_{soil} [kg soil m^{-3} soil]. This calculation is based on the assumption that soil organic matter weight consists of 48 % of organic carbon.

$$\mu = 0.48 \cdot \left(\varepsilon_{\text{org}}/100\right) \cdot \rho_{\text{soil}}$$

3A.3 Minimum oxygen concentration at the interface of the water-film and the soil air

The minimum oxygen concentration at the interface of the water-film and soil air, $C_{\text{min\_int}}$ [kg O_2 m^{-3} root], was calculated following the method proposed by De Willigen and Van Noordwijk (1984). Their method is an extension of the method by Lemon and Wiegand (1962), describing the oxygen diffusion pathway from the gas phase of the soil to the root tissue, but additionally involves microbial respiration in the root rhizosphere, i.e. in the water-film that surrounds the root:

$$C_{\text{min\_int}} = \frac{r_{\text{root\_tot}} + r_{\text{waterfilm}}}{2 \cdot \pi \cdot D_{\text{root}}} \cdot \left\{ \frac{1}{2} + \frac{(\lambda-1)\cdot\delta}{2} + \lambda \cdot \ln\left(1+\Delta/a\right) - \frac{\lambda \cdot \delta \cdot \left(1+\Delta/a\right)^2 \cdot \ln\left(1+\Delta/a\right)}{\left(\Delta/a\right)\cdot\left(2+\Delta/a\right)} \right\}$$

with:

$$\lambda = D_{\text{root}}/D_{\text{waterfilm}}$$

$$\delta = r_{\mathrm{waterfilm}} / \left(r_{\mathrm{waterfilm}} + r_{\mathrm{root\_tot}} \right)$$

The oxygen consuming processes that are involved in the method of De Willigen and Van Noordwijk (1984) are both root respiration $r_{\mathrm{root\_tot}}$ [kg O_2 m^{-1} root d^{-1}] and respiration in the water-film $r_{\mathrm{waterfilm}}$ [kg O_2 m^{-1} root d^{-1}]. Since oxygen diffusion occurs through both the water-film and the root tissue, the diffusivities of oxygen through both media are included (D_{root} and $D_{\mathrm{waterfilm}}$). The distance over which diffusion takes place is determined by the thickness of the water-film Δ and the root radius a.

3A.4 Water-film thickness

The water-film thickness Δ [m] was approximated according to the procedure proposed by Simojoki (2000), which is based on soil water retention data. Δ was approximated by the difference between the calculated distance between the pore centers (Barley 1970 *fide* Simojoki 2000) and the radii of the cylindrical gas filled pores (Simojoki 2000):

$$\Delta = 2 \cdot \left(\sqrt{\frac{1}{\pi \cdot n(\varphi)}} - \frac{2 \cdot \sigma}{\varphi} \right)$$

with φ the matric potential of the soil moisture [Pa] and σ the surface tension of water [N m^{-1}], that is given by the Eötvös rule: $\sigma = 0.07275 \cdot \left(1 - 0.002 \cdot \left(T_{\mathrm{soil}} - 291\right)\right)$.

n is the length density of air filled pores (i.e. the number of air filled pores per unit area):

$$n(\varphi) = \int_0^{\varphi} \frac{-\mathrm{d}\theta / \mathrm{d}\varphi}{\pi \cdot 4 \cdot \sigma^2 / \varphi^2} \mathrm{d}\varphi$$

which includes the derivative of the moisture retention curve according to Van Genuchten (Van Genuchten 1980):

$$\theta(\varphi) = \theta_{\mathrm{res}} + \frac{\theta_{\mathrm{sat}} - \theta_{\mathrm{res}}}{\left(1 + (\alpha \cdot \varphi)^N\right)^M}$$

$$\frac{\mathrm{d}\theta}{\mathrm{d}\varphi} = \frac{\left(\theta_{\mathrm{sat}} - \theta_{\mathrm{res}}\right) \cdot \alpha \cdot (\alpha \cdot \varphi)^{N-1} \cdot \left(1 + (\alpha \cdot \varphi)^N\right)^{M-1} \cdot M \cdot N}{\left(\left((\alpha \cdot \varphi)^N + 1\right)^M\right)^2}$$

with θ_{sat} the saturated water content [-], θ_{res} the residual water content [-] and a [Pa^{-1}], M [-] and N [-] the Van Genuchten parameters.

3A.5 Reduction of microbial respiration due to soil moisture availability

The factor f_φ that represents the reduction of microbial activity due to soil moisture availability is calculated according to Arora (2003) and Probert et al. (1998 *fide* Paul 2001). f_φ varies between 0.0 and 1.0, which represent maximum and minimum reduction, respectively. Arora (2003) proposed a reduction function for f_φ, in which f_φ is assumed to decrease linearly with the logarithm of matric potential φ, between thresholds: φ_1 (25000 Pa), φ_2 (762500 Pa) and φ_3 (1500000 Pa). These thresholds are derived from Probert et al. (1998 *fide* Paul 2001) and incorporated in the formulation of Arora (2003):

$$f_\varphi = \begin{cases} 0.5 & \varphi < \varphi_{\text{sat}} \\ 1.0 - 0.5 \cdot \dfrac{\log(\varphi_1) - \log(\varphi)}{\log(\varphi_1) - \log(\varphi_{\text{sat}})} & \varphi_{\text{sat}} \le \varphi < \varphi_1 \\ 1.0 & \varphi_1 \le \varphi < \varphi_2 \\ 1.0 - \dfrac{\log(\varphi) - \log(\varphi_2)}{\log(\varphi_3) - \log(\varphi_2)} & \varphi_2 \le \varphi < \varphi_3 \\ 0.0 & \varphi > \varphi_3 \end{cases}$$

with φ_{sat} the saturated matric potential [Pa]. On the basis of field data, Cosby et al. (1984) proposed the following equation for φ_{sat}: $\varphi_{\text{sat}} = 10^{\left(-0.0131 \cdot \varepsilon_{\text{sand}} + 1.88\right)} \cdot 100$, with $\varepsilon_{\text{sand}}$ the sand content of the soil [%].

3A.6 Oxygen concentration in the atmosphere

The oxygen concentration in the atmosphere C_{atm} [kg O$_2$ m^{-3} air] was calculated according to the general gas law, assuming 21% oxygen in the atmosphere:

$$C_{\text{atm}} = 0.21 \cdot M_{\text{O}_2} \cdot \frac{p}{\text{R} \cdot T_{\text{air}}}$$

with M_{O_2} the molar mass of oxygen [kg mol^{-1}], p the atmospheric pressure [Pa], R the universal gas constant [m^3 Pa K^{-1} mol^{-1}] and T_{air} the air temperature [K].

3A.7 Oxygen concentration in the gas phase of the soil

The oxygen concentration C [kg O$_2$ m^{-3} soil air] in the gas phase of the soil at soil depth z [m] (Fig. 3.2C) was calculated according to Cook (1995). His model is based on one-dimensional oxygen diffusion in the soil. The diffusivity of the soil is given by D_{soil} [m^{2}d^{-1}]. Additionally, his model involves a sink term that decreases exponentially with soil depth z.

Contrary to Cook (1995), we considered two separate sink terms in which both microbial and root respiration are involved (Fig. 3.2D). Each term is described both by a reference value at $z = 0$ ($R_{\text{microbial\_z0}}$ in Eq. 3.12 and $R_{\text{root\_tot\_z0}}$ in Eq. 3.10 [kg O$_2$ m^{-3} soil d^{-1}]) and by a shape factor for the exponential decrease ($Z_{\text{microbial}}$ and Z_{root} [m] in Eqs. 3.11 and 3.9, respectively).

At $z = 0$, C equals the oxygen concentration in the atmosphere C_{atm} [kg O$_2$ m^{-3} air]. Two different solutions for the oxygen concentration profile can be distinguished:

First, as for $z \rightarrow \infty$, $C \rightarrow$ constant and non-zero value. This occurs when:

$$Z_{\text{microbial}}^2 \cdot \frac{R_{\text{microbial\_z0}}}{D_{\text{soil}}} + Z_{\text{root}}^2 \cdot \frac{R_{\text{root\_tot\_z0}}}{D_{\text{soil}}} < C_{\text{atm}}$$

then:

$$C = C_{\text{atm}} - \left(Z_{\text{microbial}}^2 \cdot \frac{R_{\text{microbial\_z0}}}{D_{\text{soil}}} \right) \cdot \left(1 - \exp\left(-\frac{z}{Z_{\text{microbial}}} \right) \right) - \left(Z_{\text{root}}^2 \cdot \frac{R_{\text{root\_tot\_z0}}}{D_{\text{soil}}} \right) \cdot \left(1 - \exp\left(-\frac{z}{Z_{\text{root}}} \right) \right)$$

Second, as for $z \rightarrow \infty$, $C \rightarrow 0$. This occurs when:

$$Z_{\text{microbial}}^2 \cdot \frac{R_{\text{microbial\_z0}}}{D_{\text{soil}}} + Z_{\text{root}}^2 \cdot \frac{R_{\text{root\_tot\_z0}}}{D_{\text{soil}}} \geq C_{\text{atm}}$$

then:

$$C = C_{\text{atm}} - \left(Z_{\text{microbial}}^2 \cdot \frac{R_{\text{microbial\_z0}}}{D_{\text{soil}}} \right) \cdot \left(1 - \frac{z}{Z_{\text{microbial}}} \cdot \exp\left(-\frac{L}{Z_{\text{microbial}}} \right) - \exp\left(-\frac{z}{Z_{\text{microbial}}} \right) \right) - \left(Z_{\text{root}}^2 \cdot \frac{R_{\text{root\_tot\_z0}}}{D_{\text{soil}}} \right) \cdot \left(1 - \frac{z}{Z_{\text{root}}} \cdot \exp\left(-\frac{L}{Z_{\text{root}}} \right) - \exp\left(-\frac{z}{Z_{\text{root}}} \right) \right)$$

where z at which $C = 0$, given by L [m] (Fig. 3.2C) can be found iteratively through the Newton-Raphson method:

$$f_{\text{i}} = 0 = C(L)$$

$$f_{\text{i}}' = -\frac{R_{\text{microbial\_z0}}}{D_{\text{soil}}} \cdot L \cdot \exp\left(-\frac{L}{Z_{\text{microbial}}} \right) - \frac{R_{\text{root\_tot\_z0}}}{D_{\text{soil}}} \cdot L \cdot \exp\left(-\frac{L}{Z_{\text{root}}} \right)$$

$$L_{\text{i+1}} = L_{\text{i}} - \frac{f_{\text{i}}}{f_{\text{i}}'}$$

Appendix 3B: Repro-functions for the reduction of root water uptake of a temperate grassland under oxygen stress

We used simulations with our process-based model for oxygen stress to describe root water uptake reduction F as a continuous function of gas-filled porosity ϕ_{gas}, soil temperature T_{soil} and soil depth z. These repro-functions are based on the following assumptions and restrictions:

- The repro-functions are only valid for the plant characteristics of temperate terrestrial natural grasslands (Table 3.2) and for soil types that resemble the Staring series of Wösten at al. (2001) (Table 3B.1);
- Between minimum and maximum oxygen deficiency (points I and II in Fig. 3.1), a linear relationship between F and ϕ_{gas} is assumed (Fig. 3B.1);
- The air temperature T_{air} equals T_{soil} [K];
- The organic matter content ε_{org} = 10 % for all soils (our model, see Section "Sensitivity of $\phi_{\text{gas\_min}}$ and F to environmental parameters" appeared to be hardly sensitive to ε_{org});
- The repro-functions were derived for limited ranges of abiotic conditions: 265 K $\leq T_{\text{soil}} \leq$ 303 K and $0.05 \leq z \leq 0.5$ m.

Assuming linearity, the general shape of the relationship between F and ϕ_{gas}, can be described as $F = a \cdot \phi_{\text{gas}} + b$ ($0 \leq F \leq 1$; Fig. 3B.1), where both a and b were approximated as functions of T_{soil} and z (Fig. 3B.2):

$$a = a_1 T_{\text{soil}}^2 + a_2 z^2 + a_3 T_{\text{soil}} + a_4 z + a_5 T_{\text{soil}} z + a_6$$

$$b = b_1 T_{\text{soil}}^2 + b_2 z^2 + b_3 T_{\text{soil}} + b_4 z + b_5 T_{\text{soil}} z + b_6$$

We derived parameter values $a_{1\text{-}6}$ and $b_{1\text{-}6}$ for different soil types through curve fitting on simulated data in the following way. First, we simulated F as function of ϕ_{gas} and we computed the slope a and intercept b by linear regression. This was done for different soil types (Table 3B.1), 8 values for T_{soil} (268 K $\leq T_{\text{soil}} \leq$ 303 K and a step size of 5 K) and 10 values for z ($0.05 \leq z \leq 0.5$ m and a step size of 0.05 m). Second, for each soil type we derived values of $a_{1\text{-}6}$ and $b_{1\text{-}6}$ by non-linear least square fitting in R (www.r-project.org) on all 80 points $a(T_{\text{soil}}, z)$ and $b(T_{\text{soil}}, z)$ respectively. Examples of the thus obtained functions for a and b are presented in Fig. 3B.2. The results for the fitted parameter values for all soils, including the fit statistics, are presented in Table 3B.2 (a) and Table 3B.3 (b).

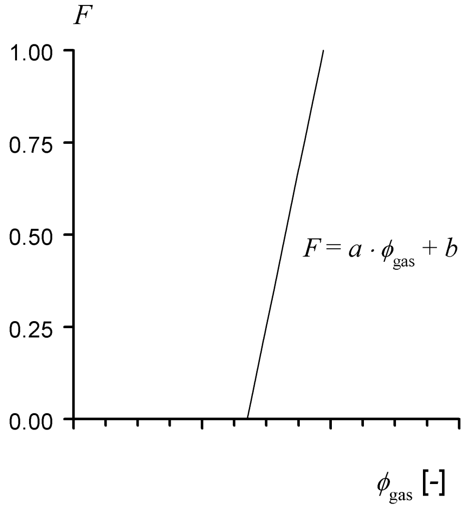

Figure 3B.1: Example of a repro-function to describe the relationship between ϕ_{gas} and *F*. Both the slope *a* and intercept *b* are functions of soil type (Table 3B.1), soil temperature T_{soil} [K] and soil depth *z* [m] (Table 3B.2 and 3B.3, Fig. 3B.2).

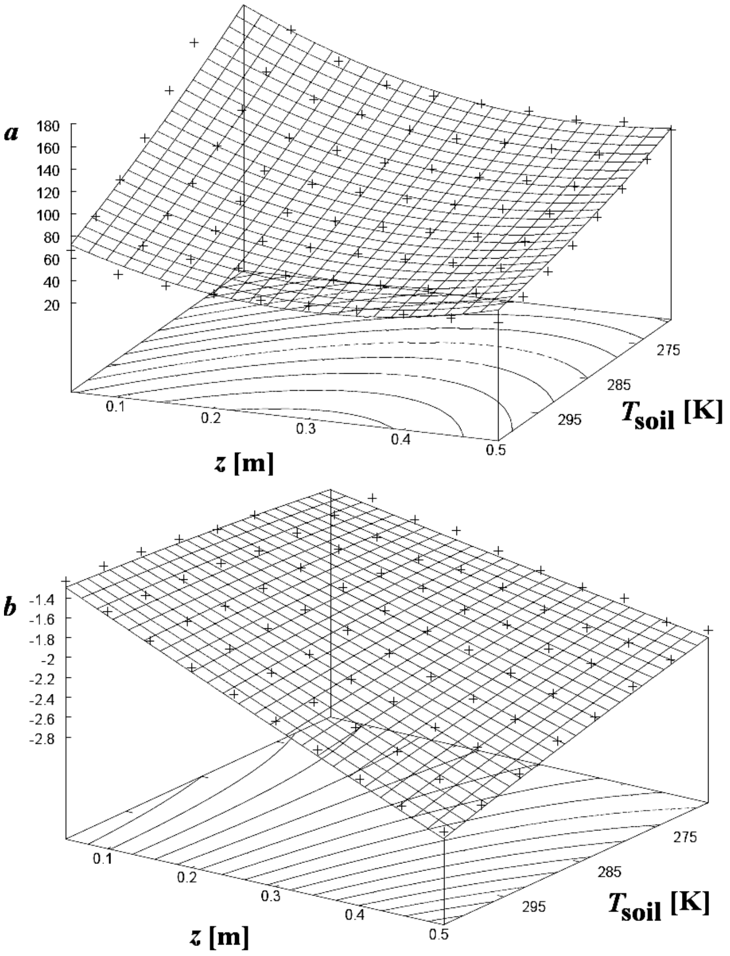

Figure 3B.2: Continuous functions, fitted on simulated data (crosses), of both the slope *a* (top figure) and intercept *b* of the repro-function $F(\phi_{\text{gas}})$ (Fig. 3B.1) for soil type B8 (Table 3B.1).

Table 3B.1: Soil types from the Staring-series (Wösten et al. 2001). Both top soils (B) and sub soils (O) are distinguished.

Top soils	Description	Sub soils	Description
B1	not loamy, very fine to moderately fine sand	O1	not loamy, very fine to moderately fine sand
B2	moderately loamy, very fine to moderately fine sand	O2	Moderately loamy, very fine to moderately fine sand
B3	loamy, very fine to moderately fine sand	O3	loamy, very fine to moderately fine sand
B4	highly loamy, very fine to moderately fine sand	O4	highly loamy, very fine to moderately fine sand
B5	coarse sand	O5	coarse sand
B6	boulder clay	O6	boulder clay
B7	light sandy clay	O7	brook loam
B8	moderately sandy clay	O8	light sandy clay
B9	heavy sandy clay	O9	moderately sandy clay
B10	light clay	O10	heavy sandy clay
B11	moderately clay	O11	light clay
B12	heavy clay	O12	moderately clay
B13	sandy loam	O13	heavy clay
B14	silty loam	O14	sandy loam
B15	peaty sand	O15	silty loam
B16	sandy peat and peat	O16	oligotrophic peat
B17	peaty clay	O17	mesotrophic and eutrophic peat
B18	clayey peat	O18	organic sublayer

Table 3B.2: Fitted parameters for the calculation of slope *a* in the repro-function $F = a \cdot \phi_{\text{gas}} + b$ $(0 \le F \le 1)$: $a = a_1 T_{\text{soil}}^2 + a_2 z^2 + a_3 T_{\text{soil}} + a_4 z + a_5 T_{\text{soil}} z + a_6$

Soil type (Table 3B.1)	a_1	a_2	a_3	a_4	a_5	a_6	residual standard error for *a*
B1	5.07e-03	2.40e+02	-4.39e+00	-6.31e+02	1.67e+00	9.08e+02	3.081
B2	1.20e-02	3.26e+02	-8.91e+00	-9.29e+02	2.49e+00	1.64e+03	4.791
B3	1.21e-02	3.64e+02	-9.09e+00	-9.90e+02	2.60e+00	1.70e+03	4.777
B4	1.67e-02	4.42e+02	-1.21e+01	-1.26e+03	3.34e+00	2.20e+03	6.448
B5	4.17e-03	1.93e+02	-3.72e+00	-5.28e+02	1.44e+00	7.77e+02	2.366
B6	2.11e-02	5.02e+02	-1.51e+01	-1.40e+03	3.69e+00	2.71e+03	7.223
B7	2.86e-02	5.57e+02	-1.97e+01	-1.67e+03	4.50e+00	3.41e+03	9.240
B8	1.75e-02	5.55e+02	-1.32e+01	-1.34e+03	3.31e+00	2.48e+03	7.140
B9	2.34e-02	6.00e+02	-1.70e+01	-1.40e+03	3.42e+00	3.09e+03	7.165
B10	3.12e-02	6.62e+02	-2.20e+01	-1.53e+03	3.65e+00	3.91e+03	7.722
B11	2.58e-02	6.42e+02	-1.83e+01	-1.61e+03	4.00e+00	3.26e+03	8.574
B12	2.50e-02	6.53e+02	-1.79e+01	-1.45e+03	3.40e+00	3.21e+03	8.596
B13	2.53e-02	5.97e+02	-1.79e+01	-1.72e+03	4.58e+00	3.18e+03	9.092
B14	2.82e-02	7.10e+02	-2.04e+01	-1.54e+03	3.56e+00	3.71e+03	8.186
B15	2.08e-02	4.72e+02	-1.46e+01	-1.37e+03	3.65e+00	2.57e+03	7.081
B16	1.99e-02	4.80e+02	-1.39e+01	-1.34e+03	3.47e+00	2.45e+03	6.845
B17	2.27e-02	6.31e+02	-1.62e+01	-1.58e+03	3.91e+00	2.91e+03	8.817
B18	2.23e-02	6.50e+02	-1.60e+01	-1.74e+03	4.45e+00	2.89e+03	10.200
O1	7.21e-04	1.76e+02	-1.59e+00	-4.33e+02	1.16e+00	4.52e+02	1.939
O2	3.75e-03	2.25e+02	-3.61e+00	-5.96e+02	1.59e+00	7.91e+02	2.803
O3	7.06e-03	2.86e+02	-5.91e+00	-7.52e+02	2.00e+00	1.19e+03	3.658
O4	1.29e-02	3.74e+02	-9.74e+00	-1.03e+03	2.72e+00	1.82e+03	5.126
O5	2.92e-03	1.86e+02	-3.06e+00	-5.07e+02	1.39e+00	6.85e+02	2.255
O6	3.00e-02	5.41e+02	-2.06e+01	-1.69e+03	4.61e+00	3.55e+03	9.061
O7	2.76e-02	6.63e+02	-1.95e+01	-1.67e+03	4.15e+00	3.48e+03	8.568
O8	1.85e-02	4.88e+02	-1.34e+01	-1.34e+03	3.50e+00	2.43e+03	7.169
O9	2.08e-02	5.46e+02	-1.50e+01	-1.50e+03	3.92e+00	2.72e+03	7.778
O10	1.85e-02	5.94e+02	-1.39e+01	-1.45e+03	3.60e+00	2.60e+03	7.867
O11	2.29e-02	6.33e+02	-1.67e+01	-1.65e+03	4.21e+00	3.05e+03	9.321
O12	2.60e-02	5.89e+02	-1.83e+01	-1.33e+03	3.12e+00	3.26e+03	6.613
O13	3.36e-02	6.27e+02	-2.29e+01	-1.40e+03	3.26e+00	3.95e+03	6.937
O14	3.84e-02	6.74e+02	-2.71e+01	-1.40e+03	3.21e+00	4.83e+03	7.449
O15	2.25e-02	6.16e+02	-1.66e+01	-1.37e+03	3.22e+00	3.05e+03	7.788
O16	1.88e-02	4.75e+02	-1.32e+01	-1.29e+03	3.31e+00	2.33e+03	6.737
O17	2.19e-02	5.40e+02	-1.53e+01	-1.50e+03	3.87e+00	2.70e+03	7.716
O18	1.98e-02	5.00e+02	-1.41e+01	-1.40e+03	3.67e+00	2.52e+03	7.372

Table 3B.3: Fitted parameters for the calculation of intercept *b* in the repro-function $F = a \cdot \phi_{\mathrm{gas}} + b$ $(0 \le F \le 1)$: $b = b_1 T_{\mathrm{soil}}^2 + b_2 z^2 + b_3 T_{\mathrm{soil}} + b_4 z + b_5 T_{\mathrm{soil}} z + b_6$

Soil type (Table 3B.1)	b_1	b_2	b_3	b_4	b_5	b_6	residual standard error for *b*
B1	1.89e-04	-3.91e-01	-8.65e-02	2.11e+01	-8.61e-02	7.12e+00	0.027
B2	5.02e-05	-7.56e-02	-1.01e-02	1.80e+01	-7.27e-02	-2.81e+00	0.021
B3	5.36e-06	3.54e-01	1.20e-02	1.73e+01	-7.09e-02	-5.51e+00	0.026
B4	-2.67e-05	4.87e-02	3.03e-02	1.76e+01	-7.02e-02	-7.90e+00	0.022
B5	2.60e-04	-1.74e+00	-1.16e-01	2.28e+01	-8.99e-02	9.67e+00	0.039
B6	-1.23e-04	-6.11e-02	8.42e-02	1.66e+01	-6.63e-02	-1.51e+01	0.023
B7	-1.02e-04	8.54e-03	7.12e-02	1.76e+01	-7.06e-02	-1.33e+01	0.025
B8	-8.09e-05	2.23e-01	5.65e-02	1.62e+01	-6.61e-02	-1.08e+01	0.024
B9	-9.68e-05	1.56e-01	6.56e-02	1.67e+01	-6.76e-02	-1.21e+01	0.025
B10	-1.37e-04	-4.78e-02	8.94e-02	1.81e+01	-7.09e-02	-1.55e+01	0.028
B11	-1.71e-04	-2.25e-01	1.08e-01	1.68e+01	-6.46e-02	-1.78e+01	0.031
B12	-1.36e-04	-5.72e-01	8.92e-02	1.02e+01	-3.91e-02	-1.54e+01	0.040
B13	-1.19e-04	-8.68e-03	8.28e-02	1.77e+01	-6.97e-02	-1.54e+01	0.029
B14	-9.91e-05	-9.32e-01	7.13e-02	1.35e+01	-5.10e-02	-1.35e+01	0.053
B15	-7.90e-05	2.75e-02	5.85e-02	1.55e+01	-6.20e-02	-1.16e+01	0.016
B16	-7.91e-05	2.32e-01	5.71e-02	1.10e+01	-4.40e-02	-1.12e+01	0.017
B17	-2.21e-04	-5.23e-01	1.39e-01	1.44e+01	-5.42e-02	-2.27e+01	0.028
B18	-1.16e-04	-3.60e-01	7.85e-02	1.05e+01	-3.96e-02	-1.41e+01	0.029
O1	4.17e-04	-1.41e+00	-2.06e-01	2.42e+01	-9.84e-02	2.20e+01	0.043
O2	2.56e-04	-4.40e-01	-1.22e-01	2.19e+01	-8.92e-02	1.16e+01	0.029
O3	1.93e-04	-2.84e-01	-8.88e-02	1.96e+01	-8.08e-02	7.68e+00	0.032
O4	5.69e-05	-7.44e-02	-1.48e-02	1.80e+01	-7.36e-02	-2.01e+00	0.029
O5	5.21e-04	-1.81e+00	-2.61e-01	1.96e+01	-7.85e-02	3.01e+01	0.045
O6	-1.10e-04	6.88e-02	7.90e-02	1.77e+01	-7.11e-02	-1.48e+01	0.023
O7	-1.76e-04	-3.81e-01	1.11e-01	1.79e+01	-6.90e-02	-1.85e+01	0.031
O8	-2.38e-05	5.72e-01	2.47e-02	1.64e+01	-6.82e-02	-6.50e+00	0.026
O9	-4.68e-05	4.19e-01	3.84e-02	1.74e+01	-7.16e-02	-8.59e+00	0.028
O10	-1.10e-04	1.03e-01	7.32e-02	1.69e+01	-6.77e-02	-1.32e+01	0.027
O11	-1.48e-04	-3.36e-01	9.58e-02	1.78e+01	-6.94e-02	-1.64e+01	0.031
O12	-1.58e-04	1.36e-01	9.92e-02	1.56e+01	-6.18e-02	-1.65e+01	0.027
O13	-2.69e-04	-6.12e-01	1.66e-01	1.27e+01	-4.80e-02	-2.65e+01	0.042
O14	-6.34e-05	-4.27e-01	5.05e-02	1.73e+01	-6.82e-02	-1.06e+01	0.063
O15	3.08e-05	5.25e-02	-6.04e-03	8.44e+00	-3.54e-02	-2.00e+00	0.043
O16	-6.20e-05	3.40e-01	4.76e-02	9.54e+00	-3.85e-02	-9.98e+00	0.020
O17	-2.90e-05	3.99e-01	2.75e-02	8.07e+00	-3.30e-02	-6.73e+00	0.020
O18	-6.76e-05	4.41e-01	5.01e-02	1.50e+01	-6.10e-02	-1.01e+01	0.023

CHAPTER

4

A climate-proof relationship between soil moisture conditions and vegetation composition

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Abstract

Reliable forecasts of the effects of climate change on the species composition of vegetation require the development of robust relationships that include the relevant climate-dependent processes, because current correlative approaches may no longer be applicable in a changing climate. Until now, the need for such relationships has been only hypothetical. In this paper, we show the need for and the application of a climate-proof process-based relationship between soil moisture conditions and vegetation composition. We considered groundwater-dependent sites, where oxygen stress, caused by a surplus of soil moisture, determines plant growth. We compared two existing indirect correlative variables for the soil oxygen status – namely mean spring groundwater level (*MSL*) and sum exceedence value (*SEV*) – with our newly developed direct measure, viz. root respiration stress (*RS*). *SEV* includes the duration and extent to which the water table rises above a certain threshold groundwater level and *RS* results from the reduction of root respiration due to insufficient oxygen supply. *RS* was simulated with a novel model. First, we defined relationships between each variable and vegetation response, in terms of the occurrence of plants that are adapted to a particular soil moisture regime. We then forecast the vegetation response for four climate scenarios for the year 2050. Although relationships were statistically equally strong for the present climate, there were very different vegetation responses upon climate change. We show that the indirect explanatory variables *MSL* and *SEV* are insufficient to predict the effect of climate change, as – unlike *RS* – essential parameters that determine oxygen stress (e.g. temperature and extreme rainfall events in the growing season) are insufficiently accounted for. We argue that the use of *RS* will increase the reliability of vegetation predictions and thus increase the future success of adaptive strategies to conserve and restore vegetation in a changing climate.

Introduction

Within global change research, much attention is being paid to our ability, or inability, to predict the effect of climate change on species groups and ecosystems (e.g. Guisan & Thuiller 2005; Botkin et al. 2007). Besides improving methods to describe processes like dispersion and competition, it is important to describe optimally the relationships between habitat characteristics and vegetation characteristics (Guisan & Zimmermann 2000). Current habitat distribution models describe the habitat of plant species by statistically derived (e.g. by generalized regression, environmental envelopes or Bayesian modelling) response curves of a set of environmental variables (e.g. Guisan & Zimmermann 2000; Bakkenes et al. 2002; Thomas et al. 2004; Guisan & Thuiller 2005; Botkin et al. 2007). Various explanatory environmental variables have been proposed (Palo et al. 2005), ranging from elevation, slope and geology (e.g. Davis & Goetz 1990; Ostendorf & Reynolds 1998), to soil moisture content (e.g. Sykes et al. 2001) and air temperature (e.g. Ashcroft 2006). However, the ecological relevance of these explanatory environmental variables is often so indirect and simple (Botkin et al. 2007) that the relationships with the vegetation have a highly correlative character (Guisan & Zimmermann 2000).

To predict the effects of climate change in a reliable manner, process-based and climate-proof relationships (i.e. relationships that are applicable under changing climatic conditions) between environmental conditions and species groups are a prerequisite because they, in contrast to indirect and correlative relationships, do not have to be calibrated for future periods or other regions. It is therefore surprising that the habitat distribution models that have been used to forecast the effects of climate change usually make use of such indirect relationships (Suding et al. 2008). Causal relationships are especially necessary for forecasting ecological effects under environmental conditions that differ strongly from those under which these relationships were derived (Guisan & Zimmermann 2000). The development of causal relationships, with physiologically meaningful explanatory variables (Franklin 1995; Guisan & Zimmermann 2000), has been identified as one of the main objectives in ecological modelling (Guisan & Zimmermann 2000). However, as far as we know, it has never been shown that direct relationships actually lead to vegetation predictions that are different from those to which indirect relationships lead.

In this paper, we will investigate relationships between soil oxygen stress (a habitat characteristic) and vegetation composition using models with different levels of climate-related causality. Together with soil acidity and soil nutrient availability, the soil moisture regime is one of the most important factors in species selection (Ellenberg 1992; Silvertown et al. 1999; Witte et al. 2007). Soil moisture affects plant growth both when it is deficient (moisture stress) and when it is superfluous (oxygen stress). The mechanisms through which these stresses act are highly different. Moisture stress limits the photosynthetic activity of plants (Tezara et al. 1999), while oxygen stress limits the metabolic activity of plants by decreased root respiration (De Willigen & Van Noordwijk 1984; Amthor 2000; Chapter 3). In this study, we focus on plant communities from groundwater-dependent sites, where oxygen stress determines plant growth.

Explanatory variables for oxygen stress have been straightforwardly derived from measured groundwater levels in terms of, for example, mean groundwater levels (Runhaar et al. 1997; Ertsen et al. 1998; Schaffers & Sýkora 2000; Dwire et al. 2004; Leyer 2005) or the period and degree that the groundwater level exceeds a certain threshold value (Gowing et al. 1998; Silvertown et al. 1999; Barber et al. 2004). However, the groundwater level has only an indirect effect on the soil moisture content and thus on the oxygen availability in the root zone, namely by capillary rise (which depends on soil texture). Effects of other variables that determine oxygen stress (e.g. precipitation, potential evapotranspiration, soil temperature and plant characteristics) are not accounted for by groundwater levels. Consequently, explanatory variables that are derived straightforwardly from groundwater levels are rough proxies that do not consider some primary but essential processes, like the oxygen demand of and the oxygen supply to plant roots (Chapter 3).

In this paper, we show the need for and application of climate-proof process-based relationships in habitat distribution models. We focus on oxygen stress and a parameter that integrates vegetation responses to the moisture regime, F_m (the average moisture indicator value, a proxy for plant adaptations to oxygen stress, derived from the species composition at a site). By using F_m we are able to predict the type of plants that grow at a site. If desired, F_m can be translated into the occurrence of specific species groups (Witte et al. 2007). We compare both existing (indirect) measures of oxygen stress and a novel measure of oxygen stress based on plant physiological and soil physical processes, and show their relationships with F_m. The change in F_m is forecast for all relationships under four climate scenarios.

Methods

General approach

We compiled a database with site information on species composition, groundwater level and soil type from a large number of sites in the Netherlands. For each site we computed the mean indicator value of the vegetation for moisture regime, F_m [-] (Witte et al. 2007), considered as the response variable of the vegetation. This variable was correlated with a number of measures of oxygen stress.

First, F_m was regressed against existing measures of oxygen stress with low levels of causality, namely mean spring groundwater level (*MSL* [m above soil surface]) and sum exceedence values (*SEV* [m d]). Additionally, we considered root respiration stress due to anoxic soil conditions (*RS* [kg O_2 m^{-2}]) as a climate-proof measure. *RS* is the most direct and process-based vegetation response to oxygen stress, as respiration is the first process inside a plant that is affected by low oxygen availability in the root zone. In a natural vegetation, plants are adapted to oxygen stress, for instance by means of aerenchyma to transport air (e.g. *Phragmites sp.*), by avoidance of anoxic conditions by growing late and rooting only superficially (*Drosera sp.*) or by the absence of root-like organs (*Sphagnum sp.*). In this way, they avoid oxygen stress. For this reason, we computed *RS* for each site using a reference vegetation, thus assessing a site factor that acts as a measure for the wetness of the soil, independent of the actual vegetation. For this, we applied a recently developed model for oxygen transport that includes relevant plant physiological and soil physical processes in the soil–plant–atmosphere continuum (Chapter 3).

Using the relationships thus obtained, we predicted F_m for four climate scenarios. Finally, we investigated differences in F_m predicted on the basis of *RS* and on the basis of *MSL* and *SEV*.

Data

We used relevés (species composition data from vegetation plots) from the datasets of Runhaar (1989) (188 relevés) and the Netherlands State Forest Service (Beets et al. 2003) (178 relevés). The relevés originate from a wide range of terrestrial vegetation types differing in succession stages, soil type, soil moisture regime, nutrient availability and soil pH. None of the investigated plots had been under the influence of a major change in hydrological conditions. All vegetation relevés were representative of natural habitats in the Netherlands, a small and flat country with a temperate climate that has small spatial differences in meteorological conditions. The mean summer and winter temperature is 289 K and 276 K, respectively, the mean yearly precipitation is 770 mm and the mean yearly reference evapotranspiration (according to Makkink (1957)) is 563 mm.

Fortnightly measurements of groundwater level data were available in or immediately next to each relevé, but only for specific periods and for a limited number of years. However, long time-series of groundwater levels are required to define generally applicable relationships, i.e. relationships that are not biased by temporal deviations in meteorological conditions (Chapter 2). Therefore, the groundwater level series of all relevés of both data sources were extended to the period 1971-2000, which is representative of the actual climatic conditions (Knotters & Van Walsum 1997; Chapter 2) and interpolated to daily values with the Menyanthes impulse response software (Von Asmuth et al. 2002). Menyanthes transforms precipitation and evapotranspiration series (impulse) into groundwater level series (response) (Chapter 2). Daily local meteorological data on air temperature, precipitation and reference evapotranspiration (according to Makkink (1957)) were available from the Royal Netherlands Meteorological Institute (KNMI) from 1970 onwards. We omitted relevés without soil descriptions, relevés with variable soil surface levels and relevés for which a reliable simulation of soil moisture conditions was impossible. Overall, 145 relevés were used for further analysis. The same time series of groundwater levels were used to compute *MSL*, *SEV* and *RS*.

A list of moisture indicator values for plant species tailored to the Netherlands (Witte et al. 2007) was used to compute the arithmetic mean moisture indicator value F_m for each relevé, using all plant species present. Following the findings of Käfer and Witte (2004), no weight was given to species abundance. F_m ranges from 1, for species from aquatic systems, to 4, for species from extremely dry systems (Fig. 4.1).

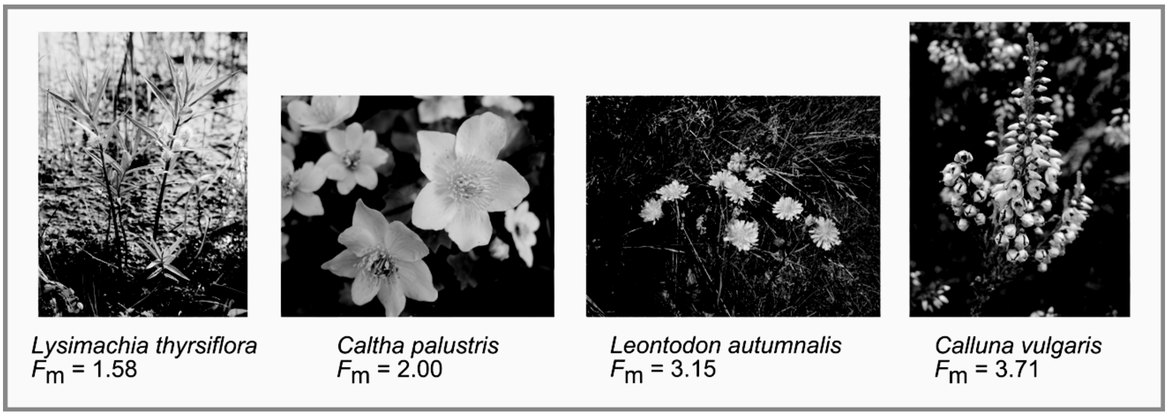

Figure 4.1: Different F_m values, illustrated by characteristic species.

Indirect measures of oxygen stress

Mean spring groundwater level

The mean spring groundwater level, *MSL* [m above soil surface], has been used as a proxy for potential oxygen stress, based on the assumption that the groundwater level at the beginning of the growing season is decisive for plant growth (Runhaar et al. 1997). *MSL* was originally selected as the best predictor of vegetation response compared to mean highest and mean lowest groundwater levels (Runhaar et al. 1997). We calculated the 30-year *MSL* based on the groundwater level on 1 April.

A disadvantage of this measure is that it depends upon the applied assumption on the start of the growing season. Irrespective of the predictive power of the relationship, which has been shown to be high (Runhaar et al. 1997; Chapter 2), it will not be applicable under changing climate conditions, when the growing season will start earlier because of rising temperatures (Menzel et al. 2006; Solomon et al. 2007). Other disadvantages are that this proxy does not account for changes in extreme precipitation events during the growing season, nor for the effects of soil temperature, soil texture or soil organic matter content on oxygen stress.

Sum exceedence values

The sum exceedence value, *SEV* [m d], has been used as a proxy for potential oxygen stress and involves the duration and extent to which the water table rises above a threshold groundwater level during the growing season (March – September inclusive) (Gowing et al. 1998; Silvertown et al. 1999; Barber et al. 2004). Like *MSL*, *SEV*s are directly derived from time series of groundwater levels. Some process knowledge is involved in *SEV*: Silvertown et al. (1999) defined the threshold groundwater level as the groundwater level at which the gas-filled porosity in the topsoil in average summer conditions is less than 10%, which was assumed to be a critical value for sufficient soil aeration (Wesseling & van Wijk 1957). This threshold value depends only on the soil type.

For each growing season, we calculated *SEV* as the cumulative difference between the daily groundwater level and the threshold value according to Silvertown et al. (1999). Only positive differences (i.e. threshold exceedences) were included. A 30-year average *SEV* was calculated.

Similar to *MSL*, this proxy depends on assumptions with regard to the growing season period, and does not account for the effects of soil temperature or soil organic matter content. It does indirectly account for precipitation and potential evapotranspiration (through their effect on the groundwater level).

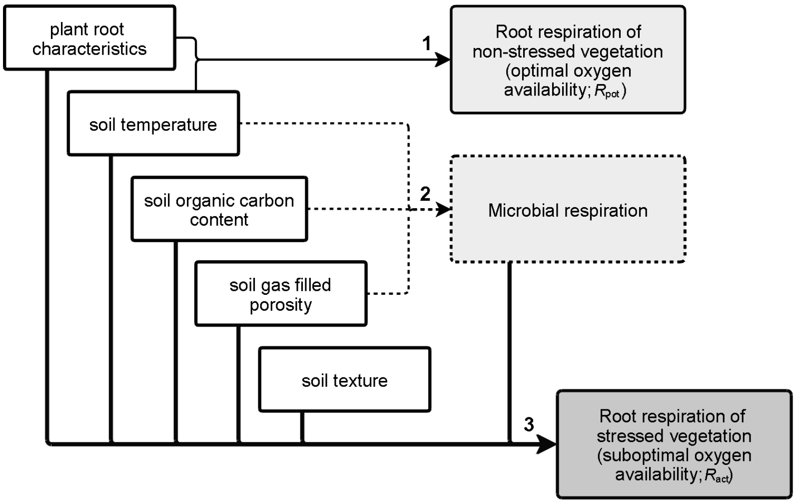

Figure 4.2: Flow chart for the calculation of potential root respiration R_{pot} (1), microbial respiration (2) and actual root respiration R_{act} (3).

Respiration stress

The respiration stress, *RS* [kg O_2 m^{-2}], is based on the most direct vegetation response to soil oxygen deficiency, and involves the relevant processes in the soil–plant–atmosphere continuum. An overview of the structure of the model used is given in Fig. 4.2 and Section "Respiration model". For details of all the equations involved, we refer to Chapter 3.

Respiration model

Soil microbial and root respiration are the main oxygen-consuming processes that take place in the soil. Root respiration is determined by interacting respiratory (i.e. oxygen consuming) and diffusive (i.e. oxygen providing) processes in and to the soil, which were described by generally applied physiological and physical relationships, respectively (see Chapter 3). Under optimal soil aeration and thus non-limiting oxygen availability, plant roots respire potentially. This potential root respiration R_{pot} corresponds to the oxygen demand of plant roots, which is determined only by plant characteristics and soil temperature (Amthor 2000) (Fig. 4.2).

Upon increasingly wetter conditions, however, the gas-filled porosity of the soil decreases and the oxygen availability becomes insufficient for potential root respiration. The method as described in Chapter 3 can be used to calculate the actual root respiration R_{act} for a given gas-filled porosity. The respiration reduction, R_{red}, due to wetter conditions determines the respiration stress.

Unfortunately, the experimental information that allows validation of our model is very limited. The only information we found, in which soil respiration was measured for a grass species at a range of temperatures, soil moisture contents and otherwise constant conditions, concerns measured soil respiration rates for a C_4-grass, *Panicum virgatum*

(Tufekcioglu et al. 1998; Raich & Tufekcioglu 2000). This is still appropriate to validate our model as the respiration rates of C_4 and C_3 plants are highly similar (Byrd et al. 1992). We simulated both microbial and root respiration based on the given soil type (fine loam), soil organic carbon content (2.83%), soil moisture content, soil temperature and plant root characteristics (Ma et al. 2000; Chapter 3). No parameter optimization was applied. Fig. 4.3 shows that our simulations describe the measured soil respiration well, and clearly demonstrates that soil respiration strongly depends upon soil temperature.

Root respiration reduction vs MSL and SEV

To test whether the simulation of root respiration actually surpasses *MSL* and *SEV* in representing the occurrence of oxygen stress for plant roots, we compared simulated respiration reduction for situations with a low soil temperature and low soil aeration vs high soil temperature and low aeration. By definition, neither *MSL* nor *SEV* includes the effect of soil temperature. Only our new respiration model describes the combined effect of a low aeration and a high temperature, a condition that is expected to occur more frequently in a future climate (Van den Hurk et al. 2006; Solomon et al. 2007). Experiments by Thompson and Fick (1981) and Tsukahara and Kozlowski (1986) demonstrated an increased plant root stress under these conditions. The combined effect of a shallow groundwater level and a high temperature reduced considerably the root dry weight (Thompson & Fick 1981) and the root growth rate (Tsukahara & Kozlowski 1986) compared to the reductions for a shallow groundwater level and a low temperature. The observed increased plant-root stress with increased soil temperature corresponds to an increased root respiration reduction. Neither *MSL* nor *SEV* reflects this increased root stress due to an increased soil temperature, and both will thus underestimate the effect of climate change on root oxygen stress. Thus, our new approach is an improvement

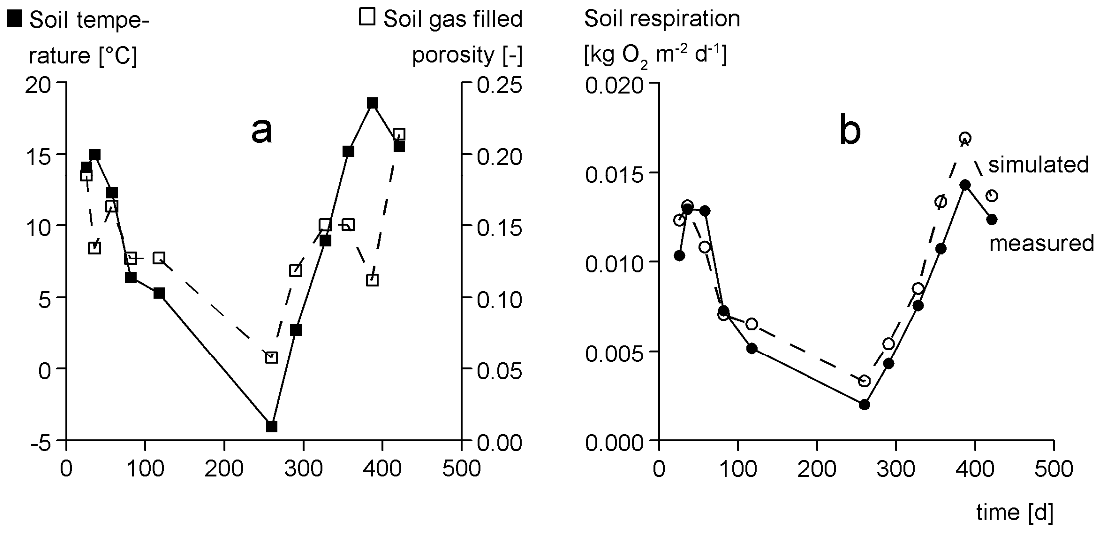

Figure 4.3: Measured (Raich & Tufekcioglu 2000) and simulated (this research) soil respiration (b) for *Panicum virgatum* for given soil temperature and soil moisture content (a). The presented graph is partly modified after Raich and Tufekcioglu (2000).

compared to using *MSL* or *SEV*.

Application of the respiration model in this research

Respiration stress was assessed as a site characteristic (like *MSL* and *SEV*) by applying plant characteristics of a reference vegetation, defined as a temperate natural grassland not adapted to oxygen stress (Chapter 3). This site characteristic reflects the oxygen status of the soil, independent of the actual (adapted) vegetation. Unlike the reference vegetation, the oxygen stress of plants that are adapted to wet and anoxic soils is practically zero, and therefore no relationship with F_m is to be expected. So, we did not attempt to assess the respiration rates of the actual vegetation at a site, but defined a process-based proxy for the wetness of the soil to which the actual vegetation is adapted, instead. This proxy is the oxygen stress of a hypothetical reference vegetation.

Simulation of R_{act} for the reference vegetation requires daily soil temperature and soil moisture contents in the root zone. These variables were simulated with SWAP (Van Dam et al. 2008), including an improved calculation procedure for nearly saturated conditions (Schaap & van Genuchten 2005; Cirkel et al. Unpublished results), for the period 1971-2000. In the original model as described in Chapter 3, the soil was considered to consist of a single soil compartment and the top boundary for soil oxygen diffusion was given by the oxygen concentration in the atmosphere. Here, we applied the model to a complete soil profile, consisting of 16 layers to allow for layer-specific soil physical properties, moisture content and temperature. Consequently, the oxygen concentration in the gas phase of the soil at the bottom of the upper layer was used as the top boundary condition of the lower layer. The difference between R_{pot} and R_{act} was calculated for each soil layer separately. These differences were summed, resulting in a daily value of respiration reduction for each site. As a measure of oxygen stress, we used the yearly maximum reduction in respiration across a 10-day period, averaged over 30 years. This measure (*RS*) enables us to account for the effects of both extreme rainfall events and high temperatures, as especially the combination of these conditions affects vegetation (e.g. Sojka et al. 1972; Drew 1983) and this combination is predicted to increase in the near future (Van den Hurk et al. 2006).

The meteorological input consisted of precipitation and reference crop evapotranspiration data corresponding to those used for the simulations of groundwater levels (Section "Data"), and temperature. Groundwater levels served as the bottom boundary conditions. Soil physical parameters according to Van Genuchten (1980) were derived from a national soil database (Wösten et al. 2001).

Climate scenarios and resulting changes in moisture regime

We considered four climate scenarios for the year 2050 (Van den Hurk et al. 2006) to predict changes in F_m. These scenarios, which were developed by the Royal Netherlands Meteorological Institute (KNMI), are based on general circulation model simulations published in the Fourth Assessment Report of the IPCC (Solomon et al. 2007) and

Table 4.1: Climate scenarios; Effects of climate change on temperature, precipitation and evapotranspiration in the Netherlands for four climate scenarios (Van den Hurk et al. 2006)

	Scenario			
Variable	G	G+	W	W+
summer (June-July-August)				
mean temperature K	+0.9	+1.4	+1.7	+2.8
mean precipitation %	+2.8	-9.5	+5.5	-19.0
wet day frequency %	-1.6	-9.6	-3.3	-19.3
precipitation on wet day %	+4.6	+0.1	+9.1	+0.3
reference evapotranspiration %	+3.4	+7.6	+6.8	+15.2
winter (December-January-February)				
mean temperature K	+0.9	+1.1	+1.8	+2.3
mean precipitation %	+3.6	+7.0	+7.3	+14.2
wet day frequency %	+0.1	+0.9	+0.2	+1.9
precipitation on wet day %	+3.6	+6.0	+7.1	+12.1

include changes in temperature, precipitation and reference crop evapotranspiration (Table 4.1). The G and W scenarios comprise a +1 K and +2 K global temperature increase, respectively, but with unchanged air circulation patterns in summer and winter. The G+ and W+ comprise the same global temperature increases, but the '+' indicates that the air circulation patterns changed (Van den Hurk et al. 2006). We transformed time series from 1971-2000 of these three climate variables to the 2050 climate, using transformation software supplied by the KNMI (Bakker & Bessembinder 2007). In addition, based on Kruijt et al. (2008), we decreased evapotranspiration values by 2% to account for the higher water use efficiency of plants at increased CO_2 levels in 2050.

Future precipitation and evapotranspiration were used to simulate future groundwater levels in Menyanthes (see Section "Data"). Subsequently, *MSL* and *SEV* were calculated. Future soil moisture and soil temperature profiles were created with SWAP for each scenario, using as input the future air temperature, precipitation, reference crop evapotranspiration and groundwater level series. Finally, future respiration stress *RS* was simulated on the basis of these soil moisture and soil temperature profiles.

Statistical analysis

We defined relationships between each of the explanatory variables (*MSL*, *SEV* and *RS*) and F_m through regression. First, we checked whether a linear regression model was suitable. If not, we tested non-linear regression equations. The optimal regression equation was selected based on the Akaike information criterion. Non-linear regression models that were conceptually incorrect, for example because of local extremes, were not considered. For comparison of the predictive power among explanatory variables, we applied both the Pearson correlation coefficient r between observed and predicted F_m values and the root mean squared error (*RMSE*) of the predictions.

For each climate scenario, we tested whether predicted F_m values based on the relationships for indirect explanatory variables (*MSL* and *SEV*) were significantly different from the predicted F_m values based on *RS*. To do so, we analysed whether the slope between two sets of F_m values deviated significantly ($P<0.05$) from 1 in a linear regression with intercept 0.

Results

Relationships between proxies for oxygen stress and F_m

The relationship between mean spring groundwater level *MSL* and F_m was best described by a sigmoid regression model (Fig. 4.4a), as it levels off at both deep and shallow groundwater levels (Witte & Von Asmuth 2003). *MSL* is not discriminating for higher F_m values, that is, for vegetation adapted to dry conditions. It was remarkable that the F_m values at deeper groundwater levels were located very close to the horizontal asymptote. A much larger spread was expected here, as at dryer sites the soil moisture regime is highly determined by soil texture. Unfortunately, at deep groundwater levels the dataset included relevés only on loamy fine sands, which resulted in F_m values that were very close to the horizontal asymptote. Had relevés on other soils (e.g. coarse sand and heavy loam) been involved, the spread around the asymptote would have been more representative of all soil types that are present in the Netherlands, and R^2_{adj} would have been lower (*RMSE* higher).

The relationship between sum exceedence value *SEV* and F_m (Fig. 4.4b), showed a vertical asymptote at $SEV \approx 0$. This relationship was best described by a power function. Most important is the shallow slope for higher *SEV* values, representing high levels of oxygen stress. The proxy apparently does not differentiate much in the range of moderate to severe oxygen stress.

The relationship *RS* vs F_m (Fig. 4.4c) was best described by a linear regression model, with the F_ms rather evenly distributed across the whole range of *RS*. The predictive power of the relationship was high and comparable to the those based on *MSL* and *SEV*.

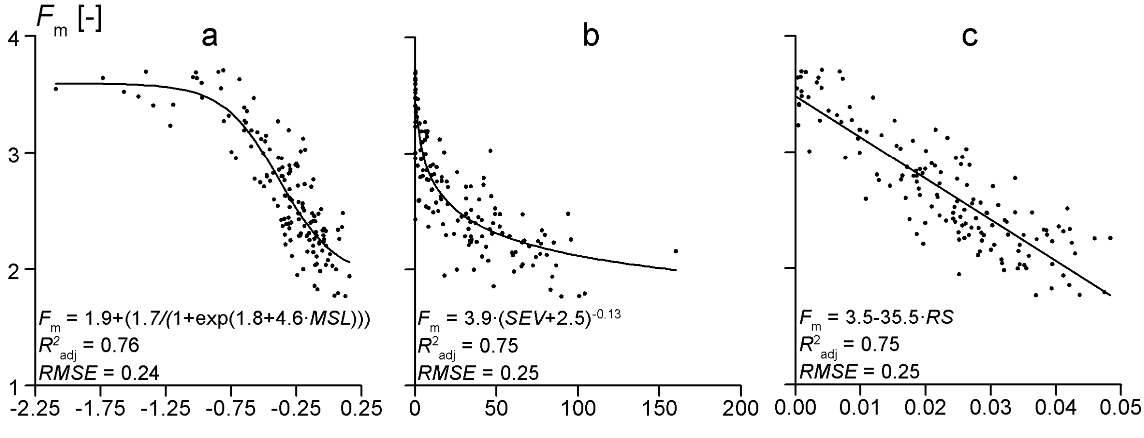

Figure 4.4: Vegetation characteristic F_m as function of root oxygen stress, represented by the indirect measures (a) mean spring groundwater level *MSL* and (b) sum exceedence value *SEV*, and by the direct measure (c) respiration stress *RS*. Each dot represents a relevé.

Vegetation predictions for different climate scenarios

All climate scenarios predicted an increase in temperature and extreme rainfall events (Table 4.1). Consequently, as demonstrated by the experiments by Thompson and Fick (1981) and Tsukahara and Kozlowski (1986) (see Section "Root respiration reduction vs *MSL* and *SEV*"), root oxygen stress was expected to increase, resulting in lower predicted F_{m} values. However, in none of the indirect measures was the increase in oxygen stress apparent, in contrast to the direct measure (Fig. 4.5). This difference was also reflected in the predicted F_{m} values (Fig. 4.6). There are large differences between future F_{m} predictions that are based on direct measures and those that are based on indirect measures of root oxygen stress for all climate scenarios (Fig. 4.7). Using *RS* as predictor consistently led to more oxygen stress, especially for low F_{m} values. A predicted $F_{\mathrm{m}}^{2050}(RS)$ of 1.8 (the lowest F_{m} value in the dataset in the present climate) deviates from $F_{\mathrm{m}}^{2050}(MSL)$ and $F_{\mathrm{m}}^{2050}(SEV)$, both of which had corresponding values of 2.1 for each of the climate scenarios (Fig. 4.7). The predictions based on *MSL* and *SEV* were significantly higher (i.e. drier) than those based on *RS* for each scenario.

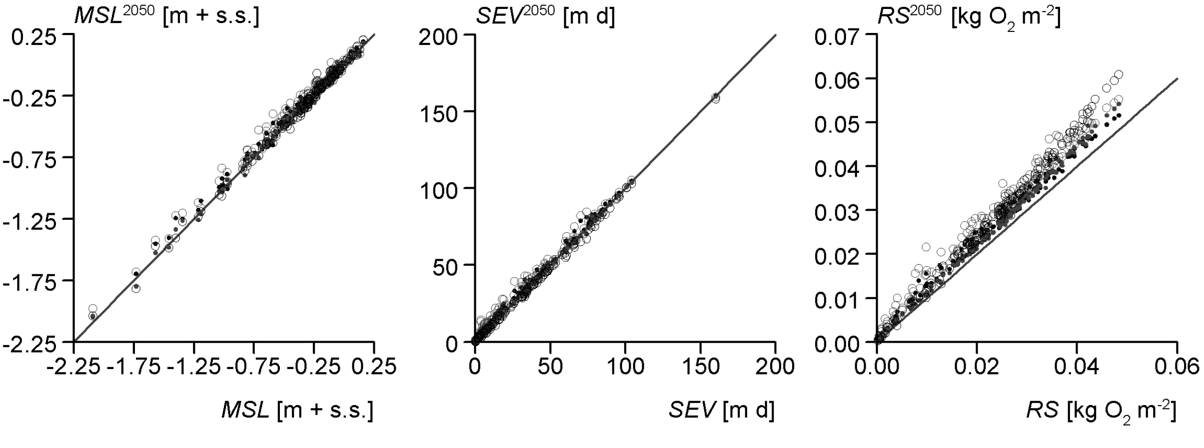

Figure 4.5: *MSL*, *SEV* and *RS* for the actual climate (horizontal axis, same as in Fig. 4.4) against calculated values for the climate scenarios G (●), G+ (●), W (○) and W+ (○) (Table 4.1). The line represents the 1:1 line. Each dot represents a relevé. Both *MSL* and *SEV* hardly change with a changing climate. The change in *RS* represents the expected pattern due to the increase of extreme precipitation events in combination with high temperatures.

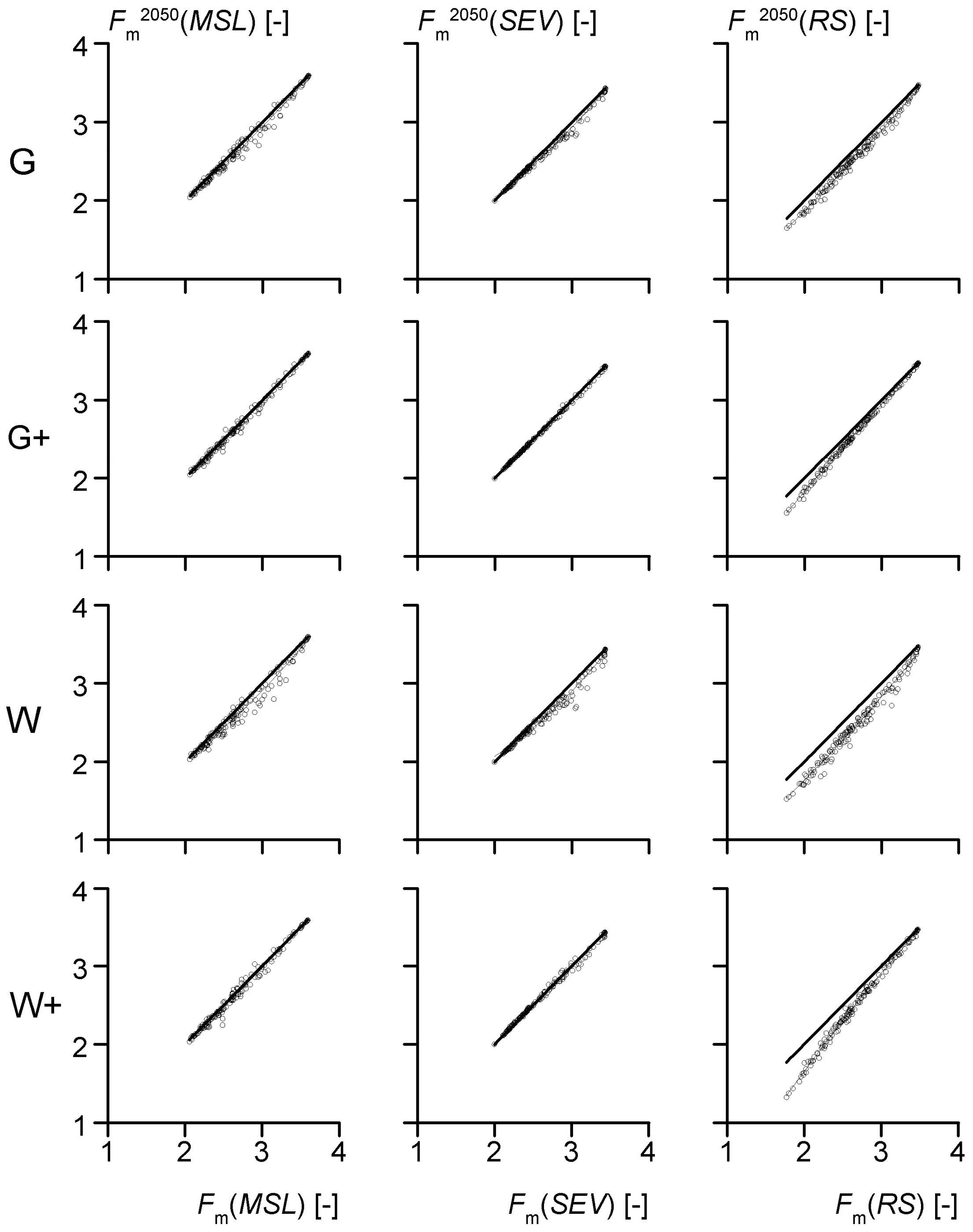

Figure 4.6: Predicted F_m values based on the relationships between *MSL*, *SEV* and *RS* and F_m as presented in Fig. 4.4 for the actual climate (x-axis) vs the climate scenarios G, G+, W and W+ (y-axis). The line represents the 1:1 line. Each dot represents a relevé. Both predictions based on *MSL* and *SEV* hardly change with a changing climate. The change in predictions based on *RS* represents the expected pattern due to the increase of extreme precipitation events in combination with high temperatures.

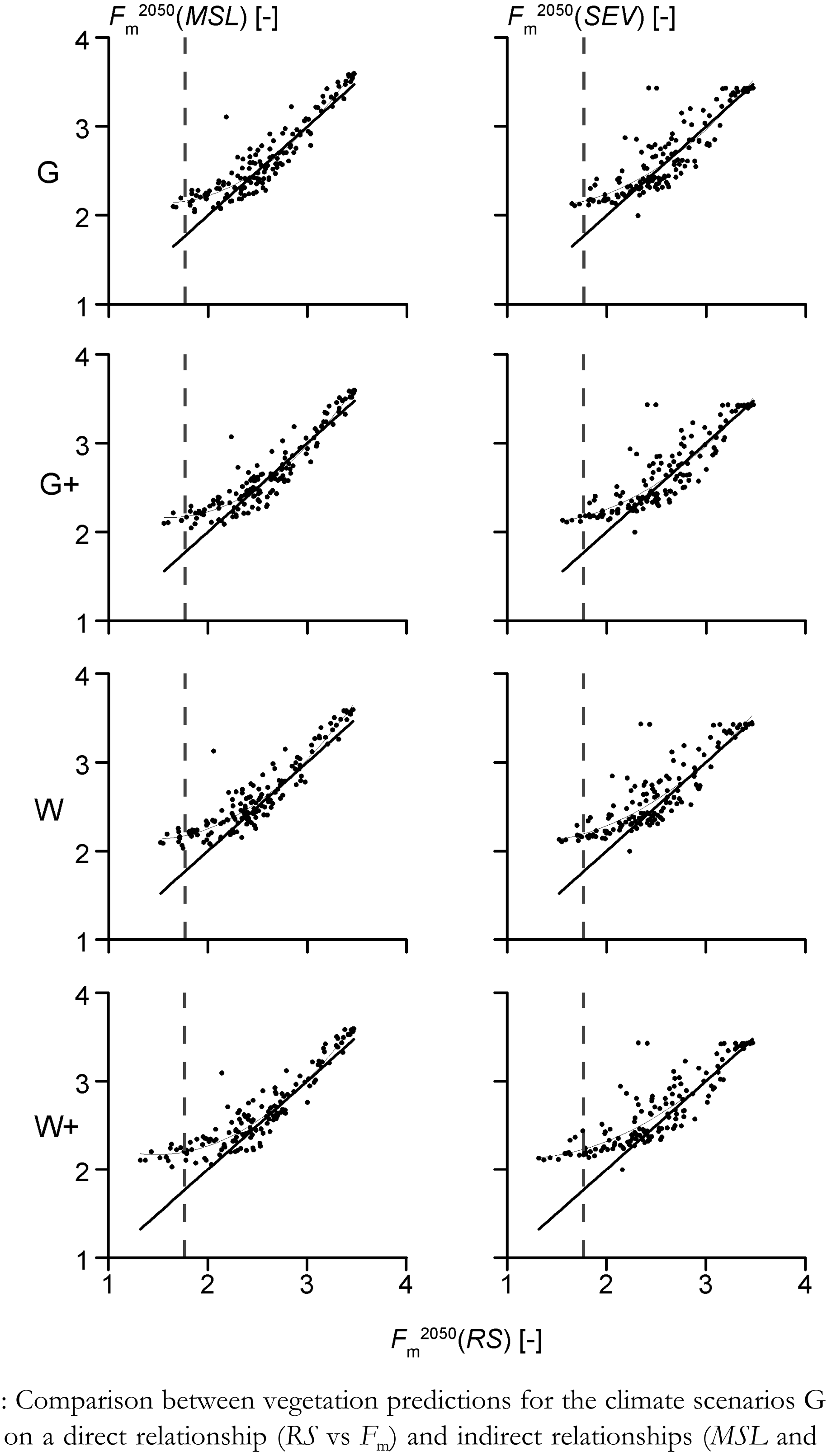

Figure 4.7: Comparison between vegetation predictions for the climate scenarios G, G+, W and W+ based on a direct relationship (*RS* vs F_m) and indirect relationships (*MSL* and *SEV* vs F_m). Each dot represents a relevé. The lines represent the 1:1 lines for the predicted $F_m^{2050}(RS)$ values. Some $F_m^{2050}(RS)$ values fall outside the regression interval (given by the vertical line). However, large deviations occur at F_m values that fall within and outside the regression interval.

Discussion

Climate-proof relationship between oxygen stress and vegetation

Our analysis clearly illustrates that there are systematic differences between vegetation predictions for future climatic conditions that are based on direct proxies (root respiration stress; *RS*) and those that are based on indirect proxies for oxygen stress (mean spring groundwater level *MSL* and sum exceedence value *SEV*) (Fig. 4.7), even though these proxies perform equally well in describing present-day vegetation patterns (Fig. 4.4).

For the predictions of changes in vegetation composition in a changing climate, we propose using our newly developed relationship between oxygen stress and vegetation composition, since it is based on relevant plant physiological, soil physical and climate-dependent processes. We focused on root respiration reduction, which is the most direct plant physiological response to oxygen stress. Plants will suffer from oxygen stress when soil oxygen availability, due to high soil moisture contents, is insufficient to provide plant roots with a sufficient amount of oxygen. This demand depends on temperature, and thus on climate. As a result, they will be outcompeted by species that are better adapted to oxygen stress (lower F_m).

For the calculation of *RS*, we selected the period with the highest oxygen stress for each year by calculating the maximum cumulative respiration reduction in a 10-day period. However, using a period of, for example, 7 or 14 days led to highly similar $F_m^{2050}(RS)$ values for each of the climate scenarios (average absolute difference 0.01 (±0.01)); thus, the measure is robust for the period chosen. We applied the respiration model to a reference vegetation to obtain a site characteristic, independent of the actual vegetation. The yearly average simulated soil respiration rates (for our reference vegetation, defined as a temperate natural grassland) were 1.47 and 1.06 kg O_2 m^{-2} yr^{-1}, based on R_{pot} and R_{act}, respectively. These simulations correspond reasonably well to measured average values for temperate grasslands (1.18 kg O_2 m^{-2} yr^{-1}; Raich & Schlesinger 1992) and respiration ranges across different terrestrial biomes (0.1 to 3.5 kg O_2 m^{-2} yr^{-1}) in general (Raich & Schlesinger 1992).

We based our current climate *RS* vs F_m relationship on a combination of two very detailed datasets, both of which were originally specifically compiled to analyse soil moisture–vegetation relationships (Runhaar 1989; Beets et al. 2003). Unfortunately, such a specific combination of accurate data is presently unavailable for different climates, obstructing the possibilities for validating the predicted F_m values of future climates. Nevertheless, there are several arguments that support the assumption that *RS* actually leads to more reliable vegetation predictions than *MSL* or *SEV*. First, the oxygen consumption of and supply to plant roots strongly depend on soil temperature, a variable that is incorporated only in *RS* (Section “Root respiration reduction vs *MSL* and *SEV*”). A combination of low soil temperatures (e.g. outside the growing season) and low soil oxygen availabilities will hardly affect plant functioning, and coincides with a low daily respiration reduction R_{red}. During the growing season, however, soil temperatures will be higher and low soil oxygen availabilities will thus cause a relatively high R_{red}. This combination is known to be strongly detrimental to plant survival (e.g. Sojka et al. 1972; Drew 1983). Second, both *MSL* and *SEV* require assumptions on the starting date and length of the growing season, which will change with the changing climate. Third, extreme precipitation events are known to have a major effect on vegetation composition, and are more directly incorporated in *RS*. Fourth, unlike *RS*, the relationship of *MSL* and that of *SEV* vs vegetation composition have to be recalibrated for all new environmental conditions, which is impossible for a future climate.

These arguments support our assumption that vegetation predictions based on relationships that have relatively low levels of causality (i.e. indirect measures) will be insufficient to predict the vegetation response under future climatic conditions. This analysis ratifies the need for causal relationships in habitat distribution models.

Naturally, adding process knowledge may be at the cost of the goodness-of-fit of derived relationships. Assumptions on model parameters, schematization of relevant processes and numerical discretizations in our detailed simulation of soil moisture, soil temperature and soil oxygen potentially introduces errors. Despite this drawback, the explained variance of the relationship between F_m and *RS* is comparable to the explained variances of the relationships between F_m and *MSL* and *SEV*, which indicates that *RS* is a robust predictor for F_m. This is also confirmed by the strong predictive power of *RS* across the complete range of F_m values, which indicates that we considered the main processes that are relevant to vegetation composition. In addition, it shows that respiration stress is a discriminating factor also at relatively dry sites ($F_m = 3 - 4$) (Appendix 4A).

The large differences between $F_m^{2050}(RS)$, $F_m^{2050}(MSL)$ and $F_m^{2050}(SEV)$ (Fig. 4.7) were not caused by the choice of the non-linear regression models for *MSL* and *SEV*. For each of these measures, an alternative design by a linear regression without asymptotes based on $F_m < 3.0$ led to highly similar differences for low F_m values. The differences are thus robust to the regression we used.

Implications of indirect vs direct relationships

Our analysis strongly suggests that indirect measures of oxygen stress underestimate the increased oxygen stress under changing climatic conditions at a given future groundwater level dynamics. These differences in calculated oxygen stress occurred despite the use of the same groundwater levels as input. In contrast to *RS*, especially the highest values for *MSL* and *SEV* (thus highest oxygen stress) are almost equal to those for the actual climatic conditions (Fig. 4.5). However, especially at shallow groundwater levels, large shifts in oxygen stress are expected with climate change, as the combination of a higher soil moisture content and an increased temperature will lead to increased oxygen stress (e.g. Sojka et al. 1972; Drew 1983).

Consequently, both *MSL* and *SEV* likely predict higher F_m values (i.e. drier vegetation) than *RS*, and there are large differences in predicted vegetation composition between the indirect and the direct measures (Figs. 4.6 and 4.7). This might have major consequences for the interpretation of habitat distribution models. For example, according to our findings differences of 0.5 on the F_m scale are expected. Under the actual climate, this comprises a difference in *MSL* of about 0.25 m, which in turn determines the occurrence vs the absence of, for example, *Molinea* meadows or *Sphagnum* dominated bogs (Runhaar et al. 2003). Therefore, we believe that indirect measures in habitat distribution models lead to systematic and ecologically significant errors in the evaluation of the impact of climate change on vegetation. Consequently, conservation policies might fail and international obligations might not be met.

Application in ecological prediction models

Because of the high level of causality and the use of a site-independent reference vegetation, our novel measure to characterize oxygen stress *RS* is applicable to vegetation types and regions that differ from those considered in this research. The process-based approach makes superfluous the calibration of the *RS* vs F_m relationship in other regions. By defining the stress of a reference vegetation, specific information about the actual vegetation characteristics at a site is not required. This increases the applicability of our approach, because databases that combine the required environmental data and actual vegetation information are currently lacking (Section "Climate-proof relationship between oxygen stress and vegetation").

Given the demonstrated ecological significance of climate-proof relationships, incorporating them into habitat distribution models is strongly advised. However, the calculation of *RS* requires extensive simulations. This may be considered undesirable or unfeasible. For the calculation of R_{act}, we therefore constructed repro functions that reproduce the behaviour of the full respiration model (Appendix 4B). The application of these repro functions simplifies and speeds up the calculations considerably. Still, the use of repro functions does not diminish the amount of soil data that is needed as input for the simulations. At least some approximations of soil type, soil moisture and soil temperature are needed. However, even when only rough descriptions of these parameters are available, *RS* can be calculated. The model predictions thus obtained correspond quite well to the predictions that are based on the detailed simulations (Appendix 4B).

Conclusions

We have demonstrated that the indirect explanatory variables for oxygen stress that have been used to predict vegetation characteristics are insufficient to analyse the effect of climate change on vegetation composition. Essential parameters that influence the occurrence of oxygen stress and that are expected to change in the future climate – namely higher temperatures and extreme rainfall events – are insufficiently accounted for. Hence, we propose a direct relationship between oxygen stress and vegetation characteristics in terms of respiration stress, which can be calculated for all possible climate change scenarios. As this approach thus allows the effects of an increasingly simultaneous occurrence of low soil aeration and high temperature in a changing climate to be taken into account, the direct measure *RS* shows ecologically significant differences in predicted vegetation characteristics compared to the correlative measures *MSL* and *SEV*.

Our novel measure of root oxygen stress is an important quantitative step following the recommendations of previous studies (Franklin 1995; Guisan & Zimmermann 2000) to define relationships with high levels of causality that are indispensable for robust vegetation predictions in a changing climate.

Acknowledgements

This study was carried out in the framework of both Project A1 'Biodiversity in a changing environment: predicting spatio–temporal dynamics of vegetation' of the Dutch national research program Climate Change and Spatial planning (www.klimaatvoorruimte.nl) and the joint research program of the Dutch Water Utility sector. We wish to thank Han Runhaar and Staatsbosbeheer for providing their valuable data.

Appendix 4A: Oxygen stress at groundwater independent sites

Fig. 4.4c illustrates that F_m is related to *RS* over the whole range of F_m-values. This indicates that respiration stress is a discriminating site factor at relatively dry sites (F_m= 3 – 4) too. Apparently, at deep groundwater levels the soil moisture conditions can incidentally be that high, that oxygen stress occurs. To investigate this, we calculated respiration stress for relevés that are groundwater independent, i.e. the groundwater levels are such deep that they do not influence the soil moisture conditions in the root zone by capillary rise. We used 17 relevés with soil descriptions from Jansen et al. (2000) and simulated soil moisture and soil temperature profiles with SWAP.

The groundwater independent sites appeared to fit nicely within the relationship between *RS* vs F_m, as derived from groundwater dependent sites (Fig. 4A.1). This can be explained by a negative correlation between oxygen stress and moisture stress: the finer the soil texture, the higher the oxygen stress, but the lower moisture stress as well. However, the F_m-values at the groundwater independent sites seem to be somewhat higher (i.e. drier) than at groundwater dependent sites, which indicates the absence of capillary rise at groundwater independent sites.

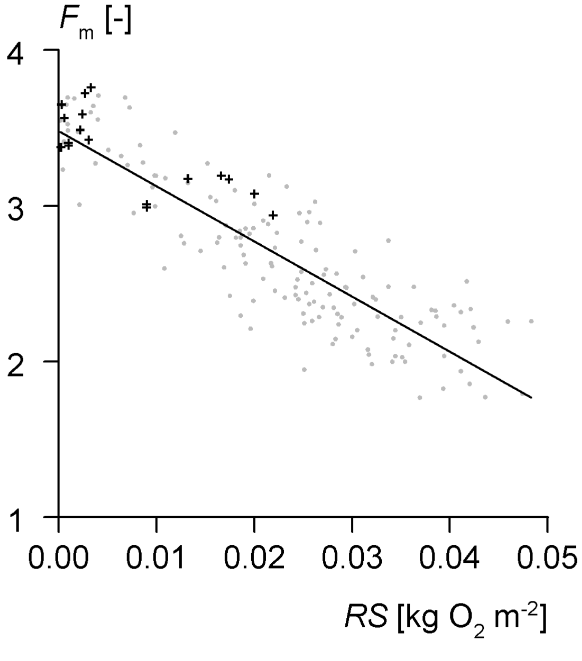

Figure 4A.1: Relationship between *RS* and F_m as given in Fig. 4.4. The crosses represent simulations for groundwater independent sites.

Appendix 4B: Shortcuts for the calculation of *RS*

The advantage of simulated daily respiration reduction as measure of oxygen stress is that relevant plant physiological and soil physical processes are considered in detail. The disadvantage is that the procedure is quite laborious en time-consuming. Therefore, we also calculated R_{act} by repro functions (Chapter 3) that reproduce the behaviour of the full respiration model. These repro functions speed up the simulations considerably.

The repro functions are based on the plant characteristics of the reference vegetation (Section "Application of the respiration model in this research") and are defined for all soil types of the Staring-series (Wösten et al. 2001). The main difference with the full model is that the top boundary condition is always defined by the atmospheric oxygen concentration C_{atm}. Consequently, the distance over which oxygen diffusion is calculated (z) is given with respect to the soil surface. Therefore, we simulated R_{act} in a certain soil layer based not on the gas filled porosity of the specific layer, but on the arithmetic mean gas filled porosity of the layer and the upper layers instead. The resulting respiration stress is denoted RS_{repro}.

In order to further increase the practical applicability of the computation, we investigated whether rough approximations of the input parameters might still result in acceptable model predictions. The following approximations were made: a) both the calculations of R_{pot} and R_{act} are based on the air temperature instead of the simulated soil temperatures, b) the soil characteristics are only defined by the most upper soil layer and c) hydrostatic equilibrium is assumed to describe the soil moisture conditions and thus gas filled porosities in each of the soil layers. Based on the data thus obtained, we simulated

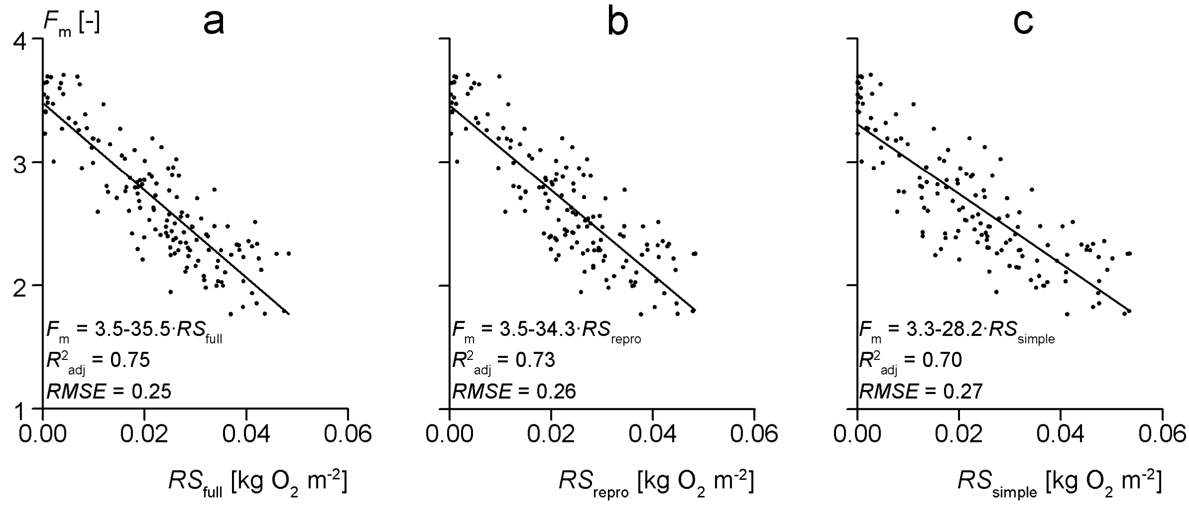

Figure 4B.1: (a) relationship of F_m with *RS*, based on detailed SWAP-simulations for soil moisture and soil temperature and the full oxygen stress module; (b) relationship based on detailed SWAP-simulations, but for the repro functions for R_{act} (and herewith *RS*) derived from the oxygen stress module; (c) relationship for the repro functions, but based on hydrostatic equilibrium conditions and on air temperature.

R_{act} with the repro functions as described above. The resulting respiration stress is denoted RS_{simple}.

The relationship RS_{repro} vs F_m (Fig. 4B.1b) resulted in an approximately similar regression line as RS_{full} vs F_m (Fig. 4B.1a) though, the predictive power of the relationship is a bit lower. The relationship RS_{simple} vs F_m (Fig. 4B.1c) resulted in a relationship with a relatively low predictive power. The assumption of hydrostatic equilibrium to describe the soil moisture conditions leads to an underestimation of the respiration stress at relatively dry sites. Consequently, both the slope and the intercept of the regression line are lower than for RS_{full} vs F_m (Fig. 4B.1a).

For each of the climate scenarios holds that predicted $F_m^{2050}(RS_{repro})$ and $F_m^{2050}(RS_{simple})$ values are not significantly different from predicted $F_m^{2050}(RS_{full})$ values.

CHAPTER

5

Intensifying interacting water-related stress amplitudes will push endangered plant species over the edge

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Submitted

Abstract

In the past century, rainfall variability, temperature and atmospheric CO_2-concentration have increased significantly and they are expected to increase even more in the near future (Karl et al. 1995; Dai et al. 1998; Easterling et al. 2000; Weltzin et al. 2003; Solomon et al. 2007; Knapp et al. 2008). The consequently increased dynamics in soil moisture contents (Fay et al. 2008; Knapp et al. 2008), together with increased plant physiological demands for both oxygen and water (Dai et al. 1998; Chapter 4), might lead to an increased variability in wet and dry extremes of plant stresses (Knapp et al. 2008), i.e. of oxygen and water stress, respectively. The correlative nature of previous studies and their focus on one stress only (Easterling et al. 2000; McCarty 2001; Levine et al. 2008) has hampered understanding the causal effect of climate change on plant species composition through changes in oxygen and water stress. Here we use process-based simulations of oxygen and water stress to show that both stresses will intensify in a future climate (Knapp et al. 2008) and that they will increasingly coincide, i.e. both stresses will occur within the same vegetation. This intensification and increased coincidence of stresses is shown to negatively affect the future presence of currently endangered plant species, while a decrease is not apparent for common species. Consequently, the species that are already threatened under the current climate will suffer most from climate change.

Introduction

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), and to affect vegetation composition (Easterling et al. 2000; Porporato et al. 2004; Knapp et al. 2008; Levine 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). In temperate climates, soil moisture, in concert with nutrient availability and soil acidity, is the most important environmental filter in determining local plant species composition (Weltzin et al. 2003; Witte et al. 2007), as it determines the availability of both oxygen and water to plant roots (Knapp et al. 2008). These resources are indispensable for meeting the physiological demands of plants. We hypothesized that the predicted increased variability in soil moisture contents (Fay et al. 2008; Knapp et al. 2008) together with increased physiological demands for both oxygen and water (Dai et al. 1998; Chapter 4) might lead to an increased variability in plant stress and therefore bring about a higher incidence of lethal conditions and a strongly reduced competitive ability. As such variable stress conditions are expected to especially affect species with narrower physiological tolerance ranges (Parmesan et al. 2000), future habitats might become inappropriate for currently endangered species.

Until now, both large-scale (global) and plot-scale effects of climate change through soil moisture on plant species composition have been investigated only through indirect environmental measures (Easterling et al. 2000; McCarty 2001; Levine et al. 2008) such as mean annual 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 (Chapter 4). Moreover, researchers only determined effects of one of the moisture related stresses, i.e. either oxygen or water stress. The neglect of causal relationships between climate change and simultaneous variation in oxygen and water stress, may explain the contradictory findings regarding the effects of soil moisture dynamics on species composition described so far (Knapp et al. 2002; Drake & Lodge 2004; Adler & Drake 2008). Here we have overcome these limitations by a novel modelling approach to quantify the occurrences of both oxygen and water stress.

In order to quantify oxygen and water stress with causal measures, one should focus on interacting meteorological, soil physical, microbial, and plant physiological processes in the soil-plant-atmosphere system. The first physiological process inhibited at high soil moisture contents is plant root respiration, i.e. oxygen consumption in the roots, which responds to increased temperatures. High soil moisture contents hamper oxygen transport from the atmosphere, through the soil -where part of the oxygen additionally disappears by soil microbial oxygen consumption (Chapter 3) - and to the root cells. Reduced respiration negatively affects the energy supply to plant metabolism. Plant transpiration, which responds to increased temperatures and atmospheric CO_2-concentrations, is the first physiological process that will be inhibited by low soil moisture contents (Porporato et al. 2004), negatively affecting both photosynthesis and cooling. As both the supply and demand of oxygen and water depend strongly on the prevailing meteorological conditions, both oxygen and water stress should be calculated dynamically in time to capture climate change effects. Our modelling approach describes the relevant interacting processes in detail, in order to analyse accurately whether climate change in fact intensifies both the wetness and drought-related plant stresses. In pursue of a recently set conceptual framework on the effects of increased rainfall variability on moisture-related plant stresses (Knapp et al. 2008), we calculated process-based oxygen and water stress for 185 terrestrial vegetation plots from a variety of natural xeric, mesic and hydric (Knapp et al. 2008) habitats in a temperate climate, i.e. the Netherlands. For each vegetation plot, oxygen and water stress were calculated for a hypothetical reference vegetation (Chapter 3) (Appendix 5A) as the reduction in potential rates of respiration and transpiration due to a surplus or shortage of soil moisture, respectively (see Section “Methods Summary”).

Results and Discussion

Model results indicate that there is a shift in habitat conditions towards more extreme coincidence of plant oxygen and water stress under future climatic conditions (Fig. 5.1). In vegetation plots with either oxygen or water stress, the degree of stress was calculated to intensify under the future climate. In vegetation plots where the stresses presently coincide (50% of the dataset has both oxygen and water stress larger than zero), however, both stresses will intensify simultaneously in the future climate (the arrows in Fig. 5.1 that move away from both axes). More severe wet and dry extremes will thus co-occur within the same vegetation plot. Consequently, there is an increased coincidence of intensified plant stresses, which is visualized by the coloured areas that encompass 90% of the vegetation plots (Fig. 5.1). This increase is large enough to result in the development of new niches, which may be potential habitats for new species.

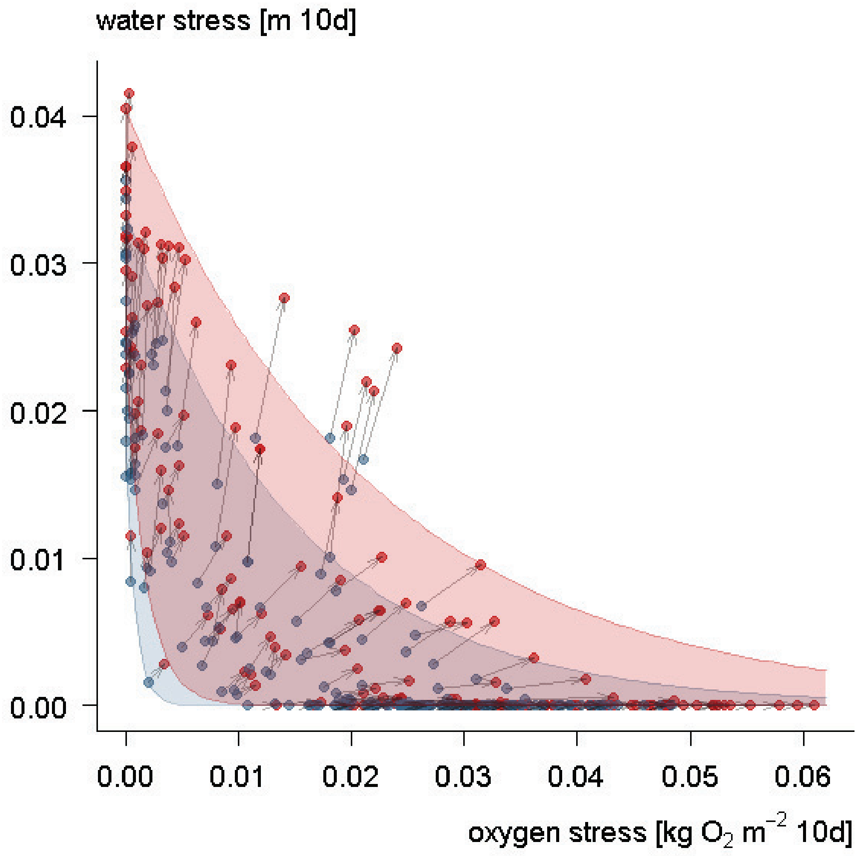

Figure 5.1: Oxygen stress and water stress for 185 vegetation plots for the current (blue) and future climate (red). Arrows indicate the direction of climate-induced shift for each vegetation plot. The polygons show the area enclosed by the 5 and 95% regression quantiles (Koenker & Basset 1978), thus encompassing 90% of the data points. Under the future climate this area represents both an increased coincidence and intensification of oxygen and water stress.

To investigate the habitat suitability of coinciding plant oxygen and water stress for currently endangered species, we first determined the current number of Red List species (Van der Meijden et al. 2000) within each vegetation plot. Then we related current oxygen and water stress to this number through quantile regression (Koenker & Basset 1978; Cade et al. 1999) to determine the number of endangered species that could potentially occur under specific stress conditions (see Section "Methods Summary"). This analysis demonstrates that under the current climate, the coincidence of oxygen and water stress is coupled to a significantly lower potential number of endangered plant species within a vegetation plot (plane and projected isolines in Fig. 5.2). There is a highly significant

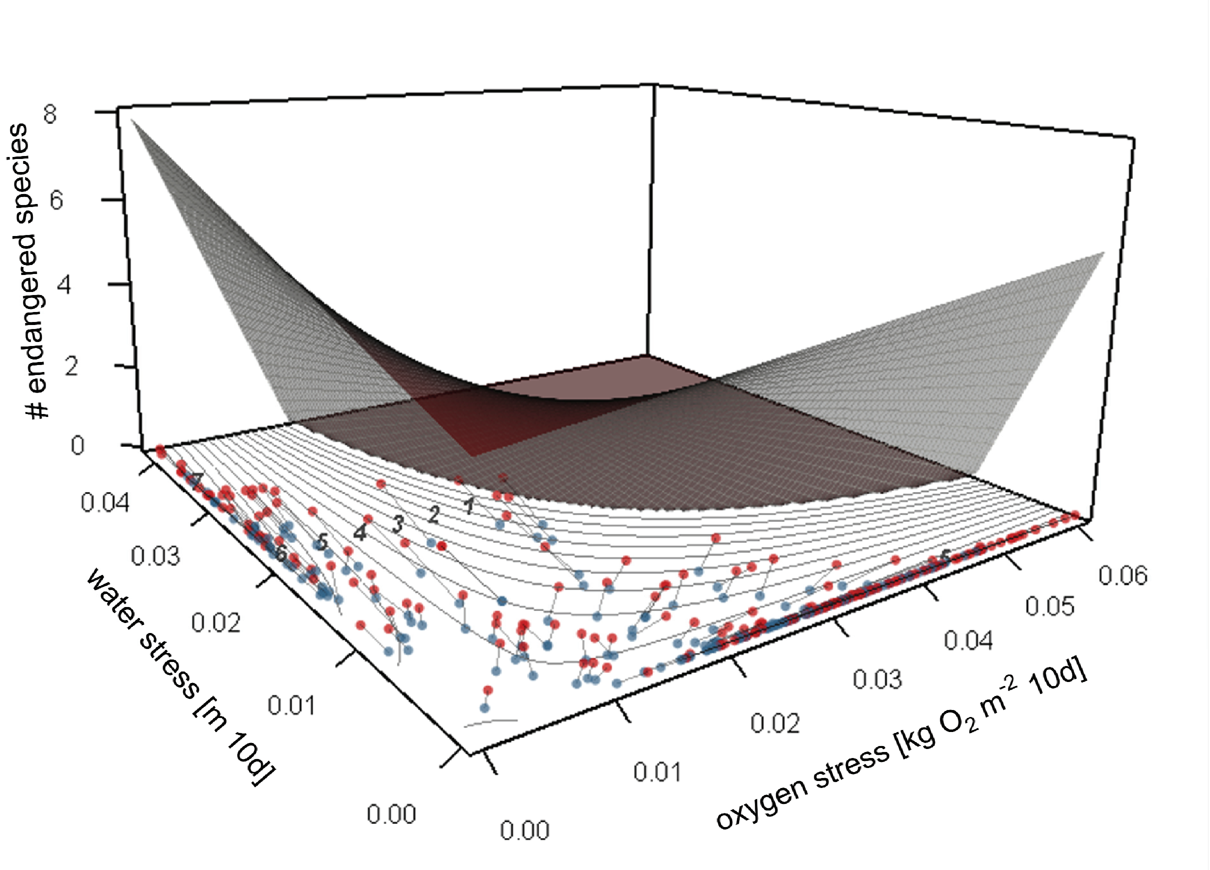

Figure 5.2: Effect of climate change on the oxygen and water stress and occurrence of endangered species within a vegetation plot. In total, the dataset includes 97 endangered species, of which 64 species occur at coinciding oxygen and water stress. The plane and the corresponding isolines represent the potential number of endangered species within a vegetation plot (# endangered species) for a specific coincidence of oxygen and water stress under the current climate, visualized by the 95% regression quantile (Koenker & Basset 1978; Cade et al. 1999) (Number of endangered species within a vegetation plot = 22.4*oxygen stress + 82.2*water stress - 13969.0*oxygen stress*water stress + 4.4 with respectively p=0.66, p=0.14, p<0.001 and p<0.001). The decreased number of endangered species within a vegetation plot under the future coincidence of oxygen and water stress is visualised by the projection of the points from Fig. 5.1 in which the red data points (future climate) generally shift to the isolines with a lower number of endangered species.

interaction for the combination of oxygen and water stress for the 95% regression quantile (Fig. 5.2), underpinning the critical influences of the coincidence of stresses on the habitat suitability of endangered species. This confirms that variable stress conditions are detrimental to species with narrow physiological tolerance ranges (Parmesan et al. 2000). This reduction is not apparent in the total number of plant species within a vegetation plot (see Appendix 5B), which implies that climate change will affect endangered species more strongly than common species.

Although nutrient availability may potentially influence the occurrence of endangered species in our dataset too (Wassen et al. 2005), soil fertility did not affect our findings (see Appendix 5B). This confirms that, by using regression quantiles, we have isolated the limiting effects of oxygen and water stress, and correctly analysed the potential number of endangered species at specific combinations of these moisture related stresses.

The projection of calculated shifts in future (2050) oxygen and water stress (Fig. 5.1) on the isolines of Fig. 5.2 shows that climate change threatens the future occurrence of currently endangered species, because the intensification and increased coincidence of oxygen and water stress concurs with a strong decrease in the number of endangered species (Fig. 5.2). This indicates that the future habitat suitability will decrease for these species. Using future oxygen and water stress (red points in Fig. 5.2) as input in the 95% regression quantile in Fig. 5.2, we found that the statistically significant negative interaction term leads to a reduction of 16% in the potential number of endangered species per vegetation plot in 2050. Increased dynamics in habitat factors other than soil moisture may further decrease the occurrence of endangered species. An increase in abundance, due to the development of no-analogue habitats, is unlikely as invasive species commonly have wide physiological ranges (Funk et al. 2008) and are consequently seldom endangered.

On the other hand if only one of the stresses prevails, climate change does not significantly affect endangered species, and the number of endangered species within a vegetation plot remains high (i.e. 8 endangered species within a single vegetation plot across a total 97 endangered species present in our dataset). Thus, climate change only decreases the habitat suitability of endangered species if it actually intensifies both oxygen and water stress.

The predicted threat to the future of currently already endangered species has direct implications for policies to maintain endangered species, as applied by international nature management organisations (e.g. IUCN). Global climate change alters the natural habitat conditions in such a way that they become increasingly unsuitable for the persistence of endangered species, which hampers the success of managing species diversity by local executive institutions.

Methods Summary

Both oxygen and water stress were based on calculations over 30 years with detailed daily values of soil moisture content and temperature for each vegetation plot, simulated with the hydrological model SWAP (Van Dam et al. 2008), for both the current and future (2050) climate (Chapter 4). Oxygen and water stress were computed by applying a hypothetical reference vegetation, instead of the actual vegetation. The stresses thus obtained reflect the oxygen and water status of the soil at which the actual vegetation persists. Oxygen stress equals the yearly maximum reduction in root respiration (i.e. potential minus actual respiration) for a 10-day period, averaged over 30 years. Respiration reduction was calculated with a recently developed model for oxygen consumption and transport (Chapter 3). Plant characteristics of a reference vegetation, actual soil type, and daily soil moisture conditions and soil temperature were model input. Unlike existing measures, this oxygen stress measure accounts for the effects of both extreme rainfall events and high temperatures, known to affect vegetation (Sojka et al. 1972; Drew 1983). Water stress equals the yearly maximum reduction in transpiration for a 10-day period, averaged over 30 years. Transpiration reduction is daily output from the SWAP-model (Van Dam et al. 2008) in terms of the difference between the potential and the actual transpiration. Plant characteristics of a reference vegetation, actual soil type, and daily groundwater levels, precipitation, air temperature and reference evapotranspiration were model input. This water stress measure accounts for the effects of both prolonged dry periods and high atmospheric demand for plant transpiration, i.e. factors that determine water stress of plants (Porporato et al. 2004). The constraining effect of oxygen and water stress on the number of endangered species present in the actual vegetation of each vegetation plot, was described by the 95% regression quantile (Koenker & Basset 1978), a measure that unlike conventional regression, excludes the effect of unmeasured limiting factors (Cade et al. 1999).

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Appendix 5A: Methods

Data

We used 185 vegetation plots that originate from a wide range of terrestrial vegetation types differing in succession stages, soil type, soil moisture regime, nutrient availability and soil pH. None of the investigated plots had been under the influence of a major change in hydrological conditions. All vegetation plots were representative of natural habitats. For groundwater-dependent sites, fortnightly 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. The groundwater level series were extended to the period 1971-2000, and interpolated to daily values with the Menyanthes impulse response software (Von Asmuth et al. 2002), to characterize temporal deviations in meteorological conditions and to show long-term average conditions (Chapter 2). Menyanthes transforms precipitation and evapotranspiration series (impulse) into groundwater level series (response) (Chapter 2). Daily local meteorological data on air temperature, precipitation and reference evapotranspiration (according to Makkink (1957)) were available from the Royal Netherlands Meteorological Institute (KNMI) from 1970 onwards.

For each site, 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 the SWAP-model (Van Dam et al. 2008). The meteorological input for the SWAP-simulations consisted of daily precipitation and reference evapotranspiration data corresponding to those used for the simulations of groundwater levels, and daily temperature. Daily groundwater levels served as the bottom boundary conditions. For each site, soil physical parameters according to Van Genuchten (1980) were derived from a national soil database (Wösten et al. 2001).

Hypothetical reference vegetation

In a natural vegetation, plants are adapted to oxygen or water stress, for instance by aerenchyma or hairy leaves, respectively. In this way, the real stresses experienced by plants are minimized. Consequently, minimal relationships between oxygen and water stress and the actual vegetation are to be expected. To objectively characterize stress levels, both oxygen and water stress were computed by applying a hypothetical reference vegetation (Chapter 3), instead of the actual vegetation. This reference vegetation is defined as a temperate natural grassland not adapted to oxygen and water stress.

Oxygen stress

Root respiration is determined by interacting respiratory (i.e. oxygen consuming) and diffusive (i.e. oxygen providing) processes in and to the soil, which were described by generally applied physiological and physical relationships, respectively (see Chapter 3). Plant roots respire at a potential rate under optimal soil aeration and thus non-limiting oxygen availability. This potential root respiration is in equilibrium with the oxygen demand of plant roots, which is determined only by plant characteristics (in this case of the reference vegetation) and daily soil temperature (Amthor 2000) (as simulated with SWAP). Upon increasingly wetter conditions, however, the gas-filled porosity of the soil decreases and oxygen availability becomes insufficient for potential root respiration. The method of Chapter 3 allows calculating the actual root respiration for a given daily gas-filled porosity, which is output of the SWAP-simulations. The difference between the potential and actual root respiration is calculated for each soil layer separately. These differences are summed, resulting in a daily value of respiration reduction for each site, quantifying the respiration stress due to wetter conditions.

Water stress

Plants transpire at a potential rate under non-limiting water availability. This potential transpiration depends on the atmospheric demand (Monteith & Unsworth 1990) (global radiation, air humidity, wind speed, air temperature and atmospheric CO_2-concentration). When water becomes limiting, however, the water uptake by plant roots and herewith plant transpiration is reduced. SWAP uses the Feddes-function (Feddes et al. 1978) to describe this reduction.

Oxygen and water stress for the future climate

For the calculations of future oxygen and water stress, we considered the W^+ climate scenario (Van den Hurk et al. 2006) for the year 2050. This scenario, which was developed by the Royal Netherlands Meteorological Institute (KNMI), 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 (Van den Hurk et al. 2006). The scenario comprises a +2 °C global temperature increase, with changed air circulation patterns in summer and winter (Van den Hurk et al. 2006). For each vegetation plot, we transformed temperature, precipitation and reference evapotranspiration time series from 1971-2000 to the 2050 climate, using transformation software supplied by the KNMI (Bakker & Bessembinder 2007). This software takes account of shifts in precipitation from summer to winter and to intensified rainfall events. In addition, we decreased evapotranspiration values by 2% to account for the higher water use efficiency of plants at increased CO_2 levels in 2050 (Kruijt et al. 2008). The W^+ scenario allows to account 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 on a scale as detailed as vegetation plots, as is done in this study.

Future precipitation and evapotranspiration were used to simulate future groundwater levels in Menyanthes. Future soil moisture and soil temperature profiles were created with SWAP, using as input the future air temperature, precipitation, reference crop evapotranspiration and groundwater level series. Future oxygen stress was simulated on the basis of these soil moisture and soil temperature profiles. Future water stress was derived from the SWAP output.

Appendix 5B

Effects of nutrient availability

Besides soil moisture, nutrient availability also potentially affects the occurrence of endangered species in our dataset. In order to test whether the result we found might be an artefact caused by a high nutrient availability coinciding with oxygen and water stress, we included a measure for nutrient availability, i.e. nutrient indicator values (see Witte et al. 2007), as covariate in the 95% regression quantile. If effects attributed to oxygen and water stress would have been caused by (correlations with) nutrient availability, then the power of the relationships between the number of endangered species and these stresses would have decreased (or eliminated) when including this covariate. In this way, we accounted for additional variation not associated with oxygen and water stress, but with nutrient availability.

The interaction term in the regression quantile remained highly significant (Table 5B.1) and the predictive power increased (t-value for the interaction term -4.8 and -5.3 for the model with and without nutrient availability, respectively). This indicates that nutrient availability decreases some of the residual variation in the regression and thereby strengthens the relationship, but this is an additional effect on top of the effect of water and oxygen stress.

Total number of species

In order to test whether the decline in the number of endangered species with increasing coincidence and intensification of oxygen and water stress deviates from trends occurring to other plant species (i.e. also to common/abundant species), we analysed whether the total number of species within a vegetation plot showed a similar trend. From the results of the 95% regression quantile (Table 5B.1) can be concluded that the significant interaction term for the number of endangered species is not apparent in the total number of species within a vegetation plot. Thus, unlike endangered species, the total number of species is not affected by coinciding oxygen and water stress.

Table 5B.1: Parameter values of the 95% regression quantiles, describing the inhibiting effect of oxygen and water stress on 1) the number of endangered plant species within a vegetation plot with nutrient availability as covariate, and 2) the total number of species within a vegetation plot. Number of species = a_1*oxygen stress + a_2*water stress + a_3*oxygen stress*water stress + a_4

	a_1	a_2	a_3	a_4
# endangered species with nutrient availability as covariate	33.8 (p=0.40)	96.2 (p=0.03)	**-15535.6 (p<0.001)**	4.1 (p<0.001)
total # species within a vegetation plot	227.4 (p=0.12)	875.1 (p<0.001)	**-29269.2 (p=0.2)**	26.2 (p<0.001)

CHAPTER

6

General discussion

Process-based relationships between water, oxygen and vegetation

Forecasting the impact of climate change on natural ecosystems is one of the main topics in current environmental research. The development of reliable climate-proof habitat distribution models, which are based on causal, process-based relationships between site factors and plant traits, has been identified as one of the main objectives in the development of robust habitat distribution models. Soil moisture is one of the main factors that determine the vegetation composition at a site, as it determines the availability of both water and oxygen to plant roots – resources that are indispensable for plant survival. Therefore, the general aim (see Chapter 1) of this thesis was *to develop robust, generally applicable and climate-proof relationships between soil moisture conditions and vegetation characteristics, and as such, to contribute to the applicability of habitat distribution models under changing climatic conditions*. In response to the specific aims stated in Chapter 1, the major results of this thesis are:

Aim: optimize the predictive power and general applicability of soil moisture-vegetation relationships by filtering out systematic errors due to climatic noise

Result: Data harmonization increases the general applicability of empirically derived relationships (Chapter 2). Systematic errors in moisture-vegetation relationships are due to temporal variations in the meteorological conditions that determine groundwater depth (i.e. precipitation and evapotranspiration). Data harmonization removes such errors and thus allows different datasets to be combined.

Aim: develop a process-based procedure for the calculation of oxygen stress to plant roots

Result: A new plant physiological and soil physical process-based model to calculate critical gas-filled porosities of the soil as thresholds for the occurrence of oxygen stress to plant roots (Chapter 3). With this model we showed that currently used constant thresholds for oxygen stress (i.e. Wesseling & van Wijk 1957; Feddes et al. 1978) are insufficient, because critical gas-filled porosities are especially sensitive to soil temperature, plant characteristics and soil depth.

Aim: define process-based and climate-proof site factors for oxygen and water stress, replacing currently used correlative site factors

Result: Process-based relationships, which should be based on harmonized data (Chapter 2), are indispensable for making reliable forecasts of the effect of climate change on the plant species composition of the vegetation (Chapter 4). In contrast to our new direct measure Respiration Stress, based on the process-based oxygen stress model (Chapter 3), currently used indirect measures of oxygen stress do not include essential climate variables like temperature and extreme rainfall. Hence, these measures underestimate the occurrence of future oxygen stress to plant roots, and result in predicted future vegetations that are systematically too dry. Besides a measure of oxygen stress, a direct measure of water stress was also defined, in terms of Transpiration Stress (Chapter 5).

Aim: predict the effect of climate change on both future oxygen and water stress, and relate this to the impact of climate change on the future species diversity

Result: Climate change intensifies both oxygen and water stress, particularly when these stresses coincide. Consequently, the variation in stress will increase with the changing climate, which results in variable stress conditions. Especially these conditions were found to negatively affect the occurrence of currently endangered plant species (Chapter 5). The future existence of such species is therefore under pressure due to climate change.

These results provide new insights into the effects of climate change on future plant stresses and consequently on the future vegetation composition. Process-based measures of both oxygen and water stress made it possible to analyse the effect of climate change on the critical moisture conditions of the soil, in terms of the stresses that actually determine vegetation composition. Until now, a thorough analysis, focussing on the relevant processes in the soil-plant-atmosphere system, had not been performed.

Moreover, in accordance with the general aim of the research, the results contribute to one of the required improvements of habitat distribution models, i.e. the development of process-based relationships between soil moisture and vegetation (Guisan & Zimmermann 2000; Pearson & Dawson 2003; Botkin et al. 2007). This should lead to a habitat distribution model that allows robust vegetation predictions, also under changing climatic conditions.

Implications and applications

This thesis shows that the use of correlative, indirect relationships between site factors and vegetation in habitat distribution models should be discouraged. Predictions made with currently used correlative models, like climate envelopes (e.g. Bakkenes et al. 2002; Thomas et al. 2004), should therefore be interpreted cautiously. In particular, Chapter 5 shows that the effect of climate change on moisture related plant stresses is complex; both wet and dry extremes might be affected, and conditions that are not present under the current climatic conditions might occur in the future. A brief outlook is given below of the implications and applications regarding data requirements and availability, the application of derived relationships on large scales and the opportunities to extend this research to other research fields.

Data requirements and availability for different spatial scales

A disadvantage of process-based site factors for moisture is that they require more detailed data than indirect measures such as mean groundwater levels. Nevertheless, since these data (such as soil type and temperature) have been shown to be key components in the occurrence and modelling of plant stresses, it is advisable to try to obtain such information. In addition, the effect of changing climate variables on plant stresses should be analysed more thoroughly than has been done so far.

Detailed meteorological data are already generally available, and as long as the spatial gradients in meteorological conditions are relatively small, plot scale data will not be needed. Soil data and time series of groundwater levels, however, may differ strongly between sites. Therefore, when plot-scale analyses are performed, as in this research, detailed soil and groundwater data should be obtained. In the Netherlands, groundwater levels are usually measured biweekly and for limited periods, but these can be extrapolated and interpolated, e.g. by using Menyanthes (see Chapter 2). Based on climate scenarios from the Royal Netherlands Meteorological Institute (Van den Hurk et al. 2006), indications of the future site conditions can also be obtained. If detailed soil data and time series for precipitation, evapotranspiration, temperature and groundwater levels are available, process-based oxygen and water stress can be simulated, in accordance with the approaches presented in Chapters 4 and 5.

To apply the site factors for oxygen and water stress to the national, European or even global scale, less accurate data will suffice. For the Netherlands, a national groundwater model is available, which includes modelling of the daily moisture content in the unsaturated zone (www.nhi.nu) on a 250x250 m scale. In the near future, a 25x25 m scale will be modelled. Soil data are available for each grid cell, and daily meteorological conditions are available from the Royal Netherlands Meteorological Institute. For Europe, simulated daily soil moisture data are available on a 5x5 km scale, based on soil data, rainfall, potential evapotranspiration and daily mean air temperature (http://natural-hazards.jrc.ec.europa.eu). It should therefore also be possible to apply this model for future climatic conditions based on the IPCC climate scenarios (Solomon et al. 2007). Using the methods presented in Chapters 4 and 5 of this thesis, such data can serve as input to characterize site factors for oxygen and water stress and to provide possibilities for performing climate-proof vegetation predictions on a large scale. Obviously, the accuracy of the predictions will decrease with the increased scale of application. Therefore, large-scale applications may be used to identify directions of shifts in future vegetation composition, rather than using the results for local nature management purposes.

Extend results to other fields of research

In this research, the oxygen stress model (Chapter 3) was applied using a hypothetical reference vegetation; potential oxygen stress was therefore calculated. However, with a slight adjustment – incorporating longitudinal oxygen transport from the atmosphere through the plant stem and to the plant roots (Colmer 2003) – the model could also be applied to the actual, physiologically adapted vegetation that is present. By doing so, the influence of low soil aeration on actual plant stress could be investigated, which would be especially useful for determining actual oxygen stress and the resulting yield suppression of (adapted) agricultural crops. Until now, such stresses have been based on constant thresholds for oxygen stress, which are inapplicable under future climatic conditions (Chapter 3). Moreover, after adjusting the model we would have the opportunity to contribute to the simulation of soil respiration rates and the related CO_2 flux of terrestrial ecosystems under current and future climatic conditions. These fluxes are of great interest, because they affect global warming (Raich & Schlesinger 1992; Schlesinger & Andrews 2000).

Perspectives

In order to further improve the presented relationships between moisture conditions and vegetation, I recommend the following research:

- Validation of the simulated reduction of root water uptake due to oxygen stress (Chapter 3) with lysimeter experiments, under controlled environmental conditions and under different levels of soil saturation.
- Validation of the vegetation predictions based on the process-based measure of oxygen stress (Respiration Stress) for future climatic conditions (Chapter 4), e.g. on the basis of detailed data from Southern Europe.
- Although a climate-proof, physiologically based variable for plant traits, i.e. the dependent variable in the moisture-vegetation relationship, was not one of the specific aims of this research, such a measure is desirable to further optimize the applicability of the relationship. Although mean indicator values may be rather robust to characterize plant traits, I recommend trying to replace these mean indicator values with functional plant traits that represent the most direct physiological adaptations of plant species to oxygen and water stress (Chapter 1). Data on moisture-related plant traits for each species should be obtained, and techniques to combine different plant traits into a single representative variable should be developed.
- In this research, the effect of alterations in the moisture regime on the vegetation composition played a central role. Therefore, this thesis focused on the derivation of site factors for moisture that determine the actual vegetation composition. However, it is expected that species-specific physiological behaviour, which has feedback to soil moisture conditions, will also change as a result of climate change. For example, due to increased atmospheric CO_2, the water loss through plant stomata might decrease (Kruijt et al. 2008), which decreases the root water uptake and increases the groundwater recharge. Such feedback mechanisms between vegetation and groundwater recharge prevent water stress from occurring. Such changes in physiological behaviour should be considered, not only to further improve habitat distribution models, but also to accurately predict groundwater recharge in a future climate. In the coming years, I intend to work on these feedbacks.

Final conclusions

Climate-proof relationships between water, oxygen and vegetation are needed to reliably predict vegetation composition under changing climatic conditions. The need for mechanistic measures for site factors has been widely recognized by the scientific community, but fundamental approaches to fill the gaps are still lacking. This thesis has shown that mechanistic measures are indeed indispensable; it offers approaches to characterize the plant stresses resulting from a shortage or surplus of soil water. Using these process-based measures, it demonstrated that climate change increases both the wet and dry extremes in plant stresses, i.e. oxygen and water stress respectively. The resulting increased variability in plant stresses threatens the future of currently endangered plant species. The process-based relationships developed in this thesis contribute to an increased understanding of the effects of climate change on future vegetation composition.

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LIST OF PUBLICATIONS

Bartholomeus R.P., Van Dongen R. & De Louw P. (2004) Onderzoek naar kwelafhankelijke vegetatie in beekdal het Merkske. *H_2O*, 10, 27-30.

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Bartholomeus R.P., Witte J.P.M., van Bodegom P.M., Van Dam J.C. & Aerts R. A climate-proof relationship between soil moisture conditions and vegetation composition. submitted.

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CURRICULUM VITAE

Ruud Bartholomeus was born in Westerhoven, the Netherlands, on 19 May 1980 and grew up in Knegsel. After graduating from secondary school (VWO, Sondervick College, Veldhoven) in 1999, he started to study Land and Water Management at Hogeschool Larenstein in Velp. In the final project of this BSc study, he investigated the main site factors that determine seepage dependent vegetation types in brook valleys, at the Netherlands Organisation for Applied Scientific Research TNO. He graduated in 2003 and continued with the MSc study Hydrology and Water Quality, with a specialisation in Soil Physics, Agrohydrology and Groundwater Management, at Wageningen University. As a minor thesis, which he conducted at Alterra, he implemented a radiation routine in the SWAP-model that improves the calculation of soil moisture conditions on inclined surfaces. As a final project he developed a finite element model on the interaction of open water flow and groundwater. He graduated in November 2005 (Cum Laude). After his graduation, he started his PhD research at the department of Systems Ecology at the Institute of Ecological Science of the VU University Amsterdam and at KWR Watercycle Research Institute. This research was part of a large project on the development of a model to predict the vegetation composition in future climatic conditions. The results of this PhD research are reported in this thesis. In November 2009 he will start as a postdoctoral researcher at KWR Watercycle Research Institute, where he will work on a climate-proof evapotranspiration module for groundwater models, taking into account the feedback mechanisms of the vegetation to climate change.