

## RESEARCH ARTICLE

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## Key Points:

- Plant competition influences vegetation-atmosphere feedbacks
- Better predictions of vegetation and atmosphere processes with plant competition
- Including competition gives larger leaf areas but lower photosynthesis

## Supporting Information:

- Supporting Information S1

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# Understanding the impact of plant competition on the coupling between vegetation and the atmosphere

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**Abstract** Competition between plants for resources is an important selective force. As a result competition through natural selection determines vegetation functioning and associated atmospheric interactions. Our aim was to investigate how the coupling between vegetation and atmosphere is influenced by plant competition. Though included in some coupled vegetation-atmosphere models, little attention has been paid to systematically study the impact of plant competition in determining the evolution of surface and atmospheric variables. We used a coupled vegetation-atmosphere model and included a new representation of plant competition. We compared the model results with diurnal data from Ameriflux Bondville site over a growing season. Including competition improved LAI (Leaf Area Index) and net ecosystem exchange of CO<sub>2</sub> (NEE) predictions; if competition was not considered, there were strong deviations from observations. Remarkably, competition increased LAI while it reduced whole stand photosynthesis, resulting in a less negative NEE. Finally, independent of competition, latent heat flux, surface temperature, specific humidity, and atmospheric CO<sub>2</sub> are well reproduced by the model. Only the sensible heat flux was overestimated, mainly due to the imbalance in the surface energy balance that can lead to lower measured sensible heat fluxes. Sensitivity analysis showed that the importance of plant competition on model outcomes increases with more nitrogen and water availability and may differ between soil types. We thus quantified the potential effect of plant competition in a coupled vegetation-atmosphere system and showed that it strongly influences this system, and therefore, we propose that competition should be considered in more vegetation-atmosphere models.

## 1. Introduction

Plants often grow in dense communities (e.g., forests or grasslands) where they share resources, such as light, water, and nutrients, with neighbor plants and where competition for these resources is often an important selective force. As a result, through natural selection, vegetation stands have often become dominated by the best competitors, whose traits therefore strongly determine vegetation functioning [McNickle and Dybzinski, 2013] and associated atmospheric interactions. However, even though inclusion of plant competition in atmospheric models has frequently been called for [Farrior, 2014; Weng et al., 2015; Zhang et al., 2015], large atmospheric models usually do not include this [Sitch et al., 2003; Boussetta et al., 2013]. Models that did include competition either followed a Lotka-Volterra competition based approach [e.g., Zhang et al., 2015] or used a gap model [e.g., Moorcroft et al., 2001]. Lotka-Volterra models assess whether competition between species is stronger than within species and then determine coexistence or exclusion. Gap models, on the other hand, predict the chance that an individual inhabits an empty area which was created by the death of others; thus, competition for light among individuals is considered. However, in contrast to those models we take an evolutionary game theoretical approach, by considering that natural selection favors plants that are the best competitors and not the ones that have the highest inherent performance. Plants assess the pay-off of a given strategy (trait values) in relation to the characteristics of neighboring plants [Reichert and Hammerstein, 1983]; the performance of one plant therefore depends on the characteristics of its neighbors.

It was shown for a variety of vegetation types that inclusion of competition between plants in a vegetation model using evolutionary game theory resulted in larger predicted leaf areas that were closer to observed values than when competition was not considered [Anten, 2002; Lloyd et al., 2010]. As leaves tend to have

lower albedo than soil, such difference in estimates of leaf area may importantly impact estimates of the available radiative energy and its partitioning between evapotranspiration and sensible heat flux. Furthermore, inclusion of plant competition in a vegetation model also resulted in lower estimated photosynthetic  $\text{CO}_2$  uptake and transpiration [Anten, 2002; Van Loon et al., 2014] which in turn may impact carbon and water cycle projections, respectively. Here our aim is to investigate how the coupling between vegetation and the atmosphere is influenced by plant competition at diurnal scales during a whole growing season. That is, if plant traits and associated vegetation functioning have evolved through natural selection on maximization of competitiveness rather than on maximization of inherent performance, how would this affect vegetation-atmosphere interactions? Our hypothesis is that plant competition affects vegetation responses and thereby could strengthen or decrease certain feedback loops in the coupling of vegetation and atmosphere, resulting in changes in the atmospheric state variables. To study plant competition, we use soybean (*Glycine max*). The choice for soybean is because this species is widely grown all over the world and might therefore have globally a large effect on atmospheric processes. But we emphasize that we perform a simple and elementary analysis meant solely to assess the impact of competition on vegetation and atmospheric processes and not to develop a fully predictive climate model.

## 2. Material and Methods

Our methodology to quantify our hypothesis is based on a coupled soil vegetation-atmosphere model that includes explicitly a new representation of plant competition, which can be defined as an evolutionary game theoretical routine that models natural selection through competition. Our research strategy is to determine the impact of this new representation on surface and atmospheric variables and processes, which include the LAI (Leaf Area Index, i.e., the leaf area per unit soil area), latent and sensible heat flux, net ecosystem exchange of  $\text{CO}_2$ , surface temperature, specific humidity, and atmospheric  $\text{CO}_2$ . The coupled vegetation-atmosphere model we use was developed by Vilà-Guerau de Arellano et al. [2015], hereafter called CLASS model. This model is a soil-water-atmosphere-plant model that predicts the energy, water, and carbon balance on a daily time scale for the atmospheric boundary layer (ABL). This model explicitly includes the coupling of surface, heat, and the exchange fluxes between the ABL and the troposphere. A short description of the CLASS model is provided in section 2.1. The vegetation part of the CLASS model is replaced with the vegetation model of Van Loon et al. [2014]. This vegetation model represents natural selection for canopy traits thereby relating photosynthesis to available nitrogen and has already been validated for soybean [Van Loon et al., 2014]. A short description of the vegetation model is provided in section 2.2, and in section 2.3 it is explained how this model is coupled to the CLASS model. We developed and explore two versions of this model: (1) CLASS<sub>SimOpt</sub>: competition between plants is omitted, which is called the simple optimization model; and (2) CLASS<sub>ComOpt</sub>: competition between plants is taken into account, which is called competitive optimization model. Here we will shortly explain the two model versions; in section 2.4 we give a more elaborate description and explain how these model versions are incorporated in the vegetation-atmosphere model.

In the first model version, CLASS<sub>SimOpt</sub> it is assumed that plant traits are optimal simply when whole stand performance is maximized, meaning that the plants individual performance is optimized as long as it is in a monoculture without any invading strategies. The theory is based on the ecological concept that natural selection may have produced plants with optimal traits that maximize whole stand net photosynthesis independent of competition between plants [Dewar et al., 2009]. We have chosen to optimize the LAI first because leaf area is an important trait driving photosynthesis, growth, and competitive ability of plants and, second, because LAI is a key vegetation parameter in many atmospheric models [Van den Hurk et al., 2003] and is generally thought to play an important role in vegetation-atmosphere feedbacks [Bounoua et al., 2000] due to its influence on the radiation balance and evapotranspiration. The optimal LAI has been defined as the value at which, for a given total canopy  $N$  and a fixed water availability, the whole canopy photosynthesis is maximized [Schieving et al., 1992; Anten et al., 1995]. The second model version, CLASS<sub>ComOpt</sub> uses a game theoretical approach assuming that plants compete for light through leaf overlap and that due to this the photosynthetic performance of one plant depends on the characteristics of its neighbors [Reichert and Hammerstein, 1983]. With this method the evolutionary stable LAI of a vegetation stand can be determined, which is defined as the LAI whereby no individual plant can increase its performance by a unilateral change in its LAI [Reichert and Hammerstein, 1983]. Thus, this method considers that natural selection favors plants that

have a competitive advantage over their neighbors rather than those with optimal trait values for maximum performance.

Both CLASS<sub>SimOpt</sub> and CLASS<sub>ComOpt</sub> are validated against seasonal half hourly data from soybean collected in the year 1998 at the Ameriflux tower site located in Bondville, Illinois (see sections 2.5 and 2.6). By doing so, we compare the ability of the two model versions to reproduce the diurnal evolution of the essential components of the soil-vegetation-atmosphere system for soybean over a whole growing season, and we can determine the effects of inclusion of competition on surface and atmospheric processes. Finally, we complete the study by performing a sensitivity analysis on leaf nitrogen availability, soil type, and soil water content in order to study the effect of competition on the coupling between surface and atmospheric processes under different environmental conditions, more explanation is provided in section 2.7.

### 2.1. The Soil-Water-Atmosphere-Plant Model (CLASS Model)

Here we briefly describe the CLASS model; a full description of the CLASS model can be found in Vilà-Guerau de Arellano *et al.* [2015]. To ensure reproducibility, we list all parameter values, the variables mentioned in the main text, and of the initial conditions in Tables S1, S2, and S3 in the supporting information, respectively, in the supporting information. The model is a 0-dimension (in space) soil-water-atmosphere-plant system that can be used for studying the evolutions of the daily interactions between the main biophysical variables that control the surface, atmospheric boundary layer (ABL), and the carbon cycle. The main governing equations of the state variables, potential temperature, specific humidity, wind, and carbon dioxide are according to the mixed layer theory. This theory assumes that these state variables are well mixed within the convective boundary layer (CBL) due to the intense convective turbulent motions. The interface between the top of the ABL—defined by the boundary layer height,  $h$ —and the free troposphere is characterized by a gradient (jump) in the state variables. The evolution of the ABL depends on the boundary layer growth, which is driven by surface fluxes of heat and moisture (buoyancy flux) and the entrainment flux of heat and moisture at the top of the CBL.

The general equation describing the diurnal evolution of an atmospheric state thermodynamic variable (potential temperature, specific humidity, or wind) or atmospheric constituents ( $\text{CO}_2$ )  $\psi$  reads as

$$\frac{\partial \langle \psi \rangle}{\partial t} = \frac{\overline{w' \psi'_s} - \overline{w' \psi'_e}}{h} \quad (1)$$

where  $\overline{w' \psi'_s}$  is the surface flux (e.g., sensible heat flux, latent heat flux, and net ecosystem exchange of  $\text{CO}_2$ ),  $\overline{w' \psi'_e}$  the entrainment flux (exchange flux between the atmospheric boundary layer properties and the free troposphere properties),  $h$  is the atmospheric boundary layer height, and  $\psi$  is parameterized as a function of the entrainment velocity ( $dh/dt$ ) and the jump of the variable at the inversion. Note that the boundary layer height modifies the dilution capacity of the ABL. Equation (1) thus describes that changes in atmospheric state variables depend on the connection between the surface conditions (represented by the surface flux) and the atmospheric entrainment fluxes modulated by the atmospheric boundary layer height. The result is a variation in time of the specific state of atmospheric composition of variables in the ABL.

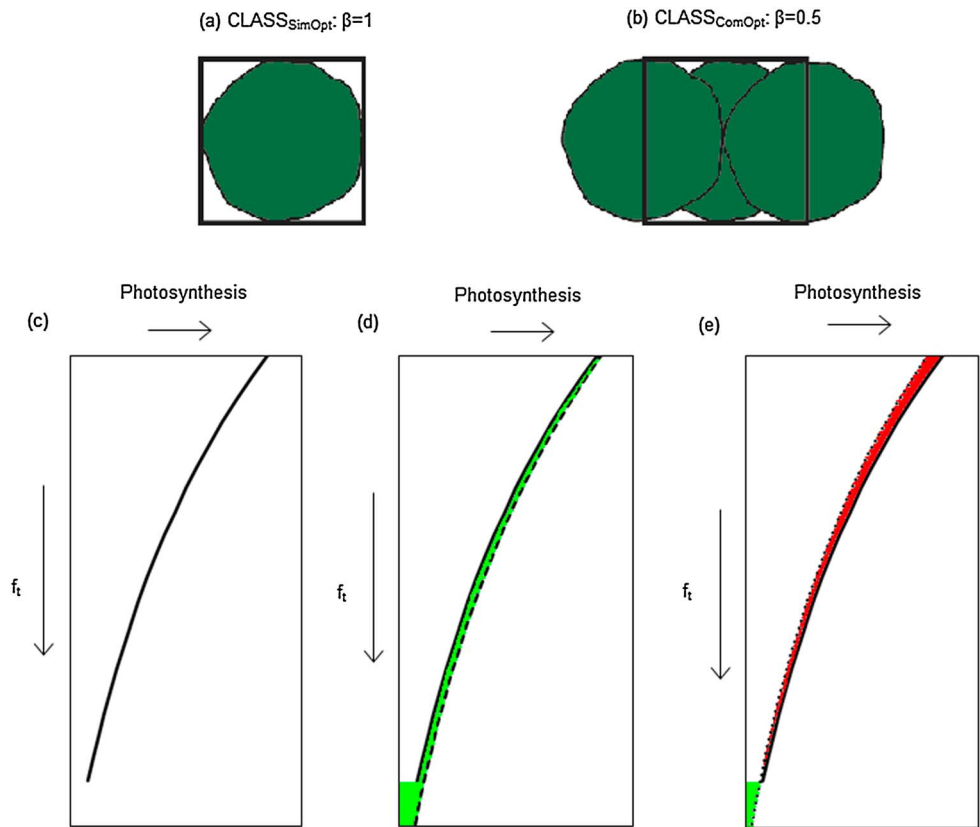
### 2.2. The Vegetation Model, CLASS<sub>OPT</sub>

The vegetation part of the original CLASS model is replaced by an optimality approach that allows to optimize LAI (Leaf Area Index) to maximize daily total canopy net photosynthesis rate (either at the individual plant or at vegetation level, see below) under the environmental constraints: total canopy leaf N content, incident light, temperature, atmospheric  $\text{CO}_2$ , and soil and atmospheric water content. Here we give a brief summary of the vegetation model emphasizing equations that influence the atmospheric part of the model most; a full description of the model can be found in Van Loon *et al.* [2014].

From a whole stand a target plant is defined, whose leaves are within area  $A$ . The ratio of the target plant's leaf area to the total leaf area ( $\beta$ ) in the area  $A$  describes the degree to which canopies of plants are mixed, which in turn determines the degree to which plants influence each other's light climate (Figure 1).

$$\beta = \text{LAI}_i / \text{LAI}_T \quad (2)$$

where  $\text{LAI}_i$  is the LAI of the target plant and  $\text{LAI}_T$  the total LAI in area  $A$ . A  $\beta$  value of 1 means that in the area  $A$ , there are only leaves of the target plant and there is no mixture with leaves of neighboring plants; therefore, the target plant is only influenced by its own light climate. This value of  $\beta$  is used for the simple optimization version of the model (CLASS<sub>SimOpt</sub>). While a  $\beta$  value smaller than 1 means that in the area  $A$ , there is a mixture of



**Figure 1.** (a) A value of  $\beta = 1$  (equation (2)), leaves of the target plant in area A (black box) are not mixed with leaves of neighboring plants, is the simple optimization model (CLASS<sub>SimOpt</sub>). (b)  $\beta = 0.5$ ; this is the competitive optimization model (CLASS<sub>ComOpt</sub>). (c) In case of the simple optimization model, the target plant has an optimal LAI to maximize its photosynthesis. The continuous line shows the maximal photosynthesis of the target plant over the cumulative LAI ( $f_t$ ). In case of the competitive optimization model, the stable LAI is determined. (d) The target plant unilaterally increases its leaf area beyond the simple optimal LAI; therefore, it captures a larger fraction of the available light at the cost of reducing its photosynthetic capacity per unit leaf area, because in the model we assume a constant canopy N content. The dashed line shows the photosynthesis of the target plant when only the target plant increases its LAI; the green area indicates the photosynthesis gain due to this increase in leaf area. (e) When this resulted in an increase in the net photosynthesis of the target plant, the LAI of the neighbors was also increased. The dotted line shows the photosynthesis of the target plant when its neighboring plants also increase their LAI; the red area indicates the photosynthesis loss due to this increase in leaf area; note that this red area is larger than the green area indicating that when all plants increase their leaf area, photosynthesis is reduced. Figures 1a and 1b are redrawn from Van Loon et al. [2014].

leaves of the target plant with leaves of neighboring plants, and this degree of mixture increases when  $\beta$  becomes smaller, indicating that the shading experienced by the target plant is mostly caused by leaves of neighboring plants. The leaf area of the target plant and of its neighbors within the area A are assumed to be uniformly distributed, horizontally and vertically. Furthermore, all plants are assumed to be identical, in terms of height, LAI, etc., but it is only the combined leaf area of the target plant and the neighboring plants in the area A that matters. Thus, competition between plants is taken into account in the competitive optimization version of the model (CLASS<sub>ComOpt</sub>). It is important to stress that  $\beta$  is fixed over the entire growing season, because the level of canopy mixing is the mean of the competitive environment a plant evolved in during natural selection. For example, trees with broad crowns would on average experience less overlap and thus have higher  $\beta$  values than herbaceous plants, and a similar distinction could be made for plants from sparse versus dense vegetation (see section 3 and also Anten and During [2011]). For further elaboration on the  $\beta$  values of the two model versions, see section 2.4.

For calculation of light (i.e., photosynthetically active radiation, PAR) partitioning within the canopy we follow the approach of Spitters et al. [1986] that distinguishes between the distribution of direct solar beam and diffuse radiation. The leaf photosynthesis [Farquhar et al., 1980] is a function of PAR [Spitters et al., 1986],

nitrogen [Anten *et al.*, 1995; Harley *et al.*, 1992], temperature [Johnson *et al.*, 1942; Farquhar *et al.*, 1980], CO<sub>2</sub> and soil and atmospheric water content [Tuzet *et al.*, 2003]. In this model the gross photosynthesis rate of a leaf ( $P_{gl}$ ) is the minimum of the carboxylation or Rubisco limited photosynthesis rate ( $P_{cl}$ ) and the electron transport limited photosynthesis rate ( $P_{jl}$ ) [Farquhar *et al.*, 1980]. Net leaf photosynthesis ( $P_{nl}$ ) is calculated as the gross photosynthesis rate of a leaf per unit ground area minus the leaf respiration rate ( $R_l$ ). Integration of the leaf gross and net daily photosynthesis rates over the cumulated LAI of the canopy and subsequently multiplying the integrands by  $\beta$  yields the canopy net photosynthesis rate ( $P_{nT}$ ) and gross photosynthesis rate ( $P_{gT}$ ), respectively.

We assumed a fixed total amount of leaf N ( $N_T$ ), and because this is fixed results an increase in leaf area in a reduced leaf N content. As leaf photosynthetic capacity (i.e., the light-saturated rate of photosynthesis) is strongly correlated with leaf N content an increase in LAI at fixed canopy N will thus entail a reduction in photosynthetic capacity per unit leaf area [Evans, 1989]. It is important though to note that roots are not represented in our model, but instead, we simply assume a given total N that plants can allocate to leaves.

We assumed a steady state of inflow of CO<sub>2</sub> into the plant and consumption of CO<sub>2</sub> by the plant. Meaning that the stomatal conductance times the difference in atmospheric and internal CO<sub>2</sub> is equal to the photosynthesis. The stomatal conductance of the canopy is described as [Tuzet *et al.*, 2003]

$$G_{sT} = G_{s0} + \frac{c \cdot P_{gT}}{(C_i - \Gamma^*) / Pa} \cdot g_{\psi} \quad (3)$$

where  $G_{s0}$  is the residual stomatal conductance;  $c$  is a scaling parameter and  $g_{\psi}$  is an empirical logistic water stress function to describe the sensitivity of stomata to leaf water potential  $\psi_l$ ,  $C_i$  the internal CO<sub>2</sub>,  $\Gamma^*$  the CO<sub>2</sub> compensation point, and  $Pa$  the atmospheric pressure [Tuzet *et al.*, 2003].

Furthermore, we assumed a steady state of plant transpiration and plant water transport through the stem [Sterck and Schieving, 2011]. Meaning that the whole plant stomatal conductance times the vapor pressure difference between leaf and air is equal to the stem conductance times the difference between soil water potential and leaf water potential. The steady state assumptions of water transport and of CO<sub>2</sub> inflow and consumption were solved with the given parameters and for the given constraints (total canopy leaf N content, soil and atmospheric water content, incident light, temperature, and atmospheric CO<sub>2</sub>).

### 2.3. Coupling of the CLASS Model With the Vegetation Model

The ABL is influenced by vegetation in two ways: (1) vegetation determines the surface albedo, which influences how the net radiation available is partitioned between latent and sensible heating (LE and SH respectively), and (2) vegetation controls the plant transpiration and therefore the moisture flux into the atmosphere. It is important to stress that the ABL hereby evolves over the day changing atmospheric moisture and potential temperature thereby feeding back on the net ecosystem exchange of CO<sub>2</sub> ( $NEE = -\text{net photosynthesis rate} + \text{soil respiration rate}$ ), evapotranspiration, and SH, and thus influencing the atmospheric processes (equation (1)). Additionally, increase in vegetation coverage, reduces the surface albedo (except when the soil is very dark, as we will show), thereby influencing the energy balance, and this could increase the SH and in turn increase the temperature in the ABL. Finally, the photosynthesis is also calculated in a different way compared to the original CLASS model; now it relates to the available nitrogen, and this will thus affect NEE and thereby also atmospheric CO<sub>2</sub>.

To study the vegetation-albedo feedback and in order to simulate seasonal changes in surface albedo, we calculated the overall albedo ( $\alpha$ ) combining the albedo's of pure soil ( $\alpha_{soil}$ ) and pure canopy ( $\alpha_{canopy}$ ), the LAI, and the extinction coefficient ( $k$ ) [e.g., Oguntunde *et al.*, 2007; Zeng and Yoon, 2009].

$$\alpha = \alpha_{soil} + (\alpha_{canopy} - \alpha_{soil}) e^{-k \frac{LAI}{P}} \quad (4)$$

Note that our model explicitly addresses the target plant and its interaction with neighbors, calculated as the ratio between the target plants' LAI ( $LAI_i$ ) and its fraction presence in the vegetation ( $\beta$ ) (equation (2)).

The soil vegetation coverage ( $c_{veg}$ ) is a function of the LAI and the extinction coefficient [Sitch *et al.*, 2003].

$$c_{veg} = 1 - e^{-k \frac{LAI}{P}} \quad (5)$$



#### 2.4. The Optimization Model Versions, CLASS<sub>SimOpt</sub> and CLASS<sub>ComOpt</sub>

Our goal is to analyze two model versions of vegetation responses: (1) CLASS<sub>SimOpt</sub>: a simple optimization approach that assumes that plant communities respond optimally to atmospheric influences such that net photosynthesis of the whole community is maximized, without including competition between plants; and (2) CLASS<sub>ComOpt</sub>: a competitive optimization approach which assumes that vegetation stands will evolve through natural selection whereby the plant type with the highest plant level photosynthesis prevails. It is thus assumed that through natural selection vegetation stands are dominated by the best competitors rather than by the ones that have the best inherent performance. Below we briefly describe their implementation.

CLASS<sub>SimOpt</sub>: the optimization procedure determined the optimal LAI that maximized whole stand net photosynthesis ( $P_{nT}$ ) for the given environmental constraints, and we thus assumed that there is no competition between plants ( $\beta = 1$  equation (2), Figure 1a). The simulated photosynthesis is depending on the penetration of light within the canopy (Figure 1c). At the top of the canopy (cumulative LAI,  $f_t = 0$ ) photosynthesis is highest while it decreases with increased cumulative LAI ( $f_t$ ). In the simulation, leaf area of all plants in the vegetation is increased simultaneously until maximum net photosynthesis was reached which is then the optimal LAI. Such an optimal LAI exists, as light interception increases with LAI but with decreasing marginal returns while at fixed N increasing LAI also entails a reduction in leaf N content and thus in leaf photosynthetic capacity [Anten *et al.*, 1995]. The underlying assumption of simple optimization is that trait acclimation to atmospheric conditions will be such that whole stand performance is maximized.

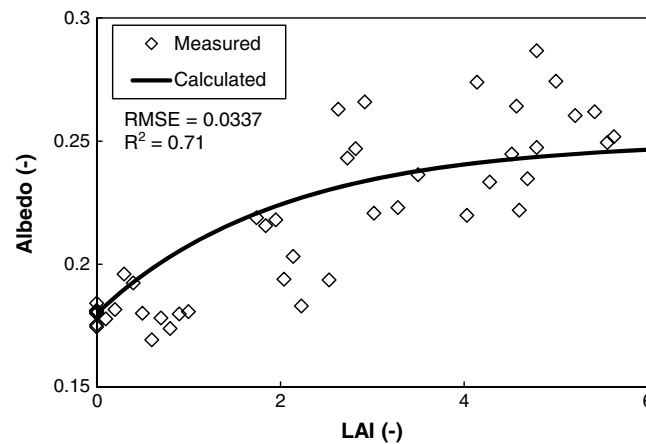
CLASS<sub>ComOpt</sub>: with this model the stable LAI of the stand, i.e., the LAI at which no individual can increase its performance with a change of its leaf area, is determined. Thus, plant competition is taken into account to determine the optimal trait values of individuals. In CLASS<sub>ComOpt</sub>, the degree of mixture between target and neighbor plants, and  $\beta$  was set to 0.5 (equation (2), Figure 1b); these values were chosen, because it has given satisfactory predictions of LAI of herbaceous stands in other studies [Anten 2002; Van Loon *et al.*, 2014]. After setting  $\beta$  to 0.5 the LAI of the target plant ( $LAI_t$ ) was unilaterally increased by 5%, while the LAI of the neighbors was kept constant (Figure 1d). By this increase in its leaf area, the target plant captures a larger fraction of the available light at the cost of reducing its photosynthetic capacity per unit leaf area. When this resulted in an increased net photosynthesis rate of the target plant, the LAI of the neighbors was also increased by 5%, and as such  $LAI_T$  also increased by 5% (Figure 1e). This process was repeated until a value of  $LAI_T$  was found at which a further change in  $LAI_t$  did not increase the net photosynthesis rate of the target plant, which is the stable LAI for the given environmental constraints. This iteration process thus simulates the process of natural selection for evolutionary stable traits. In this calculation a lower  $\beta$  value means that a mutant plant has a relatively greater benefit of unilaterally increasing its leaf area, because it would get a greater fraction of the light that otherwise came available to neighbors; while if  $\beta = 1$ , the plant only shades itself. Thus, with declining  $\beta$  there is increased selection to produce larger leaf areas. As each day has different environmental constraints (e.g., atmospheric CO<sub>2</sub>, N availability, and soil water content; see Table S3) we determined the stable LAI for each day separately. Additionally, we set the constraint that all leaves must have a daily net photosynthesis above zero [Reich *et al.*, 2009], meaning that each of the leaf layers in the model is not allowed to have a negative average daily net photosynthesis rate which sets a limit to leaf area production.

#### 2.5. Vegetation and Soil Conditions

The input values used in defining the total canopy N content are summarized in Table S4 in the supporting information and all other input values can be found in Table S1. Below a description is given of the estimation of the parameters of the albedo function, the total canopy N content, and the parameters of the soil respiration.

For the albedo function (equation (4)) we estimated parameter values of the albedo of pure soil ( $\alpha_{soil}$ ) and pure canopy ( $\alpha_{canopy}$ ), from shortwave incoming and outgoing radiation data of soybean of the growing season 2002 of the Ameriflux tower in Bondville. The albedo is the average ratio of outgoing to incoming shortwave radiation during daytime, and if plotted against LAI, we can obtain the parameter values.

In our case we find that the albedo is lower without vegetation cover than with vegetation cover (Figure 2); this is because the soil is a very dark silt loam soil that is typically found throughout much of the midwestern United States.



**Figure 2.** Measured LAI of soybean and albedo (average daily outgoing shortwave radiation/incoming shortwave radiation) during the growing season of the year 2002 (diamonds) and calculated LAI-albedo function (continuous line) and the root-mean-square error (RMSE) and  $R^2$ .

of Ameriflux per day of the year and used these  $N_t$  values as input in both  $CLASS_{SimOpt}$  and  $CLASS_{ComOpt}$  (Table S4).

The soil respiration rate (Resp) depends on a water stress function ( $f_w$ ); whereby the soil respiration rate decreases with increasing soil water content, as it is assumed that in this case, diffusive oxygen is limiting. Furthermore, the soil respiration rates depend on temperature according to a Q-10 relationship.

$$Resp = (1 - f_w) R_{10} e^{\left(\frac{E_0}{283.15 R}\right) \left(1 - \frac{283.15}{T_{soil}}\right)} \quad (6)$$

where  $R_{10}$  is the respiration rate at 10°C,  $E_0$  is the activation energy,  $R$  is the universal gas constant, and  $T_{soil}$  is the soil temperature.

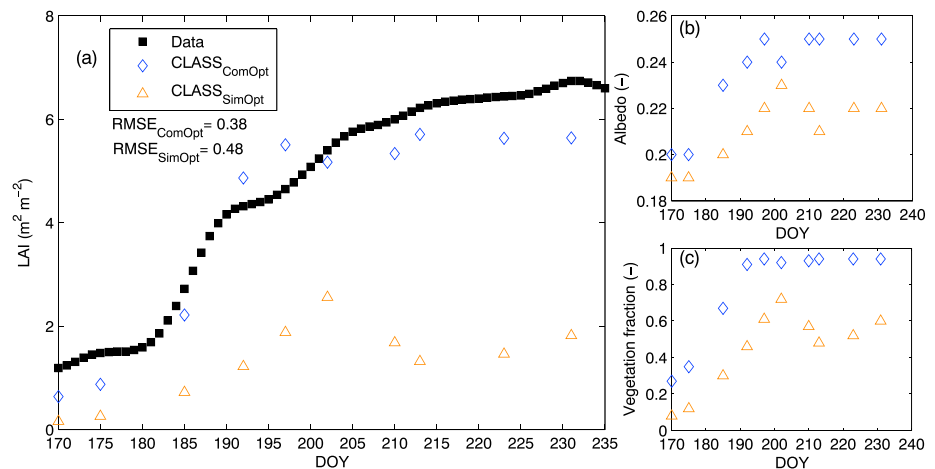
The parameter value  $R_{10}$  is estimated from data of  $CO_2$  fluxes to the atmosphere (net ecosystem exchange, NEE). This is estimated from days without vegetation present, so  $CO_2$  flux comes only from soil surface and is thereby only influenced by top soil layer temperature and soil moisture.

## 2.6. Data for Model Comparison

The model results of both  $CLASS_{SimOpt}$  and  $CLASS_{ComOpt}$  were compared with data of state variables and surface fluxes collected every half hour from soybean in the year 1998 at the Ameriflux tower site located in Bondville, Illinois (40° latitude, −88° longitude); in order to study if we get accurate predictions of the diurnal evolution of the main components, namely, LAI, LE, SH, NEE, surface temperature, specific humidity, and atmospheric  $CO_2$ , of the soil-vegetation-atmosphere system for the soybean plot. These main components have been chosen to be adequate metrics to represent both vegetation responses as well as atmospheric responses. We selected 10 days during the whole growing season for this comparison. All input values per day can be found in Table S1 in the supporting information. These 10 days have been chosen based upon the following criteria: cloudless days and with enough data available for use of input of initial and boundary conditions and for comparison with model results. The focus is on cloudless days, because the model assumptions are based on convective turbulent conditions (equation (1)) [Vilà-Guerau de Arellano *et al.*, 2015]. In addition, we focused on diurnal conditions under cloudless days when the surface friction velocity is above  $0.2 \text{ ms}^{-1}$  to ensure that the eddy-covariance measurements are gathered under enough turbulence [Pattey *et al.*, 2002]. To provide some extra insight in the model results, we point out the results of three specific days of those 10 days (1 day in the beginning, middle, and end of the growing season). To analyze how well the model predicts the observed values, we performed a linear regression and calculated the  $R^2$ , root-mean-square error (RMSE, standard deviation of the data about the regression line) and the average deviation between the observed and predicted values (5%).

$$S\% = \frac{100}{n} \sum_{i=1}^n \frac{|y_{pr} - y_{obs}|}{y_{obs}} \quad (7)$$

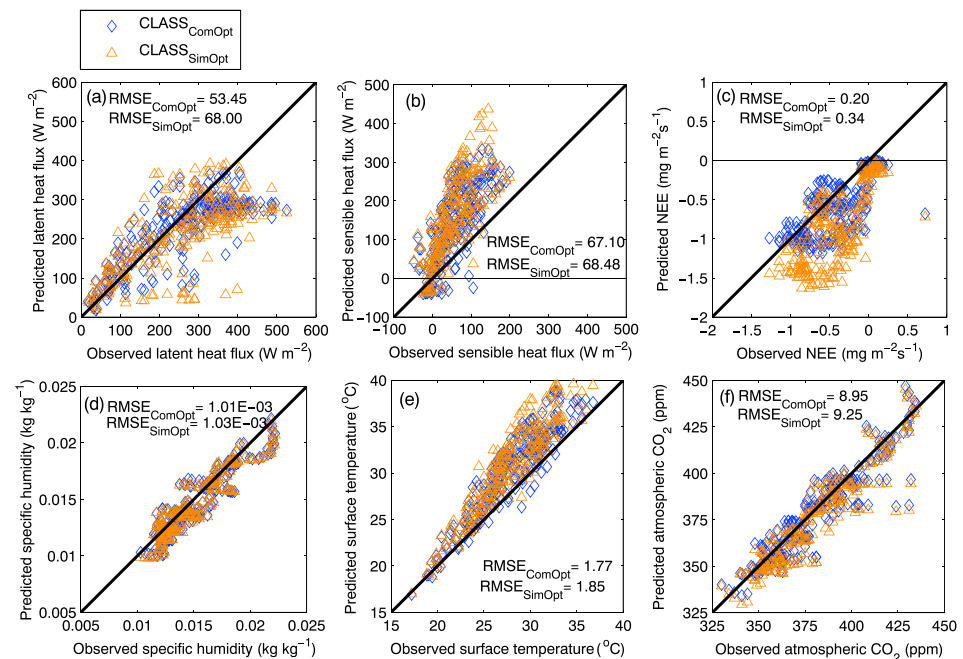
where  $n$  is the number of observations,  $y_{pr}$  the predicted value, and  $y_{obs}$  the observed value.



**Figure 3.** (a) Soybean data on LAI from the Ameriflux Bondville tower site for the whole growing season (filled black squares) compared with the modeled LAI values of the competitive optimization model (CLASS<sub>ComOpt</sub>, blue diamonds) and of the simple optimization model (CLASS<sub>SimOpt</sub>, orange triangles) for the 10 selected days, and for these 10 days also the (b) predicted albedo and (c) vegetation fraction.

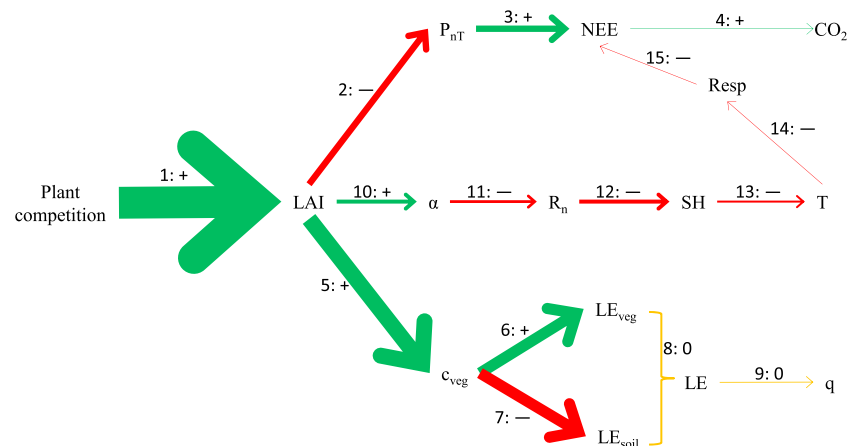
## 2.7. Sensitivity Analysis

For the sensitivity analyses we studied in detail one representative day in the growing season, namely, day of year (DOY) 213, as on this day the canopy was fully grown. We show the most representative outcomes of the model runs; these include the LAI, NEE, and the evaporative fraction (EF). The evaporative fraction is the LE divided by LE plus SH and is to quantify the partitioning of the surface energy balance.



**Figure 4.** For the whole soybean growing season the (a) half hourly predicted latent heat flux, (b) sensible heat flux, (c) net ecosystem exchange (NEE), (d) specific humidity air, (e) surface temperature, and (f) atmospheric  $\text{CO}_2$  for the competitive optimization model (CLASS<sub>ComOpt</sub>) and the simple optimization model (CLASS<sub>SimOpt</sub>) versus the observed values from Ameriflux 1998 Bondville for DOY 170, 175, 185, 192, 197, 202, 210, 213, 223, and 231 and the root mean square error of both the competitive optimization model and the simple optimization model (RMSE<sub>ComOpt</sub> and RMSE<sub>SimOpt</sub> respectively). All the results of the linear regression can be found in Table 1 and all the results over the days can be found in Figure S1 in the supporting information.





**Figure 5.** Conceptual diagram connecting the effect of accounting for plant competition on modeled surface variables. This effect can either be positive (green arrow with plus sign), negative (red arrow with minus sign), or no effect (yellow arrow with zero sign). The size of the arrow gives an indication about the size of the effect. Inclusion of (1) plant competition results in a higher leaf area index, LAI, and (2) a lower photosynthesis rate,  $P_{nT}$ . The lower photosynthesis rate increases the net ecosystem exchange of  $\text{CO}_2$ , (3) NEE (indicates the removal of  $\text{CO}_2$  from the atmosphere and it is a negative value, with a lower photosynthesis it becomes less negative) and as a result the (4) atmospheric  $\text{CO}_2$  increases. (5) The higher LAI also increases the fraction of vegetation,  $c_{veg}$ ; resulting in a higher latent heat flux of the vegetation, (6)  $LE_{veg}$  while the (7) soil heat flux,  $LE_{soil}$ , is reduced. These counterbalance each other and thereby the (8) total latent heat flux,  $LE$ , is almost not changed leading to also (9) almost no change in specific humidity of the air,  $q$ . An increase in LAI also increases the (10) albedo,  $\alpha$ ; and thereby reducing the (11) total net radiation,  $R_n$ , (12) sensible heat flux,  $SH$ , and (13) temperature,  $T$ . The lower temperature reduces the (14) soil respiration rate,  $Resp$ , but it only slightly reduces the (15) NEE.

With the coupled vegetation-atmosphere model we investigated the inclusion of plant competition on total canopy N content, because it is an important factor in regulating the total canopy photosynthesis rate and LAI and thus can have a large impact on the energy fluxes. Additionally, N input is also an anthropogenic forcing, with large spatial and temporal differences around the globe.

We also performed a sensitivity analysis on other soil types than silt loam, which was found on the location we had chosen, namely, sand and clay. We chose to do this sensitivity analysis, because the soil albedo for the silt loam soil is lower (albedo = 0.18) than the albedo of full canopy closure (albedo = 0.25, see section 2.5), which is rather unusual as most soils have a higher albedo than the vegetation and this might therefore have large influences on the energy fluxes. The input values for the different soil types are shown in Table S5 in the supporting information.

Next to this we also performed for each soil type a sensitivity analysis on the effect of changes in soil moisture index of the top and deeper soil layers. The soil moisture index is the water content of the soil (top or deeper soil layer) minus the water content at wilting point divided by the water content of at field capacity minus the water content at wilting point (soil moisture index,  $SMI = \frac{W_2 - W_{wilt}}{W_{fc} - W_{wilt}}$ ). It reflects the ability of the soil to supply moisture to plants, a value of 0 means that there is no supply of water to plants while a value of 1 means that there is ample water available. This is simulated, because the water content of the soil in combination with the texture of the soil might also affect the energy fluxes. Additionally, the original experiment had relatively wet soils; therefore, it is also interesting to analyze how the effect of inclusion of competition will be on dry soils.

### 3. Results and Discussion

#### 3.1. Model Validation With Observations

Figures 3 and 4 show soybean data, from the Ameriflux Bondville tower, during the growing season of 1998 in comparison with predictions of the competitive optimization model ( $CLASS_{ComOpt}$ ) and the simple optimization model ( $CLASS_{SimOpt}$ ) for 10 selected days (see also Figure S1). This is shown to validate model outcomes and to investigate the influence of competition on the coupling between the vegetation and the atmosphere diurnal scales during a whole season. Figure 5 is a conceptual figure showing the effect of accounting for

**Table 1.** Results of the Linear Regression (Slope, Intercept, RMSE, and  $R^2$ ) With the Competitive Optimization Model (CLASS<sub>ComOpt</sub>) and the Simple Optimization Model (CLASS<sub>SimOpt</sub>) as a Dependent Variable and the Observed Values of Ameriflux 1998 Bondville for Several Days Over the Growing Season (DOY 170, 175, 185, 192, 197, 202, 210, 213, 223, and 231) During Daytime as the Independent Variables, and the Average Deviation Between Estimated Values and Observed Values (S%)

	Model	Slope (S.E.)	Intercept (S.E.)	RMSE	$R^2$	S%
Atmospheric CO <sub>2</sub> (ppm)	CLASS <sub>ComOpt</sub>	0.923 (0.023)	26.720 (8.972)	8.95	0.87	1.7
	CLASS <sub>SimOpt</sub>	0.935 (0.024)	19.667 (9.267)	9.25	0.86	4.5
Ground heat flux (W m <sup>-2</sup> )	CLASS <sub>ComOpt</sub>	0.467 (0.029)	21.181 (1.297)	14.39	0.52	158.8
	CLASS <sub>SimOpt</sub>	0.484 (0.030)	23.682 (1.346)	14.93	0.52	171.1
LAI (—)	CLASS <sub>ComOpt</sub>	0.961 (0.103)	−0.182 (0.507)	0.64	0.92	18.9
	CLASS <sub>SimOpt</sub>	0.296 (0.076)	−0.027 (0.374)	0.47	0.65	72.8
Latent heat flux (W m <sup>-2</sup> )	CLASS <sub>ComOpt</sub>	0.575 (0.028)	76.444 (7.753)	52.92	0.64	27.4
	CLASS <sub>SimOpt</sub>	0.545 (0.036)	73.120 (10.022)	68.40	0.49	32.0
Net ecosystem CO <sub>2</sub> exchange (mg m <sup>-2</sup> s <sup>-1</sup> )	CLASS <sub>ComOpt</sub>	0.724 (0.045)	−0.296 (0.024)	0.25	0.52	225.4
	CLASS <sub>SimOpt</sub>	0.986 (0.059)	−0.427 (0.032)	0.33	0.54	326.6
Net radiation (W m <sup>-2</sup> )	CLASS <sub>ComOpt</sub>	1.010 (0.015)	27.501 (6.194)	42.60	0.95	16.1
	CLASS <sub>SimOpt</sub>	1.038 (0.017)	29.566 (6.731)	46.29	0.94	19.4
Sensible heat flux (W m <sup>-2</sup> )	CLASS <sub>ComOpt</sub>	1.447 (0.082)	56.170 (6.272)	65.93	0.56	339.9
	CLASS <sub>SimOpt</sub>	1.604 (0.086)	67.235 (6.569)	69.05	0.59	375.9
Specific humidity (kg kg <sup>-1</sup> )	CLASS <sub>ComOpt</sub>	0.906 (0.023)	0.001 (0.000)	1.01E−03	0.87	6.0
	CLASS <sub>SimOpt</sub>	0.907 (0.023)	0.001 (0.000)	1.03E−03	0.87	6.2
Temperature air (°C)	CLASS <sub>ComOpt</sub>	1.066 (0.034)	−1.250 (0.910)	1.75	0.80	5.0
	CLASS <sub>SimOpt</sub>	1.085 (0.035)	−1.591 (0.934)	1.80	0.80	5.3
Temperature surface (°C)	CLASS <sub>ComOpt</sub>	1.102 (0.029)	−0.492 (0.824)	1.77	0.85	8.8
	CLASS <sub>SimOpt</sub>	1.165 (0.031)	−1.630 (0.860)	1.85	0.86	10.6

plant competition on modeled surface variables, by comparing the results obtained from the CLASS<sub>SimOpt</sub> with CLASS<sub>ComOpt</sub>.

The inclusion of competition between plants in a coupled vegetation-atmosphere model resulted in a better agreement of the calculations of LAI (Leaf Area Index, i.e., the leaf area per unit soil area) with the data. CLASS<sub>SimOpt</sub> strongly underestimated the LAI observations for the whole growing season (Figure 3a). After DOY 202 the LAI simulated by CLASS<sub>SimOpt</sub> declined, the reason is a decrease in light intensity after this day. In contrast, CLASS<sub>ComOpt</sub> predictions are much more in line with the data observations (Figure 3a). The LAI increases during the beginning of the growing season and stabilizes after DOY 195 closely following the observed pattern (Figure 3a). The LAI values are 1.5, 3.6, and 4.4 m<sup>2</sup> m<sup>-2</sup> higher for CLASS<sub>ComOpt</sub> compared to CLASS<sub>SimOpt</sub> on DOY 185, 197, and 213, respectively. Simulated albedo and vegetation fraction do also show clear differences between CLASS<sub>ComOpt</sub> and CLASS<sub>SimOpt</sub> (Figures 3b and 3c, respectively). Data on albedo and on vegetation fraction was not available.

The higher LAI for CLASS<sub>ComOpt</sub> compared to CLASS<sub>SimOpt</sub> can be explained according to game theoretical principles. Because plants compete for light, a unilateral increase in LAI of a given plant above the optimal LAI results in a relatively smaller increase in self-shading for that plant while it is able to capture a larger fraction of the available light. As a result, this plant can increase its carbon gain by increasing its LAI (Figure 1d) even if this reduces photosynthesis of the stand as a whole [Anten, 2002] (Figure 1e). In the model the canopy N content remains constant, and production of extra leaf area to shade competitors therefore results in reduction of the leaf photosynthetic capacity. Consequently, CLASS<sub>ComOpt</sub> predicts a lower total canopy net photosynthesis rate than CLASS<sub>SimOpt</sub> while having a larger LAI. This suggests that natural selection under competition results in evolutionary stable communities that have a higher LAI than needed for maximization of whole stand photosynthesis [see also Anten, 2002; Lloyd *et al.*, 2010].

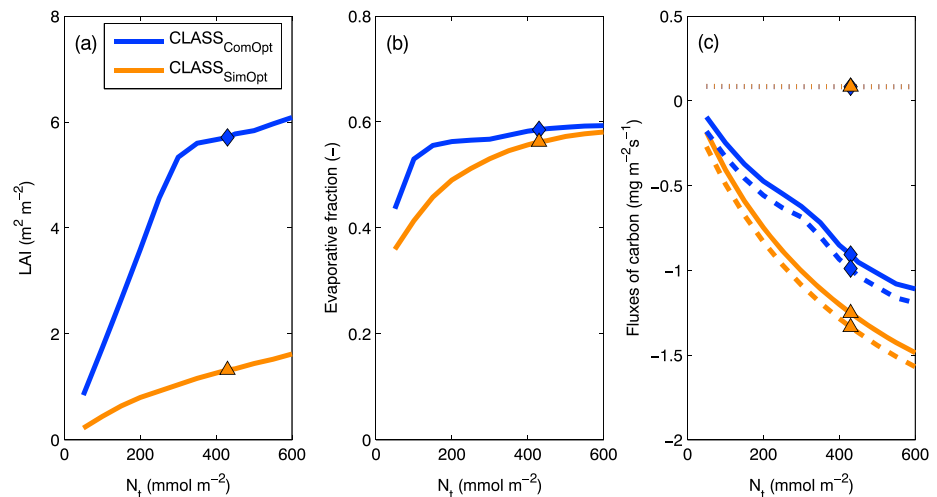
Here we show that inclusion of game theory to account for competition between plants not only improves simulations at the canopy level but also at the ecosystem level; as the modeled net ecosystem exchange rates of CO<sub>2</sub> (NEE = −net photosynthesis rate + soil respiration rate) by CLASS<sub>ComOpt</sub> are in clear agreement with the observations, while the NEE values from CLASS<sub>SimOpt</sub> are not (Figure 4c; Table 1). The NEE becomes 35%, 34%, and 28% less negative for DOY 185, 197, and 213, respectively, with inclusion of competition between plants (negative entailing CO<sub>2</sub> being taken from the atmosphere). A less negative NEE is caused by a lower photosynthesis rate (Figure 5, arrow 2), as soil respiration only has a marginal influence. The soil

respiration rate is only slightly reduced (Figure 5, arrow 14), which is due to lower soil temperature resulting from the higher albedo (Figure 5, arrow 10). Although the predicted NEE values by CLASS<sub>ComOpt</sub> are in close agreement with observations, uncertainty in observed NEE values is present due to the difficulties in measuring soil respiration and photosynthesis at leaf or canopy level. This is mostly the case when wind speed is low, as this leads to less mixing of floor and canopy air and thus higher uncertainty of CO<sub>2</sub> fluxes recorded [Hollinger and Richardson, 2005]. In summary, including competition in a coupled vegetation-atmosphere model increases the LAI while it reduces whole stand photosynthesis, thus resulting in a less negative NEE.

Although CLASS<sub>ComOpt</sub> predicted a higher LAI than CLASS<sub>SimOpt</sub>, it resulted in an almost similar latent heat flux (LE) (Figure 4a; Figure 5, arrow 8), though RMSE and S% (average deviation between estimated values and observed values) of CLASS<sub>ComOpt</sub> are slightly lower than of CLASS<sub>SimOpt</sub> (Table 1). This is predicted, because of a high LAI, and thus, a high leaf coverage (the fraction of soil covered by vegetation is during most of the growing season above 0.9 for CLASS<sub>ComOpt</sub>, see Figure 3c and Figure 5, arrow 5) results in a high LE of the vegetation (Figure 5, arrow 6) but reduces soil LE (Figure 5, arrow 7), while it is the other way around for a low LAI. As a result, both the simple and the competitive optimization models estimate LE reasonably well compared to the observations (Figure 4a, Table 1). Thus, especially during the beginning of the growing season, when there is no full canopy closure, the LE is fully determined by the soil LE and at the end of the growing season by the LE of the vegetation (Figures 3c and S2). However, at the end of the growing season both model versions underestimate the maximum daily LE values obtained during noon (Figure S1b). On DOY 185, 197, and 213, the observed daily maximum LE values were 384, 410, and 525 W m<sup>-2</sup>, respectively. Model predictions of daily maximum LE values for these days were 336, 294, and 275 W m<sup>-2</sup> for CLASS<sub>ComOpt</sub> and 369, 271, and 297 W m<sup>-2</sup> for CLASS<sub>SimOpt</sub>, respectively. To conclude, while the LAI was thought to have a large impact on the water cycle [Eltahir and Bras, 1996], here we show that on the particular soil type in our experiment changes in LAI have almost no effect on the total LE and thereby also not on the atmospheric moisture content; in contrast, the soil LE has a large impact on the total LE.

During the beginning of the season very high values of sensible heat flux (SH) were found (Figure S1c), as during this period there was little canopy coverage indicating that most of the SH was emitted by the soil [Bernacchi *et al.*, 2007]. Sensible heat fluxes were overestimated by both model versions with a factor of around 1.5 (Figure 4b). There could be several reasons for this. First, it could be that the representation of the surface energy balance in our model does not include all processes involved, such as heat storage within the canopy, horizontal advection of heat [Wilson *et al.*, 2002], and aerosol loading that influence the partitioning between direct and diffuse radiation, and it can reduce PAR [Barbaro *et al.*, 2014]. Second, the model underestimates the LE with around 5% during the end of the growing season at midday when the LE is high (Figure S1b) leading to more energy available for SH and for the ground heat flux. The discrepancy between modeled and measured values could, however, also be related to uncertainty in observations as inaccuracies of 10–30% in measurements are common [e.g., Brotzge and Crawford, 2003; Wilson *et al.*, 2002]. Latent heat fluxes for example can have systematic errors due to for instance change in fetch conditions due different wind direction and wind speed [e.g., Dekker *et al.*, 2001a] while random errors at half hourly resolutions can easily become 10% of the measured flux [e.g., Dekker *et al.*, 2001a]. This is further corroborated by the imbalance in the surface energy budget, as there is a gap in energy balance of the data between the net observed radiation and the sum of the surface heat fluxes (latent, sensible, and ground heat flux); we found that the observed radiation is on average 25 W m<sup>-2</sup> higher (16 W m<sup>-2</sup>–30 W m<sup>-2</sup>, 95% confidence interval) compared to the observed sum of the surface heat fluxes (Figure S3 in the supporting information). However, these measurement inaccuracies could at best explain about 60% of the difference between the model and observations.

Finally, both model versions (CLASS<sub>ComOpt</sub> and CLASS<sub>SimOpt</sub>) calculate surface temperature, specific humidity, and atmospheric CO<sub>2</sub> reasonably well (Table 1, Figures 4d and 4f), where RMSE and S% of CLASS<sub>ComOpt</sub> are always slightly better compared to CLASS<sub>SimOpt</sub> (Table 1). To conclude, for this location it was shown that inclusion of competition between plants (CLASS<sub>ComOpt</sub>) greatly improves predictions of a number of key characteristics in the vegetation atmosphere system, especially LAI and NEE (Figures 3 and 4, Table 1). However, it is important to note that the value given to the degree to which plants are mixed and thus influence each other's light climate ( $\beta$  value, equation (2)) has a strong influence on predicted vegetation responses [Van Loon *et al.*, 2014]. Here we chose a  $\beta$  value of 0.5 as it was shown that it was a good value for the prediction of vegetation processes for soybean [Van Loon *et al.*, 2014], as well as other herbaceous



**Figure 6.** The (a) LAI, (b) evaporative fraction ( $LE/(SH + LE)$ ), and the (c) fluxes of carbon represented by the contribution of  $CO_2$  assimilation by photosynthesis (dashed lines), soil respiration (dotted lines), and net ecosystem exchange (continuous lines) for different total canopy leaf N contents ( $N_t$ ) for DOY 213 of the competitive optimization model (blue line; CLASS<sub>ComOpt</sub>) and of the simple optimization model (orange line; CLASS<sub>SimOpt</sub>). The blue diamond and the orange triangle in the figures indicate, respectively, for CLASS<sub>ComOpt</sub> and for CLASS<sub>SimOpt</sub> the original result corresponding to DOY 213.

stands [Anten, 2002]. But the degree of interaction between plants strongly depends on the type of plant. Trees for example have relatively broader canopies and thus higher  $\beta$  than herbaceous plants [Anten and During, 2011]. This could entail that the coupling between vegetation and the atmosphere would be less affected by plant competition for forests than for herbaceous stands. More research is needed to assess how competition may affect vegetation-atmosphere coupling in different vegetation types.

### 3.2. Sensitivity Analysis: Total Canopy N Content

Here we show that the canopy N content ( $N_t$ ) has a large impact on the LAI (Figure 6a), which is consistent with general findings [e.g., Reich, 2012; Dewar et al., 2012]. As LAI affects the surface albedo (equation (4)) and the canopy stomatal conductance (via affecting the photosynthesis rate, equation (3)) and thus the available radiative energy and the partitioning between the latent and the sensible heat flux,  $N_t$  indirectly influences the evaporative fraction ( $EF = LE/(LE + SH)$ ) (Figure 6b). Canopy N content also had a large effect on the NEE (Figure 6c) due to its positive effect on photosynthesis and stomatal conductance; i.e., more nitrogen entails higher photosynthetic enzyme contents and associated photosynthetic activity in the canopy [Ollinger et al., 2008].

The effects of including plant competition on vegetation and atmospheric variables also depended strongly on  $N_t$ . The difference in LAI simulated by CLASS<sub>ComOpt</sub> and CLASS<sub>SimOpt</sub> increases with  $N_t$  (Figure 6a), because with more N availability, light becomes more limiting and there is a greater selective advantage of large leaf areas if light competition is considered (Figure 6a). This trend is consistent with the general consensus that light competition is weaker in habitats limited by nutrients as it limits growth [Grime, 1973].

We also found that the net canopy photosynthesis (not shown) is increased by more N availability and that this increase is larger for CLASS<sub>SimOpt</sub> than for CLASS<sub>ComOpt</sub>. This reflects the competitive effect where selective advantage of overinvesting in leaf area to compete with neighbors increases with  $N_t$ . Furthermore, an increase in  $N_t$  leads also to a decrease in soil respiration. This is because on our soil type LAI increases entail increases in surface albedo and thus a slightly lower soil temperature. We do note, however, that this simulation does not consider potential direct effects of N availability in the soil on microbial activity and thus soil respiration. CLASS<sub>ComOpt</sub> simulated a higher LAI than CLASS<sub>SimOpt</sub>, resulting therefore in a lower soil respiration for CLASS<sub>ComOpt</sub>. As a result of the increased net photosynthesis and decreased soil respiration when  $N_t$  increases, the NEE will become lower (Figure 6c), i.e., more  $CO_2$  is extracted from the atmosphere. The photosynthesis increases more for CLASS<sub>SimOpt</sub> compared to CLASS<sub>ComOpt</sub> while having similar soil respiration rates, resulting in a more negative NEE for CLASS<sub>SimOpt</sub> (Figure 6c).

CLASS<sub>ComOpt</sub> simulated a higher EF than CLASS<sub>SimOpt</sub> at low  $N_t$ , but the values converged as  $N_t$  increased (Figure 6b). The higher LAI of CLASS<sub>ComOpt</sub> resulted in a larger surface albedo and thereby a lower SH and thus a higher EF at low  $N_t$ . With higher values of  $N_t$  the predicted EF of CLASS<sub>ComOpt</sub> and CLASS<sub>SimOpt</sub> converge, because of similar SH and LE values. The converging SH values between the two model versions are explained by the fact that the albedo is a saturating function of LAI (equation (4)), and thus, at high  $N_t$  and associated LAI values, differences in LAI predicted by the two model versions do not impact the albedo very much. LE values are similar, because although CLASS<sub>SimOpt</sub> has a lower vegetation coverage and therefore a lower LE of the vegetation, this is compensated by the higher LE of the soil (Figure 6b). Thus, the inclusion of plant competition has a larger impact on the predicted LAI and NEE when N availability is high, while it has the largest impact on the EF for medium values of N. These interactive effects of competition and N availability on model outcomes are important as an increase in N deposition rates is forecasted [Galloway *et al.*, 2004; IPCC, 2014].

### 3.3. Sensitivity Analysis: Soil Moisture Index and Soil Types

Here we show that the effect of inclusion of plant competition on model outcomes strongly depends on the soil water content of both the top and the deeper soil layer. We conducted a sensitivity analysis on the soil moisture index of both the deeper and top soil layer (SMI; 0 means water level is at wilting point thus (almost) no water available, 1 means water level is at field capacity thus ample water available) and on the soil type. The original soil type is silt loam with a relatively high soil moisture content of both the top and deeper soil layer (SMI close to 1). Note that the water content of the deeper soil layer is constant over the day and that it determines plant water uptake and the drainage from top to the deeper soil layer. The effect of the SMI of the deeper soil layer is pointed out in equation (3), the stomatal conductance function, via a logistic water stress function. The water content of the top soil layer (first 2 cm) influences the soil evaporation.

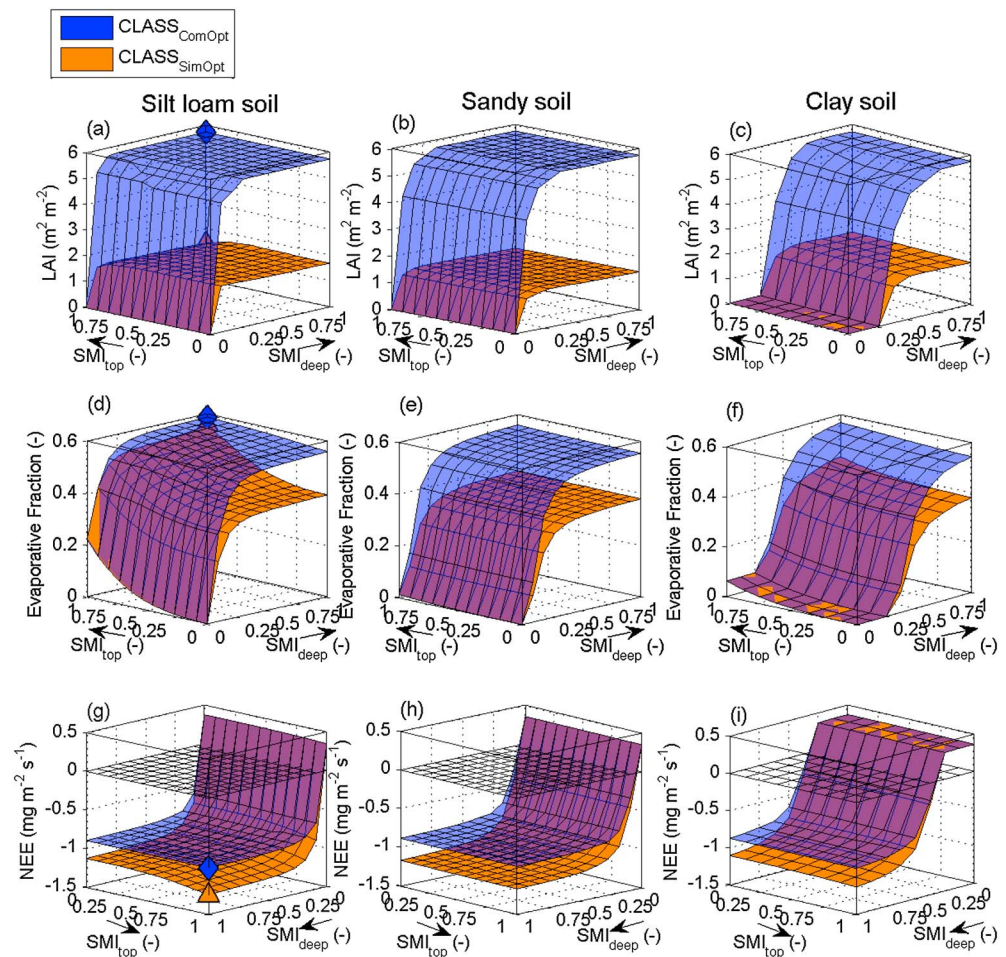
#### 3.3.1. Soil Moisture Index

The general pattern of the effects of increasing the SMI on the LAI, EF, and NEE was similar across the three soil types (Figure 7). First, we will explain these general patterns and followed by a discussion of the sensitivity on the differences between the soil types. Very low values of SMI of the deeper soil layer strongly limit plant water uptake and thus stomatal conductance and thereby photosynthesis is strongly reduced, and NEE even becomes positive (Figures 7g–7i). Therefore, the LAI is, for both CLASS<sub>ComOpt</sub> and CLASS<sub>SimOpt</sub>, decreased (Figures 7a–7c), and transpiration rate is also strongly reduced. When the SMI of the deeper soil layer is increased, both models predict an increase in LAI (Figures 7a–7c). But this increase is stronger for CLASS<sub>ComOpt</sub> than for CLASS<sub>SimOpt</sub>, because as water availability increases, plants can increase their LAI and thus competition for light also increases. This is in agreement with the general notion that light competition is less important in habitats with soil water deficit, because plant growth is then limited by water stress rather than by light [Grime, 1977]. This larger LAI for CLASS<sub>ComOpt</sub> than the optimal LAI simulated with CLASS<sub>SimOpt</sub> results in a lower photosynthesis, leading to less negative values of NEE (Figures 7g–7i). The higher LAI for CLASS<sub>ComOpt</sub> also results in a higher vegetation fraction and thus in a higher EF (Figures 7d–7f).

#### 3.3.2. Difference Between the Soil Types

On a silt loam soil at low SMI of the deeper soil layer, both CLASS<sub>SimOpt</sub> and CLASS<sub>ComOpt</sub> predict a decrease in EF when the SMI of the top soil layer was reduced (Figure 7d). Due to the low LAI (Figure 7a) and thus the low vegetation coverage, the total LE is almost completely determined by the LE of the soil. A reduction in SMI of the top soil layer leads thus to a reduction of the soil LE and thereby also in total LE and EF (Figure 7d). This results in a reduction of the specific humidity of the air and thus an increase in the vapor pressure difference between leaf and air ( $D_s$ ). This increased  $D_s$  caused a reduction in the leaf water potential, as a high  $D_s$  corresponds in general to plant water stress [Drewry *et al.*, 2010], and thereby also a reduction of the stomatal conductance, which is in line with literature [e.g., Oren *et al.*, 1999; Dekker *et al.*, 2001b]. For plants, a high  $D_s$ , in general, corresponds to plant water stress, because stomatal closure usually occurs when atmospheric demands for water vapor increases due to rapid depletion of soil water content around the roots when atmospheric demand is high and thereby the soil is not able to supply the water [Denmead and Shaw, 1962]. In our model results, this reduced stomatal conductance under low SMI of the top soil layer resulted in a decrease in photosynthesis. Additionally, the soil respiration rate also increased because of the lower SMI (diffusive oxygen is not limiting) and thus resulting in a less negative NEE (Figure 7g), though we do note that we did not consider potential negative effects of soil drying on microbial activity and respiration which could somewhat mitigate the reduction in NEE.





**Figure 7.** (a, d, and g) On a silt loam, (b, e, and h) sandy, and (c, f, and i) on clay soil; the (Figures 7a–7c) LAI, (Figures 7d–7f) evaporative fraction ( $LE/(SH + LE)$ ), and (Figures 7g–7i) the net ecosystem exchange (NEE) for different soil moisture index (SMI) of the top soil layer ( $w_{c,top}$ ) and of the deeper soil layer ( $w_{c,deep}$ ) for DOY 213 of the simple optimization model ( $CLASS_{SimOpt}$ , orange surface) and the competitive optimization model ( $CLASS_{ComOpt}$ , blue surface). The blue diamond and the orange triangle on the figures for silt loam soil (Figures 7a, 7d, and 7g) indicates, respectively, for the competitive optimization model and for the simple optimization model the original result of DOY 213; note that for the evaporative fraction these points are very close (Figure 7d).

On a sandy soil, the increase in EF with SMI of the top soil layer was much smaller compared to the other two soil types (Figures 7d–7f). This is because on sandy soils, increasing the SMI of the top soil layer leads only to minor increase in soil LE, as the water content of the top soil layer is still quite low compared to other soil types. Although the albedo of a sandy soil is higher compared to a silt loam and clay soil and therefore a lower SH was found, the EF was still lower due to the low total LE resulting from the low soil LE (Figure 7e).

On the clay soil there was a much stronger effect of reducing the SMI on LAI, EF, and NEE compared to the other soil types. This is because at low SMI the matric potential of a clay soil drops more rapidly compared to a sandy and silt loam soil (Figure S4, equation (S1), Table S5) [Tuzet *et al.*, 2003]. The ensuing greater water retention of clay soils entails that a reduction in SMI causes a stronger reduction in water availability to the plant and thus a greater stomatal closure [Tuzet *et al.*, 2003]. Therefore, LAI and EF increase less rapidly and NEE decreases less rapidly with an increase in SMI of the deeper soil layer (Figures 7c, 7f, and 7i).

To summarize, independent of the type of soil the largest effect of including competition between plants on the EF and the NEE can be obtained on well-watered soils and top and deeper soil layer, and this also holds for changes in atmospheric state variables. However, there are still some interesting and significant differences in atmospheric state variables between the soil types. The difference in LAI between  $CLASS_{SimOpt}$



and CLASS<sub>ComOpt</sub> on a well-watered silt loam and clay soils caused on both soil types an increase in albedo of 12% and thereby led to a decrease in air temperature of 0.7°C. In comparison, *Bounoua et al.* [2000] showed with a coupled vegetation-atmosphere model that 3% increase in albedo, when the LAI increased, reduces the annual air temperature with 0.8°C, in contrast on a well-watered sandy soil increase up to 0.2°C. Here we also show that the effects of including competition for well-watered conditions were fairly similar across soil types, i.e., atmospheric CO<sub>2</sub> increased with 3, 2, and 2 ppm and specific humidity increased with  $3.5 \text{ E}^{-4}$ ,  $3.5 \text{ E}^{-4}$ , and  $3.9 \text{ E}^{-4} \text{ kg kg}^{-1}$ , respectively, for silt loam, clay, and sandy soil. Thus, independent of the type of soil, inclusion of plant competition led to an increase of the atmospheric CO<sub>2</sub>.

Though it is important to note that the degree to which plants are mixed, the parameter  $\beta$ , was held constant during both the sensitivity analysis on the total canopy N content as well as on the soil water content. However, under natural conditions high water or N availability likely allows for denser stands and thus lower  $\beta$  values ( $\beta = 1$  indicates that leaves of plants are not overlapping, and decreasing values of  $\beta$  indicates that the degree of overlap increases). Selection for competitive traits in such habitats may thus be stronger than what we assumed suggesting that the increased competition effect could also be larger than what we predicted.

#### 4. Conclusions and Outlook

Here we show that the inclusion of plant competition for light through canopy overlap in a coupled vegetation-atmosphere model led to an improvement of the daily predictions of both a number of atmospheric state variables and vegetation responses throughout the whole growing season. Remarkably, including competition, thus considering that natural selection favored plants with the highest competitive ability, results in an increase in LAI while this causes a reduction in whole stand photosynthesis (i.e., due to the assumed fixed total canopy N results an increase in leaf area in a reduced photosynthetic capacity), a less negative NEE and an increased atmospheric CO<sub>2</sub> (+3 ppm). In addition, the increased LAI also caused a higher albedo for this site resulting in a decreased air temperature (−0.8°C). Our findings also indicate that the impact of competition on the coupling between vegetation and the atmosphere depends on the available nitrogen content and the soil water content and to a lesser extent to the soil type (i.e., differences in water retention capacities). Regardless of the type of soil, we show that the largest effects of including plant competition on both vegetation as well as atmospheric processes is found on well-watered soils which are not limited by nitrogen.

Our findings thus indicate that plant competition may strongly influence vegetation and atmospheric processes, and we therefore strongly recommend including it in more coupled vegetation-atmosphere models. However, it should be emphasized that are results are based on a single soybean growing season and are meant solely to understand the impact of plant competition on the coupling between vegetation and the atmosphere, by using a relatively simple parameter to describe plant competition. Several aspects could be considered in future studies. First as already noted, other plant types have a different degree of interaction, and therefore, the influence on the coupling between the vegetation and atmosphere could be altered. Second, our model does not consider root competition, while recent studies [e.g., *Farrior et al.*, 2013, 2015] showed that water limited conditions may result in overinvestment in fine roots drawing resources away from leaf area production.

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