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Optimum vegetation characteristics, assimilation, and transpiration during a dry season: 2. Model evaluation

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[1] In a companion paper, a conceptual model was presented to predict two important vegetation parameters from climatic constraints in water limited conditions, notably photosynthetic capacity and internal carbon dioxide concentration. In this study, the model is evaluated using data of four experimental forest plots in sub-Mediterranean Slovenia which were selected for their topography induced differences in climate and contrasting vegetation characteristics. Data were collected during a regular (2004) and an exceptionally dry year (2003). Measurements showed that photosynthetic capacity decreases with vapor pressure deficit, and internal carbon dioxide concentration correlates positively with available water. Variations in soil water storage at the start of the dry season and vapor pressure deficit during the dry season are responsible for a large part of these differences. Winter precipitation has a large effect on the shape of the seasonal course of transpiration during the following season. The model explained observed differences among sites and years in photosynthetic capacity and the seasonal cycle of transpiration. Although the magnitude of calculated optimum internal carbon dioxide concentrations agreed with observations, the model could not explain observed differences in internal carbon dioxide concentration or the correlation between internal carbon dioxide concentration and water availability. The optimality hypothesis, despite its limitations, can be used to predict the seasonal cycle of transpiration.

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1. Introduction

[2] The effect of vegetation characteristics on the fluxes of carbon dioxide and water is reasonably well understood, at least better than the effect of climatic variables on the development of vegetation characteristics. Although the effect of climate on vegetation has long been a matter of research, the prediction of vegetation parameters from climatic constraints is still qualitative. Most studies which predict optimum vegetation characteristics for a certain climate use some sort of an ecological optimality hypothesis (EOH). However, the validation of EOHs is extremely difficult [*Kerkhoff et al.*, 2004] because of the lack of long-term data, variability of climate and vegetation, and the nonlinearity of the interactions.

[3] In a companion paper [*Van der Tol et al.*, 2008], a simple model was presented which uses a physiological optimality hypothesis to predict two important parameters of a green canopy: photosynthetic capacity and internal carbon dioxide concentration. The model is not a typical ecological model, since it does not predict vegetation structure parameters nor competition between individuals. It rather predicts the evolution of transpiration and photosynthesis over time that results in the highest total net photosynthesis. The two parameters are species- and site-dependent and relevant for the calculation of the surface exchange fluxes of carbon dioxide and water.

[4] In this study, the model is applied to forests in a sub-Mediterranean climate and data collected in a field experiment are used for evaluation. A field evaluation was preferred above a controlled laboratory experiment because the vegetation in the field experiment had been allowed to develop naturally in interaction with climate for at least 50 years. Data were collected at four experimental forest plots in sub-Mediterranean Slovenia, which were selected for their contrasting water availability and humidity. Only soil and climate measurements are used to constrain the biochemical properties and seasonal cycles of assimilation and transpiration and independent measurements of biochemistry and transpiration as evaluation. We speak of evaluation rather than validation, since a true validation requires statistically robust criteria which are not feasible in this case.

[5] Owing to the thin soils, the low precipitation in summer and the high potential evaporation, the forests at these sites are water limited. A disadvantage of the sites is that the vegetation is perennial. Perennial vegetation carries a history of previous years, whereas theory aims to predict independent values for a season. Moreover, in perennial

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vegetation survival may be more important in the long term than optimizing photosynthesis at the short, seasonal timescale. However, since we focus on physiologic characteristics of a canopy consisting of annually replaced leaves, the physiological optimality hypothesis is a reasonable assumption.

[6] Measurements were carried out during an average (2004) and an exceptionally dry year (2003). For four plots in 2004 and two plots in 2003, photosynthetic capacity and internal carbon dioxide concentration were calculated with the model and (for 2004) compared to leaf nitrogen content, leaf photosynthesis measurements and ^{13}C isotope discrimination. The calculated parameter values are used to calculate seasonal cycles of transpiration, which are evaluated using transpiration measurements.

2. Methods and Materials

2.1. Site Description

[7] Measurements were carried out in a naturally reforested area, in the catchment of the Dragonja River in Mediterranean Slovenia (N45°28′ E13°46′). The sub-Mediterranean climate is classified as Caf (mild winter, hot summer, no dry season) in the Köppen system. Mean annual precipitation is 1100 mm. The parent material in the Dragonja catchment is flysch: a sequence of calcareous shales and thin sandstone banks. In the upper part of the catchment, broad plateaus are intersected with narrow, steep river valleys of two contributing streams. In the lower part, the valley is broad and the plateaus narrow. The elevation ranges between 0 and 330 m above sea level. Soils in the whole catchment are Rendzina soils [*Keesstra*, 2006] and consist of clay loam (30% sand, 50% silt, 20% clay). Soil depth ranges from a few decimeters on the slopes to several meters of alluvial deposits in the valley.

[8] Four experimental plots were selected in deciduous forests, which contrasted in aspect, local hydrological and climate conditions, and vegetation composition. The forests had developed with minimum human interference during the last 50 years. Both texture and chemical composition of the soils at the plots were similar. One plot was located on a north-facing and one on a south-facing slope (north and south plot), one was located at the foot of a converging west-facing slope (west plot), and one with younger forest was located on a diverging south-facing slope (south-young plot). For a complete site description and a map showing the locations of the plots we refer to *Van der Tol et al.* [2007]. Two plots experience a high (north and south-young) and two plots a low (south and west) water availability. In this way, each of the four combinations of high and low vapor pressure deficit and high and low soil moisture content was present.

[9] The plots not only contrasted in microenvironment but also in species composition, stem density, and forest structure. The dominant species were *Carpinus betulus* at the two shaded plots (north and west), and *Quercus pubescens* at the two exposed plots (south and south-young). Trees at the shaded plots were taller than at the sunlit plots. The forest at the south-young plot was younger, and pioneer vegetation was present (*Juniperus communis*).

2.2. Measurements

[10] At the plots, vegetation and soil parameters, meteorological variables, and the water balance were measured between April and November 2003 and between May and September 2004. For 2003, data of the two plots which contrast both in soil water availability and humidity deficit (north and south plot), and for 2004, data of all four plots were available. The measurements are described in detail in *Van der Tol et al.* [2007]. Measurements consisted of biochemical characteristics of the vegetation (^{13}C isotope discrimination, leaf nitrogen content, leaf area index, leaf chamber photosynthesis), the water balance (soil moisture content, precipitation, throughfall and stemflow, transpiration) and basic meteorological variables (wind speed, diffuse and direct incoming shortwave radiation, and reflected shortwave radiation). Basic meteorological variables were measured at a meteorological station 3 km east of the experimental plots. Leaf chamber photosynthesis measurements were carried out on two species at the south and the south-young plot and leaf nitrogen content and ^{13}C isotope discrimination at all four plots, but only in 2004.

[11] Temperature, relative humidity, vertical profiles of soil moisture content, and sap flux density were measured continuously at each plot. Soil moisture content measurements at the north plot in 2003 were incomplete: only the subsoil at 5 cm depth was measured continuously, and gravimetric measurements were carried out only on 30 May. Precipitation was measured with recording tipping bucket systems at three stations within 500 m of the forest plots. Temperature and relative humidity were measured at 2 m height with aspirated, shielded humicaps (HMP45AC, Vaisala Oyj, Finland), which were calibrated against a wet and dry bulb copper-constantan thermocouples (Vrije Universiteit Amsterdam) before and after the study. Soil moisture was measured at five depths per plot (three for the south-young plot) with TDR sensors (CS616, Campbell Sci. Inc., and TRIME). Soil depth was measured by drilling boreholes. Sap flux density was measured with 12 sensors per plot with the method of *Granier* [1987], and transpiration was calculated by scaling the measurements to the plot scale as described by *Van der Tol et al.* [2007]. Incoming and outgoing short wave and long wave radiation and net radiation were measured at the south plot with a CNR1 radiometer (Kipp and Zonen, Delft, Netherlands) mounted on a tower above the canopy.

[12] Isotope discrimination and leaf nitrogen content were measured with an elemental CNHO-analyzer Flash 1112 (Finnegan MAT, Bremen, Germany) for 83 leaf samples, collected at the start and the end of the dry season of 2004. Each sample consisted of approximately 10 leaves of the most abundant species. An average for each plot was calculated by weighting the measurements with the relative contribution of each species to the total sapwood area. Light response curves of leaf photosynthesis were measured at the south (from a measurement tower) and south-young plot (at breast height) on leaves of *Fraxinus ornus* and *Quercus pubescens* between 14 and 21 July and 17 (19 leaves) and 26 August 2006 (15 leaves) with a LCA3 gas analyzor with leaf chamber and portable light unit (ADC BioScientific Ltd., UK).

2.3. Model Input

[13] The model described in the companion paper was used to calculate optimum photosynthetic capacity and internal carbon dioxide concentration and the seasonal cycle of transpiration. Table 2 shows measured components of the

Table 1. A Priori Parameter Values for the Model

K_c (μbar)	K_o (mbar)	O (mbar)	Γ^* (μbar)	C_s (μbar)	m_n	m_d	α
460	330	210	30	360	0.05	0.05	1.0

water balance during the dry seasons of 2003 and 2004 which were used as input, and Table 1 shows a priori parameter values used in the model.

[14] For the start of the dry season, the day when leaves had fully developed was developed (DOY 150; the development of leaf area was monitored weekly with PAR measurements below and above the canopy). For the end of the dry season the moment was chosen when soil moisture content reached its seasonal minimum value (DOY 250 in 2003 and DOY 255 in 2004).

[15] The initial amount of soil moisture in the soil is calculated as initial soil moisture content integrated over soil depth to the impermeable layer. During the experiment, the soil water reservoir was recharged by six rainstorms. The model was developed for dry periods with no recharge, making analytical solutions possible. In order to be able to apply the model, the parameter s_0 is calculated as the sum of the initial amount of moisture in the soil and the total amount of rainfall during the season. This necessary simplification has two disadvantages. First, it has consequences for the seasonal cycle of transpiration. Second, it has consequences for the optimality hypothesis: the vegetation may be able to respond to initial soil water content, but not to future rain events. The optimized parameters are based on information that is not yet available when the leaves are formed.

[16] For parameters s_f (the soil water storage at the onset of drought stress) and s_r (the soil water storage at wilting point), the soil water storage at pF = 3.0 (θ = 0.30) and pF = 4.2 (θ = 0.195) is used, respectively, for all plots.

[17] Parameters in Table 1 are a priori values, except for m_d and m_n, which were estimated from leaf photosynthesis measurements as discussed in the next section. Application of the model is straightforward, using the parameters in Tables 1 and 2. Optimum photosynthetic capacity, initial transpiration and photosynthesis rate can be calculated with equations (30)–(32) of the companion paper. The decrease with time during water stress is calculated with equations (15), (18), and (22).

3. Results

[18] In this section, first, the water balance of the four plots is presented, and second, some of the underlying assumptions of the model are evaluated. Third, the performance of the model to predict photosynthesis, internal carbon dioxide concentration, and the seasonal cycles of transpiration is evaluated.

3.1. Water Balance

[19] Table 2 shows measured components of the water balance during the dry seasons of 2003 and 2004. Precipitation and temperature in 2004 were close to the 30-year average, whereas precipitation in 2003 was one of the lowest and temperature the highest in a 500 year record of the region [*Casti et al.*, 2005]. Variations in vapor pressure deficit can be explained from topographic position: two plots at shaded locations had lower vapor pressure deficit than two plots located at the sunlit side of a hill (south slope). Soil moisture content at the start of the dry season was used as input. It is unknown what caused the differences in soil moisture content at the start of the dry season because drainage, soil evaporation, and transpiration (of the undergrowth) before the start of the dry season were not measured. Throughfall and stemflow were measured throughout the whole year. These measurements showed that evaporation of intercepted water was higher at the south than at the north slope during the winter, which may explain part of the difference in soil moisture content between these two plots in spring. At the west plot, initial soil moisture content is relatively low, which may be explained by drainage to a coarse sand layer just below the root zone.

[20] The greatest uncertainty in the estimates of soil water availability is rooting depth because its spatial variability was not measured. The uncertainty in the rooting depth was estimated as 25%, which results in an error of 15% in available water [*Van der Tol*, 2007].

[21] Total measured transpiration is close to the amount of available water in the summer s_0, and thus nearly all available water transpires. The fact that this holds for all plots suggests that transpiration is indeed water limited. Not only mean transpiration differs among plots, but also the shape of its seasonal course. Figure 1 shows, for example, measured daily transpiration versus time for the north and the south plot for 2003 and 2004. Transpiration in 2004 was a factor two higher than in 2003. In both years, transpiration at the north plot is initially higher than at the south plot, but later in the season this sequence reverses. In 2003, transpiration rates at the north and the south plot intersect at an earlier date than in 2004. It is the question whether this behavior can be predicted using the assumption of maximum growth.

Table 2. Length of the Season t_e, Gross Precipitation P_g and Net Precipitation (Throughfall Plus Stemflow) P_n, Mean Soil Moisture Content at the Start of the Dry Season, Weighted Over the Soil Profile θ_0, Rooting Depth RD, Available Water s_0, Soil Water Storage Below Which Stress Occurs s_f, Soil Water Storage at Wilting Point s_r, and Mean Daytime Vapor Pressure Deficit D for Two Plots in 2003 (30 May and 7 September) and Four Plots in 2004 (29 May and 11 September)[a]

Year	Plot	t_e, d	P_g, mm	P_n, mm	θ_0	RD, m	s_0, mm	s_f, mm	s_r, mm	D, hPa
2003	north	100	138	79	0.25	1.0	329	300	195	19.4
	south	100	138	76	0.23	1.0	311	300	195	24.5
2004	north	105	175	131	0.39	1.0	519	300	195	12.3
	south	105	175	129	0.32	1.0	449	300	195	15.6
	west	105	175	152	0.30	1.0	456	300	195	12.1
	south-young	105	175	146	0.37	0.8	445	240	156	16.4

[a]Daytime is defined as the time when incoming shortwave radiation $R_{si} > 20$ W m^{-2}. Available water s_0 is the initial soil water content integrated over the root zone plus net precipitation.

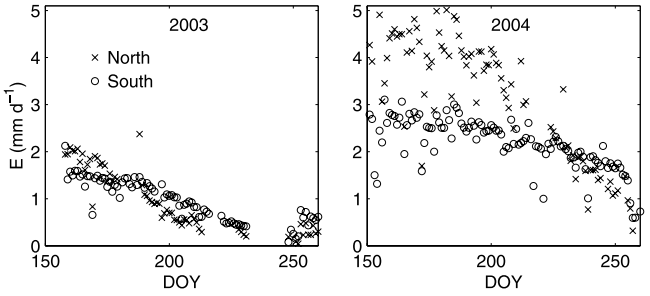

Figure 1. Daily transpiration for the north and the south plot in 2003 and 2004 versus day of the year (DOY).

3.2. Evaluation of Model Assumptions

[22] In the model, a water stress response function ξ was used, being the ratio of actual to potential (unstressed) transpiration. Theoretically, ξ is a function of soil water potential ψ_s. In Figures 2 and 3 the relationship between transpiration, soil water potential, and soil moisture content is evaluated, using data of the four forest plots. Figure 2 shows daily transpiration versus soil water potential calculated from measured soil moisture data and a pedotransfer function [*Van Genuchten*, 1978] calibrated against data of laboratory experiments. Data for the north plot in 2003 were not available because no continuous soil moisture data for the whole profile were measured.

[23] Figure 2 shows that transpiration is linearly proportional to soil water potential. Water transport between soil and leaf is gradient driven:

$$E = K(\psi_s - \psi_l) \tag{1}$$

where ψ_s and ψ_l are soil and leaf water potential, respectively, and K hydraulic conductivity. The fact that measured transpiration is linearly proportional to soil water potential implies that equation (1) can be used for E, where ψ_l and K are considered constants, the values of which can be derived from linear regression. The unstressed transpiration rate E_0 is the transpiration rate at ψ_s = 0, leaf water potential the value of ψ_s for which E = 0, and hydraulic conductance the slope of the regression line. Figure 2 shows that the value of E_0 differs among the plots. It also shows that the higher the value of E_0 is, the higher also the value of ψ_l, which indicates that a tradeoff exists between high transpiration rates in unstressed conditions and resistance to drought, as suggested in literature [*Smith and Huston*, 1989].

[24] The circles in Figure 2 represent data of 2003. The response of transpiration to water potential differs between 2003 and 2004. This in an important observation, because it indicates that the hydraulic parameters are flexible enough to adapt to variations between years. In 2003, ψ_l was lower than in 2004, while E_0 was not different.

[25] In the model, transpiration in water stressed conditions is calculated as a function of soil moisture storage rather than soil water potential (see companion paper). Figure 3 shows the ratio of daily transpiration to mean transpiration in unstressed conditions (E/E_0) versus soil moisture content for the four plots in 2004. The quantity on the vertical axis (E/E_0) is the measured equivalent of the model parameter ξ.

[26] The difference in response to drought among the plots can in principle be modeled by adjusting parameter α in equation (18) of the companion paper. The application of the optimality hypothesis in its current form, i.e., optimizing with respect to photosynthetic capacity and internal carbon dioxide concentration, does not say anything about the value α takes. The data suggest that vegetation with a high E_0 is sensitive to water stress (high α). From equation (31) in the companion paper it can be seen that, had this correlation between parameters been incorporated into the model, then high values of optimum E_0 would become lower and low values of E_0 higher. In other words, the range of values for E_0 would be smaller because too high values of E_0 imply a relatively high risk of stress. In this study, an a priori value of α = 1 is used, and differences in the response of transpiration to soil moisture are neglected.

[27] Parameters s_f, the soil water storage below which transpiration is reduced, and s_r, the soil water storage at wilting point, are also constants in this study. These param-

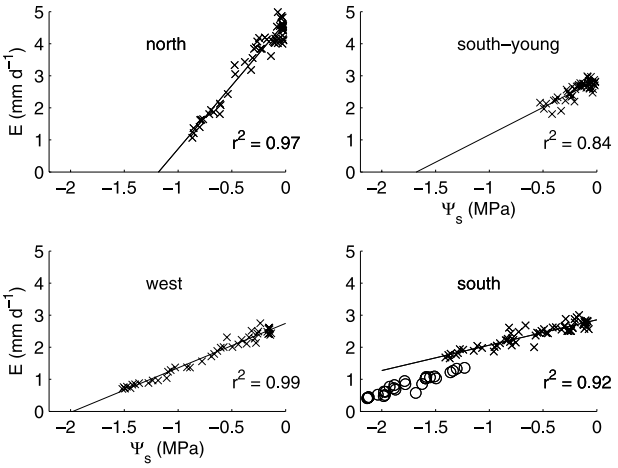

Figure 2. Daily transpiration E versus soil water potential ψ for the four plots in 2004 (crosses) with linear regression lines, and for the south plot in 2003 (circles).

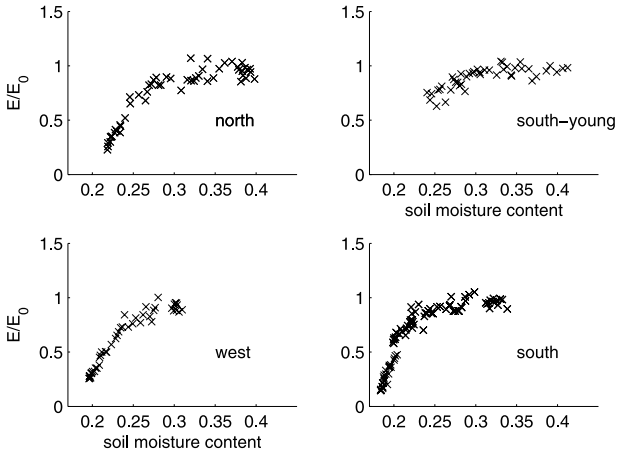

Figure 3. The quotient of daily transpiration over mean transpiration in unstressed conditions E/E_0 versus soil moisture content θ for the four plots in 2004. Unstressed transpiration rate E_0 is calculated as the means measured transpiration rate at pF > 3.0.

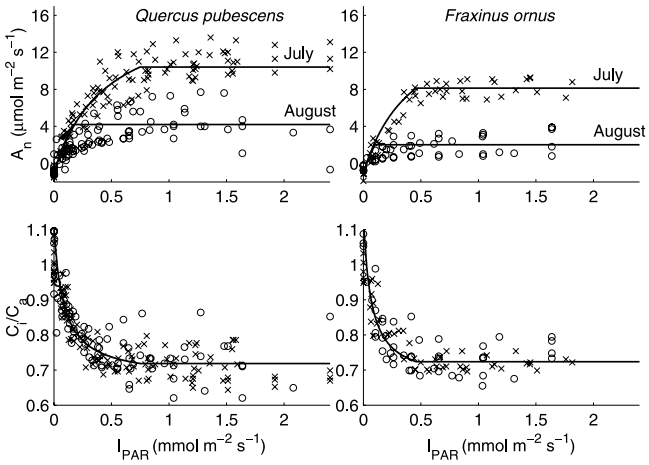

Figure 4. Photosynthesis rates and the ratio of internal over ambient carbon dioxide concentration of different leaves of two species (*Quercus pubescens* and *Fraxinus ornus*) at the south and the south-young plot versus PAR irradiance, measured with a leaf chamber gas analysis system between 14 and 21 July 2004 (crosses) and between 17 and 26 August 2004 (circles).

eters may be species- and site-dependent as well. The current model is unable to address this.

[28] One of the assumptions in the model is that drought causes a decrease in Rubisco activity and photosynthetic capacity rather than stomatal closure only. Figure 4 shows photosynthesis rate and the ratio of internal to ambient carbon dioxide concentration versus irradiance for leaves of *Quercus pubescens* and *Fraxinus ornus* measured at the south and the south-young plot in July and August 2004 with leaf chamber measurements. The rate of photosynthesis in August was two times lower than in July, while internal carbon dioxide concentration did not change significantly. This indicates that stomatal conductance and the rate of photosynthesis decreased proportionally, while water use efficiency remained constant. In Figure 5, leaf photosynthesis data and chemical leaf sample data are combined. This figure shows internal over ambient carbon dioxide concentration, leaf nitrogen content, and maximum carboxylation capacity for enzyme limited conditions V_{cm} of the model of *Farquhar et al.* [1980] at the south plot versus day of the year in 2004. Although leaf nitrogen content remained relatively constant, V_{cm} decreased with a factor two or three. Apparently, downregulation of photosynthetic capacity during the season does not necessarily cause a decrease in leaf nitrogen content. This confirms that leaf nitrogen content is proportional to V_{cm} in unstressed conditions, and at canopy scale to photosynthetic capacity ν_0 rather than to the actual ν. The change in internal carbon dioxide concentration is not significant ($p = 0.95$). *Wilson et al.* [2000] found similar results for maple and oak trees, and concluded that changes in photosynthetic capacity take a dominant role in the reduction of photosynthesis during the season, even if leaf nitrogen remains unchanged.

[29] The leaf photosynthesis measurements are also used to evaluate the model assumption that dark respiration remained constant during the season, and to derive a value for maintenance parameter m_d. While carboxylation capacity decreased by a factor two to three between July and August 2004, dark respiration rates of individual leaves remained 1.0 μmol m^{-2} s^{-1}. These measurements indicate that dark respiration does not decrease while V_{cm} decreases as a result of drought. Dark respiration of the canopy was calculated by multiplying the respiration rate of an individual leaf by leaf area index. Parameter m_d is calculated as R_{dd}/ν_0, using an a priori estimate of ν_0 of 80 μmol m^{-2} s^{-1}. This results in a value of $m_d = 0.05$. No data are available that make an estimation of nighttime maintenance respiration parameter m_n possible. In this study it is assumed that nighttime respiration equals daytime dark respiration, i.e., $m_n = m_d$, acknowledging that this is an approximation. By doing so, some respiration terms, such as that of roots, are excluded. Consequently, in this study, the growth of green tissue is optimized rather than that of a whole canopy. To optimize growth of a whole canopy, all respiration terms should be included.

[30] Figure 6 shows measurements of leaf nitrogen content and internal carbon dioxide concentration calculated from ^{13}C isotope discrimination for the four plots. Neither leaf nitrogen content at the two plots with low vapor pressure deficit (north and west), nor that at the two plots with high vapor pressure deficit (south and south-young) differ significantly from each other ($\alpha = 0.95$). However, leaf nitrogen content at the plots with low vapor pressure deficit is significantly higher than that at the plots with high vapor pressure deficit. Leaf nitrogen content closely correlates with vapor pressure deficit ($r^2 = 0.95$), and hardly with water availability ($r^2 = 0.04$, not shown). The values for internal carbon dioxide concentration also vary among the plots but in a different way than leaf nitrogen content. Internal carbon dioxide concentration is significantly higher at the two plots with high soil moisture content than at the two plots with low soil moisture content. Internal carbon dioxide concentration closely correlates with water availability ($r^2 = 0.89$) but not with vapor pressure deficit ($r^2 = 0.00$, not shown).

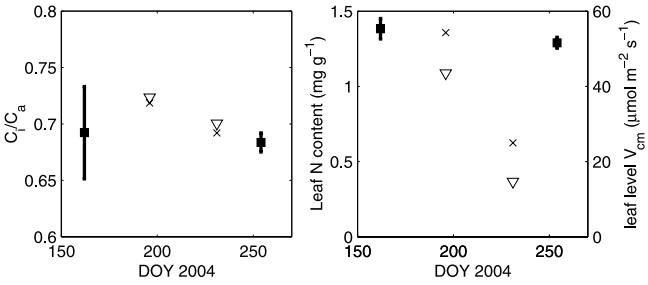

Figure 5. (left) The ratio of internal over ambient carbon dioxide concentration, derived from ^{13}C isotope discrimination analysis of leaf materials (boxes) and from leaf photosynthesis measurements of *Quercus pubescens* (crosses) and *Fraxinus ornus* (triangles) at the south plot, versus DOY 2004. The error bar represents the 95% confidence interval. (right) Leaf nitrogen content from leaf samples (boxes), and photosynthetic capacity for enzyme limited conditions ν (V_{cm}) for *Quercus pubescens* (crosses) and *Fraxinus ornus* (triangles) at the south plot versus DOY 2004.

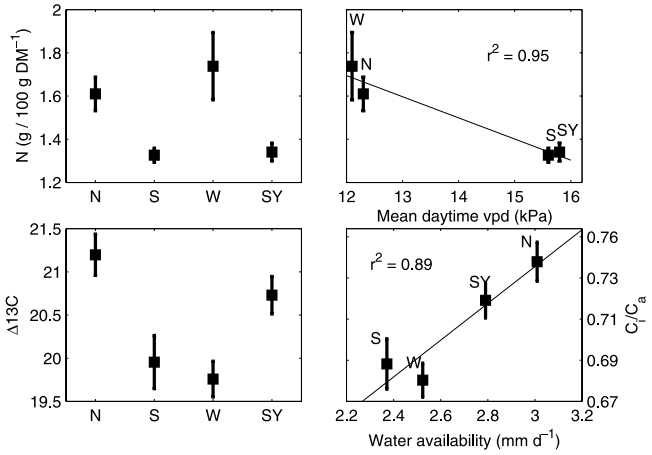

Figure 6. Measured leaf nitrogen content and ^{13}C isotope discrimination for the four plots in 2004 (left), and leaf nitrogen content versus vapor pressure deficit (upper right), and internal over ambient carbon dioxide concentration (lower right) versus water availability, with 95% confidence intervals. The vertical axes of the lower two panels are exchangeable. Data were derived from analysis of 83 leaf samples of the most abundant species, together covering at least 95% of the sapwood area, and averages for the plots were calculated by scaling samples with the relative contribution of species to total sapwood area.

[31] The differences in C_i among the plots are small but significant. The data suggest a positive relationship between water availability and internal carbon dioxide concentration. This implies that the lower the water availability is, the higher the water use efficiency. A lower water availability is then compensated by a more efficient use, which explains why differences in nitrogen content (photosynthetic capacity) among the plots do not correlate with water availability. The fact that photosynthetic capacity does not correlate spatially with water availability is remarkable, because photosynthetic capacity (although not leaf nitrogen content) at the plots changes strongly with time as a result of drought during a season. This suggests that the response of photosynthetic capacity to changes in drought during a season is a faster process than the structural adaptation of leaf nitrogen to long-term conditions of droughts.

3.3. Evaluation of Model Predictions

[32] The model was first used to calculate optimum internal carbon dioxide concentration. The ratio of calculated optimum internal to ambient carbon dioxide concentration was 0.71, 0.73, 0.69 and 0.71 for the north, south, west and south-young plot, respectively, which is close to measured values of 0.74, 0.69, 0.68, and 0.73 for these plots. The range of these values is only small, and the model is able to predict the right order of magnitude. However, we discussed before that measured C_i correlates with water availability, which also agrees with literature [*Lloyd and Farquhar*, 1994]. This is not the case for calculated optimum C_i. Moreover, there is no correlation between the four measured and modeled values of C_i. This is not surprising because the model was based on the assumption that photosynthetic capacity, and not carbon dioxide concentration, responds to drought. As a result, optimum C_i is independent of available water.

[33] In what follows, measured values for internal carbon dioxide concentration are used to calculate optimum photosynthetic capacity. This implies that now, photosynthetic capacity is optimized given C_i. The resulting photosynthetic capacity is the optimum value for ν_0 similar to that on the dashed line in Figure 7 of the companion paper at the measured C_i. In this case, we do not use a probability density function of s_0, but the actual measured value for the particular season (Table 1). Note that in the measured value of s_0, also rainfall during the season was included. For 2003, no measured values of C_i were available. Because 2003 was drier than 2004, and the observations of 2004 suggest a positive relationship between available water and C_i, lower values for C_i can be expected. However, we have not measured this. For this reason, and because the range of C_i values in 2004 was small, the mean of the measured values for the four plots in 2004 was used for C_i/C_a (0.71).

[34] Figure 7 shows calculated optimum photosynthetic capacity ν_0 versus measured leaf nitrogen content for the four plots in 2004. Calculated ν_0 correlates well with measured nitrogen content (r^2 = 0.96). Although leaf nitrogen is not the only factor affecting canopy level photosynthetic capacity (leaf area index and correction factor ε also play a role), does the high correlation indicate that the modeled differences in photosynthetic capacity are realistic. Dots in this figure refer to literature values of *Reich et al.* [1999] for individual leaves. Although canopy and leaf values of photosynthetic capacity cannot be compared directly, the factor two between the modeled canopy values and leaf values of photosynthetic capacity indicates that photosynthetic capacity is modeled within the right order of magnitude. *Van der Tol et al.* [2007] found leaf values for V_{cm} of 50 to 70 μmol m^{-2} s^{-1} for the same plots based on leaf chamber measurements, which is also a factor two lower than the currently modeled canopy values.

[35] Figure 8 shows modeled (solid lines) and measured transpiration (symbols), for all plots in 2004, and for the north and the south plot in 2003. A statistical analysis of these data is unfortunately not feasible. Instead, we will focus on the main issues: the value of initial transpiration rate E_0, the day when water stress starts, and the shape of the stress response function ξ.

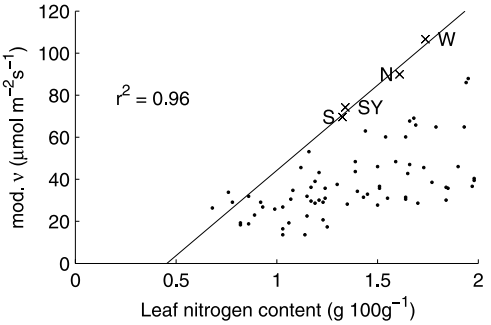

Figure 7. Modelled photosynthetic capacity at canopy level ν_0 versus leaf nitrogen content for the four plots in 2004. Dots are values for photosynthetic capacity at leaf level derived from data of *Reich et al.* [1999] for various ecosystems.

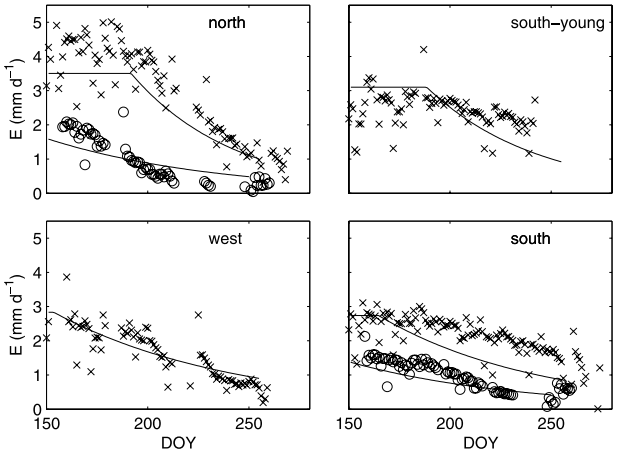

Figure 8. Measured and calculated transpiration for the four plots for 2003 (circles) and 2004 (crosses).

[36] The model is able to predict differences in E_0 among plots and between years. This means that it is possible to predict transpiration at the start of the season using only available water, long-term mean vapor pressure deficit and respiration coefficients as input. Other models may predict transpiration more accurately, but most of them will use vegetation characteristics and net radiation as input.

[37] The model is also able to predict the day when stress starts reasonably well. At the north and south-young plot, initial soil moisture content is relatively high. As a result, water stress starts at a later date than at the south and the west plot: soil water storage remains above the threshold below which water stress occurs, s_f, and transpiration remains at the initial, unstressed rate E_0 for a longer period of time. The latter is also visible in the measured data.

[38] The decrease of transpiration (the shape of the stress response function ξ) is only predicted well for the west plot. Because rainfall during the season was added to the initial soil water reservoir, jumps in transpiration caused by rainstorms are not reproduced by the model. For the south and the south-young plots, modeled and measured transpiration at the end of the season do not agree. This can be explained by parameters s_f, s_r, and α.

[39] Figure 1 showed that measured transpiration at the north plot is initially higher than at the south plot, but this sequence reverses later in the season. There are two reasons why this is the case. First, internal carbon dioxide concentration differs between the plots. Water availability and internal carbon dioxide concentration affect the course of transpiration in different ways. Increasing s_0 (for constant s_f/s_0) shears the vertical scale: initial transpiration rate is higher but $\xi(t)$ does not change, and thus the transpiration curves for two different values of s_0 cannot intersect. Internal carbon dioxide concentration affects both E_0 and $\xi(t)$: a lower internal carbon dioxide concentration corresponds to a more conservative water use and a slower decrease of ξ with time, and thus, transpiration curves for two different values of C_i can intersect. Second, Figure 2 shows that a tradeoff between high transpiration and resistance to drought exists (not included in the model because of the constant s_f, s_r, and α). Vegetation with a high E_0 (north plot) is more sensitive to drought stress than vegetation with a low E_0 (south plot). Because this is apparently the case (Figure 2), transpiration is overestimated at the north plot and underestimated at the south plot at the end of the dry season.

4. Discussion and Conclusions

[40] In a companion paper, a conceptual model was described for vegetation which is constrained by water availability. A relationship between photosynthetic capacity and internal carbon dioxide concentration was derived from the constraint that the soil-vegetation-atmosphere continuum of water flow must be conserved. Optimum values for the two parameters are calculated by assuming maximum growth. The only input of the model is available water, long-term average vapor pressure deficit and respiration coefficients. Despite the simplicity of the model, internal carbon dioxide concentration C_i, photosynthetic capacity ν and the seasonal cycles of transpiration are satisfactory modeled.

[41] Predicted values of optimum C_i are within the natural range. In literature, a positive relationship between internal carbon dioxide concentration C_i and water availability is often suggested [*Lloyd and Farquhar*, 1994; *Damesin et al.*, 1998; *Swap et al.*, 2004]. The data of this study point into the same direction. This effect is not included in the model because a constant C_i throughout the season was assumed.

[42] Predicted values of optimum photosynthetic capacity correlate positively with leaf nitrogen content, and negative with vapor pressure deficit. Both phenomena are in agreement with global findings by *Wright et al.* [2005], although they considered relationships at leaf scale instead of canopy scale. *Wright et al.* [2005] found that for deciduous forests leaf mass correlates negatively with vapor pressure deficit, but it does not correlate with precipitation. In this study, similar phenomena were observed. The exact mechanisms, and the effects of climate on the ratio of leaf area to leaf mass and leaf area index are beyond the scope of this study and remain to be studied.

[43] Predicted values for the initial (unstressed) transpiration rate were in agreement with measurements. Differences between years and among plots could be explained from climatic boundary conditions (water availability and vapor pressure deficit). The day when stress starts was modeled satisfactorily. The shape of the modeled stress response curve was for the south and south-young plot not in agreement with measurements. This can be explained by the fact that the same relationship between transpiration and soil moisture content was used for all plots, and thus a possible tradeoff between high unstressed transpiration rate and drought sensitivity was not taken into account. This tradeoff would be worth a separate investigation. In such a study it is important to realize that the parameters s_f, s_r, and α depend on both vegetation and soil characteristics. Tree height may also be important, since it limits possibilities for water transport, and thus it affects parameters s_f, s_r, and α.

[44] In the study area, winter precipitation played a key role. Soil moisture storage was the main supply of water, and recharge of the soil reservoir took place during the winter months. Some rainstorms occurred during the summer. As a simplification, the model was executed as if these rainstorms occurred all at the start of the season. This simplification was necessary, since the model requires a soil water reservoir which is not recharged during the dry

season. Because a large part of the available water was already present at the start of the season, this simplification did not lead to erroneous results. This indicates that in such a climate, the shape of the seasonal cycle of transpiration can already be predicted in the early spring.

[45] In some climates it may be more realistic to represent the growing season as a sequence of different dry seasons, between which the soil reservoir is recharged. In that case, the plasticity of photosynthetic capacity may be a problem: if the dry periods are relatively short, ν_0 can probably not adapt to each dry period. A stochastic approach describing the expected cumulative growth or risk of damage should then be used.

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