How useful are plant functional types in global simulations of the carbon, water, and energy cycles?

Paul B. Alton

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[1] Land-surface and vegetation models divide the globe into discrete vegetation classes or plant functional types (PFTs). The current study quantifies some of the limitations of this simplification on global predictions of carbon, water, and energy fluxes. First, a state-of-the-art land-surface model, JULES-SF, is optimized against a diversity of calibration data sets (eddy covariance fluxes, field measurements of net primary production (NPP), and remotely sensed surface albedo) in order to retrieve a range of values for four key plant parameters within each PFT. This is done for 112 sites and 1200 1° land points. Second, global simulations are compared in which the parameter values per PFT are either fixed (standard method) or vary according to either the retrieved parameter range or the satellite-observed range (new methods). Retrieved key plant parameters exhibit a broad range, and the range overlap between PFTs is significant. The impact on the global simulation depends on the surface flux/state in question. Thus, the difference between the new and old method is small for albedo, net shortwave radiation, and continental runoff (0.005, 0.7%, and 2%, respectively) compared to current model-observation differences (0.05, 7%, and 20%, respectively). In contrast, carbon fluxes are more sensitive to the categorization of plant properties, with predicted global NPP varying by ≤15% (6.2 Gt yr⁻¹) according to whether the standard or one of the new methods is implemented.


1. Introduction

[2] Land-surface models are a widespread and indispensable tool with which to simulate global fluxes under past, current and future climate [Intergovernmental Panel on Climate Change, 2007]. Previous studies focused on the limitations of such models, particularly with respect to spatial resolution [Müller and Lucht, 2007], uncertain parameterization via field measurements [Zaeleh et al., 2005] and inadequate representation of biophysical processes [Cramer et al., 1999; Knorr and Heimann, 2001]. However, the uncertainty introduced into global simulations through the use of discrete vegetation classes or PFTs has received much less attention. (Acronyms and abbreviations used frequently in the text are listed in Table 1.) Traditionally, global vegetation is divided into various groups according to physiognomy [Raunkiaer, 1934], climatic tolerances [e.g., Koeppen, 1936; Holdridge, 1947; Prentice et al., 1992], physiology [e.g., Bonan et al., 2002] or remotely sensed cover type [e.g., DeFries et al., 1999]. The usefulness and accuracy of such an approach in land-surface modeling has recently been questioned by field ecologists who record a broad range of leaf traits within any given PFT and significant overlap between PFTs [Reich et al., 2007]. Indeed, what is the validity of compressing ~250,000 vascular plant species into a few PFTs? Such considerations have led to a call for a more continuous parameterization based on either PFT-dependent [Körting et al., 2009] or PFT-independent [Wright et al., 2004] empirical relationships or, alternatively, use of a substantially increased number of PFTs (TRY, A communal network to compile and share plant trait data, http://www.try-db.org/, 2010). Conventionally, global land-surface models are kept simple for computational expediency and compatibility with the land cover type distinguishable by satellite [Sellers et al., 1996]. Moreover, sufficient field measurements have only become available fairly recently permitting a more refined parameterization of plant properties.

[3] In this study, a simulation of global fluxes is conducted using key plant properties which are fixed per PFT. This conventional simulation (standard method) is then compared with simulations in which plant properties assume a range of values within each PFT (new methods). The fixed parameter values, as well as the parameter range adopted in one of the new methods, are derived from the optimization of a complex, process-based land-surface model against three calibration data sets (eddy-covariance, field-based annual NPP, and satellite albedo) which collectively cover 112 sites and 1200 1° land points. This is the first time that the PFT paradigm has been tested in this way. Moreover, it is unusual for a global land-surface model to be constrained
against a wide diversity of data sources. Multiple constraints are important owing to significant covariance amongst parameters (equifinality) which severely limits the amount of information that can be derived from any given data set [Medlyn et al., 2005]. The main objective is to determine the loss of precision in global fluxes through the use of fixed PFT parameters. A secondary aim is to determine the extent to which key plant properties retrieved in the optimization disaggregate into predefined PFTs. In terms of research questions we ask ourselves how useful PFTs are within global models. More specifically, we investigate whether PFTs provide sufficient precision compared to current model-observation discrepancies. In this context we calculate the precision as the difference between the standard and new methods described above. [4] In section 2 we first introduce the model and data sets and then discuss the model calibration and global experiment required to test the PFT paradigm.

2. Methods

2.1. Land-Surface Model

[5] The current study uses the Joint UK Land Environmental Simulator (JULES-SF) which is an enhanced version of the new UK Met.Office Surface Exchange Scheme [Cox et al., 1999]. JULES-SF takes account of diffuse and direct sunlight at multiple heights within the canopy and is one of most elaborate land-surface models which operates globally in terms of light interception [Alton et al., 2007a]. The energy calculation central to JULES-SF is the standard Penman-Monteith approach [Monteith, 1965], ensuring the balance of ingoing and outgoing energy fluxes at the land-surface. Photosynthesis is calculated separately within each of five leaf layers according to a biochemical compartmental model [Collatz et al., 1991], before summing to produce a canopy total. Leaf photosynthesis is linked to transpiration through a Ball-Berry stomatal model [Ball et al., 1987]. Plant respiration depends on maintenance and growth terms [Ryan, 1991]. The former includes separate, additive terms for leaf and root respiration according to Q10 relationships based on canopy and soil temperature [Law et al., 1999]. Surface albedo is estimated according to the two-stream approximation of Sellers et al. [1996].

[6] To represent vegetation, JULES-SF uses five PFTs: broadleaf forest, needleleaf forest, C3 grass, C4 grass and shrubland. However, given the importance of the tropics to global gross primary production (GPP), for the purposes of this study an additional, sixth PFT is created for tropical broadleaf forest. In the global simulation, the fraction of each PFT at each 3° land point is taken from International Geosphere-Biosphere Project classification [Hansen and Reed, 2000] which has been simplified for use with JULES and its predecessor, the Met.Office Surface Exchange Scheme [Cox et al., 1999]. For the site simulations a single PFT is adopted. JULES-SF uses a small number of PFTs. However, a diversity of biomes can be created through various combinations of the tile fractions (e.g., mixed forest from broadleaf and needleleaf) and the use of leaf area index time series required to drive the model (e.g., deciduous rather than evergreen needleleaf). Land-surface models accommodating a larger number of PFTs tend to prescribe identical parameter values to more than one PFT owing to a paucity of parameterization data [e.g., Bonan et al., 2002; Hickler et al., 2006]. The spatial distribution of soil thermal and hydrological properties is taken from the Global Soil Wetness Project database [Dirreyer et al., 1999]. Detailed equations for JULES-SF, and its very similar predecessor the Met. Office Surface Exchange Scheme, are contained in the works of Cox et al. [1999] and Alton and Bodin [2010].

2.2. Data Sets

[7] As input, JULES-SF requires biophysical parameter values, meteorological forcing and a leaf area index time series. Many of the biophysical parameters are PFT-specific and include plant attributes which are either structural (e.g., rooting depth, canopy height), optical (e.g., leaf absorbance) or physiological (e.g., photosynthetic capacity, minimum stomatal conductance). Key plant parameters (defined below) are derived from an optimization of the model against calibration data sets. The rest of the biophysical parameters are assigned using average collated field measurements [Alton and Bodin, 2010].

[8] The calibration data sets comprise:

[9] 1. Half-hourly eddy covariance fluxes from the Marconi FLUXNET archive [Falge et al., 2002], consisting of net ecosystem exchange (NEE), latent heat (LE), sensible heat (H) and net radiation (Rn) for 31 sites. To minimize the impact of incomplete energy closure [Wilson et al., 2002; Foken, 2008], we exclude fluxes recorded under low frictional velocity (<0.16 m s⁻¹ [Goulden et al., 1996; Reichstein et al., 2003]) or, if frictional velocity is unrecorded, where wind speed <2 m s⁻¹ [Medlyn et al., 2003].

[10] 2. Annual NPP from the Ecosystem Model-Data Intercomparison (EMDI) archive for 81 EMDI class A sites, combining both aboveground and belowground NPP [Olson et al., 2008]. Note that this data set constitutes a new release correcting a significant previous error in tropical NPP.

[11] 3. Sixteen day visible (αVIS) diffuse albedo for 1200 land points (200 per PFT, where ≥75% of the land point is covered by the relevant PFT) selected randomly from the 1° Moderate Resolution Imaging Spectroradiometer (MODIS) product [Hall et al., 2006].

[12] 4. Sixteen day near-infrared (αNIR) diffuse albedo for the same land points as αVIS using the MODIS product for the near-infrared wave band. The selection of MODIS data is limited by the maximum number of land points for shrubland. For αVIS the MODIS wave bands b1, b2 and b3 are averaged while αNIR uses wave band b5 only. In each
case only the highest-quality (full-inversion) measurements are assimilated [Schaaf et al., 2002].

[13] The above four data sets are chosen to provide observational constraints for each of the three primary global cycles (carbon, water, and energy). Note that albedo determines net shortwave radiation and therefore provides a major control on surface energy balance. A summary of location and vegetational composition for the FLUXNET locations is provided by Alton and Bodin [2010], who adopt the same stations, although we refer to Law et al. [2002] for a more complete site description with references to the original publication of data. Olson et al. [2008] provide positions and vegetational composition for the EMDI locations.

[14] For the Marconi sites, JULES is forced with the tower-based meteorology averaged to a 3 h time step, while the EMDI simulations are forced with the Global Soil Wetness Project reconstructed 3-hourly climatology [Dirmeyer et al., 1999]. In both cases the first 5 years of the Global Soil Wetness Project climatology (1986–1990) serve as spin-up for model soil moisture (present-day soil carbon stocks are prescribed according to Schlesinger [1997] and do not require spin-up). For all locations, leaf area index is provided by the satellite-based advanced very high resolution radiometer time series in the ISLSCP archive [Los et al., 2000]. The time series is normalized so that the maximum satellite value equals the in situ value where recorded (all Marconi sites and half of EMDI sites). For MODIS locations, the last 5 years of the available AVHRR time series are averaged (1991–1995) to produce an annual phenological cycle. This period occurs somewhat earlier than the MODIS calibration data set (2002). However, the shift in the growing season over one decade is not too large (3–7 days [Myneni et al., 1997; Angert et al., 2005]) compared to the 10 day time step of the leaf area index time series. In principle, it is possible to adopt the MODIS leaf area product but this is based on reflectance which is already used to optimize the key plant parameters. Instead, it is preferable to retain an independence between data sources used to drive the model (leaf area index from the advanced very high resolution radiometer) and those used for calibration or validation purposes (MODIS albedo). In section 3.3, we test the sensitivity of our results to model forcing by adopting the first, rather than the last, 5 years of the Global Soil Wetness Project forcing and advanced very high resolution radiometer leaf area time series for EMDI and MODIS locations.

[15] Given the importance of the tropics to global photosynthesis, eddy covariance fluxes for two further tropical forest sites (Jaru and Tapajós [Saleska et al., 2003; Iwata et al., 2005]) are added to the single Marconi tropical broadleaf site (Manaus). For Marconi measurements recorded after 1995 the corresponding leaf area index time series from the advanced very high resolution radiometer were kindly provided by S. Los. An overview of the calibration and forcing data sets is given in Table 2.

### 2.3. Model Calibration

[16] The model is calibrated (optimized) by minimizing the cost function:

$$
\chi^2 = \sum_{i=1}^{n} \frac{(F_{\text{sim}} - F_{\text{obs}})^2}{(\Delta F_{\text{obs}})^2}
$$

where $F_{\text{obs}}$ and $F_{\text{sim}}$ are, respectively, the observed and simulated fluxes (or state vectors in the case of albedo). For the observational error $\Delta F_{\text{obs}}$ we adopt values of: 30 W m$^{-2}$ for LE, H and Rn [Hollinger and Richardson, 2005]; 0.02 for $\alpha_{\text{EVS}}$ and $\alpha_{\text{NIR}}$ [Jin et al., 2003]; 3 μmol m$^{-2}$ s$^{-1}$ for NEE [Medlyn et al., 2005; Hollinger and Richardson, 2005]; and 0.1 kg m$^{-2}$ yr$^{-1}$ for NPP. Hollinger and Richardson [2005] recommend a cost function based on absolute deviation, rather than square deviation, when calibrating against eddy-covariance fluxes since observational errors exhibit a double exponential rather than a Gaussian distribution. However, the corresponding modification to equation (1) changes the retrieved optimal parameter values by only 2%.

[17] To identify key plant parameters (i.e., those possessing greatest influence over model fluxes and state vectors), we conduct a sensitivity analysis of JULES-SF. This follows closely the precepts set out by Alton et al. [2007b] and Alton and Bodin [2010]. Therefore, we provide only a brief summary here. A default 5 year simulation is conducted for 200 locations per PFT (the MODIS land points referred to above) using the Global Soil Wetness Project spin-up meteorology mentioned in section 2.2. Then, each parameter is varied in turn according to it probable range from the literature while keeping the remaining parameters at constant, literature (default) values. Alton and Bodin [2010] already collate literature values and their ranges (see also Table 3) except for root respiration, discussed below, which is based on measurements of Law et al. [1999]. Parameters are ranked in influence according to the greatest fractional change in model output, e.g., $\Delta \text{NEE/NEE}_1$ where NEE is the annual net ecosystem exchange of the default simulation averaged over all 1200 locations and $\Delta \text{NEE}$ is the average annual change after parameter perturbation. Note that a more elaborate sensitivity analysis using latin hypercube or...
A schematic overview of the model calibration. A G01030 V A R inferred from the Marconi simulations Alton et al. plays for NPP; (3) and m (1.79) R (1.03) (visible and near (0.01) m (leaf dark respiration as a (0.10) for grasses [2010], A (0.12) are found for the appropriate EMDI ‐ R for visible surface albedo; and AMR (‐ V for near (0.20) are found for the remaining plant functional types); and dzm is the change in roughness length with canopy height (0.1 ± 0.05 m m ‐1 for grasses/shrubs and 0.05 ± 0.025 m m ‐1 for the remaining plant functional types).

Table 3. Ranking of the Most Influential Parameters per Model Flux/State According to the Fractional Change in Average Model Output (in Parentheses) *

<table>
<thead>
<tr>
<th>Flux/State</th>
<th>Primary Parameter</th>
<th>Secondary Parameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>NEE</td>
<td>R (1.79)</td>
<td>Vmax (1.31)</td>
</tr>
<tr>
<td>LE</td>
<td>m (0.08)</td>
<td>Vmax (0.04)</td>
</tr>
<tr>
<td>H</td>
<td>ASR (0.22)</td>
<td>m (0.12)</td>
</tr>
<tr>
<td>Rn</td>
<td>ANIR (0.10)</td>
<td>AVIS (0.01)</td>
</tr>
<tr>
<td>NPP</td>
<td>R (1.03)</td>
<td>Vmax (0.74)</td>
</tr>
<tr>
<td>αVIS</td>
<td>AVIS (0.20)</td>
<td>dzm (0.01)</td>
</tr>
<tr>
<td>αNIR</td>
<td>ANIR (0.31)</td>
<td>dzm (0.01)</td>
</tr>
</tbody>
</table>

*The fractional change for NEE is relatively high as this flux is quite close to zero when averaged over the whole year. NEE, LE, H, Rn, αVIS, and αNIR are net ecosystem exchange, latent heat, sensible heat, net radiation, visible albedo, and near‐infrared albedo, respectively. Parameters are as follows (default value and perturbation given in parentheses): R is root respiration at 25°C (5.8 ± 2.9 μmol m ‐2 s ‐1); m is the slope of the Ball‐Berry stomatal model (8 ± 4); A VIS is visible leaf absorptance (0.85 ± 0.05); ANIR is near‐infrared leaf absorptance (0.20 ± 0.15); Vmax is top‐of‐canopy rubisco‐limited photosynthetic capacity (42 ± 24 μmol m ‐2 s ‐1 for grasses and 84 ± 48 μmol m ‐2 s ‐1 for the remaining functional types); and dzm is the change in roughness length with canopy height (0.1 ± 0.05 m m ‐1 for grasses/shrubs and 0.05 ± 0.025 m m ‐1 for the remaining plant functional types).

Monte‐Carlo sampling [Zaehle et al., 2005; Alton et al., 2007b] is beyond the scope of the current study owing to the large number of locations (1200) used for the sensitivity analysis. In Table 3, our analysis reveals the importance of Vmax (top‐of‐canopy rubisco‐limited photosynthetic capacity) for NEE, LE, H, Rn (Marconi fluxes) and A VIS and ANIR (visible and near‐infrared leaf absorptance) for the prediction of albedo. The two most influential parameters for NPP are Vmax and R (root respiration at 25°C). Similar sets of key parameters are identified in the past for other global models, in particular the important role of photosynthetic capacity for carbon fluxes [Dang et al., 1998; Knorr and Heimann, 2001; Wang et al., 2007]. Note that the current version of JULES‐SF differs from that used by Alton and Bodin [2010] who find that FR (leaf dark respiration as a fraction of photosynthetic capacity [Collatz et al., 1991]) plays an important role in carbon exchange. In the current version, root respiration is formulated separately using a more physiologically based relationship with soil temperature (Q10 = 2.3 [Law et al., 1999]). Thus, R possesses a strong influence on NPP via its large contribution to autotrophic respiration. In the work of Alton and Bodin [2010], plant respiration is simply scaled from leaf respiration according to the plant‐to‐leaf nitrogen ratio.

[18] To avoid problems of parameter covariance and equifinality in the model calibration [Medlyn et al., 2005] we chose only the four most influential parameters for optimization (one per data set). Therefore, we ascribe tuning parameters as follows: (1) Vmax for eddy‐covariance fluxes; (2) R for NPP; (3) AVIS for visible surface albedo; and (4) ANIR for near‐infrared surface albedo. Although Vmax plays an important role for NPP we assign this parameter to eddy covariance fluxes owing to its influence on both NEE and LE. These four key plant parameters are optimized to minimize the cost function in equation (1).

[19] The optimization is conducted for each PFT separately. Thus all locations in each calibration data are assigned to one of the six PFTs defined in the model according to the site description in the literature (Marconi and EMDI) or their selection from the International Geosphere‐Biosphere Project land cover classification (MODIS). The number of locations per PFT and calibration data set is given in Table 2. The optimization is performed stepwise using the Levenberg‐Marquardt method which is a gradient‐based minimization [Press et al., 1992]. First, optimal values of Vmax are found for all Marconi sites for the PFT in question (step 1). Then optimal values of R are found for the appropriate EMDI sites (step 2). Finally, AVIS and ANIR are retrieved for the corresponding MODIS locations (step 3). At this stage, optimal parameter values across all sites are averaged to create the mean retrieved value per PFT for each key plant parameter. These mean values are pooled in order to initialize simulations in the next iteration (Figure 1). Further iterations are necessary since some parameters influence more than one flux or state vector. For example, R has a primary influence over predicted NPP but also a secondary impact on predicted NEE. Therefore, the three

Figure 1. A schematic overview of the model calibration. Parameters Vmax, R, AVIS, and ANIR are the top‐of‐canopy rubisco‐limited photosynthetic capacity, the root respiration at 25°C, the visible leaf absorptance, and the near‐infrared leaf absorptance, respectively. Parameters are pooled at the end of each iteration and thus serve to constrain subsequent tuning against each data source. For example, Vmax inferred from the Marconi simulations enters the EMDI simulations (as a fixed parameter) and thus modifies the values of R, inferred from the EMDI simulations in the subsequent iteration.
minimization steps described above are reiterated until there is convergence (≤2% change) in the mean of the optimal parameter values retrieved for each PFT (3–5 iterations). After convergence, the mean retrieved value per PFT for each key plant parameter is stored, along with the standard deviation from the mean (across the PFT), for implementation in the global simulations discussed below.

[20] It may be possible to tune all four key parameters for each location within all data sets. However, conservatively, we prefer to adjust a single parameter per data set in order to avoid parameter covariance and equifinality. There is no single, ideal way to carry out data assimilation and opinions differ as to the maximum information that can be extracted and how best to extract it [Trudinger et al., 2007; Williams et al., 2009]. Furthermore, as yet no guidelines exist within the literature on how best to weight parameters derived from diverse data sources. To gauge sensitivity to the number and choice of optimization parameters we conduct three separate sensitivity tests by: (1) replacing \( R_r \) with the leaf respiration parameter \( F_{GR} \); (2) retrieving both \( R_r \) and \( F_{GR} \) for EMDI sites; and (3) retrieving both \( V_{max}^{0} \) and \( F_{GR} \) for Marconi sites.

[21] The adopted minimization method (Levenberg-Marquardt) is well suited to a large number of calibration data and makes the solution in the current investigation computationally manageable. Although Bayesian minimization techniques are favored by some authors (e.g., Metropolis algorithm [Sacks et al., 2005]), such methods are several orders of magnitude more computationally expensive. They are also very sensitive to errors assumed for the observations [Katteg et al., 2009] which, for eddy covariance measurements in particular, are difficult to quantify [Lasslo et al., 2008]. We estimate the error in our minimization technique, in particular its ability to find the absolute (rather than local) minimum to equation (1), by conducting 100 repetitions of the optimization per PFT, with a random selection of initial values for key plant parameters. The impact of observational uncertainties are gauged using the standard bootstrap technique which is well suited to problems where measurements errors are poorly known [Richardson and Hollinger, 2005; Rocha and Goulden, 2009]. In this case, the observational data are subject to random resampling (with replacement) creating 100 samples, each equal in size to the original number of observations. The minimization is conducted separately for each of these samples. Note that the resampling is only possible for the eddy covariance and albedo measurements since the EMDI database consists of a single measurement per site. Within the above two tests, the standard deviation across the 100 repetitions suggests a 2–4% error in the mean retrieved parameter values owing to either the minimization technique or observational uncertainty. As shown in the results, this error is an order of magnitude smaller than the parameter range derived for each PFT.

2.4. Global Experiment

[22] The experiment consists of three global simulations with parameter values within each PFT configured differently in each case. Thus: (1) key plant parameters are set to a fixed value equal to the mean PFT value retrieved from the optimization (P-fixed); (2) parameter values are selected randomly from a Gaussian (normal) probability distribution with mean and standard deviation corresponding to the range of optimal values derived for each PFT during optimization (P-gauss); and (3) leaf absorptance (visible and near-infrared) and top-of-canopy photosynthetic capacity are ascribed values according to next nearest location measured by satellite (P-next).

[23] Within P-gauss, the assumption of a true Gaussian distribution is tested in the results by examining the distribution of retrieved optimal values. P-next allows for the possibility that parameter values within any given PFT may be spatially clustered rather than completely random as assumed in P-gauss. It is difficult to test the assumption of randomness except for visible and near-infrared leaf reflectance where the land points used for calibration provide fairly good global coverage. For these properties, values are ascribed according to the next nearest single location, rather than via spatial interpolation, since the separation between each grid cell of the global simulation and the next-nearest calibration land point is already quite large (≥5°). To increase the number of parameters which are varied within P-next, a tentative 1° global map of \( V_{max}^{0} \) is also created using the MERIS Terrestrial Chlorophyll Index [Dash and Curran, 2004]. This index provides a measure of leaf chlorophyll concentration (g chlorophyll m\(^{-2}\) ground) by exploiting the position of increased reflectance going from red to near-infrared wavelengths (“red-edge” effect [Curran et al., 2007]). By taking account of the vertical gradient in leaf nitrogen within the canopy, it is possible to infer \( V_{max}^{0} \) from this index (see Appendix A for details). Values of \( V_{max}^{0} \) are averaged over 3° grid cells when implemented in P-next owing to the coarser resolution of the global simulation (see below). Within P-next, \( R_r \) is assigned the fixed values from P-fixed as no spatially explicit information is currently available.

[24] Global simulations cover the Global Soil Wetness Project period (1986–1995). The first 5 years constitute spin-up ensuring that global fluxes converge within 2%. The last 5 years are averaged to produce annual fluxes of carbon, water, and energy. Global simulations are run at 3° resolution which is sufficient to simulate individual land point fluxes with <5% precision [Müller and Lucht, 2007]. Zonal and global output is compared amongst the three simulations to determine the loss in precision in using fixed parameter values per PFT. This modeling error is compared against the corresponding model-observation discrepancy. To quantify the latter, there are relatively few global data sets available. The following are selected on the basis that they provide a measure of model performance over each of the main cycles (carbon, water, and energy): (1) the relatively complete global data set of continental discharge published recently by Dai et al. [2009] to test the water cycle; (2) annually averaged zonal shortwave (visible + near-infrared) albedo measured with MODIS to test energy balance (via its impact on net shortwave radiation); and (3) current best estimates of global NPP from land-surface model intercomparison studies to test the carbon cycle. NPP is selected for the carbon cycle on the basis that this quantity has been the focus of many previous modeling studies [Cramer et al., 1999; Knorr and Heimann, 2001] and the intermodel dispersion owing to, for example, different representations of land-surface and vegetation processes is fairly well quantified (±20%). Note that zonal albedo (data set 2) does not provide a completely independent check since a small subset of the MODIS data set (<10%) is used to calibrate visible
The interplay of these constraints gives rise to a

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increases from,

is the same and the retrieved parameter

is retrieved as a second optimization parameter

Lloyd et al.

(as opposed to

, Simulated and observed values of 16 day albedo,

is the number of retrieved values is 200 per PFT.

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R

and

the number of retrieved values is given in parentheses

(dashed).

Lines are shown for the best fit (solid; p < 0.001) and y = x

infrared leaf absorptance. Model surface runoff in

data set 1 is linked to continental discharge via the global river routing map of Oki and Sud [1998].

The experiment outlined above is the first (crude)

attempt to introduce some spatial variability into the key

plant parameters adopted for vegetation classes in order to

gauge the impact on global flux estimates. Some of the

variability introduced by P-gauss can be expected to cancel

since zonal/global fluxes represent an average across many

land points. However, many land-surface processes possess

a highly nonlinear dependence on surface properties which

would preclude complete cancelation. For example, leaf

photosynthesis is known to be colimited by light, tempera-

ture and water availability [Collatz et al., 1991] and would

not, therefore, be expected to vary proportionally with

. The interplay of these constraints gives rise to a

canopy response (NEE and GPP) which is highly nonlinear,
saturating in a dramatic fashion against shortwave radiation

[Lewis et al., 2000; Lloyd et al., 2002; Gu et al., 2003; Saleska et al., 2003].

3. Results and Discussion

3.1. Retrieved Plant Parameters

The optimization of the model is fairly successful
(Figure 2). The greatest improvement compared to pre-

optimization, when all parameters are set to average litera-

ture values, is for NEE, NPP and albedo (R² increases from,

respectively, 0.60, 0.13 and 0.85 to 0.67, 0.94 and 0.95). The

improvement in the remaining fluxes is less pronounced,

possibly owing to their initially high correlations against the observations. The overall high correlation in

Figure 2, relative to preoptimization, suggests that the

optimization procedure makes profitable, simultaneous use of all the calibration data sets in order to constrain the model. Note that the order in which parameters are tuned within the iterative technique is not important. Thus, the postoptimization R² is the same and the retrieved parameter values change by <2% when retrieving 

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for either the EMDI or the Marconi locations, the

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, the postoptimization R² is poor, particularly for NPP (0.32), compared to the original tuning (0.94). If 

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is retrieved as a second optimization parameter for either the EMDI or the Marconi locations, the improvement in R² is marginal (e.g., 0.94→0.98 for NPP). It might be argued that 

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should be added to the retrieval even if the the improvement is marginal. However, for the vast majority of NPP points in Figure 2 there is no improvement when adding 

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d

and for these same points we risk overestimating the true parameter range by introducing too many covariant parameters [Medlyn et al., 2005].

Table 4. Retrieved Parameter Values per Plant Functional Type Shown as Mean ± Standard Deviation

<table>
<thead>
<tr>
<th>PFT</th>
<th>( V_{\text{max}}^0 ) (μmol m⁻² s⁻¹)</th>
<th>( R_r ) (μmol m⁻² s⁻¹)</th>
<th>( A_{VIS} )</th>
<th>( A_{NIR} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nontropical broadleaf</td>
<td>74 ± 36 (n = 8)</td>
<td>4.9 ± 2.3 (n = 4)</td>
<td>0.89 ± 0.03</td>
<td>0.30 ± 0.07</td>
</tr>
<tr>
<td>Tropical broadleaf</td>
<td>96 ± 32 (n = 3)</td>
<td>1.2 ± 1.0 (n = 20)</td>
<td>0.89 ± 0.02</td>
<td>0.26 ± 0.04</td>
</tr>
<tr>
<td>Needleleaf</td>
<td>52 ± 26 (n = 13)</td>
<td>2.8 ± 2.1 (n = 26)</td>
<td>0.94 ± 0.03</td>
<td>0.35 ± 0.09</td>
</tr>
<tr>
<td>C3 grass</td>
<td>68 ± 40 (n = 2)</td>
<td>1.3 ± 1.4 (n = 9)</td>
<td>0.93 ± 0.05</td>
<td>0.16 ± 0.10</td>
</tr>
<tr>
<td>C4 grass</td>
<td>13 ± 8 (n = 3)</td>
<td>0.89 ± 1.3 (n = 22)</td>
<td>0.93 ± 0.06</td>
<td>0.21 ± 0.13</td>
</tr>
<tr>
<td>Shrubland</td>
<td>37 ± 18 (n = 2)</td>
<td>2.2 ± 1.6 (n = 0)</td>
<td>0.93 ± 0.04</td>
<td>0.29 ± 0.10</td>
</tr>
</tbody>
</table>

\( * \) Key plant parameters are top-of-canopy rubisco-limited photosynthetic capacity (\( V_{\text{max}}^0 \)), root respiration at 25°C (\( R_r \)), visible leaf absorptance (\( A_{VIS} \)), and near-infrared leaf absorptance (\( A_{NIR} \)). For \( V_{\text{max}}^0 \) and \( R_r \), the number of retrieved values is given in parentheses as \( n \). For shrubland, \( R_r \), and its standard deviation are set to the average of the other plant functional types (PFTs) (no EMDI locations available). For both \( A_{VIS} \) and \( A_{NIR} \) the number of retrieved values is 200 per PFT.
The mean and standard deviation of the parameter values retrieved from the model calibration are given in Table 4. The mean retrieved values appear reasonable compared to collated field measurements. Thus, measured\( A_{VIS} \) and \( A_{NIR} \) average, respectively, 0.85 ± 0.05 and 0.20 ± 0.15 [Williams, 1991] compared to 0.89–0.93 and 0.16–0.35 in Table 4. Empirical relationships established between leaf nitrogen and photosynthetic capacity [Kattge et al., 2009] suggest mean values for \( V_{cmax}^0 \) of 97, 84, 63, 84 and 67 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) for nontropical broadleaf, tropical broadleaf (nonoxisols soils), needleleaf, C3 grass (crops) and shrubland, respectively, after substituting the values of leaf nitrogen used within JULES-SF. These values differ by 16 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) (root-mean-square (RMS)) from the corresponding mean retrieved values in Table 4. The greatest discrepancy is for shrubs (Figure 3) which constitute a diverse group which is not particularly well represented in the calibration data sets. Note that, for the four key parameters, the spread of retrieved values across any given PFT is generally large. Furthermore, the standard deviation does not decline against the number of sites as might be expected if the retrieved value range is limited by sample size (Figure 4). Thus, at least some of the retrieved PFT range appears to be inherent. Figure 3 also demonstrates that the retrieved range is realistic, though perhaps slightly too broad on average, compared to collated field measurements.

Only the MODIS locations are sufficiently numerous to determine with confidence the detailed distribution of retrieved parameter values. Visual absorptance (\( A_{VIS} \)) exhibits a fairly narrow range of values and mean values are clustered (Table 4). Near-infrared absorptance shows well defined peaks for tropical broadleaf, needleleaf and shrubland, a spread distribution for grasses and a bimodal distribution for nontropical broadleaf (Figure 5). Some of the PFTs conform poorly to a Gaussian distribution. Therefore,
Table 5. Zonal Differences With Respect to the Simulation P-Fixed for Annual Net Primary Production, Annual Diffuse Shortwave Albedo, and Annual Runoff

<table>
<thead>
<tr>
<th></th>
<th>NPP (kg m(^{-2}) yr(^{-1}))</th>
<th>Albedo</th>
<th>Runoff (kg m(^{-2}) yr(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>P-gauss</td>
<td>0.18 (21%)</td>
<td>0.003 (1%)</td>
<td>4.3 (1%)</td>
</tr>
<tr>
<td>P-next</td>
<td>0.11 (13%)</td>
<td>0.006 (2%)</td>
<td>4.6 (2%)</td>
</tr>
</tbody>
</table>

\(^{a}\)This is the root-mean-square difference averaged over all latitude bands from \(-60^\circ\) to \(+80^\circ\). The corresponding percentage change with respect to P-fixed is given in parentheses. NPP, net primary production.

we check below (section 3.3) the impact of the assumed parameter distribution within the global experiment. Values of near-infrared absorptance in Figure 5 exhibit some disaggregation according to PFT although the distributions overlap greatly. Note that the retrieved dispersion in near-infrared absorptance (standard deviation = 0.04–0.13) is greater than the uncertainty of the original MODIS albedo measurements (0.02 [Jin et al., 2003]).

[29] Other key plant parameters in Table 4 also exhibit a large amount of overlap. In order to quantify overlap we define, for each parameter, the “PFT-separation” as the RMS deviation of the PFT-mean from the mean averaged across all PFTs. Thus, for \(V_{\text{max}}\) in Table 4, RMS = \(\{(74-57)^2+(96-57)^2+(105-57)^2\}/n\)^0.5 where PFTs range from 1 to n. Similarly, for each parameter, we define the “half-width” as the RMS average of the standard deviations within each PFT, i.e., \(\{(\sigma_1^2+\sigma_2^2+...)/n\}\)^0.5 where, for \(V_{\text{max}}\), \(\sigma_1=36\) and \(\sigma_2=32\), etc. On this basis, the PFT-separation/half-width ratio exceeds 2 for PFTs that are fairly well separated and ≤1 when two distributions overlap over at least half of their range. For \(V_{\text{max}}\), \(R_s\), \(A_{\text{VIS}}\), and \(A_{\text{NIR}}\) the corresponding ratios from Table 4 are 0.94, 0.77, 0.46, and 0.67. The ratio for \(V_{\text{max}}\) (0.94) agrees fairly well with the corresponding ratio derived from the empirical data shown in Figure 3 (0.81).

[30] Measured field properties of plants belonging to the same PFT often span a wide range. For example, \(V_{\text{max}}\), measured for three nontropical broadleaf species (birch, oak, and beech) covers a range 65–115 \(\mu\)mol m\(^{-2}\) s\(^{-1}\) [Meir et al., 2002] which is almost as broad as the corresponding range in Table 4 (±36 \(\mu\)mol m\(^{-2}\) s\(^{-1}\)). A few field-based studies find fairly constant values for some plant parameters. For example, leaf quantum efficiency differs by only 6% between a needleleaf plantation and a mature needleleaf site [Ibrum et al., 2006]. In general, however, collated field measurements reveal a broad range of properties for any given PFT [Wright et al., 2004]. For example, a compilation of plant properties measured for 2500 species from 175 sites suggests that PFTs based on growth form, leaf habit and phylogeny only account for 1/3–2/3 of variation in leaf traits such as photosynthetic capacity [Reich et al., 2007]. This suggests a PFT-separation/half-width ratio of 0.5–2.0 (1/3–2/3 PFT-related, 1/3–2/3 PFT-intrinsic). Although this empirical ratio varies greatly according to plant property, it encompasses the corresponding ratios derived above for \(V_{\text{max}}\), \(R_s\), \(A_{\text{VIS}}\), and \(A_{\text{NIR}}\) (0.46–0.94).

[31] Note that there are few previous attempts to retrieve parameter values for several sites within the same PFT. In general, a larger number of parameters are estimated for just one or two FLUXNET sites [Medlyn et al., 2005; Knorr and Katge, 2005; Santaren et al., 2007]. However, the calibration of a land-surface model against three needleleaf and four nontropical broadleaf sites yielded values of \(V_{\text{max}}\) which vary, respectively, by 70% and 19% across each PFT [Wang et al., 2007]. The corresponding variation in the current study is 51% for 13 needleleaf sites and 48% for eight nontropical broadleaf sites. Apart from the number of sites used, the main differences between our study and that of Wang et al. [2007] are the formulation of the model (multilayer canopy versus two big leaf), the number of calibration data sources (four versus one) and the number of parameters tuned (one versus six per data source).

3.2. Global Simulations

[32] As explained in section 2.4, we focus on annual runoff, annually averaged shortwave albedo and annual NPP when testing the differences between global simulations. However, the impact on related quantities is also included in the discussion below.

[33] For zonal runoff, the difference between a global simulation with fixed parameter values per PFT (P-fixed) and one that allows for a range of parameter values per PFT (P-gauss and P-next) is 1–2%. Here, “difference” refers to the RMS difference in model output averaged over 10° latitude bands from \(-60^\circ\) to \(+80^\circ\) (i.e., over all vegetated landmasses; Table 5). The model-model 1–2% difference is an order of magnitude smaller than the corresponding discrepancy between model and observation (21%). Similarly, the differences between the simulations of zonal albedo are small (0.005 per 10° latitude, equivalent to 0.7% in net shortwave radiation) compared to the corresponding model-observation discrepancy (0.045 or ~7% in net shortwave radiation; Figure 6). The three simulations (P-fixed, P-gauss, P-next) predict a range for global annual evapotranspiration (63 ± 1 × 10\(^3\) Gt yr\(^{-1}\)) which is small compared to the current observational range (63–72 × 10\(^3\) Gt yr\(^{-1}\)) inferred recently from satellite and river discharge measurements [Schlosser and House, 2007; Dai et al., 2009]. These results suggest that fixed PFT values are sufficient for modeling certain surface states and fluxes. Albedo and the calculation of net shortwave radiation have a fairly linear dependence on leaf reflectance, thus allowing some of variation across each PFT to cancel. Evapotranspiration and runoff depend strongly on soil properties which may explain their relative insensitivity to the manner in which PFTs are configured.

[34] In contrast, annual carbon fluxes are much more sensitive to the representation of key plant parameters. Regionally, P-fixed differs from P-gauss and P-next by ≤11% for GPP and by ≤21% for NPP (RMS difference per 10° latitude band). For global annual GPP, P-fixed (129 Gt yr\(^{-1}\)) differs from P-gauss and P-next by ≤6 Gt yr\(^{-1}\) (≤4%). The corresponding differences for global annual NPP is ≤6 Gt yr\(^{-1}\) (≤15%; Table 6) which approaches the corresponding dispersion in current state-of-the-art global land-surface models (±20% [Cramer et al., 1999]). Global NEE depends strongly on soil parameters (e.g., microbial respiration) which are not tuned in the current experiment. However, differences between the simulations for global NEE, owing to plant representation (1–6 Gt yr\(^{-1}\)), are important in the context of current carbon sinks (≥2–3 Gt yr\(^{-1}\) [House et al., 2003]).

[35] Note that the current model-observation discrepancies are not unusual for global land-surface models. Model-observation discrepancies arise from inter alia imperfect model processes [Cramer et al., 1999; Knorr and Heimann,
which tends both to dampen the impact of any given parameter change and to prevent complete cancelation.

[37] Both simulations which allow for spatial variability within each PFT (P-gauss and P-next) deviate comparably from the fixed parameter simulation (P-fixed). This is somewhat surprising given that the values of \( V_{cmax} \) calculated for P-next are clearly nonrandom within at least some PFTs (e.g., C3 grass and tropical broadleaf; Figure 7). The similarity between P-gauss and P-next suggests that spatial gradients in primary plant properties may be of minor importance to the calculation of some regional fluxes/properties (runoff, evapotranspiration, and albedo) and some global fluxes (GPP), at least compared to current uncertainties in model processes [Cramer et al., 1999; Knorr and Heimann, 2001].

3.3. Limitations and Sensitivity of the Methodology

[38] Although the current study optimizes a small number of parameters, some equifinality will be present in the retrieved values owing to parameter covariances. This implies an overestimation of the true parameter range for any given PFT and, by corollary, an upper limit to the error introduced into the global simulation. An upper limit is also likely to apply to models using a greater number of PFTs compared to the current study since a less coarse classification would reduce the parameter range within any given PFT. This idea is difficult to test for the Marconi and EMDI data sets where the small number of available locations precludes division of the data into a greater number of PFTs. However, for the more numerous MODIS locations, we test the impact of an increased number of PFTs on the parameter retrieval by introducing a further three categories (Mediterranean broadleaf, deciduous needleleaf, and agricultural land) to the original six PFTs, and reassigning the original 1200 land points to the resultant nine PFTs. As before, land cover attribution follows the International Geosphere-Biosphere Project and the distribution of agricultural land is taken from Goldewijk [2001]. The parameter range is reduced only slightly by this process (standard deviation from 0.043 to 0.042 for \( A_{VIS} \) and from 0.093 to 0.087 for \( A_{NIR} \)). Likewise, the corresponding PFT-separation/half-width ratio increases only slightly to 0.50 and 0.83, for \( A_{VIS} \) and \( A_{NIR} \) respectively, compared to the original retrieval using six PFTs (0.46 and 0.67, respectively). Thus, for leaf reflectance at least, a significant range and overlap still occur even when adopting a greater number of vegetation categories.

[39] We test the sensitivity to model forcing by adopting the first, rather than the last, 5 years of the Global Soil Wetness Project forcing and satellite leaf area time series for EMDI and MODIS locations. The greatest impact is for the mean values of \( R_{e} \) with a change \( \pm 12\% \). However, the

![Figure 6](image)

**Figure 6.** The simulated and observed (obs) zonal distributions of (a) annual net primary productivity (NPP), (b) mean annual albedo for diffuse shortwave radiation, and (c) annual total runoff. Simulations are shown for fixed key parameter values per PFT (P-fixed) and for Gaussian-distributed values (P-gauss). For NPP and albedo, an additional simulation is shown using next nearest parameter values (P-next). For runoff, P-next is omitted as the profile is indistinguishable from P-gauss and P-fixed (P-gauss and P-fixed overlap greatly too).

2001], poorly known values for nonoptimized field-based parameters [Zaehle et al., 2005], errors in observational data sets [e.g., Coe, 2000; Lasslop et al., 2008] and problems in scaling from site to global level [e.g., Hickler et al., 2006]. The current global experiment seeks only to determine the precision associated with the PFT paradigm and does not reveal the total uncertainty in global simulations of carbon, water and energy fluxes which is almost certainly larger.

[36] The differences in global carbon budget between the simulations are smaller than the relative size of the standard deviation adopted in P-gauss for the key plant parameters (52% of the mean when averaging across all parameters derived for all PFTs in Table 4). By summing across many land points some of the variation introduced by the Gaussian can be expected to cancel. However, several land-surface processes possess a highly nonlinear dependence on surface properties (e.g., the dependence of canopy GPP on \( V_{cmax} \))
Figure 7. (top) Global top-of-canopy photosynthetic capacity \( (V_{\text{can}, \text{top}}^{0}; \mu\text{mol m}^{-2} \text{s}^{-1}) \) estimated from the MERIS Terrestrial Chlorophyll Index. (bottom) The dominant PFT within the International Geosphere-Biosphere Project classification [Hansen and Reed, 2000] is shown for reference only. Although the color scale is continuous (owing to restrictions within the plotting software), the PFTs are set according to the following discrete values: no vegetation (0), broadleaf (1), needleleaf (2), C3 grassland (3), C4 grassland (4), shrubland (5), and tropical broadleaf (6). Note that a dominant PFT is assigned to all ice-free land points even if vegetation is very sparse, e.g., desert regions.
impact on inferences drawn from the global experiment is marginal. For example, model-model differences for global and zonal NPP change by ≤1%. The impact is small because the adopted parameter range is broad (typically ±52%) with respect to the mean value. Note that the 12% error associated with the forcing period provides an upper limit to the impact of 2–4% errors estimated for the minimization routine and observational uncertainty (section 2.3).

[40] Some of the PFTs in Figure 5 exhibit extended tails in their parameter distribution, a characteristic shared with collated field measurements of leaf properties [Wright et al., 2005; Katteg et al., 2009]. Therefore, we check the impact of a non-Gaussian (extended) distribution on the global experiment. Thus, within P-gauss, we replace the Gaussian with a double-exponential (Laplace) distribution, setting the exponential scale length to 0.88 for all parameters to ensure that 68% of values lie within 1σ of the mean (as in a Gaussian distribution). The greatest impact on the global experiment is an increase in the difference between P-fixed and P-gauss for both global (from 15% to 21%) and zonal (from 21% to 33%) NPP. This suggests a moderate sensitivity to the assumed parameter distribution, particularly if extended tails are present. However, the retrieved range for \( V_{cmax}^0 \) is already somewhat too broad (by 23% on average) with respect to collated field measurements (Figure 3). This consideration, along with the relatively small number of PFTs defined in the model, suggest that the difference between P-gauss and P-fixed that we derive in the original global experiment is likely to be an upper limit to the precision lost in global fluxes through the use of fixed PFT parameters.

4. Conclusions and Future Work

[41] Adopting fixed parameter values for key plant properties, rather than a range of values for each PFT, provides sufficient precision in the calculation of some surface fluxes and states (e.g., albedo and net shortwave radiation, evapotranspiration, and runoff) compared to current model-observation discrepancies. However, simulated fluxes of carbon are relatively sensitive to the representation of plant properties. In particular, important regional differences exist in predicted GPP and NPP (≤11% and ≤21% RMS difference per 10° latitude) according to the use of fixed or variable values of photosynthetic capacity within each PFT. Global totals of NPP differ by ≤15% which approaches the current intermodel dispersion in global NPP (±20% [Cramer et al., 1999]) and the errors associated with process-representation [Knorr and Heimann, 2001]. Our conclusions for carbon fluxes are somewhat sensitive to the parameter value distribution assumed within each PFT. For example, when assuming an extended (Laplace) parameter distribution, rather than a Gaussian (normal) distribution, regional differences increase to 33%. However, a simulation using MODIS and MERIS global data sets to represent spatial variability in leaf absorptance and photosynthetic capacity deviates from the fixed parameter regime in a comparable manner to the Gaussian distribution.

[42] Key plant parameters retrieved from model optimization show some disaggregation into PFTs but the overlap between PFTs is generally large, as found in field measurements in the literature. The impact of parameter range depends on the parameter in question and the particular output quantities that it influences in the model. For example, the PFT-separation/half-width ratio is quite low for near-infrared leaf absorptance (0.67) but adopting a fixed value for each of the six PFTs appears to provide sufficient precision (0.005) for the calculation of global shortwave albedo. In contrast, mean retrieved values of photosynthetic capacity (\( V_{cmax}^0 \)) exhibit greater separation (PFT-separation/half-width ratio = 0.94) but fixed values for both this and the respiration parameter \( R_G \) provide only 15% precision for global NPP. Note that, by adopting a relatively small number of PFTs (six), our calculation is likely to provide an upper limit to both the parameter range and the precision error in the global calculation.

[43] Future work will extend the current model calibration to the LaThuile FLUXNET archive [Stoy et al., 2009] and compare retrieved parameter values against the TRY (A communal network to compile and share plant trait data, http://www.try-db.org/, 2010) plant trait archive, once both of these large databases become generally available. More extensive assimilation of global remote-sensing products is required in the future in order to assess spatial variability of plant properties.

Appendix A

[44] The 1° MERIS Terrestrial Chlorophyll Index (MTCI; g chlorophyll m⁻² ground) is derived by Dash and Curran [2004] from global hyperspectral measurements recorded by the satellite-borne Medium Resolution Imaging Spectrometer Instrument (MERIS [see also Curran et al., 2007]). It combines chlorophyll leaf concentration (g chlorophyll m⁻² leaf) with leaf area index (m⁻² leaf per m⁻² ground). Noting the strong correlation observed between electron transport (\( J_{cmax} \)) and rubisco-limited photosynthetic capacity \( V_{cmax}^0 \) [e.g., Wullschleger, 1993; Meir et al., 2002] and assuming that \( J_{cmax} \) is proportional to leaf chlorophyll concentration:

\[
\text{MTCI} = N(PFT) \times V_{cmax}^0 \times \int_0^{L_\text{fl}} \exp(-k_{\text{rub}} \times L) dL \quad (A1)
\]

where \( L \) is the cumulative leaf area index (m²m⁻²) from the top of the canopy downward and \( k_{\text{rub}} \) is the leaf nitrogen allocation coefficient (vertical gradient) which is assumed to be 0.15 in JULES consistent with field measurements [Lewis et al., 2000; Meir et al., 2002]. \( N(PFT) \) is the normalization constant which, once known, allows \( V_{cmax}^0 \) to be calculated via inversion of equation (A1).

[45] The normalization of \( N(PFT) \) is conducted independently for each PFT using 1° land points covered by ≥75% of the relevant PFT (the same calibration land points used to determine leaf reflectance). The value of \( N(PFT) \) is set so that average growing season \( V_{cmax}^0 \) obtained from equation (A1) for these land points is equal to the mean value obtained during model optimization. Thus, the final global map of \( V_{cmax}^0 \) possesses mean values across each PFT which are consistent with the model optimization but contains spatial variability at 1° resolution consistent with the heterogeneity of MTCI. The MERIS data adopted in equation (A1) are taken from the earliest complete year of measurement (2003).

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**ALTON: USEFULNESS OF PLANT FUNCTIONAL TYPES**


P. B. Alton, Geography Department, Swansea University, Swansea SA2 8PP, UK. (p.alton@swansea.ac.uk)