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An analysis of some diverse approaches to modelling terrestrial net primary productivity

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Abstract

We inter-compare the mathematical formulation of ten models of terrestrial net primary productivity (NPP) and their functional responses to temperature (T), carbon dioxide (CO_2), soil water (W) and photosynthetically active radiation (PAR). The models span a broad spectrum of complexity of approaches from the original, empirical Miami model, through β-factor, and global-average box models, to the dynamic global vegetation models (DGVMs) TRIFFID and BIOME3. Five of the models separate photosynthesis and respiration, although only three directly consider biochemistry. Equations for all the models are given in a complete, compact, standardized format.

NPP responses to temperature differ markedly: β-factor models show only a tiny increase with temperature, empirical models predict a modest S-shaped response saturating above 35 °C (a surrogate for drought effects), biochemical and quasi-biochemical models show a peaked response with an optimum in the range 15–25 °C except for DEMETER ($<$10 °C). Qualitative differences in whether respiration exhibits a peaked or exponential response to temperature have only a modest effect on NPP. The CO_2 response of NPP is qualitatively similar in all but one model that misrepresents it. Where a water stress response of NPP is represented, it is saturating in all but the same model, where NPP declines under high soil moisture. Where represented, the PAR response of NPP is saturating, but the saturation point differs considerably.

When responses to two environmental variables are combined, the second variable typically just scales the response to the first. In biochemical models, the temperature optimum of NPP increases with CO_2, and it also increases noticeably with PAR in TRIFFID and a derivative of it. Where different plant functional types (PFTs) are represented, C_4 grasses have the greatest maximum NPP at a higher optimum temperature than any C_3 PFT. Boreal, needle-leaf trees generally have the lowest NPP. Additional uncertainties in modelling respiration, stomatal conductance, light-use efficiency, and scaling to the canopy level are discussed. We suggest that a concerted effort to standardize definitions, notation, units and PFTs would add a degree of transparency that is currently lacking in NPP modelling.

Keywords: Terrestrial net primary productivity; NPP; Comparison; Models

1. Introduction

Over the past 30 years a considerable number of global vegetation models have been developed to investigate many different aspects of the terrestrial carbon cycle, including changing vegetation distributions

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and the land carbon sink. At the core of most of these models is a net primary productivity submodel but many of the mechanisms behind global terrestrial productivity are still not properly understood. As a consequence of this, as well as the availability of data and computational capacity at the time of development, models proposed to calculate net primary productivity and simulate the global vegetation are quite diverse in their approaches. At one end of the spectrum is the simple, empirically derived, correlation of net primary productivity with air temperature and precipitation used in the Miami model (Leith, 1975a). At the other end is the detailed simulation of biochemistry used, for instance, in TRIFFID (Cox, 2001) and BIOME3 (Haxeltine and Prentice, 1996a,b). Despite their different approaches, the published output of most global vegetation models compares fairly well with observations and it is not always clear exactly what the differences are between these models, why they have these differences and whether any one model can be said to be better than the others. In this paper a number of previously published NPP formulations are presented in a clear, concise, standardised format and then their mechanisms and behaviour are systematically compared. The main aim of this paper is to provide a clear review of some of the techniques of NPP modelling for anyone wishing to incorporate such a model into a wider system but we hope that it will also inspire those already engaged in such work.

Two other recent studies have compared the output of NPP models but not the mechanisms that can help explain the differences in output. The Potsdam NPP Model Intercomparison (Cramer et al., 1999) compared seventeen global models of terrestrial biogeochemistry. All were driven by standardised gridded monthly mean air temperature, precipitation and solar radiation from observation databases. This led to immediate discrepancies as models designed and calibrated to work at a specific resolution were much less accurate when it was altered, perhaps itself an indicator that all is not well with these models. Standardised input datasets for humidity, wind speed and the initial soil and vegetation distributions could not be established. In the latter two cases this was because of the use of different classifications for soil types, plant types, biomes and ecosystems. It is also notable that one model uses an atmospheric carbon dioxide level of 280 ppmv, the others between 340 and 360 ppmv. It is curious that this was not standardised. The fundamental result given in Cramer et al. (1999) is that predicted NPP varied between 39.9 and 80.5 GtC per year, more than a factor of two. Estimates of global NPP exhibit a smaller range from 45.09 GtC per year (Leith, 1975b) to 59 GtC per year (Amthor, 1998) with considerable uncertainty surrounding these figures due to interannual variation, relatively sparse measurement (both spatially and temporally, Running et al., 2000) and difficulties estimating the contribution of below ground biomass. So the variability in predictions does not refute any of the models, but neither does it validate them or help to increase confidence. Other papers in the same series consider the significance of model vegetation structure (Bondeau et al., 1999), light use submodels (Rumy et al., 1999) and water use submodels (Churkina et al., 1999). All tend to focus on the output of the models in the comparison and attempts at explaining the underlying causes of the differences are limited.

Cramer et al. (2001) compare six dynamic global vegetation models under different climate change scenarios (including no change) generated by the HadCM2-SUL general circulation model. Under the no change scenario predicted NPP varies between 45 and 60 GtC per year. Kappa statistic tests (Monserud and Leemans, 1992) also found ‘fair’ agreement between the predicted and observed maps of dominant vegetation classes. Although the results of this comparison are more promising than those of Cramer et al. (1999), its authors remain cautious about the veracity of predictions, particularly at a regional scale.

Both of the studies discussed above focus on the output of the vegetation models, rather than the fine details of their construction. By contrast, this study focuses on the mechanisms driving the models, paying particular attention to the net primary productivity submodels. It is hoped that this will lead to a better understanding of the results of ‘output’ comparison studies as well as illuminating some of the practical and philosophical issues involved in formulating vegetation models.

A brief description and commentary for each model considered in this study is given in Section 2. Detailed equations and parameter values for each model are presented in a standardised format in Appendices A and B. In Section 3 each model (as given by the equations in Appendix A) is used to calculate net primary productivity and, where appropriate, photosynthesis and respiration over a range of values for temperature, carbon dioxide, water and light intensity. For those models which specify multiple plant types the impact of these alternative parameterisations is also investigated. In Section 4 the pros and cons of different classes of model are discussed and some of the issues involved in modelling respiration, stomatal conductance and light-use efficiency are highlighted. The study concludes with a summary of the main points it has raised and some suggestions for future work.

2. Model descriptions

The models studied in this paper are only a small sample of the considerable number of published vegetation models. They were chosen to be representative of a range of approaches for modelling vegetation productivity. Ten models are considered in detail. In the following section each model is briefly described and any distinctive features or particular problems are highlighted. Complete equations for each model (as gleaned from the literature but transformed into a standardised and relatively concise format) are given in Appendix A.

2.1. Broad structural classification

Before embarking on a detailed study of individual models it is helpful to have some broad idea of the different forms global vegetation models can take. The simplest approach is to divide them into two groups, biogeographical (or correlative) models and biogeochemical (or process-based) models. Biogeographical models such as BIOME (Prentice et al., 1992) and ALBIOC (Roelandt, 2001) use a gridded map of climate variables to determine which of a number of plant types could be present in that grid cell. Biomes or ecosystems are then defined as particular combinations of plant types. Biogeographical models are based on the potential equilibrium vegetation and do not simulate any biochemical processes of the vegetation. Thus, they can be used to investigate the response of the equilibrium vegetation distribution to climate change but net primary productivity can only be studied as far as it depends on the type of vegetation present. Biogeographical models do not allow for changes in vegetation density within a biome. Nor do they predict transient changes in the vegetation distribution.

In contrast biogeochemical models assume a constant distribution of vegetation, again in the form of plant types or biomes. Biochemical processes such as photosynthesis and respiration are then simulated according to the local climate. These processes can be expressed implicitly or explicitly and there is considerable diversity of formulations for both. Models using the implicit formulation calculate NPP from climate variables without ever formulating functions for photosynthesis or respiration. A common approach is to modify a maximum or benchmark NPP by factors accounting for a temperature response, water stress and carbon dioxide fertilisation. Models using the explicit formulation use functions motivated by plant biochemistry. Rates for each component of the photosynthesis–respiration–growth process are then calculated according to the local environment, usually described by the temperature, atmospheric carbon dioxide, photosynthetically active radiation and soil water or precipitation. NPP for the system is given by combining these components. Biogeochemical models can be used to predict changes in vegetation density and productivity under climate change. They will not predict any change in either the transient or equilibrium vegetation distribution.

In practise many models fall between these two groups, combining aspects of both in an attempt to model changes in density and distribution. The common restriction of both methods and their hybrids is their reliance on an equilibrium vegetation distribution. Even if it is assumed that the vegetation can reach an equilibrium state, it will certainly not re-adjust to a new equilibrium on the same time-scales as the scenarios of rapid climate change currently of interest. In light of this Dynamic Global Vegetation Models have been developed to predict transient changes in the vegetation structure. Again there is considerable diversity in approaches. The biogeochemical TRIFFID model (Cox, 2001), incorporates Lotka-Volterra type competition to formulate a system of differential equations describing changes in both area and density of each vegetation type. In contrast, the IBIS model (Foley et al., 1996) extends the biogeographical approach by considering the changing productivity, and thus density, of each element of the potential vegetation in a grid cell.

A second broad classification arises from the structure of the NPP submodel that is employed. Empirical models (e.g. Miami, Leith, 1975a; King et al., 1997) relate NPP to temperature and precipitation using functions deduced from real world data. β-factor models (e.g. Polglase and Wang, 1992; King et al., 1995, 1997) modify a base rate of productivity by a biotic growth factor (β) to account for carbon dioxide fertilisation. This may also involve some temperature dependency in the determination of the carbon dioxide compensation point. The quasi-biochemical models (e.g. Svirezhev and von Bloh, 1998; Lenton, 2000, DEMETER; Foley, 1994) use environmental response functions based, to a greater or lesser degree, on the biochemistry of plants but do not consider the biochemistry explicitly. They usually employ these factors to modify a base productivity rate or the component photosynthesis and respiration rates. The biochemical models (e.g. simple TRIFFID, Huntingford et al., 2000; TRIFFID, Cox, 2001 and BIOME3, Haxeltine and Prentice, 1996a,b) treat some, or all, of the plant biochemistry explicitly to determine photosynthesis, respiration and net primary productivity rates.

With these broad classifications in mind, each of the models considered in this study is now briefly described. Where specific equations or parameters are mentioned in the following text this refers to the standardised form of the model as presented in Appendix A, not the original publication.

2.2. Miami model—Leith (1975a)

The empirical Miami model, developed by Leith (1975a), is considered to be the first global vegetation model and is often used as a baseline for comparisons. It can be thought of as a biogeographical model with implicit plant types. Empirically derived functions correlate mean annual temperature and precipitation with NPP. Plant types are not distinguished but are implicitly included in the derivation of the correlation functions.

The Miami model gives reasonable estimates of current NPP rates and their distribution but this is only to be expected given its empirical basis. However, predictions of future NPP made with the Miami model must be treated cautiously. Firstly, there is no mechanism to account for changing vegetation density. Secondly, like other biogeography models, it assumes that the implicit vegetation distributions will immediately adjust to changes in climate. If the Great Plains of America were to get the warm, wet climate of the tropical rain forest then they would also acquire the NPP of a rain forest and, by implication, its vegetation.

2.3. King et al. (1997), Post et al. (1997)

King et al. (1997) and Post et al. (1997) investigate changes in ecosystem carbon density resulting from climate change using a model combining the empirical and β-factor approaches by adding a carbon dioxide fertilisation term to the Miami model. This additional term is derived from the Farquhar photosynthesis formulation (Farquhar and von Caemmerer, 1982). It assumes that photosynthesis is always light limited, rather than Rubisco or transport limited, and is a function of both atmospheric carbon dioxide and temperature. In contrast to the Miami model, this model also distinguishes 30 plant functional types. Their distribution is fixed and based on maps of observed vegetation. Carbon is allocated to leaf, branch, stem and root components at appropriate ratios for each plant type. Turnover rates and rooting depth (which is used for the soil submodel) are the only other characteristics differentiated.

Although 30 vegetation types are distinguished in this model, none use a C_4 photosynthesis pathway and exactly the same very simple Miami model is used to calculate the base NPP of all of them. Then a quasi-Farquhar photosynthesis scheme, the complexity of which is out of keeping with the rest of the model, is bolted on. Finally a parameter (k_1) is introduced as a scaling factor. This is supposed to account for efficiency losses believed to be responsible for an observed disparity between the potential and actual increases in vegetation carbon density as a result of carbon dioxide fertilisation. Some justification for such a factor is given but, with no reliable empirical estimates, it is impossible to assign it a meaningful value. Indeed, King et al. (1997) find it convenient to use a value of 0.6 but admit that the actual value is almost certainly lower than that.

2.4. Polglase and Wang (1992)

Polglase and Wang (1992) use a β-factor approach to develop a biogeochemical model with multiple vegetation types. Space is not treated explicitly but 10 biomes are distinguished and a characteristic climate and productivity, based on observed averages, is determined for each. This baseline productivity is then modified by a biotic growth factor accounting for carbon dioxide fertilisation. An electron-transport limited Farquhar formulation is used to derive temperature and carbon dioxide dependencies for this function. However, this formulation is not actually used in the simulations. Instead, a simplified form is preferred in which the temperature dependency is absorbed by a single parameter (k_{10}). This is estimated for each biome using the mean growing season temperature. Equations for both models are given in Appendix A, #1 is the full model, #2 the simplified form. Carbon is allocated to leaf, branch, stem and root components.

As with the model by King et al. (1997) discussed above, Polglase and Wang's (1992) model is intended to investigate changes in vegetation density resulting from changes in the climate but the biotic growth factor formulation is problematic. The simplifying parameter (k_{10}) is particularly suspect as it is determined from the biotic growth factor and the CO_2 compensation point functions using the average temperature for each biome. As the authors themselves admit, there are significant problems with this, particularly in biomes with pronounced seasonal temperature variation.

2.5. *King et al. (1995)*

Another β-factor model designed to investigate changing vegetation carbon density is given by King et al. (1995). It has elements of both the biogeochemical and biogeographical approaches. Productivity for each biome is described by a logistic growth equation modified by an environmental response factor. This is essentially Polglase and Wang's (1992) model, with a temperature and atmospheric carbon dioxide dependent biotic growth factor derived from the Farquhar photosynthesis model. Similarly to Polglase and Wang, the full form of the model, (described in #1 of Section A.4), is replaced by a simplified form, (described in #2 of Section A.4). Again the parameterisation for this simplified form is based on the mean growing season temperature together with a scaling factor to account for photosynthetic efficiency losses. This NPP scheme is applied to 13 biomes that are considered to occupy a fixed area of each of 10 continental regions. Although this area does not explicitly change a fairly sophisticated scheme (due to Emanuel, 1995) is used to describe the area–density distribution of the vegetation within it and so some change in area is implicitly captured.

As discussed in the review of Polglase and Wang's (1992) model above, using mean annual temperature to determine the carbon dioxide response function is problematic, particularly in biomes where there is significant seasonal variation. As discussed in the review of King et al.'s (1997) model, the efficiency scaling factor is unquantified empirically and thus an extremely elastic parameter. The logistic growth term is not unreasonable. However, it only relates to intraspecific competition within that biome. Given that an area–density distribution for each biome is also calculated, it seems more logical to use this in the calculation of competition than the carbon density. This would also facilitate an interspecific competition term.

2.6. *Lenton (2000)*

In contrast to the empirical and β-factor models described above, Lenton (2000) employs a quasi-biochemical model. It is zero-dimensional and no distinction is made between vegetation types and locations. Photosynthesis is a function of temperature and atmospheric carbon dioxide but not vegetation carbon density. Respiration depends on temperature and the vegetation carbon density. Plant biochemistry is not explicitly modelled but both functions are formulated to have the correct general form and then parameterised to give a reasonable estimates of NPP for the preindustrial climate.

A particular problem with Lenton's (2000) model is the independence of photosynthesis and actual vegetation carbon. This appears to assume that the photosynthetic (i.e. canopy) area is constant even though vegetation density may change, which is consistent with other biogeochemical models and essentially equivalent to defining a baseline photosynthesis rate. Although this is reasonable for small deviations from the preindustrial carbon density, it becomes a dubious assumption if vegetation carbon changes significantly as this will affect the model respiration rate but not the photosynthesis rate. Any predictions from this model must also be treated cautiously since the global vegetation and climate are compressed to a zero-dimensional average and this may not behave in the same way as the a group of more diverse biomes represented by the same model structure.

2.7. Svirezhev and von Bloh (1997, 1998)

Svirezhev and von Bloh (1997, 1998) also develop a quasi-biogeochemical model not dissimilar to that of Lenton (2000) although photosynthesis and respiration are not explicitly modelled. Instead, maximum potential net primary productivity is supplied as a parameter and modified by factors representing temperature response, water stress, carbon dioxide fertilisation and intraspecific competition. These response functions are constructed to give a reasonable general form but are not based on rigorous biochemical or empirical analysis. In fact, the functions describing carbon dioxide fertilisation and competition are not explicitly stated at all but immediately combined into a single function, presumably for mathematical convenience. Although total carbon is the principle descriptive variable for the vegetation this is related to the vegetated area fraction to calculate evapotranspiration. Note that the model calculates NPP in terms of kgC per year so the vegetated area of the Earth (as given in Appendix B) is used in this study (but not in the original model) to convert to kgC/m^2 per year. The vegetation area function described above could also be used but the constant value is preferred for simplicity.

Svirezhev and von Bloh (1997, 1998) model is intended as a tool for qualitative investigation of the interaction between climate and vegetation and particular attention has been paid to making the equations mathematically tractable. While this is an understandable requirement, the combination of the carbon dioxide fertilisation and competition terms confuses the mechanisms of the model and makes understanding its behaviour more difficult. As with the Lenton (2000) model, the compression of the global vegetation and climate (in this case including hydrology) to a zero-dimensional average means that any predictions arising from this model must be treated cautiously.

2.8. Simple TRIFFID—Huntingford et al. (2000)

Huntingford et al. (2000) present a simplified version of the biogeochemical TRIFFID model (Cox, 2001) described in Section 2.9 below. It is based on a single plant type, parameterised according to an ‘average’ forest and net primary productivity is calculated by simulating photosynthesis and respiration. Photosynthesis is based on the full Farquhar process, although a simplification is also proposed. Two functions of temperature are suggested to describe leaf respiration (although only one will be considered in this study) and whole plant respiration is taken as a constant fraction of leaf respiration. Carbon is divided between biomass density and vegetated area at a ratio based on the leaf area index, defined as a constant fraction of biomass. The rate of expansion of area is logistic which introduces some intraspecific competition by saturating with increasing vegetation coverage.

The simple TRIFFID model is designed to investigate the qualitative response of the global vegetation to climate change. As such the simplifications that have been made seem reasonable and allow for some mathematical analysis of the model. However, the full Farquhar formulation may not be the most appropriate photosynthesis scheme. It is out of keeping with the simplicity elsewhere in the model and the combination of a such detailed biochemical expression with a very basic respiration scheme and a very broad parameterisation for a single generic vegetation type seems awkward. Clearly the model also suffers from the same limitations arising from a global average vegetation and climate as the Lenton (2000) and Svirezhev and von Bloh (1997, 1998) models described above.

2.9. TRIFFID—Cox (2001)

The TRIFFID model is a biogeochemical–biogeographical hybrid dynamically simulating changes in both vegetation density and distribution. Photosynthesis is calculated using the full Farquhar formulation while canopy respiration is related to the rate of Rubisco carboxylation. Both are modified by a piecewise linear water stress factor and scaled to the canopy level using Beer’s law. An additional water stress factor for photosynthesis is included via an integrated stomatal conductance function which relates internal leaf carbon dioxide to atmospheric carbon dioxide and humidity. The maintenance respiration rate is derived from the canopy rate and growth respiration is taken to be a constant fraction of net productivity. Modifications are made for plant types using the C_4 pathway. Five vegetation types are defined. Carbon is partitioned between leaf, root, stem and areal expansion at a ratio depending on the leaf area index. Phenology is described via a temperature dependent leaf litter fall function. An allometric relationship relates wood carbon to leaf area and a pipe model relates the canopy height to wood carbon. The area of each vegetation type is dynamically described by a partial differential equation with intra- and inter-specific competition being introduced via a Lotka-Volterra type process.

TRIFFID is a relatively comprehensive vegetation model, incorporating quite detailed biochemistry, physiognomy and dynamics. Although it is fairly elegant mathematically, having only a few step functions and no rule-based behaviour, it remains a very complicated model which is somewhat opaque and mathematically intractable.

2.10. DEMETER—Foley (1994)

DEMETER is a quasi-biogeochemical biogeographical model. Sixteen plant functional types are distinguished and the global distribution at each time step is determined from a set of ecophysiological constraints. A potential photosynthesis rate is calculated by modifying a maximum photosynthesis rate by a piecewise linear factor accounting for the temperature response and a water stress function based on the evapotranspiration rate. This is then transformed by functions accounting for canopy scaling and the quantum efficiency. Carbon is allocated to leaf, stem and root components. Maintenance respiration is calculated separately for each by modifying a base value with a Q_{10} temperature function. Growth respiration is taken to be a fixed proportion of any positive productivity. Minor modifications are made to account for plants using the C_4 pathway. Leaf area index is a prescribed constant during each of the growing, dry and winter seasons.

The DEMETER model utilises an intermediately complex formulation for vegetation functional processes. Of particular note is the constancy of the temperature response function over a broad range of growing temperatures. This is based on the assumption that plant biochemistry acclimatises to temperature changes within this range on a sub-monthly time scale. The water stress factor is a linear function of a water index. Closer inspection reveals that this index is calculated as the difference between supply and demand for soil moisture. The demand part of this relationship is based on the rate of evapotranspiration from the land surface and appears to be independent of any vegetation present. These points aside, the utility of the model in climate change studies is compromised by the absence of carbon dioxide fertilisation and competition between plant types.

2.11. BIOME3—Haxeltine and Prentice (1996a,b)

BIOME3 is a biogeographical–biogeochemical hybrid model. Seven plant functional types are identified. The potential distribution of woody plant types is determined by their minimum temperature thresholds. Grass is assumed to potentially occur everywhere. Photosynthesis is calculated by simultaneously solving two equations. The first is based on a light and Rubisco limited Farquhar model but is actually calculated based from an optimisation of daytime productivity and Rubisco carboxylation rates. The second is based on a stomatal conductance model and thus incorporates the effects of water stress. Respiration is divided into leaf, root and transport components. Leaf respiration is calculated from the rate of Rubisco carboxylation, the transport rate is related to temperature and the root rate is constant. An additional growth respiration tax is applied to all positive productivity. Some modifications are made to account for the C_4 pathway. Phenology is based on rules driven by temperature and water levels. Competition is simulated by selecting the dominant tree and grass type according to NPP and then applying additional rules to account for drought, fire and shading. Leaf area index can be considered the main descriptive variable for each vegetation type. It is found by optimising NPP and leaf area index with the restriction of a minimum leaf area requirement.

BIOME3 is the most comprehensive, and complicated, model considered in detail in this study. It is also the most impenetrable and computationally intensive. Notwithstanding the generally involved equations of the model, the two expression for photosynthesis are solved simultaneously by a bisection method. Then the NPP and leaf area index are experimentally optimised by calculating an ‘extensive range’ of values. All of this contributes to relatively high overheads. It is also interesting to note that different vegetation types in BIOME3 are effectively differentiated by a single parameter —their minimum canopy transpiration rate, and that a fairly simple rule-based system is used to simulate competition and determine the global vegetation distribution.

3. Comparison of model behaviour

In order to compare the behaviour of the models presented in Section 2 net primary productivity and, where appropriate, photosynthesis and respiration, were calculated for each formulation over a range or temperature, carbon dioxide, soil water/precipitation and light values. Since it is not possible to constructively compare the response to simultaneous changes in more than two of these variables, some had to be held constant in each run. The constant temperature value was chosen to be the global average, 15 °C. Carbon dioxide was set to the current level in the Earth's atmosphere, 350 ppmv. Water and photosynthetically active radiation were set to be saturating, or close to saturating in those models where saturation does not always occur, in order to remove any secondary impact they may have on the variable under consideration. The way in which water is represented in the various models is particularly non-standard. Some models (Leith, 1975a; King et al., 1997) use precipitation in mm per year, others (Svirezhev and von Bloh, 1998) actual soil water, others (Cox, 2001; Foley, 1994; Haxeltine and Prentice, 1996a,b) use a volumetric soil water scale. To overcome this, all non-volumetric scales are transformed to the interval [0,1] (i.e. equivalent to the volumetric scale), based on a maximum precipitation of 4000 mm per year in Leith et al. (1975) and King et al.'s (1997)models, and a maximum soil moisture content of 20 g/cm^2 in Svirezhev and von Bloh's (1998) model. Thus, to ensure saturation, water was set to be 1 (i.e. saturated on the volumetric scale), except in Svirezhev and von Bloh's (1998) model where productivity decreases if soil water exceeds 9.5 g/cm^2 and so a value of 9.5 g/cm^2 $= 0.475$ after the transform to [0,1] was used. Incident photosynthetically active radiation was set at 120 W/m^2 $= 0.00055$ Ein/(m^2 s) and a day length of 12 h was assumed. Where the vegetation carbon density was required, this was taken to be 4.13 kgC/m^2. Values for all non-plant functional type specific parameters were as stated in the appropriate table of Appendix B. Where plant type specific parameters were required a generic set of values, based on the values given for forest plant types, was used for the general comparison of all models. Where possible the responses of different vegetation types within a model and equivalent vegetation types in different models were also compared. All carbon fluxes are given in kgC/m^2 per year.

The results are broken down into four main sections. Three sections deal with the generic responses of photosynthesis, respiration and net primary productivity and are further divided into subsections dealing with each of the environmental variables. The flaws, merits and differences of the models are discussed along with the general problems associated with modelling the process in question. The fourth section looks at the modelled responses of different vegetation types.

3.1. C_3 Photosynthesis

Only five of the ten models considered in this study calculate photosynthesis explicitly. Of these the DEMETER and Lenton (2000) models do not directly consider any biochemistry. Instead, both modify a base photosynthesis rate by factors accounting for the prevalent environmental conditions. In contrast, versions of the Farquhar and von Caemmerer (1982) biochemical formulation are used in the simple TRIFFID, TRIFFID and BIOME3 models.

3.1.1. Temperature response of photosynthesis

In broad terms all five models show a similar response to changes in temperature (Fig. 1). The curves are approximately parabolic. The maximum occurs at about 28 °C in the Lenton (2000), simple TRIFFID and TRIFFID models, at 20 °C in BIOME3 and about 8 °C in DEMETER. Photosynthesis declines to 0 at about 48 °C in all models except Lenton's (2000) for which it is zero at 40 °C. Lenton (2000) and DEMETER also predict that no photosynthesis occurs below 0 °C, TRIFFID and BIOME 3 predict small amounts of photosynthesis until temperatures fall below −10 °C, while simple TRIFFID predicts that photosynthesis will continue in temperatures as low as −60 °C.

The Lenton (2000) model clearly predicts much lower photosynthesis rates at all temperatures. This is because it is calibrated for the average global vegetation under average global solar radiation and water

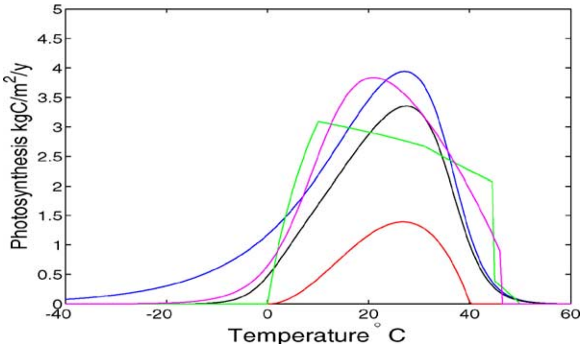

Fig. 1. Temperature response of photosynthesis when other variables are held constant at: $C_a = 350$ ppmv, $W = 1$, $I = 120$ W/m^2: (red line) Lenton, (blue line) simple TRIFFID, (black line) TRIFFID, (green line) DEMETER, (magenta line) BIOME3.

levels whereas the others are parameterised for a light and water saturated forest vegetation type. The early maximum and subsequent linear decrease between 10 and 40 °C in the DEMETER model arises from a combination of factors. The linearity is a result of the piecewise linear function used to describe the direct effect of temperature (Eq. (A.9.3)). The early decrease is a result of the temperature dependence in the light use efficiency (Eqs. (A.9.5) and (A.9.6)). The difference between the two TRIFFID models, particularly at low temperatures, comes from their treatment of the maximum rate of Rubisco carboxylation V_m. As well as some parameter differences, the formulation used in TRIFFID (Eq. (A.8.11)) includes a low temperature inhibition function which is not used in the simple TRIFFID formulation (Eq. (A.7.11)). The location of the maximum in the BIOME3 model is probably a result of the of the optimised Rubisco carboxylation rate (Eq. (A.10.11)).

3.1.2. *Carbon dioxide response of photosynthesis*

All four models which include carbon dioxide (DEMETER does not) exhibit nearly identical responses (Fig. 2). The obvious differences in magnitude arise from the differing bases rate of photosynthesis at 15 °C.

3.1.3. *Water stress and photosynthesis*

All three models which consider the effects of water stress on photosynthesis (simple TRIFFID considers water in the form of atmospheric humidity which

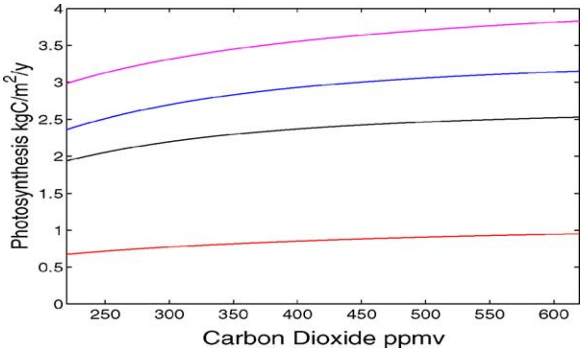

Fig. 2. Response of photosynthesis to atmospheric carbon dioxide levels when other variables are held constant at: $T = 15$ °C, $W = 1$, $I = 120$ W/m^2. (red line) Lenton, (blue line) simple TRIFFID (black line) TRIFFID, (magenta line) BIOME3.

is taken to be a function of temperature in this study) predict a saturating response (Fig. 3). The main difference is in the from of saturation and location of the saturation point. TRIFFID predicts a piecewise linear response, saturating when W is approximately 0.38. DEMETER also predicts a piecewise response which is near linear until saturation when W is approximately 0.75. BIOME3 predicts a continuous response, saturating when W is approximately 0.65.

The water stress responses are remarkably similar given that treatment of water stress differs significantly between the three models. TRIFFID employs a very simple, piecewise linear function (Eq. (A.8.20)) with a fixed saturation point to represent the effects

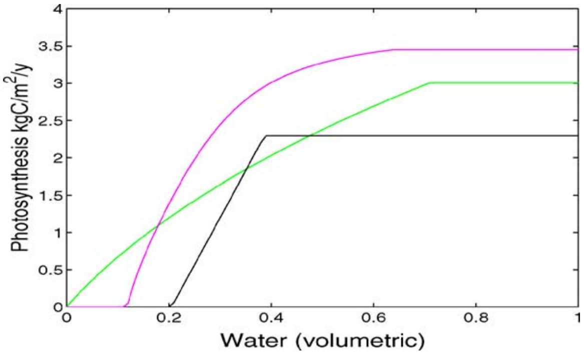

Fig. 3. Response of photosynthesis to water stress when other variables are held constant at: $T = 15$ °C, $C_a = 350$ ppmv, $I = 120$ W/m^2: (green line) DEMETER, (black line) TRIFFID, (magenta line) BIOME3.

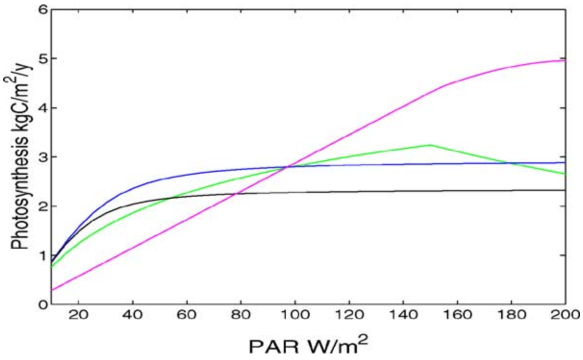

Fig. 4. Response of photosynthesis to photosynthetically active radiation levels when other variables are held constant at: $T = 15\,^{\circ}\mathrm{C}$, $C_a = 350$ ppmv, $W = 1$: (blue line) simple TRIFFID, (green line) DEMETER, (black line) TRIFFID, (magenta line) BIOME3.

of soil water levels. (Although it should be pointed out that atmospheric humidity can also have an impact though the equation for internal leaf carbon dioxide level (Eq. (A.8.10)) but this depends only on temperature, which is constant, in this study). Water stress in DEMETER is based on evapotranspiration supply and demand rates which are calculated using the ambient temperature and solar radiation levels but apparently independently of the state of the vegetation. The saturation point is thus determined by the temperature and incident solar radiation. When the water level is below the saturation point the dominant effect is the action of a linear water stress function (Eq. (A.9.4)) on the base photosynthesis rate (Eq. (A.9.2)) but a small degree of non-linearity creeps in as the base photosynthesis rate also occurs in the canopy scaling function (Eq. (A.9.1)). BIOME3 employs a similar model to calculate evapotranspiration but factors the canopy conductance of the vegetation into the evapotranspiration demand equation (Eq. (A.10.13)) and then uses a stomatal conductance model, rather than a simple linear factor, to calculate the effects of water stress. This gives a smoothly saturating response. The saturation point is determined by temperature, solar radiation and the state of the vegetation itself.

3.1.4. Photosynthetically active radiation and photosynthesis

There is some difference in the response of photosynthesis to photosynthetically active radiation levels (Fig. 4). Simple TRIFFID and TRIFFID show a saturating response with a saturation point around 80 W/m^2. DEMETER shows a very gently saturating response in photosynthesis until around 145 W/m^2 after which it begins to decline. BIOME3 predicts a linear increase in photosynthesis up to 150 W/m^2 at which point the response begins to slowly saturate.

The saturation in the DEMETER model arises from the interplay of the two inverse logarithmic functions of photosynthetically active radiation in the light use efficiency formulations (Eqs. (A.9.5) and (A.9.6)). The negative response at very high levels of photosynthetically active radiation appears to occur because of water stress. Evapotranspiration is directly related to solar radiation in DEMETER and, even when soil water is saturating, very high solar radiation levels result in evapotranspiration demand exceeding supply. Photosynthetically active radiation is incorporated into the TRIFFID models as a linear factor of the light limited photosynthesis rate (Eqs. (A.7.5) and (A.8.5)). The saturating response emerges as the RuBP and transport limited photosynthesis rates start to limit the overall photosynthesis rate at high light levels. This does not occur in BIOME3 as the optimisations in that model assume that nitrogen and Rubisco activity are redistributed through the canopy so as to utilise all available light and give a light use efficiency which is independent of photosynthetically active radiation. This results in a linear response with slight saturation occurring at very high light levels due to water stress. This can be seen in the model formulation with photosynthetically active radiation appearing only as a linear factor in Eqs. (A.10.1) and (A.10.11).

3.1.5. Summary of photosynthesis responses

Photosynthesis shows a similar near-parabolic response to temperature in all the models considered. The main differences are in the threshold temperatures. The low temperature threshold for photosynthesis ranges from 0 to $-60\,^{\circ}\mathrm{C}$, the optimum temperature ranges from 8 to $28\,^{\circ}\mathrm{C}$ and the high temperature threshold ranges from 40 to $50\,^{\circ}\mathrm{C}$. All models show a very similar, saturating response to atmospheric carbon dioxide. Water responses are also all saturating although the location of the saturation point varies considerably due to the diverse functions used to represent water stress and their interplay with the solar radiation level. The way in which photosynthetically active radiation is treated in the models is also quite variable. This leads to saturating responses in simple TRIFFID and TRIFFID, a near linear increase then decline in DEMETER and a linear response in BIOME3. The interplay between solar radiation and soil water can be important in the latter two models.

3.2. *Respiration*

Five of the models considered in this study explicitly calculate plant respiration. Approaches are varied. The Lenton (2000) model bundles all respiration processes into a single response function based on the total vegetation carbon. Simple TRIFFID recognises leaf respiration and non-leaf respiration. Leaf respiration is related to the rate of Rubisco carboxylation. Non-leaf respiration is just a constant fraction of the leaf respiration. TRIFFID recognises leaf and non-leaf maintenance respiration. Leaf respiration is a function of temperature (not the rate of Rubisco carboxylation). Non-leaf maintenance respiration is based on the non-water stressed leaf respiration rate and an elaborate calculation to determine the amount of carbon stored in the stem and roots from the leaf area index. An additional growth respiration tax of 25% is levied on any positive productivity remaining. DEMETER recognises leaf, stem and root respiration. All are calculated by modifying a base respiration rate with the same temperature response function. The carbon in each plant component is determined according to constant allocation ratios for each plant type. An additional growth respiration tax of 33% is levied on any positive productivity remaining. BIOME3 recognises leaf, wood and root respiration. Leaf respiration is related to the rate of Rubisco carboxylation. Stem respiration responds to temperature, with stem carbon being diagnosed from leaf area index. Root respiration occurs at a constant rate proportional to the leaf area index. A growth respiration tax of 20% is applied to any positive productivity remaining.

3.2.1. *Temperature response of respiration*

In all models temperature is the dominant environmental factor determining the respiration rate but the nature of the response is quite different (Fig. 5). All models predict that respiration declines to 0, or very close to 0, at temperatures below $-10\,^\circ$ C. Between -10 and $30\,^\circ$ C all five models predict increasing respiration although the form and magnitude of the increase differs slightly. Simple TRIFFID and Lenton (2000) predict a concave up curve, TRIFFID and BIOME3 a concave down curve. Although always positive, the gradient of the DEMETER response curve changes suddenly around $8\,^\circ$ C. The most significant differences in the respiration response occur when the temperature exceeds $30\,^\circ$ C. Lenton (2000) and DEMETER predict a continued exponential increase in respiration rate. TRIFFID predicts a brief decrease followed by an exponential increase. Simple TRIFFID predicts that respiration will decrease to 0 at $60\,^\circ$ C. BIOME3 predicts that respiration decreases a little up to $45\,^\circ$ C when it drops suddenly and then begins to increase slowly.

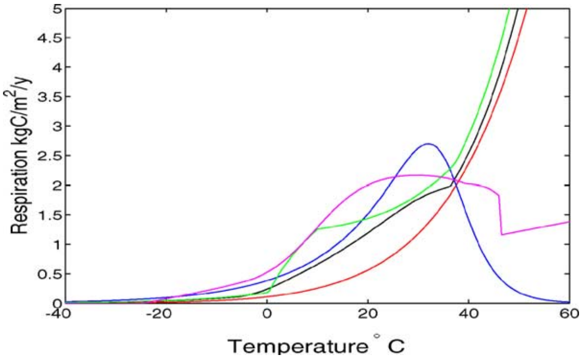

Fig. 5. Temperature response of respiration when other variables are held constant at: $C_{\mathrm{a}} = 350$ ppmv, $W = 1$, $I = 120\,\mathrm{W/m^2}$: (red line) Lenton, (blue line) simple TRIFFID, (black line) TRIFFID, (green line) DEMETER, (magenta line) BIOME3.

The difference in magnitude of respiration rates is hard to diagnose. Clearly it is lower for the Lenton (2000) model as it is parameterised for globally averaged water and solar radiation levels. In the other models it may be due to the base photosynthesis rate and associated growth tax for the specified environment, the basic parameterisation of the functions used, or the way in which carbon is allocated to the individual plant components. The sudden gradient change in the DEMETER model corresponds to a similar shift in photosynthesis rate at about the same point and shows up here as a result of the growth respiration tax. The same is true for the brief downward trend predicted by TRIFFID and BIOME3 above $30\,^\circ$ C. In both cases non-growth respiration regains dominance as photosynthesis declines, resulting in an increasing respiration rate.

3.2.2. *Response of respiration to carbon dioxide, water and photosynthetically active radiation*

Only two of the models considered in this study include a direct response of respiration to any environmental variables besides temperature. In TRIFFID, leaf respiration depends on soil water and temperature, in BIOME3 it depends on soil water, atmospheric carbon dioxide, photosynthetically active radiation and temperature via the Rubisco optimisation scheme (Eq. (A.10.11)). However, in both of these models, the growth respiration tax on photosynthesis dominates the respiration rate compared to the response to these environmental factors. In fact, their impact is sufficiently limited that (non-growth) respiration can be taken to depend on temperature alone in all models considered in this study.

3.2.3. *Summary of respiration responses*

Temperature is the main environmental variable determining the respiration rate. Carbon dioxide, water and photosynthetically active radiation levels have a small impact in some models but this is over-shadowed by the growth respiration tax on photosynthesis. In all models respiration rates increase in a fairly similar way up to 30 °C. Above this temperature there is a difference of opinion. Three predict a continued exponential increase in respiration rate, one a decline to zero and one a rapid decline followed by a slow increase. The respiration models are relatively straightforward and there is no mystery about why the response functions have the shape that they do, only whether or not they should have that shape.

3.3. *Net primary productivity*

3.3.1. *Temperature response of net primary productivity*

The temperature responses of net primary productivity fall into three main groups (Fig. 6). The empirical models predict that NPP increases with temperature up to approximately 35 °C and then remains at that rate. The β-factor models show only a very small, slow increase in NPP with temperature. The quasi-biochemical and biochemical models all show a similar form of parabolic response between 0 and 45 °C. Below 0 °C they all predict slightly negative NPP which returns to 0 as temperature decreases further. The exceptions are Svirezhev and von Bloh's (1998) model and simple TRIFFID, for which NPP is always non-negative at sub-zero temperatures. At temperatures above 40 °C Lenton (2000), TRIFFID, DEMETER and BIOME3 all predict significant negative NPP. In contrast, Svirezhev and von Bloh (1998) predict that NPP declines to zero but never becomes negative, while simple TRIFFID shows a slight dip into negative NPP which returns to 0 when the temperature reaches 60 °C. Among the biochemical models there is some variation in the optimal, high and low temperatures for NPP. As well as a difference in form between all the models studied, there is also a considerable difference in the magnitude of the predicted rate of NPP.

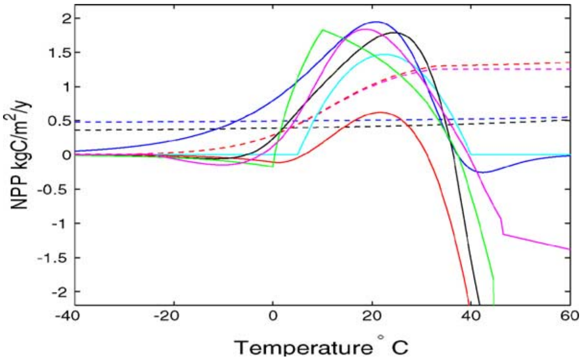

Fig. 6. Temperature response of net primary productivity when other variables are held constant at: $C_a = 350$ ppmv, $W = 1$, $I = 120$ W/m^2: (dashed magenta line) Miami, (dashed red line) King et al. (1997), (dashed blue line) Polglase and Wang #1, (dashed black line) King et al. (1995) #1, (cyan line) Svirezhev and von Bloh, (red line) Lenton, (blue line) simple TRIFFID, (black line) TRIFFID, (green line) DEMETER, (magenta line) BIOME3.

The empirical models saturate at high temperatures but do not decline in the way that might be expected because of the way in which they are structured. The data used to construct these models is based on annual averages. An average annual temperature above 30 °C is very unlikely and there is no data available with which to construct the response to such conditions, so the given model functions were extrapolated in this study. In practise this is probably pushing the model beyond its intended purpose and so results at very high temperatures should be treated cautiously. The near absence of a temperature response in the β-factor models is highly suspect. It arises because the temperature dependence only occurs in the β-factor itself and this is then multiplied by a factor based on the deviation of atmospheric carbon dioxide from a base value (Eqs. (A.3.1) and (A.4.2)). Since this deviation is generally small the potential impact of the β-factor, and the associated temperature dependency, is limited. The true temperature dependence in these models is built into the constant base NPP rate attributed to each biome type. The form of the quasi-biochemical and biochemical models can be most easily understood by studying their photosynthesis and respiration functions which are described in Sections 3.1 and 3.2. The parabolic responses of the Lenton (2000) and Svirezhev and von Bloh (1998) models are probably more appropriate high temperature extrapolations of the empirical models. The other biochemical models predict much higher NPP rates but this is probably an artifact of the methodology used in this study. Since output is scaled to an annual rate, a temperature of 40 °C in these models is applied day and night, 365 days a year. They also assume saturating water and solar radiation levels as opposed to the average levels built into the parameterisations of the other models. As such it is probably not appropriate to attempt to compare the magnitude of NPP rates between the different types of model.

3.3.2. Carbon dioxide response of net primary productivity

The response to carbon dioxide fertilisation is very similar for all models except that of Svirezhev and von Bloh (1998) (Fig. 7). There is a general upward, but saturating, trend in NPP with increasing carbon dioxide. NPP actually decreases with increasing carbon dioxide in Svirezhev and von Bloh's model (1998). This is because that model is not really set up to deal with extra carbon being added to the atmosphere and it leads to an increase in competition in the combined fertilisation/competition function (Eq. (A.6.3)) even though vegetation carbon is unchanged. The difference in magnitude of NPP is an artifact of the base NPP rate at 15 °C and should be disregarded.

3.3.3. Water stress and net primary productivity

Six of the ten models considered here include a water stress function. The empirical Miami and King et al. (1997) models show a saturating relationship, as do DEMETER, TRIFFID and BIOME3 (Fig. 8). In contrast to this, Svirezhev and von Bloh's (1998) model gives a parabolic relationship with a maximum when $W = 0.475$.

The empirical models indicate that there is an upper limit for W of approximately 0.35 (equivalent in these models to precipitation of 1500 mm per year) above which further precipitation does not enhance NPP unless the temperature is also increased. TRIFFID, DEMETER and BIOME3 are largely in agreement with this although the location of the saturation

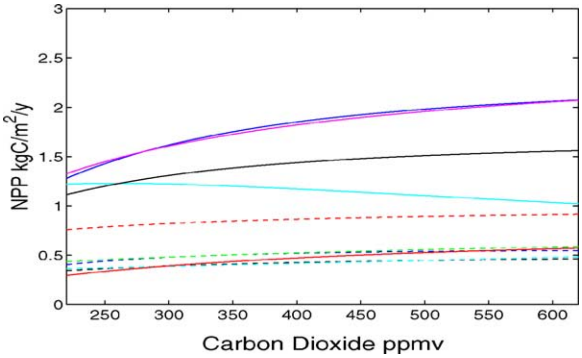

Fig. 7. Response of net primary productivity to atmospheric carbon dioxide levels when other variables are held constant at: $T = 15\,^{\circ}\mathrm{C}$, $W = 1$, $I = 120\,\mathrm{W/m^2}$: (dashed red line) King et al., 1997, (dashed blue line) Polglase and Wang #1, (dashed green line) Polglase and Wang #2, (dashed black line) King et al., 1995 #1, (dashed cyan line) King et al., 1995 #2, (cyan line) Svirezhev and von Bloh, (red line) Lenton, (blue line) simple TRIFFID, (black line) TRIFFID, (magenta line) BIOME3.

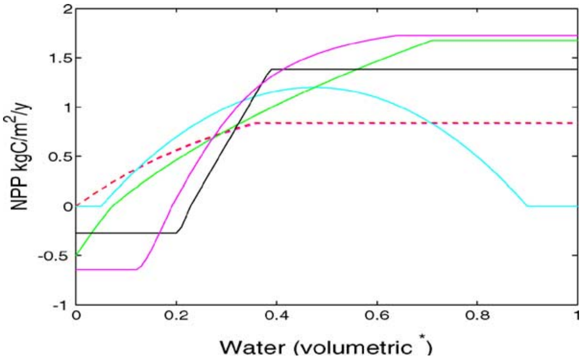

Fig. 8. Response of net primary productivity to water stress when other variables are held constant at: $T = 15\,^{\circ}\mathrm{C}$, $C_a = 350\,\mathrm{ppmv}$, $I = 120\,\mathrm{W/m^2}$: (dashed magenta line) Miami/King et al., 1997, (cyan line) Svirezhev and von Bloh, (green line) DEMETER, (black line) TRIFFID, (magenta line) BIOME3.

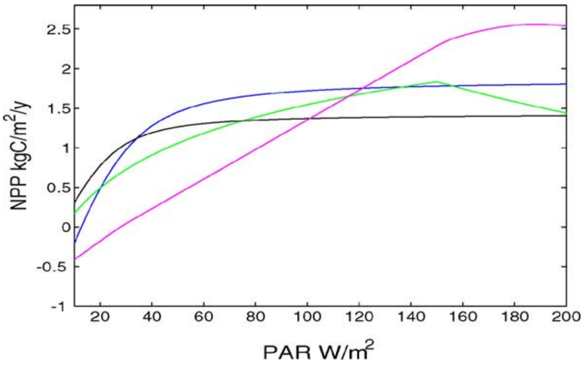

Fig. 9. Response of net primary productivity to photosynthetically active radiation levels when other variables are held constant at: $T = 15\,^{\circ}\mathrm{C}$, $C_a = 350\,\mathrm{ppmv}$, $W = 1$: (blue line) simple TRIFFID, (green line) DEMETER, (black line) TRIFFID, (magenta line) BIOME3.

point varies. The reasons behind this response are best understood through the responses of photosynthesis and respiration discussed in Sections 3.1 and 3.2. The parabolic response of Svirezhev and von Bloh's (1998) model is in stark contrast to all the others. At first sight is appears incorrect as very wet ecosystems can be among the most productive in the world (Leith, 1975b). However, Svirezhev and von Bloh's (1998) model is based on a single, generic global vegetation type. If the composition of this vegetation is assumed to be static, or at least relatively slow to change, then very high soil water levels could be expected to lead to a severe reduction in productivity among the many plants which will not tolerate water logged soils. Indeed, there is a case to be made for including a similar response in at least some of the vegetation types of the biogeochemical models.

3.3.4. *Photosynthetically active radiation and net primary productivity*

Only four models, simple TRIFFID, TRIFFID, DEMETER and BIOME3 include a response to photosynthetically active radiation. They all show a near linear increase followed by saturation although the position of the saturation point varies considerably (Fig. 9). This echoes the form of photosynthesis and respiration responses for these models and is best understood by reference to those processes (Sections 3.1 and 3.2).

3.3.5. *Summary of net primary productivity responses*

All models considered in this study show a strong temperature response for NPP. The empirical models predict a saturating response as water becomes a limiting factor although extrapolation to high temperatures is probably not valid for these models. The β-factor models show only a very weak response as temperature dependency is mostly built into the constant parameterisation. The quasi-biochemical and biochemical models predict a parabolic response. All models, except Svirezhev and von Bloh's (1998), show a similar increasing but saturating response to atmospheric carbon dioxide levels. Of the models which include water stress all except that of Svirezhev and von Bloh (1998) show a saturating response as water levels increase and other factors become limiting. Svirezhev and von Bloh's (1998) model predicts a parabolic response with NPP decreasing as water levels pass a critical threshold. The response of NPP to photosynthetically active radiation is predicted to be saturating in all models which consider it although the location of the saturation point is highly variable.

3.4. *Net primary productivity response to changes in two variables*

So far only responses to changes in a single environmental variable have been considered. But what happens if more than one factor is affecting NPP? In particular, do the intricate interactions between variables in the complicated biochemical models result in significantly different behaviour to the multiplicative combination of several independent factors used in the quasi-biochemical models? It is not really possible to effectively compare the surfaces generated by two simultaneously changing variables. Although differences in magnitude can be filtered out by normalising or comparing gradients, the inherent differences in critical threshold values between all models hinders the extraction of useful information from such surfaces. Instead, a general idea of how two variables may be interacting is sought by comparing the response curves for a particular variable, such as temperature, at three fixed values for another, such as water.

Six cases are shown in Fig. 10: (a and b) temperature and carbon dioxide, (c and d) temperature and photosynthetically active radiation, (e) temperature and water, (f) carbon dioxide and water, (g) carbon

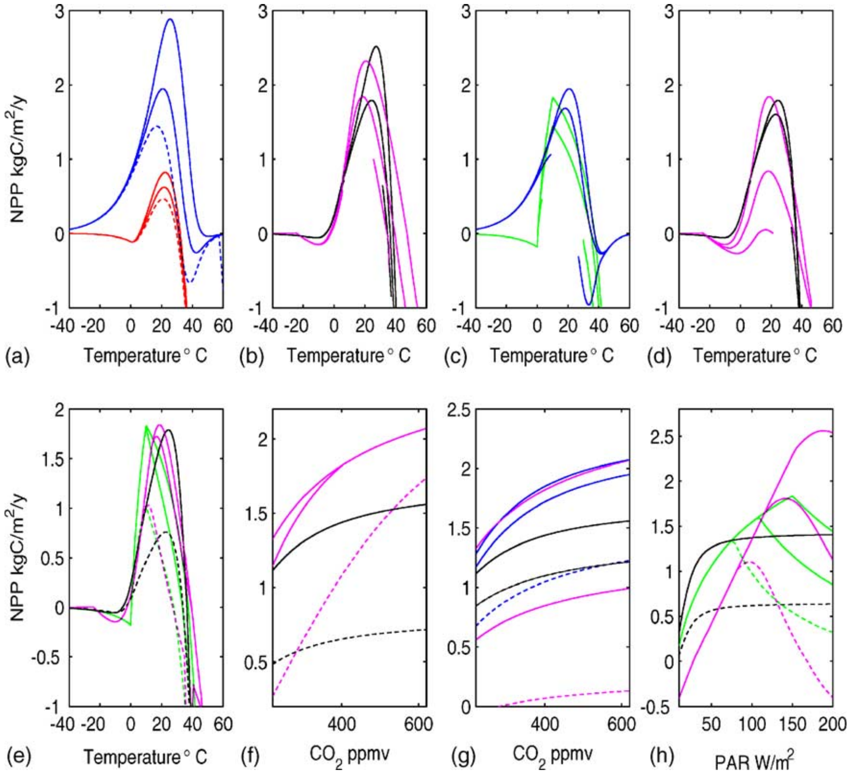

Fig. 10. Responses of net primary productivity to changes in one environmental variable at three fixed values of another. The coloured lines correspond to different models: (red line) Lenton, 2000, (blue line) simple TRIFFID, (green line) DEMETER, (black line) TRIFFID, (magenta line) BIOME3. The line styles correspond to different values of the second variable: (a and b) response to temperature with - - - $C_a = 250$, — (thick) $C_a = 350$, — (thin) $C_a = 350$; (c and d) response to temperature with - - - $I_{PAR} = 30$, — (thin) $I_{PAR} = 70$, — (thick) $I_{PAR} = 120$; (e) response to temperature with - - - $W = 0.3$, — (thin) $W = 0.6$, — (thick) $W = 1.0$; (f) response to atmospheric carbon dioxide levels with - - - $W = 0.3$, — (thin) $W = 0.6$, — (thick) $W = 1.0$; (g) response to atmospheric carbon dioxide levels with - - - $I_{PAR} = 30$, — (thin) $I_{PAR} = 70$, — (thick) $I_{PAR} = 120$; (h) response to photosynthetically active radiation levels with - - - $W = 0.3$, — (thin) $W = 0.6$, — (thick) $W = 1.0$. In all cases, if a variable is not one of the two being considered it is held fixed at: $T = 15\,^{\circ}\mathrm{C}$, $C_a = 350$ ppmv, $W = 1$ volumetric scale, $I_{PAR} = 120\,\mathrm{W/m^2}$.

dioxide and photosynthetically active radiation, (h) photosynthetically active radiation and water. As can be seen, the effect of the second variable is essentially to scale the response to the first. Some small differences in curvature do occur, notably in the response to atmospheric carbon dioxide and water in BIOME3, but they do not appear to be significant. Of course, there may be more complicated effects concealed in the covariance of two factors over their full range or the combined effect of three or more variables but the limited investigation undertaken here does seem to imply that simple multiplicative factors will yield similar results to more intricate functions.

3.5. *Responses of different plant types including those using the C_4 pathway*

Five of the models (Polglase and Wang, 1992; King et al., 1995, TRIFFID, DEMETER and BIOME3) include parameterisations for different vegetation types. The β-factor models are of little interest as their generic responses to environmental conditions are limited and the vegetation type parameterisation amounts to little more than defining the base NPP rate. The other models are more interesting with several important parameters in the model being adjusted for different plant types and fundamental changes being made to the model formulations to account for

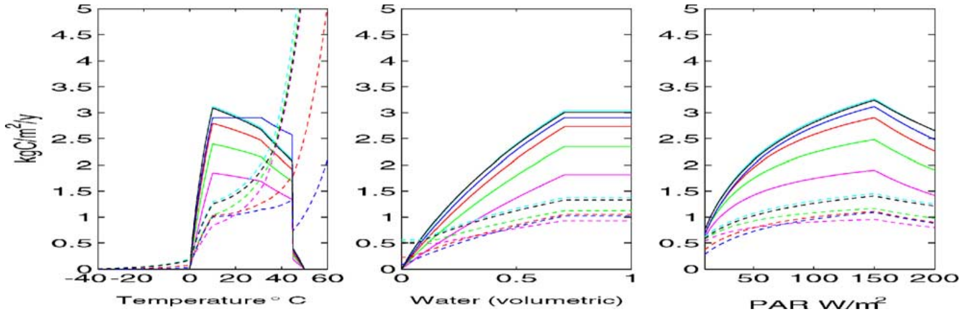

Fig. 11. Photosynthesis and respiration responses of different plant types in the DEMETER model to temperature, carbon dioxide, soil water and photosynthetically active radiation. Solid lines are photosynthesis, dashed lines respiration: (cyan line) humid tropical forest, (green line) temperate deciduous forest (magenta line) boreal forest, (red line) C_3 grass, (blue line) C_4 grass, (black line) generic.

C_4 photosynthesis. In this section the responses of the various plant types are compared for each model.

3.5.1. Plant types in DEMETER

The NPP of all plant types in DEMETER shows a similar form of response to temperature (Fig. 12). The C_3 grass is more productive than other C_3 plant types between 35 and 40 °C. It can be seen in Fig. 11 that this is because of a lower respiration rate at these temperatures which is determined by the base respiration rate parameterisation. C_4 grasses are more productive than any C_3 plant type between 10 and 45 °C, particularly in the higher part of this range. This is due to both a higher photosynthesis and a lower respiration rate. All plant types have the same response to changes in water and photosynthetically active radiation. Although NPP in all the C_3 plant types show essentially the same form of response to all environmental variables, it does vary in magnitude. Boreal forest is the least productive, followed by temperate deciduous forest, humid tropical forest and C_3 grass. This is mostly due to the different constant base rates used for photosynthesis and respiration.

3.5.2. Plant types in TRIFFID

The NPP of all plant types in TRIFFID also shows a similar form of response to temperature (Fig. 14). However, the maxima for all the C_3 plant types occur around 30 °C and the maximum for C_4 grass occurs close to 40 °C by which point NPP is close to 0 in the C_3 types. NPP only becomes positive for C_4 grass around 5 °C, compared with −5 °C for C_3 types and remains lower until around 32 °C. All of this is determined by the form of the photosynthesis response (Fig. 13) as the respiration response is very similar to that of C_3 plant types. All plant types show the same saturating response to increasing carbon dioxide levels except C_4 types which show no response. All

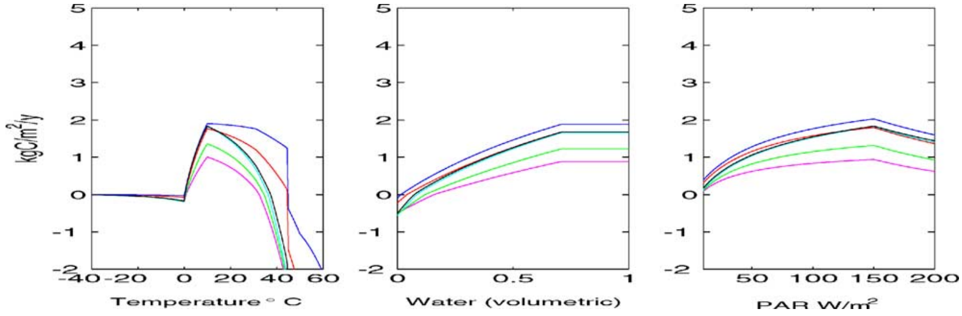

Fig. 12. Net primary productivity response of different plant types in the DEMETER model to temperature, carbon dioxide, soil water and photosynthetically active radiation: (cyan line) humid tropical forest, (green line) temperate deciduous forest, (magenta line) boreal forest, (red line) C_3 grass, (blue line) C_4 grass, (black line) generic.

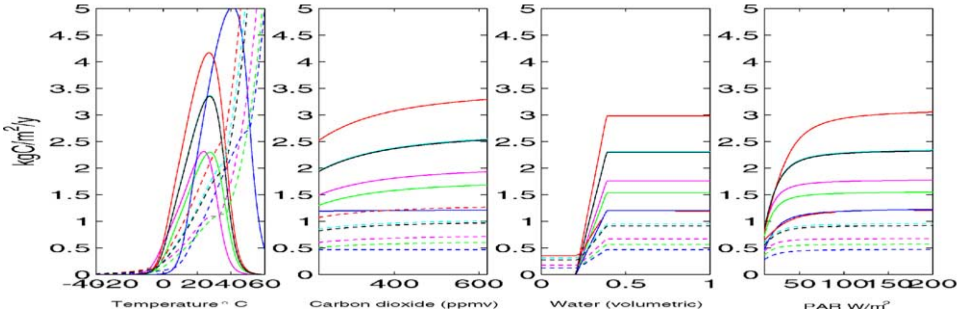

Fig. 13. Photosynthesis and respiration responses of different plant types in the TRIFFID model to temperature, carbon dioxide, soil water and photosynthetically active radiation. Solid lines are photosynthesis, dashed lines respiration: (cyan line) broadleaf tree, (magenta line) needleleaf tree, (green line) shrub, (red line) C_3 grass, (blue line) C_4 grass, (black line) generic.

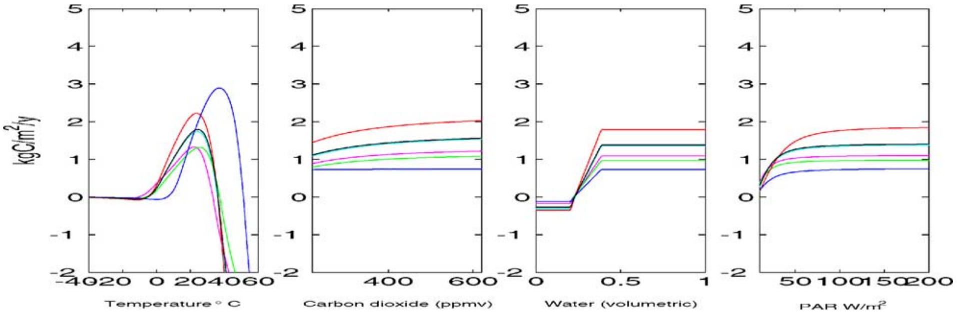

Fig. 14. Net primary productivity response of different plant types in the TRIFFID model to temperature, carbon dioxide, soil water and photosynthetically active radiation: (cyan line) broadleaf tree, (magenta line) needleleaf tree, (green line) shrub, (red line) C_3 grass, (blue line) C_4 grass, (black line) generic.

plant types show the same response to water stress and photosynthetically active radiation although NPP in C_3 grasses appears to saturate at a higher light level than for other types. As regards the magnitude of NPP, needleleaf trees are least productive except below approximately 2 °C when they gain a slight advantage. Shrubs are the second least productive except above approximately 40 °C. Next are broadleaf trees, then C_3 grass. The maximum of C_4 grass is significantly greater than that of any C_3 type.

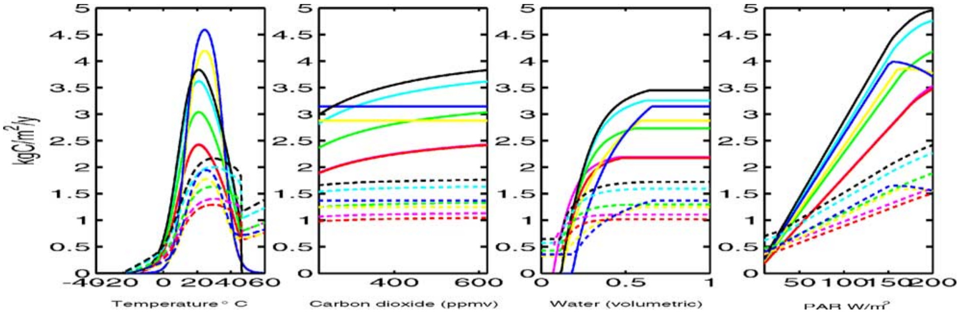

Fig. 15. Photosynthesis and respiration responses of different plant types in the BIOME3 model to temperature, carbon dioxide, soil water and photosynthetically active radiation. Solid lines are photosynthesis, dashed lines respiration: (cyan line) humid tropical forest, (green line) temperate deciduous forest, (magenta line) boreal forest, (red line) C_3 cool grass, (yellow line) C_4 cool grass (blue line) C_4 warm grass, (black line) generic.

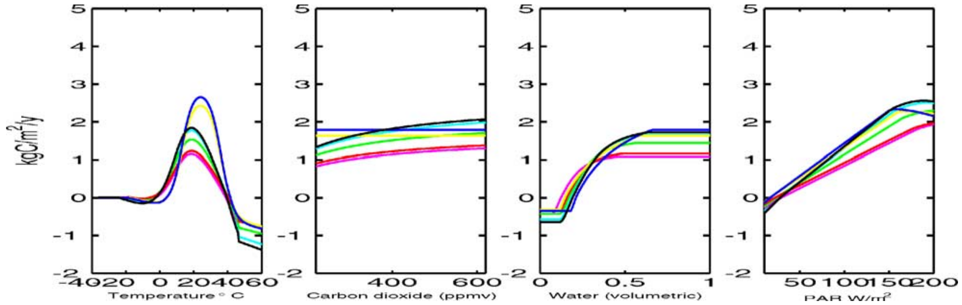

Fig. 16. Net primary productivity response of different plant types in the BIOME3 model to temperature, carbon dioxide, soil water and photosynthetically active radiation: (cyan line) humid tropical forest, (green line) temperate deciduous forest, (magenta line) boreal forest, (red line) C_3 cool grass, (yellow line) C_4 cool grass, (blue line) C_4 warm grass, (black line) generic.

3.5.3. Plant types in BIOME3

As with the previous models, all plant types in BIOME3 have a similar form of response to temperature (Fig. 16). NPP becomes positive at approximately 0 °C for C_3 plant types and 10 °C for the C_4 grass types. Maximum NPP occurs close to 18 °C for C_3 plant types and 25 °C for C_4 grasses. In all cases NPP becomes negative again when the temperature reaches approximately 40 °C. At very high temperatures NPP of the humid tropical forest type is significantly more negative than the others as a result of a higher respiration rate (Fig. 15). All plant types have the same response to carbon dioxide levels except the C_4 grasses which show no response. Although all plant types have the same saturating response to water levels, the C_3 cool grass and boreal forest types achieve maximum NPP at a much lower water level than the other types. The C_4 warm grass requires the highest water level to achieve maximum photosynthesis. Responses to photosynthetically active radiation are the same for all plant types except at very high levels when saturation, or even decline, occurs as a result of water stress. This occurs for both cool and warm C_4 grasses around 150 W/m^2 and not at all (for light levels below 200 W/m^2) for the C_3 grass or boreal forest plant types. In general, the boreal forest plant type has the lowest NPP, followed by C_3 cool grass, temperate deciduous forest and humid tropical forest. The maximum NPP of both the C_4 grasses is significantly greater than any C_3 type for carbon dioxide levels around 350 ppmv.

3.5.4. Summary of the responses of different plant types

There is a general consensus among the three models studied here that C_4 photosynthesis is more efficient at high temperatures than the C_3 pathway. TRIFFID and BIOME3 also predict that the C_4 pathway has a higher minimum temperature threshold for positive NPP than the C_3 pathway although DEMETER does not recognise this. DEMETER predicts that C_3 grass has a higher temperature threshold than other C_3 plant types but TRIFFID and BIOME3 do not agree. The two models which include a carbon dioxide response agree that all C_3 plant types show the same response to carbon dioxide levels but C_4 plants show no response. DEMETER predicts that all plant types have the same response to water and photosynthetically active radiation levels. TRIFFID predicts the same response to water levels but a higher light level before saturation occurs for C_3 grass. BIOME3 predicts that saturation occurs at a lower water level for boreal forest and C_3 grass types than humid tropical forest and C_4 grass types. This water stress also appears in the response to photosynthetically active radiation, with saturation occurring earlier for the humid tropical forest and C_4 plant types as water stress takes effect. All models agree that C_4 plants have the largest optimum productivity and boreal forest/needleleaf trees the least. DEMETER and TRIFFID predict that C_3 grass has a greater optimum productivity then humid tropical forest/broadleaf trees but BIOME3 places these the other way round. However, the opportunity of a direct comparison between models is limited because plant type definitions are not identical in all models.

4. Discussion

There is broad agreement between all models considered in this study except those using a β-factor approach. The main differences occur in the definition of critical thresholds and at the extremes of all variable ranges. The former is probably a result of both the model structure and the compression of data to fit a few broad vegetation types. The latter probably reflects a shortage of data on the way plants behave in such extreme environments. It is also clear that the intended use of the model affects the way in which it is formulated. None of the models considered in this study can be said to be wrong within the context for which they were intended. However, extension beyond these limits is not always possible or appropriate. This means that, when combining vegetation models with models of other components of the Earth system, care must be taken to ensure that they are truly compatible.

The main advantages and disadvantages of each class of model are now discussed.

4.1. The advantages and disadvantages of different classes of model

4.1.1. Empirical models

The empirical models should, by definition, give good estimates of NPP. However, their use in a changing environment is limited as they implicitly assume that the vegetation will be immediately transformed to the most appropriate type for that environment. They are also limited by the necessity to extrapolate in order to calculate the vegetation's response to an environment (for instance very high temperature and rainfall) that does not currently exist on the Earth. Nevertheless, they remain a helpful reference point for comparison with other types of model.

4.1.2. β-Factor models

The β-factor models are solely intended to investigate the effects of carbon dioxide fertilisation. As a result temperature dependence only occurs in the form of the carbon dioxide compensation point. The formulation of this function is such that temperature dependence is very weak. In the simple form of the models it is parameterised out altogether. This works for relatively modest increases in temperature associated with relatively small increases in atmospheric carbon dioxide. However, if changing carbon dioxide levels lead to a greater temperature increase, a more significant impact would be expected in both the response and structure of terrestrial ecosystems. Therefore, these models would need to be greatly extended to be of more general use in studying the integrated dynamics of the Earth system.

4.1.3. Quasi-biochemical and biochemical models

The quasi-biochemical models of Svirezhev and von Bloh (1998) and Lenton (2000) appear to give reasonable estimates of global NPP but, because they have been set up for use in zero-dimensional models, they do not properly consider spatially heterogeneous environmental factors such as soil water or light use efficiency. Lenton (2000) neglects both of these factors. Svirezhev and von Bloh (1998) include a water function, although this must be treated very cautiously when used in a globally averaged context. Indeed, the use of a globally averaged temperature in both models may also problematic as small changes in extreme temperature environments such as the tropical forests or tundra may have a significant impact on global NPP that an average global temperature will not pick up. That said, the framework used in either model could be extended to include spatial effects but some reparameterisation would be necessary to account for the shift from a global average environment to a spatially heterogeneous one. The DEMETER model attempts to step in this direction and falls between simple quasi-biochemical models such as Lenton (2000) and true biochemical models such as TRIFFID or BIOME3. Both of these latter biochemical models give similar estimates of photosynthesis, respiration and NPP but employ different methods to get there. Although the physiology and biochemistry of plants is fairly well understood, there is no agreement on the best way to model it. The Farquhar and von Caemmerer (1982) photosynthesis model and its derivatives are in widespread use although, even if this is assumed to be correct, it should be noted that it always relies on an external stomatal conductance model to calculate the internal leaf carbon dioxide level c_i. The representation of respiration, water stress, light use and scaling from the leaf to the canopy level varies. This is discussed further below. In general, the full biochemical models are likely to provide the most accurate predictions of vegetation productivity and dynamics. However, their complexity makes it difficult to understand the results they are producing, leaves them open to computational errors and incurs large computational overheads.

4.2. *Models of plant processes*

Many models break net primary productivity down in photosynthesis and respiration, which may themselves depend on functions representing water stress (or stomatal conductance) and light-use efficiency. As discussed above the Farquhar and von Caemmerer (1982) model is widely used for photosynthesis but models for other processes are more variable. Here some of the issues involved in modelling these processes are discussed along with some other major submodels not already discussed.

4.2.1. *Modelling respiration*

The main issue with respiration in the models considered in this study is the response to high temperatures. Does it continue to increase exponentially as extrapolating the Q_{10} reaction rate function suggests, or do other factors take effect and reduce the respiration rate? Larcher (1983) suggests the latter, but it remains a contentious issue. Besides this there are several other issues. Some models distinguish between different parts of the vegetation such as leaf, branch and root. This requires a method for calculating the amount of carbon, and the respiration rate, for each part. There is no agreement on the correct way to approach, or parameterise, this. There is also no agreement regarding how to distinguish different forms of respiration. Some models just use a single rate for the whole plant, others calculate leaf and non-leaf rates, others leaf, maintenance and transport plus a growth tax. This itself is problematic with the estimated proportion of NPP to be levied ranging from 20% in BIOME3 to 33% in DEMETER. In fact it is likely that this is one of the main parameters that can be adjusted to tune the output to match current data.

Ryan (1991) suggests that respiration can be adequately modelled using construction, maintenance and transport components for each plant part. But he believes that each of these components will show a different response to a changing environment. He also suggests that internal carbon and nitrogen concentrations affect the respiration rate (as they do in TRIFFID and BIOME3) but that their distribution throughout the plant may change in response to environmental changes (as happens in BIOME3). Ryan (1991) also notes that plants appear to acclimatise to local conditions. Thus, long term respiration rates may not change as significantly as the standard Q_{10} response would suggest.

Ryan’s (1991) model, like all of the others considered in this study, makes a basic separation of the plant respiration processes. In fact, the numerous respiration processes going on in a plant could be resolved in more detail. Thornley and Cannell (2000) consider this. They suggest that the substrate and structure of a plant should be separated. Then substrates can be can be transported around the plant and local concentrations used to calculate the rates of energy consuming processes. This leads them to define seven different forms of respiration in seven different plant tissues. Respiration rates are calculated for: growth, phloem loading, ammonium uptake, nitrate uptake, N_2-fixation, mineral ion uptake and residual maintenance. Although this is more comprehensive, parameterisation for any but the most extensively studied plant types may be vague. This is a general problem with any respiration model as data are not as easy to collect as they are for photosynthesis.

4.2.2. *Modelling stomatal conductance and water stress*

The models in this study use a variety of methods to deal with stomatal conductance and water stress. Svirezhev and von Bloh (1998) use a straightforward multiplicative stress function. DEMETER is similar but relates water availability to the (vegetation-independent) evapotranspiration rate. TRIFFID uses a combination of a basic multiplicative factor and an integrated stomatal conductance function relating internal leaf carbon dioxide to atmospheric carbon dioxide and humidity. BIOME3 uses a more complex model involving the soil water, evapotranspiration rate, canopy conductance and photosynthesis.

Various other models have been put forward for stomatal conductance and water use efficiency. Like respiration, it is a complicated issue and there is no agreement on the most appropriate way to approach it. According to Collatz et al. (1991) a truly mechanistic model is not plausible and empirical, or semi-empirical models, are used instead. There are two basic approaches. A maximum rate of stomatal conductance can be modified by multiplicative environmental stress functions. This is exemplified in a model by Jarvis (1976) which uses stress factors depending on the ambient temperature, solar radiation and vapour pressure deficit. An alternative approach recognises that stomatal conductance and photosynthesis are mutually influencing processes. Thus, the submodels for each process are coupled and solved simultaneously (as in BIOME3). This is the general approach taken by Ball et al. (1987), Leuning (1995) and Collatz et al. (1991), among others. Other important issues in the calculation of stomatal conductance include the use of environmental variables measured at the leaf surface rather than ambiently and scaling from the leaf to the canopy level. Both of these issues are made all the more important by the observation that temperature and leaf level humidity deficit, as well as solar radiation, can show great variability with canopy depth (Jarvis and McNaughton, 1985).

4.2.3. Modelling light-use efficiency and scaling to the canopy level

There is good data available on the way light intensity affects the rate of photosynthesis in individual leaves. This shows a saturating response (Larcher, 1983). However, scaling from a single leaf to the canopy level is a more complicated issue as the leaves at the top of the canopy receive more light than those below them. Furthermore, the photosynthesis rate is related to leaf nitrogen content which may not be uniform throughout the canopy. Friend (2001) reviews two methods for scaling from the leaf to the canopy level. The first, as employed by Sellers et al. (1992), assumes that the distribution of canopy nitrogen matches the distribution of solar radiation through the canopy. This means that a change in photosynthetically active radiation causes the photosynthesis rate of each leaf to change by the same relative amount in each leaf. A smoothing function is then used to make the transition from light-limited to Rubisco limited photosynthesis resemble observations. This leads to a saturating response, as seen in the TRIFFID model. The second model Friend (2001) considers is due to Kull and Krujit (1998). This assumes that, although the uppermost leaves of the canopy are light saturated, the lower ones may not be. At low light intensities, all leaves are light limited. When a critical light intensity is reached, determined by the leaf nitrogen content, an increasing proportion of the canopy becomes light saturated. At the canopy level both models show a saturating response as light intensity increases but the second model, with a uniform nitrogen distribution, predicts maximum photosynthesis rates 26% higher than the first. Friend (2001) considers that the second of these models is likely to be more accurate. In contrast to both of these models, BIOME3 tackles the canopy scaling problem by assuming that nitrogen is always optimally distributed for the light intensity at any canopy level and thus light use efficiency is maximised. This results in a linear, not saturating, response to increasing light intensity. As with the other plant processes, there is no agreement on which of these formulations is most appropriate, although Friend (2001) concludes his review by asserting that the only way to accurately model canopy photosynthesis is by explicitly modelling multiple canopy layers.

5. Conclusion

This study has investigated ten published terrestrial NPP models which were broadly classified as empirical, β-factor, quasi-biochemical and biochemical. All of the models considered here claim to make reasonable predictions of current or preindustrial NPP and, with the exception of the β-factor models, show broadly similar responses to changes in environmental variables. This suggests that choosing, or developing, an NPP submodel for use in a wider model should be a largely pragmatic decision based on the context of the model and the nature of the information required from it.

The empirical Miami model is very easy to implement and understand. It relies on very few parameters and should, by definition, give reasonable estimates of NPP. However, it may be compromised by the omission of vegetation carbon density and responses to several environmental factors, the need to extrapolate to environments that do not currently exist on the Earth and the implicit assumption of spontaneous changes in vegetation composition, although it may be possible to parameterise this out. The β-factor models considered here are tightly bound to their intended context and probably of limited general applicability. Their utility in rapid climate change scenarios is particularly compromised by a formulation that produces a temperature response which is either very weak or non-existent.

The responses of the quasi-biochemical models considered here generally show reasonable agreement with more sophisticated biochemical models and so may offer more appropriate responses for extreme environments, and generally be more versatile, than empirical models. However, the compression of data required to construct and parameterise the functions they use, particularly when employed in zero-dimensional contexts, suggests that even qualitative output should be considered cautiously. Furthermore, pairing causes and effects when interpreting results is not always straightforward, even in the simplest of formulations. The true biochemical models should be expected to provide the most reliable estimates of NPP, albeit at the cost of much higher computational overheads and opacity. However, there are significant uncertainties concerning respiration, stomatal conductance and canopy scaling schemes and, although the responses of the models considered here are similar, they are certainly not the same. Furthermore, the fact that predicted NPP for different plant types within these models shows relatively small differences, and that these differences are not consistent between models, suggests that ecophysiological constraints, phenology and competition submodels have a strong influence on the vegetation distributions these models predict. So, although these models provide the best estimates of NPP currently possible, their output must still be treated cautiously until further empirical work can soften some of the uncertainties in their formulations. Meanwhile, empirical or quasi-biochemical models may be sufficient for all but the most comprehensive simulations.

On a different note, carrying out this investigation has been made unnecessarily difficult by the non-standard use of definitions, notation, units of measurement and plant types in the literature. There has been some movement towards tackling these problems through the ETEMA project (Sykes et al., 2001), a pan-European working group using standardised data and parameter sets to investigate a number of issues in vegetation modelling, and we hope that the standardised equations presented in Appendix A may also be of some use. However, given the current widespread interest in modelling the terrestrial vegetation and its role in a changing Earth system, the general implementation of some form of standardisation would undoubtedly be of great benefit.

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Appendix A. Full equations for each model considered in this paper

Complete equations for all of the NPP models considered in this paper are presented below. These have been taken from the literature but transformed into a standardised, and relatively compact, format to allow easy comparison between them and facilitate a straight forward translation into computer code. The main notation is given below. All parameters have been generalised to letters and the only numbers in the given equations correspond to unit conversions, except where 1 is used as an identity element. Tables of parameter values are given in Appendix B. Units for input and output of the models are standardised and are given below. Units within models can vary and are detailed with each model description.

- NPP: net primary productivity (kgC/m^2 per year)
- C_v: carbon in the vegetation (kgC/m^2)
- C_a: carbon in the atmosphere (Pa)
- A_v: fraction of vegetated land area
- T: air temperature at the surface ($^\circ$C)
- W: soil water or precipitation—volumetric (see note below)
- P: gross photosynthesis rate (kgC/m^2 per year)
- R: respiration rate (kgC/m^2 per year)

- L: litter rate (kgC/m^2 per year)
- I_{PAR}: photosynthetically active radiation reaching the canopy (Ein/(m^2 s))
- Λ: leaf area index (m^2 leaf/m^2 area)
- β: biotic growth factor
- Γ: CO$_2$ compensation point for photosynthesis
- c_{i}: internal leaf CO$_2$ partial pressure (Pa)
- J_{C}: Rubisco limited gross photosynthesis rate
- J_{L}: light limited gross photosynthesis rate
- J_{E}: transport limited gross photosynthesis rate
- D: evapotranspiration demand
- S: evapotranspiration supply
- g_{c}: canopy conductance
- g_{p}: potential canopy conductance
- H: humidity deficit at leaf surface (kg/kg)
- d: day length (h)

Where NPP, C_{v} or R is partitioned between different parts of the plant, subscripts of l(eaf), b(ranch), s(tem), w(ood) and r(oot) are applied. Functions are always written as f_{i} except for those used in widespread use in which case the standard notation, as set out above, has been retained for clarity. Constants are always given as k_{i}. They are described and enumerated in Appendix B.

Note on water: The way in which water is represented is particularly non-standard. Some models (Leith, 1975a; King et al., 1997) use precipitation in mm per year, others (Svirezhev and von Bloh, 1998) actual soil water, others (Cox, 2001; Foley, 1994; Haxeltine and Prentice, 1996a,b) use a volumetric soil water scale. To overcome this, all scales are transformed to the interval [0,1], based on a maximum precipitation of 4000 mm per year in Leith et al. (1975) and King et al.'s (1997)models, and a maximum soil moisture content of 20 g/cm^2 in Svirezhev and von Bloh's (1998) model.

A.1. Miami model—Leith (1975a)

Inputs:

Temperature (T) (°C)
Precipitation (W) (volumetric transform of mm per year)

Productivity:

Net primary productivity (kgC/m^2 per year):

$$NPP(T, W) = \frac{1}{1000}\min\{f_1(T), f_2(W)\} \quad \text{(A.1.1)}$$

Temperature-dependent NPP (gC/m^2 per year):

$$f_1(T) = 0.45\frac{k_1}{1 + \mathrm{e}^{k_2 - k_3 T}} \quad \text{(A.1.2)}$$

Precipitation-dependent NPP (gC/m^2 per year):

$$f_2(W) = 0.45 k_4 (1 - \mathrm{e}^{-4000 k_5 W}) \quad \text{(A.1.3)}$$

A.2. King et al. (1997), Post et al. (1997)

Inputs:

Temperature (T) (°C)
Precipitation (W) (volumetric transform of mm per year)
Atmospheric CO$_2$ (C_{a}) (Pa)

Productivity:

Net primary productivity (kgC/m^2 per year):

$$\mathrm{NPP}(T, W, C_{\mathrm{a}}) = \frac{1}{1000}\min\{f_1(T), f_2(W)\} f_3(T, C_{\mathrm{a}}) \quad \text{(A.2.1)}$$

Temperature-dependent NPP (gC/m^2 per year):

$$f_1(T) = 0.45\frac{k_1}{1 + \mathrm{e}^{k_2 - k_3 T}} \quad \text{(A.2.2)}$$

Precipitation-dependent NPP (gC/m^2 per year):

$$f_2(W) = 0.45 k_4 (1 - \mathrm{e}^{-4000 k_5 W}) \quad \text{(A.2.3)}$$

CO$_2$ fertilisation function (dimensionless):

$$f_3(T, C_{\mathrm{a}}) = 1 + k_6 \beta(T, C_{\mathrm{a}}) \frac{9.901 C_{\mathrm{a}} - k_7}{k_7} \quad \text{(A.2.4)}$$

Biotic growth factor (dimensionless):

$$\beta(T, C_{\mathrm{a}}) = \frac{9.901 k_8 k_9 C_{\mathrm{a}} \Gamma(T)}{(9.901 k_8 C_{\mathrm{a}} - \Gamma(T))(9.901 k_8 C_{\mathrm{a}} + k_{10} \Gamma(T))} \quad \text{(A.2.5)}$$

CO$_2$ compensation point, ppmv (not given, taken from Polglase and Wang, 1992):

$$\Gamma(T) = k_{11} + k_{12}(T - k_{14}) + k_{13}(T - k_{14})^2 \quad \text{(A.2.6)}$$

A.3. Polglase and Wang (1992)

Inputs:

Temperature (T) (°C)
Atmospheric CO$_2$ (C_a) (Pa)

Productivity:

#1
Net primary productivity (kgC/m^2 per year):

$$\mathrm{NPP}(T, C_\mathrm{a}) = \frac{1}{10}k_1\left(1+\beta(T, C_\mathrm{a})\ln\left(\frac{9.901C_\mathrm{a}}{k_2}\right)\right) \tag{A.3.1}$$

Biotic growth factor (dimensionless):

$$\beta(T, C_\mathrm{a}) = \frac{9.901k_3k_4C_\mathrm{a}\Gamma(T)}{(9.901k_4C_\mathrm{a}-\Gamma(T))(9.901k_4C_\mathrm{a}+k_5\Gamma(T))} \tag{A.3.2}$$

CO$_2$ compensation point (ppmv):

$$\Gamma(T) = k_6 + k_7(T-k_9) + k_8(T-k_9)^2 \tag{A.3.3}$$

#2
Net primary productivity (kgC/m^2 per year):

$$\mathrm{NPP}(C_\mathrm{a}) = \frac{1}{10}k_1\left(1+k_{10}\ln\left(\frac{9.901C_\mathrm{a}}{k_2}\right)\right) \tag{A.3.4}$$

A.4. King et al. (1995)

Inputs:

Temperature (T) (°C)
Atmospheric CO$_2$ (C_a) (Pa)
Vegetation carbon density (C_v) (kgC/m^2)

Productivity:

#1
Net primary productivity (kgC/m^2 per year):

$$\mathrm{NPP}(T, C_\mathrm{a}, C_\mathrm{v}) = f_1(T, C_\mathrm{a})f_2(C_\mathrm{v}) \tag{A.4.1}$$

CO$_2$ fertilisation function (dimensionless):

$$f_1(T, C_\mathrm{a}) = 1+\beta(T, C_\mathrm{a})\frac{9.901C_\mathrm{a}-k_1}{k_1} \tag{A.4.2}$$

Biotic growth factor (dimensionless):

$$\beta(T, C_\mathrm{a}) = \frac{9.901k_2k_3C_\mathrm{a}\Gamma(T)}{(9.901k_3C_\mathrm{a}-\Gamma(T))(9.901k_3C_\mathrm{a}+k_4\Gamma(T))} \tag{A.4.3}$$

CO$_2$ compensation point (ppmv):

$$\Gamma(T) = k_5 + k_6(T-k_8) + k_7(T-k_8)^2 \tag{A.4.4}$$

Logistic growth rate (kgC/m^2 per year):

$$f_2(C_\mathrm{v}) = k_9C_\mathrm{v}(k_{10}-C_\mathrm{v}) \tag{A.4.5}$$

#2
Net primary productivity (kgC/m^2 per year):

$$\mathrm{NPP}(T, C_\mathrm{a}, C_\mathrm{v}) = f_3(C_\mathrm{a})f_2(C_\mathrm{v}) \tag{A.4.6}$$

CO$_2$ fertilisation function (dimensionless):

$$f_3(C_\mathrm{a}) = 1 + \frac{k_{11}(9.901C_\mathrm{a}-k_1)}{k_1} \tag{A.4.7}$$

A.5. Lenton (2000)

Inputs:

Temperature (T) (°C)
Atmospheric CO$_2$ (C_a) (Pa)
Vegetation carbon density (C$_\mathrm{v}$) (kgC/m^2)

Photosynthesis:

Photosynthesis rate (GtC/m^2 per year):

$$P(T, C_\mathrm{a}) = \frac{k_1k_2k_3}{k_4}f_1(T)f_2(C_\mathrm{a}) \tag{A.5.1}$$

Temperature response (dimensionless):

$$f_1(T) = \begin{cases} \dfrac{(k_5+T+273-k_6)^2(k_7-(T+273-k_6))}{k_8} & \text{if} \quad k_5 < T+273-k_6 < k_7 \\ 0 & \text{else} \end{cases} \tag{A.5.2}$$

CO$_2$ fertilisation function (dimensionless):

$$f_2(C_\mathrm{a}) = \frac{9.901C_\mathrm{a}-k_9}{9.901C_\mathrm{a}+k_{10}-k_9} \tag{A.5.3}$$

Respiration:

Respiration rate (GtC/m^2 per year):

$$R(T, C_\mathrm{v}) = k_{11}k_{12}C_v f_3(T) \times 10^{-12} \tag{A.5.4}$$

Temperature response (dimensionless)

$$f_3(T) = \mathrm{e}^{-k_{13}k_{14}(T+273)} \tag{A.5.5}$$

Productivity:

Net primary productivity (kgC/m^2 per year):

$$\mathrm{NPP}(T, C_\mathrm{a}, C_\mathrm{v}) = (P(T, C_\mathrm{a}) - R(T, C_\mathrm{v})) \times 10^{12} \tag{A.5.6}$$

A.6. Svirezhev and von Bloh (1997, 1998)

Inputs:

Temperature (T) (°C)
Atmospheric CO$_2$ (C_a) (Pa)
Total vegetation carbon (C_v) (kgC/m^2)
Soil water (W) (volumetric transform of g/cm^2)

Productivity:

Net primary productivity (kgC/m^2 per year)

$$\mathrm{NPP}(T, C_\mathrm{a}, C_\mathrm{v}, W) = \frac{k_1}{k_2} f_1(T) f_2(C_\mathrm{a}) f_3(C_\mathrm{v}) f_4(W) \times 10^{12} \tag{A.6.1}$$

Temperature response (dimensionless):

$$f_1(T) = \begin{cases} \dfrac{k_3(T-k_4)(k_5-T)}{(k_5-k_4)^2} & \text{for } k_4 \le T \le k_5 \\ 0 & \text{else} \end{cases} \tag{A.6.2}$$

CO$_2$ fertilisation/competition (dimensionless):

$$f_2(C_\mathrm{a}) f_3(C_\mathrm{v}) = \frac{(9.901 \times 12.011(1.773 \times 10^{20}/10^{21})k_6 C_\mathrm{a})(k_2 C_\mathrm{v} \times 10^{-12})}{[(9.901 \times 12.011(1.773 \times 10^{20}/10^{21})C_\mathrm{a}) + (k_2 C_\mathrm{v} \times 10^{-12})]^2} \tag{A.6.3}$$

Water response (dimensionless):

$$f_4(W) = \begin{cases} \dfrac{k_7(20W - k_8)(k_9 - 20W)}{(k_9 - k_8)^2} & \text{for } k_8 \le 20W \le k_9, \\ 0 & \text{else} \end{cases} \tag{A.6.4}$$

A.7. Simple TRIFFID—Huntingford et al. (2000)

Inputs:

Temperature (T) (°C)
Atmospheric CO$_2$ (C_a) (Pa)
Photosynthetically active radiation (I_PAR) (Ein/(m^2 s))

Photosynthesis:

Gross photosyn. rate (kgC/m^2 per year):

$$P(T, C_\mathrm{a}, I_\mathrm{PAR}) = 0.012 \times 31557600 \times f_1(J_\mathrm{C}, J_\mathrm{L}, J_\mathrm{E}) f_4(\Lambda) \tag{A.7.1}$$

Gross photosynthesis rate (mol CO$_2$/(m^2 s)):

$$f_1(J_\mathrm{C}, J_\mathrm{L}, J_\mathrm{E}) = \text{smallest root of :}$$
$$k_1 J^2 - J(J_\mathrm{P} + J_\mathrm{E}) + J_\mathrm{P} J_\mathrm{E} = 0 \tag{A.7.2}$$

where

$$J_\mathrm{P} = \text{smallest root of :}$$
$$k_2 J_\mathrm{P}^2 - J_\mathrm{P}(J_\mathrm{C} + J_\mathrm{L}) + J_\mathrm{C} J_\mathrm{L} = 0 \tag{A.7.3}$$

RuBP limited photosynthesis rate (mol CO$_2$/(m^2 s)):

$$J_\mathrm{C}(T, C_\mathrm{a}) = V_\mathrm{m}(T) \frac{c_\mathrm{i}(T, C_\mathrm{a}) - \Gamma(T)}{c_\mathrm{i}(T, C_\mathrm{a}) + f_2(T) \times (1 + (k_3/f_3(T)))} \tag{A.7.4}$$

Light limited photosyn. rate, mol CO$_2$/(m^2 s):

$$J_\mathrm{L}(T, C_\mathrm{a}, I_\mathrm{PAR}) = k_4(1 - k_5) I_\mathrm{PAR} \frac{c_\mathrm{i}(T, C_\mathrm{a}) - \Gamma(T)}{c_\mathrm{i}(T, C_\mathrm{a}) + k_6 \Gamma(T)} \tag{A.7.5}$$

Transport limited photosynthesis rate (mol CO_2/(m^2 s)):

$$J_E(T) = k_7 V_m(T) \tag{A.7.6}$$

Photo-respiration compensation point (Pa):

$$\Gamma(T) = \frac{k_3}{k_8 (k_9)^{k_{10}(T-k_{11})}} \tag{A.7.7}$$

Michaelis–Menton constant for CO_2 (Pa):

$$f_2(T) = k_{12} k_{13}^{k_{10}(T-k_{11})} \tag{A.7.8}$$

Michaelis–Menton constant for O_2 (Pa):

$$f_3(T) = k_{14} k_{15}^{k_{10}(T-k_{11})} \tag{A.7.9}$$

Internal leaf CO_2 partial pressure (Pa):

$$c_i(T, C_a) = k_{16} \left(1 - \frac{H(T)}{k_{17}}\right) (C_a - \Gamma(T)) + \Gamma(T) \tag{A.7.10}$$

Maximum rate of Rubisco carboxylation (mol CO_2/(m^2 s)):

$$V_m(T) = \frac{k_{18} k_{19}^{k_{10}(T-k_{11})}}{1 + e^{k_{20}(T-k_{21})}} \tag{A.7.11}$$

Leaf humidity deficit (kg/kg):

$$H(T) = H_{max}(T) - k_{22} \tag{A.7.12}$$

Saturated atmospheric humidity, kg/kg (not given, from Buck (1981)):

$$H_{max}(T) = \frac{k_{23}}{k_{24}} e^{(k_{25} T / k_{26} + T)} \tag{A.7.13}$$

Beer's law scaling to canopy level (dimensionless):

$$f_4(\Lambda) = \frac{1 - e^{-k_{27}\Lambda}}{k_{27}} \tag{A.7.14}$$

Respiration:

Respiration rate (kgC/m^2 per year):

$$R(T) = R_L + R_P \tag{A.7.15}$$

Leaf respiration rate (kgC/m^2 per year):

$$R_L(T) = 0.012 \times 31557600 \times k_{28} V_m(T) f_4(\Lambda) \tag{A.7.16}$$

Non-leaf respiration rate (kgC/m^2 per year):

$$R_P(T) = f_5(T) = k_{29} R_L(T) \tag{A.7.17}$$

Productivity:

Net primary productivity (kgC/m^2 per year):

$$\mathrm{NPP}(T, C_a, I_{PAR}, \Lambda) = P(T, C_a, I_{PAR}) - R_L(T) - R_P(T) \tag{A.7.18}$$

A.8. TRIFFID—Cox (2001)

Inputs:

Temperature (T) (°C)
Atmospheric CO_2 (C_a) (Pa)
Photosynthetically active radiation (I_{PAR}) (Ein/(m^2 s))
Water (W) volumetric

Photosynthesis:

Gross photosynthesis rate (kgC/m^2 per year):

$$P(T, C_a, I) = 0.012 \times 31557600 \times f_1(J_C, J_L, J_E) f_7(W) f_8(\Lambda) \tag{A.8.1}$$

Gross photosynthesis (mol CO_2/(m^2 s)):

$$f_1(J_C, J_L, J_E) = \text{smallest root of}: \quad k_1 J^2 - J(J_P + J_E) + J_P J_E = 0 \tag{A.8.2}$$

where:

$$J_P = \text{smallest root of}: \quad k_2 J_P^2 - J_P(J_C + J_L) + J_C J_L = 0 \tag{A.8.3}$$

RuBP limited photosynthesis rate (mol CO_2/(m^2 s)):

$$J_C(T, C_a) = V_m(T) \frac{c_i(T, C_a) - \Gamma(T)}{c_i(T, C_a) + f_2(T)(1 + (k_3)/(f_3(T)))} \tag{A.8.4}$$

Light limited photosynthesis rate (mol CO_2/(m^2 s)):

$$J_L(T, C_a, I_{PAR}) = k_4(1 - k_5) I_{PAR} \frac{c_i(T, C_a) - \Gamma(T)}{c_i(T, C_a) + k_6 \Gamma(T)} \tag{A.8.5}$$

Transport limited photosynthesis rate (mol CO_2/m^2/s):

$$J_E(T) = k_7 V_m(T) \tag{A.8.6}$$

Photorespiration compensation point (Pa):

$$\Gamma(T) = \frac{k_3}{k_8 k_9^{k_{10}(T-k_{11})}} \tag{A.8.7}$$

Michaelis–Menton constant for CO$_2$ (Pa):

$$f_2(T) = k_{12}(k_{13})^{k_{10}(T-k_{11})} \tag{A.8.8}$$

Michaelis–Menton constant for O$_2$ (Pa):

$$f_3(T) = k_{14}(k_{15})^{k_{10}(T-k_{11})} \tag{A.8.9}$$

Internal leaf CO$_2$ partial pressure (Pa):

$$c_i(T, C_a) = k_{16}\left(1 - \frac{H(T)}{k_{17}}\right)(C_a - \Gamma(T)) + \Gamma(T) \tag{A.8.10}$$

Maximum rate of Rubisco carboxylation (mol CO$_2$/(m^2 s)):

$$V_m(T) = \frac{k_{18}k_{19}k_{20}^{k_{10}(T-k_{11})}}{(1+e^{k_{21}(T-k_{22})})(1+e^{k_{21}(k_{23}-T)})} \tag{A.8.11}$$

Leaf humidity deficit (kg/kg):

$$H(T) = H_{\max}(T) - k_{24} \tag{A.8.12}$$

Saturated atmospheric humidity, kg/kg (not given, from Buck (1981)):

$$H_{\max}(T) = \frac{k_{25}}{k_{26}} e^{(k_{27}T/k_{28}+T)} \tag{A.8.13}$$

Respiration:

Respiration rate (kgC/m^2 per year):

$$\begin{aligned} &R(T, W, \Lambda, C_{v(r)}, C_{v(w)}) \\ &\quad = R_L(T, W, \Lambda) + R_M(T, W, \Lambda, C_{v(r)}, C_{v(w)}) \end{aligned} \tag{A.8.14}$$

Leaf respiration rate (kgC/m^2 per year):

$$\begin{aligned} &R_L(T, W, \Lambda) \\ &\quad = 0.012 \times 31557600 k_{29}k_{18}k_{19} f_4(T) f_7(W) f_8(\Lambda) \end{aligned} \tag{A.8.15}$$

Temperature response (dimensionless):

$$f_4(T) = k_{30}^{k_{10}(T-k_{11})} \tag{A.8.16}$$

Non-leaf plant maintenance respiration (kgC/(m^2 s)):

$$\begin{aligned} &R_M(T, W, \Lambda, C_{v(r)}, C_{v(w)}) \\ &\quad = f_5(T, W, \Lambda, C_{v(r)}, C_{v(w)}) \\ &\quad = \left(\frac{R_{\text{leaf}}(T, W, \Lambda)}{f_7(W)}\right) \\ &\qquad \times \left(\frac{k_{19}k_{31}k_{32}\Lambda + k_{19}k_{33}k_{34} f_6(C_{v(w)})\Lambda}{k_{19}k_{32}\Lambda}\right) \end{aligned} \tag{A.8.17}$$

Pipe model to diagnose canopy height (m):

$$f_6(C_{v(w)}) = \frac{C_{v(w)}}{k_{34}k_{35}} \left(\frac{k_{36}}{C_{v(w)}}\right)^{k_{37}} \tag{A.8.18}$$

Productivity:

NPP (kgC/m^2 per year):

$$\begin{aligned} &\text{NPP}(T, C_a, W, H, I, \Lambda) \\ &\quad = (1 - k_{38})[P(T, C_a, H, I) - R_L(T) \\ &\qquad - R_M(T, \Lambda, C_{v(w)})] \end{aligned} \tag{A.8.19}$$

Water stress response modifier (dimensionless):

$$f_7(W) = \begin{cases} 1 & W > k_{39} \\ \dfrac{W - k_{35}}{k_{39} - k_{40}} & k_{40} \le W \le k_{39} \\ 0 & W < k_{39} \end{cases} \tag{A.8.20}$$

Beer's law scaling to canopy level (dimensionless):

$$f_8(\Lambda) = 1 - \frac{e^{-k_{41} f_9(\Lambda)}}{k_{41}} \tag{A.8.21}$$

Adjustments for C$_4$ photosynthesis:

$$J_C(T) = V_m(T) \tag{A.8.22}$$

$$J_L(I) = k_{42}(1 - k_5) I_{\text{PAR}} \tag{A.8.23}$$

$$J_E(T, C_a, H) = k_{43} V_m(T) \frac{c_i(T, C_a, H)}{k_{26}} \tag{A.8.24}$$

$$V_m(T) = \frac{k_{44}k_{19}k_{45}^{k_{10}(T-k_{11})}}{(1+e^{k_{21}(T-k_{22})})(1+e^{k_{21}(k_{23}-T)})} \tag{A.8.25}$$

$$R_L(T) = 0.012 \times 31557600 k_{46}k_{44}k_{19} f_4(T) f_8(\Lambda) \tag{A.8.26}$$

A.9. DEMETER—Foley (1994)

Note: equations marked (*) below are not stated in the literature but have been estimated from published graphs.

Inputs:

Temperature (T) (°C)
Photosynthetically active radiation (I_{PAR}) (Ein/(m^2 s))
Water (W) (volumetric)
Vegetation carbon density (C_{v}) (kgC/m^2)

Photosynthesis:

Gross photosynthesis rate (kgC/m^2 per year):

$$\begin{aligned}P(T, W, \Lambda, I_{\mathrm{PAR}}) &= 0.012 \times 31557600 f_1(T, W, I_{\mathrm{PAR}})[\Lambda \\ &\quad - f_4(f_1, T, I_{\mathrm{PAR}}, \Lambda) + f_5(f_1, T, I_{\mathrm{PAR}})]\end{aligned} \tag{A.9.1}$$

Light saturated photosynthesis rate (mol CO$_2$/(m^2 s)):

$$f_1(T, W, I_{\mathrm{PAR}}) = k_1 f_2(T) f_3(T, W, I_{\mathrm{PAR}}) \tag{A.9.2}$$

Temperature response of photosynthesis (dimensionless) (*) :

$$f_2(T) = \begin{cases} 0 & T < k_2 \\ \dfrac{T}{k_3} & k_2 < T < k_3 \\ 1 & k_3 \le T \le k_4 \\ 1 - \dfrac{T}{k_5} & k_4 < T \le k_5 \\ 0 & k_5 < T \end{cases} \tag{A.9.3}$$

Available water index (dimensionless):

$$f_3(T, W, I_{\mathrm{PAR}}) = \frac{f_7(T, I_{\mathrm{PAR}}, W)}{D(T, I_{\mathrm{PAR}})} \tag{A.9.4}$$

Light use efficiency factor (mol CO$_2$/Ein):

$$\begin{aligned}&f_4(T, W, I_{\mathrm{PAR}}, \Lambda) \\ &\quad = \frac{1}{k_6} \ln\left(f_6(T) + \frac{f_1(T, W, I_{\mathrm{PAR}})}{I_{\mathrm{PAR}} \mathrm{e}^{-k_6 \Lambda}}\right)\end{aligned} \tag{A.9.5}$$

Light use efficiency factor (mol CO$_2$/Ein):

$$\begin{aligned}&f_5(T, W, I_{\mathrm{PAR}}) \\ &\quad = \frac{1}{k_6} \ln\left(f_6(T) + \frac{f_1(T, W, I_{\mathrm{PAR}})}{I_{\mathrm{PAR}}}\right)\end{aligned} \tag{A.9.6}$$

Quantum efficiency (molC/Ein):

$$f_6(T) = k_{11} - k_{12} T \tag{A.9.7}$$

Actual evapotranspiration (mol/(m^2 s)):

$$f_7(T, W, I_{\mathrm{PAR}}) = \min\{D(T, I_{\mathrm{PAR}}), S(W)\} \tag{A.9.8}$$

Evapotranspiration demand (mol/(m^2 s)):

$$\begin{aligned}&D(T, I_{\mathrm{PAR}}) \\ &\quad = \frac{f_8(T)}{f_8(T) + k_7}\left(\frac{2 \times 2.18 \times 10^5 I_{\mathrm{PAR}} - k_8(k_9 - T)}{k_{10}}\right)\end{aligned} \tag{A.9.9}$$

Potential evapotranspiration rate (mol/(m^2 s)):

$$S(W) = k_{13} W \tag{A.9.10}$$

Rate of change of saturated water vapour pressure (Pa/°C (not given, from BIOME3):

$$f_8(T) = \frac{k_{14} \mathrm{e}^{(k_{15} T / k_{16} + T)}}{(k_{17} + T)^2} \tag{A.9.11}$$

Respiration:

Leaf and plant maintenance respiration (kgC/m^2 per year):

$$\begin{aligned}R_M(T) &= f_9(T) \\ &= \sum_i 365.25 k_{18(i)} k_{19(i)} C_v k_{20}^{k_{21}(T - k_{22})} \\ i &= l, s, r\end{aligned} \tag{A.9.12}$$

Productivity:

Net primary productivity (kgC/m^2 per year):

$$\begin{aligned}&\mathrm{NPP}(P, T, W, \Lambda, I) \\ &\quad = (1 - k_{26})(P(T, W, \Lambda, I) - R_M(T))\end{aligned} \tag{A.9.13}$$

Adjustments for C$_4$ photosynthesis:

$$f_7(T) = k_{27} \tag{A.9.14}$$

A.10. BIOME3—Haxeltine and Prentice (1996a,b)

Inputs:

Temperature (T) °C

Atmospheric CO$_2$ (C_a) Pa
Photosynthetically active radiation (I_{PAR}) (Ein/(m^2 s))
Water (W) volumetric scale

Photosynthesis:

Light and RuBP co-limited net daily photosynthesis rate (kgC/m^2 per year):

$$f_1(T, c_i, I_{PAR}, \Lambda, d) = f_2(T, c_i) f_3(I_{PAR}, \Lambda)(1 - f_4(T, c_i, d)) \tag{A.10.1}$$

Auxiliary function for f_1 and V_m:

$$f_2(T, c_i) = k_2 f_7(T) k_3 k_4 k_5 \left(\frac{c_i - \Gamma(T)}{c_i + \Gamma(T)}\right) \tag{A.10.2}$$

Canopy scaling (Ein/m^2 per day):

$$f_3(\Lambda, I_{PAR}) = (1 - e^{-k_6 \Lambda}) \times 86400 I_{PAR} \tag{A.10.3}$$

Auxiliary function for f_1 and V_m:

$$f_4(T, c_i, d) = \left[1 - \left(\frac{f_5(T, c_i) - f_6(d)}{f_5(T, c_i) - k_1 f_6(d)}\right)\right]^{1/2} \tag{A.10.4}$$

Auxiliary function for f_1 and V_m:

$$f_5(T, c_i) = \frac{c_i - \Gamma(T)}{c_i + f_6(T)(1 + k_7/f_7(T))} \tag{A.10.5}$$

Auxiliary function for f_1 and V_m:

$$f_6(d) = \frac{24 k_{14}}{d} \tag{A.10.6}$$

Photosynthesis low temperature inhibition function (dimensionless):

$$f_7(T) = \frac{1}{1 + e^{k_8(k_9 - T)}} \tag{A.10.7}$$

Michaelis–Menton constant for CO$_2$ (Pa):

$$f_8(T) = k_{10}(k_{11})^{k_{12}(T - k_{13})} \tag{A.10.8}$$

Michaelis–Menton constant for O$_2$ (Pa):

$$f_9(T) = k_{14}(k_{15})^{k_{12}(T - k_{13})} \tag{A.10.9}$$

CO$_2$ compensation point (Pa):

$$\Gamma(T) = \frac{k_7}{k_{16} k_{17}^{k_{12}(T - k_{13})}} \tag{A.10.10}$$

Optimised maximum rate of Rubisco carboxylation (gC/m^2 per day):

$$V_m(T, c_i, d, \Lambda, I_{PAR}) = \frac{f_2(T, c_i)}{k_{18} f_5(T, c_i)} \left[(2k_1 - 1) f_6(d) - (2k_1 f_6(d) - f_5(T, c_i)) f_4(T, c_i, d)\right] f_3(I_{PAR}, \Lambda) \tag{A.10.11}$$

Gross daily photosynthesis rate as determined by canopy conductance (gC/m^2 per day):

$$f_{11}(T, C_a, c_i, W, I_{PAR}, \Lambda, d) = 12 \left[\frac{g_c(T, C_a, c_i, W, I_{PAR}, \Lambda, d) - k_{19}}{1.6}\right] \times \left[\frac{C_a}{k_{20}(1 - c_i/C_a)}\right] \tag{A.10.12}$$

Canopy conductance (mol CO$_2$/(m^2 per day)):

$$g_c(T, C_a, c_i, W, I_{PAR}, \Lambda, d) = \begin{cases} g_p(T, C_a, W, c_i, I_{PAR}, \Lambda, d) & S(W) > D(T, C_a, c_i, I_{PAR}, \Lambda, d) \\ -k_{21} \ln(1 - \dfrac{S(W)}{k_{22} f_{10}(T, I_{PAR})}) & S(W) \leq D(T, C_a, c_i, d, \Lambda, I_{PAR}) \end{cases} \tag{A.10.13}$$

Maximum potential canopy conductance (mol/(m^2 per day)):

$$g_p(T, C_a, c_i, I_{PAR}, \Lambda, d) = k_{19} + \frac{1}{12} \left[\frac{1.6 f_1(T, c_i, I_{PAR}, \Lambda, d) - (d/24) R_L(T, c_i, I_{PAR}, \Lambda, d)}{(C_a/k_{20})(1 - k_{23})}\right] \tag{A.10.14}$$

Transpiration demand (mol/(m^2 per day)):

$$D(T, C_a, c_i, I_{PAR}, \Lambda, d) = k_{22} f_{10}(T, I_{PAR})(1 - e^{(-g_p(T, C_a, c_i, I_{PAR}, \Lambda, d)/k_{21})}) \tag{A.10.15}$$

Supply rate of water for evapotranspiration (mol/(m^2 per day)):

$$S(W) = k_{24} W \tag{A.10.16}$$

Equillibrium transpiration rate (mol/(m^2 per day)):

$$f_{10}(T, I_{\mathrm{PAR}}) = \frac{f_{11}(T)}{f_{11}(T) + k_{25}} \left[\frac{2 \times 2.18 \times 10^5 I_{\mathrm{PAR}} - k_{26}(k_{27} - T)}{k_{28}} \right] \times 86400 \tag{A.10.17}$$

Rate of increase of saturated water vapour pressure with temperature (Pa/ °C):

$$f_{11}(T) = \frac{k_{29} \mathrm{e}^{(k_{30} T / k_{31} + T)}}{(k_{32} + T)^2} \tag{A.10.18}$$

Photosynthesis rate accounting for all factors (gC/m^2 per day):

$$P(T, C_{\mathrm{a}}, c_{\mathrm{i}}, W, I_{\mathrm{PAR}}, \Lambda, d) = \text{simultaneous solution, for } P_1 \text{ and } c_{\mathrm{i}}, \text{ of :} \tag{A.10.19}$$

$$P_1 = f_1(T, c_{\mathrm{i}}, I_{\mathrm{PAR}}, \Lambda, d) - \frac{d}{24} R_{\mathrm{L}}(T, C_{\mathrm{a}}, c_{\mathrm{i}}, d, \Lambda, I_{\mathrm{PAR}}) \tag{A.10.20}$$

$$P_1 = f_{11}(T, C_{\mathrm{a}}, c_{\mathrm{i}}, W, I_{\mathrm{PAR}}, \Lambda, d) \tag{A.10.21}$$

Respiration:

Leaf respiration rate (gC/m^2 per day):

$$R_{\mathrm{L}}(T, c_{\mathrm{i}}, I_{\mathrm{PAR}}, \Lambda, d) = k_{18} V_{\mathrm{m}}(T, c_{\mathrm{i}}, I_{\mathrm{PAR}}, \Lambda, d) \tag{A.10.22}$$

Stem and woody root respiration (gC/m^2 per day):

$$R_S(\Lambda, T) = k_{33} f_{12}(\Lambda) \mathrm{e}^{k_{34} f_{13}(T)} \tag{A.10.23}$$

Root respiration (gC/m^2 per day):

$$R_R(\Lambda) = k_{35} \Lambda \tag{A.10.24}$$

Pipe model diagnosis of stem carbon from leaf area index (gC/m^2):

$$f_{12}(\Lambda) = k_{36} \Lambda \tag{A.10.25}$$

Temperature response of stem respiration (°C^{-1}):

$$f_{13}(T) = \frac{1}{k_{37} - k_{38}} - \frac{1}{T - k_{38}} \tag{A.10.26}$$

Total respiration rate (kgC/m^2 per year):

$$R(T, c_{\mathrm{i}}, I_{\mathrm{PAR}}, \Lambda, d) = \frac{365.25}{1000} (R_{\mathrm{L}}(T, c_{\mathrm{i}}, I_{\mathrm{PAR}}, \Lambda, d) + R_T(T, \Lambda) + R_R(\Lambda)) \tag{A.10.27}$$

Productivity:

NPP (kgC/m^2 per year):

$$\mathrm{NPP}(T, C_{\mathrm{a}}, c_{\mathrm{i}}, W, I_{\mathrm{PAR}}, \Lambda, d) = \frac{4}{5} \left[\frac{365.25}{1000} P(T, C_{\mathrm{a}}, c_{\mathrm{i}}, W, I_{\mathrm{PAR}}, \Lambda, d) - R(T, C_{\mathrm{a}}, c_{\mathrm{i}}, d, \Lambda, I_{\mathrm{PAR}}) \right] \tag{A.10.28}$$

Adjustments for C$_4$ photosynthesis:

$$f_2(T, C_{\mathrm{a}}, c_{\mathrm{i}}) = \frac{c_{\mathrm{i}}}{C_a k_{39}} f_5(T) k_3 k_4 k_{40} \tag{A.10.29}$$

$$f_4(d) = \left[1 - \frac{1 - f_6(d)}{1 - k_1 f_6(d)} \right]^{1/2} \tag{A.10.30}$$

$$f_5(T) = 1 \tag{A.10.31}$$

$$f_6(d) = \frac{24 k_{41}}{d} \tag{A.10.32}$$

$$f_7(T) = \frac{1}{1 + \mathrm{e}^{k_{42}(k) 43 - T)}} \frac{1}{1 + \mathrm{e}^{k_{44}(T - k_{45})}} \tag{A.10.33}$$

$$V_{\mathrm{m}}(T, C_{\mathrm{a}}, c_{\mathrm{i}}, \Lambda, d) = \frac{f_2(T, C_{\mathrm{a}}, c_{\mathrm{i}})}{k_{41}} \left[(2k_1 - 1) f_6(d) - (2k_1 f_6(d) - 1) f_4(d) \right] f_3(I_{\mathrm{PAR}}, \Lambda) \tag{A.10.34}$$

$$g_{\mathrm{p}}(T, C_{\mathrm{a}}, c_{\mathrm{i}}, I_{\mathrm{PAR}}, \Lambda, I_{\mathrm{PAR}}) = k_{19} + \frac{1}{12} \times \left[\frac{1.6 f_1(T, c_{\mathrm{i}}, I_{\mathrm{PAR}}, \Lambda, d) - d/24 R_{\mathrm{leaf}}(T, c_{\mathrm{i}}, d, \Lambda, I_{\mathrm{PAR}})}{C_{\mathrm{a}}/k_{20}(1 - k_{39})} \right] \tag{A.10.35}$$

$$R_{\mathrm{L}}(T, c_{\mathrm{i}}, I_{\mathrm{PAR}}, \Lambda, d) = k_{41} V_{\mathrm{m}}(T, c_{\mathrm{i}}, I_{\mathrm{PAR}}, \Lambda, d) \tag{A.10.36}$$

Appendix B. Tables of parameter values and units conversions used

See in appendix Tables 1–17

Table B.1
Units conversions used in this paper

Atmosphere	Pa CO_2 → CO_2 ppmv	×9.901
Atmosphere	mol CO_2 → kgC	×0.012
Atmosphere	GtC → kgC	$\times 10^{12}$
Atmosphere	ppmv CO_2 → GtC	×9.901 × 1.773 × 0.12011
Solar energy	Ein/(m^2 s)→ W/m^2	$\times 2.18 \times 10^5$ (Larcher, 1983)
Solar energy	μEin → Ein	$\times 10^{-6}$
Temperature	K → °C	−273
Evapotranspiration	mm/s → kg/(m^2 day)	×1 (Azam-Ali and Squire, 2001)
Evapotranspiration	mm per day → mol H_2O/m^2 per day	×55.6
Canopy conductance	mm/s → mol/(m^2 s)	×0.04 (Collatz et al., 1991)
Vegetation carbon	kg dry matter → kgC	×0.45
Vegetation carbon	tC/ha → kgC/m^2	×0.1
Time	years → seconds	×31557600
Time	years → days	×365.25
Time	days → seconds	×86400

Table B.2
Constants used in this paper

Atmospheric pressure	101000 Pa
Proportion of solar radiation photosynthetically active	0.5
Latent heat of vaporisation of water	2.26×10^6 J/kg
Latent heat of vaporisation of water	40660 J/mol
Vegetated area of the Earth	1.33×10^{14} m^2

Table B.3
Parameter values used in the Miami model, Leith (1975a)

Parameter	Description	Value
k_1	Temperature response parameter	3000
k_2	Temperature response parameter	1.315
k_3	Temperature response parameter	0.119
k_4	Precipitation response parameter	3000
k_5	Precipitation response parameter	0.000664

Table B.4
Parameter values used in King et al. (1997)

Parameter	Description	Value
k_1	Temperature response parameter	3000
k_2	Temperature response parameter	1.315
k_3	Temperature response parameter	0.119
k_4	Precipitation response parameter	3000
k_5	Precipitation response parameter	0.000664
k_6	Efficiency scaling parameter	0.6
k_7	CO_2 reference concentration	320 ppmv
k_8	Ratio of intracellular to atmospheric CO_2	0.7
k_9	Biotic growth factor parameter	3
k_{10}	Biotic growth factor parameter	2
k_{11}	CO_2 compensation point parameter	42.7
k_{12}	CO_2 compensation point parameter	1.68
k_{13}	CO_2 compensation point parameter	0.012
k_{14}	CO_2 compensation point reference temperature	25 °C

Table B.5
Parameter values used in Polglase and Wang (1992)

Parameter	Description	Value
k_1	Baseline NPP	See below (tC/ha per year)
k_2	CO_2 reference concentration*	320 ppmv
k_3	Biotic growth factor parameter	3
k_4	Ratio of intracellular to atmospheric CO_2	0.7
k_5	Biotic growth factor parameter	2
k_6	CO_2 compensation point parameter	42.6
k_7	CO_2 compensation point parameter	1.68
k_8	CO_2 compensation point parameter	0.012
k_9	CO_2 compensation point reference temperature	25 °C
k_{10}	Biotic growth factor	Varied in range 0.27–0.54

* Not given. Taken from King et al. (1997).

Table B.6
Plant type-specific parameters for Polglase and Wang (1992)

	Humid tropical forest	Seasonal tropical forest	Savanna	Temperate forest	Boreal forest	Grassland	Agricultural land	Desert	Tundra	Generic*
k_1	10.1	7.2	7.87	6.13	3.58	3.52	4.25	4.7	1.0	4.89

* Not published. Calculations here based on the values given for the forest vegetation types.

Table B.7
Parameter values used in King et al. (1995)

Parameter	Description	Value
k_1	CO_2 reference concentration	280 (ppmv)*
k_2	Biotic growth factor parameter	3
k_3	Ratio of intracellular to atmospheric CO_2	0.7
k_4	Biotic growth factor parameter	2
k_5	CO_2 compensation point parameter	42.7
k_6	CO_2 compensation point parameter	1.68
k_7	CO_2 compensation point parameter	0.012
k_8	CO_2 compensation point reference temperature	25 °C
k_9	Intrinsic growth rate	See below (per year)
k_{10}	Carrying capacity	See below (kgC/m^2)
k_9	Alternative constant for response function	See below

* This value is not clearly stated in the text, only implied.

Table B.8
Plant type-specific parameters for King et al. (1995)

	Moist. tropical forest	Seasonal tropical forest	Temperate Eg. forest	Temperate deciduous forest	Boreal forest	Tropical wood/ shrub	Temperate wood/ shrub	Tropical grassland	Temperate grassland	Tundra	Desert	Cult. Land	Pasture	Generic*
k_9	0.007	0.009	0.009	0.011	0.016	0.109	0.054	0.814	1.047	2.442	2.442	2.931	2.093	0.01
k_{10}	20.0	16.0	16.0	13.5	9.0	2.7	2.7	1.8	0.7	0.3	0.3	0.5	0.7	13.33
k_{11}	0.21	0.19	0.11	0.11	0.08	0.22	0.15	0.07	0.05	0.07	0.16	0.13	0.13	0.11

Table B.9
Parameter values used in Lenton (2000)

Parameter	Description	Value
k_1	Steady-state vegetation carbon density	550 GtC
k_2	Photosynthesis rate constant	0.184 per year
k_3	Photosynthesis normalising constant	1.578
k_4	Vegetated area of the Earth	1.33×10^{14} m^2
k_5	Maximum negative deviation from photosynthesis reference temperature	15 K
k_6	Photosynthesis reference temperature	288.15 K
k_7	Maximum positive deviation from photosynthesis reference temperature	25 K
k_8	Temperature response parameter	5625
k_9	CO_2 compensation point	29 ppmv
k_{10}	CO_2 half saturation point	145 ppmv
k_{11}	Respiration rate constant	0.092 per year
k_{12}	Respiration normalising constant	8.7039×10^9
k_{13}	Respiration activation energy	54,800 J/mol
k_{14}	Ideal gas constant	8.314 J/(mol K)

Table B.10
Parameter values used in Svirezhev and von Bloh (1997, 1998)

Parameter	Description	Value
k_1	Maximum potential NPP	200 (GtC per year, 1998)
k_2	Vegetated area of the Earth*	1.33×10^{14} (m^2)
k_3	Temperature response parameter	4
k_4	Minimum growth temperature	5 °C
k_5	Maximum growth temperature	40 °C
k_6	CO_2 fertilisation function parameter	4
k_7	Water response function parameter	4
k_8	Minimum soil water for growth	1 g/cm^2
k_9	Maximum soil water for growth	18 g/cm^2
k_{10}	Constant for conversion of biomass to area	600 GtC
k_{11}	Vegetation turnover rate constant	0.08 per year

* Not used by Svirezhev and von Bloh but added here to standardise output units. Taken from Lenton (2000).

Table B.11
Parameter values used in simple TRIFFID, Huntingford et al. (2000)

Parameter	Description	Value
k_1	Photosynthesis co-limitation coefficient	0.93
k_2	Photosynthesis co-limitation coefficient	0.83
k_3	Atmospheric oxygen concentration	21200 Pa
k_4	Quantum efficiency	0.08 mol electrons/Ein
k_5	Light scattering rate	0.15
k_6	Parameter for J_L	2
k_7	Ratio of light limited photosynthesis to Rubisco carboxylation	0.5
k_8	Photo-respiration compensation point parameter	5200
k_9	Photo-respiration compensation point parameter	0.57
k_{10}	Q_{10} function parameter	0.1
k_{11}	Q_{10} function reference temperature	25 °C
k_{12}	Michaelis–Menton constant for CO_2 parameter	30 Pa
k_{13}	Michaelis–Menton constant for CO_2 parameter	2.1
k_{14}	Michaelis–Menton constant for O_2 parameter	30000 Pa
k_{15}	Michaelis–Menton constant for O_2 parameter	1.2
k_{16}	Maximum ratio of internal to external CO_2	0.875
k_{17}	Critical humidity deficit	1.0 kg/kg
k_{18}	Maximum Rubisco carboxylation rate	0.00004 mol $CO_2/(m^2\ s)$
k_{19}	Rubisco carboxylation rate parameter	2
k_{20}	Rubisco carboxylation rate parameter	0.3
k_{21}	Rubisco carboxylation rate parameter	36 °C
k_{22}	Leaf level humidity	0.005 kg/kg
k_{23}	Atmospheric humidity parameter	$1.004 \times 6.112 \times 0.6220$ (Pa)
k_{24}	Atmospheric pressure	100100 Pa
k_{25}	Atmospheric humidity parameter	17.502
k_{26}	Atmospheric humidity parameter	240.97
k_{27}	Light extinction coefficient	0.5
k_{28}	Ratio of respiration to Rubisco carboxylation rates	0.015
k_{29}	Whole plant–leaf respiration ratio	3.85

Table B.12
Parameter values used in TRIFFID, Cox (2001)

Parameter	Description	Value
k_1	Photosynthesis co-limitation coefficient	0.93
k_2	Photosynthesis co-limitation coefficient	0.83
k_3	Atmospheric oxygen concentration	21200 Pa
k_4	Quantum efficiency	0.08 mol electrons/Ein
k_5	Light scattering rate	0.15
k_6	Parameter for J_L	2
k_7	Ratio of light limited photosynthesis to Rubisco carboxylation	0.5
k_8	Photo-respiration compensation point parameter	5200
k_9	Photo-respiration compensation point parameter	0.57
k_{10}	Q_{10} function parameter	0.1
k_{11}	Q_{10} function reference temperature	25 °C
k_{12}	Michaelis–Menton constant for CO_2 parameter	30 Pa
k_{13}	Michaelis–Menton constant for CO_2 parameter	2.1
k_{14}	Michaelis–Menton constant for O_2 parameter	30000 Pa
k_{15}	Michaelis–Menton constant for O_2 parameter	1.2
k_{16}	Maximum ratio of internal to external CO_2	See below
k_{17}	Critical humidity deficit	See below (kg/kg)
k_{18}	Ratio of leaf N to maximum Rubisco carboxylation rate	0.0008 mol $CO_2/(m^2$ s kgN)
k_{19}	Leaf nitrogen concentration	See below (kgN/kgC)
k_{20}	Rubisco carboxylation rate parameter	2
k_{21}	Rubisco carboxylation rate parameter	0.3
k_{22}	Carboxylation rate temperature parameter	See below (°C)
k_{23}	Carboxylation rate temperature parameter	See below (°C)
k_{24}	leaf level humidity (from simple TRIFFID)	0.005 kg/kg
k_{25}	Atmospheric humidity parameter	$1.004 \times 6.112 \times 0.6220$ Pa
k_{26}	Atmospheric pressure	100100 Pa
k_{27}	Atmospheric humidity parameter	17.502
k_{28}	Atmospheric humidity parameter	240.97
k_{29}	Ratio of respiration to Rubisco carboxylation rates	0.015
k_{30}	Respiration temperature response parameter	2
k_{31}	Ratio of root nitrogen to leaf nitrogen	1
k_{32}	Specific leaf density	See below (kgC/m^2)
k_{33}	Ratio of stem nitrogen to leaf nitrogen	See below
k_{34}	Ratio of stem wood to canopy height×leaf area	0.01 (kgC/m^3)
k_{35}	Ratio of wood carbon to respiring stem carbon	See below
k_{36}	Ratio of wood carbon to leaf carbon	See below (kgC/m^2)
k_{37}	Unknown	0.6
k_{38}	Growth respiration fraction	0.25
k_{39}	Wilting soil moisture concentration	0.387*
k_{40}	Critical soil moisture concentration	0.205*
k_{41}	Light extinction coefficient	0.5
k_{42}	C_4 quantum efficiency	0.04 (mol electrons/Ein)
k_{43}	PEP-carboxylase limitation parameter	2×10^4
k_{44}	C_4 ratio of leaf N to Rubisco carboxylation rate	0.0004
k_{45}	C_4 ratio Rubisco carboxylation parameter	2
k_{46}	C_4 ratio of respiration to Rubisco carboxylation rates	0.025

* From Cox et al. (1998)

Table B.13
Plant type-specific parameters for TRIFFID

Vegetation type	k_{16}	k_{17}	k_{19}	k_{22}	k_{23}	k_{32}	k_{33}	k_{35}	k_{36}
Broadleaf tree	0.875	0.09	0.04	36	0	0.0375	0.1	10	0.65
Needleleaf tree	0.875	0.06	0.03	31	−5	0.1	0.1	10	0.65
C_3 grass	0.9	0.1	0.06	36	0	0.025	1	1	0.005
C_4 grass	0.8	0.075	0.03	45	13	0.05	1	1	0.005
Shrub	0.9	0.1	0.03	36	0	0.05	0.1	10	0.1
Generic*	0.875	0.08	0.04	36	0	0.05	0.1	10	0.65

* Not published. Calculations here based on the values given for the forest vegetation types.

Table B.14
Parameter values used in DEMETER, Foley (1994)

Parameter	Description	Value
k_1	Maximum rate of photosynthesis	See below (mol $CO_2/m^2/s$)
k_2	Minimum temperature for photosynthesis	0 °
k_3	Lower limit for optimum photosynthesis	10 °
k_4	Upper limit for optimum photosynthesis	45 °
k_5	Maximum temperature for photosynthesis	50 °
k_6	Light extinction coefficient	0.5
k_7	Psychrometer constant	65 (Pa/ °C)
k_8	Evapotranspiration demand parameter	0.6
k_9	Evapotranspiration demand parameter	107
k_{10}	Latent heat of vaporisation of water	40660 J/mol
k_{11}	Quantum efficiency intercept	0.075 mol electrons/Ein
k_{12}	Quantum efficiency gradient	0.001
k_{13}	Maximum rate of evapotranspiration	0.000008903 (mol/m^2/s)*
k_{14}	Rate of change of water vapour pressure parameter	2.5×10^6
k_{15}	Rate of change of water vapour pressure parameter	17.269
k_{16}	Rate of change of water vapour pressure parameter	237.3
k_{17}	Rate of change of water vapour pressure parameter	237.3
$k_{18(i)}$	Carbon allocation fraction	See below
$k_{19(l)}$	Leaf respiration rate	See below (per day)
$k_{19(s)}$	Stem respiration rate	0.018 (per day)
$k_{19(r)}$	Root respiration rate	0.073 (per day)
k_{20}	Respiration temperature parameter	2
k_{21}	Q_{10} function parameter	0.1
k_{22}	Q_{10} function reference temperature	20 °C
k_{23}	Leaf area index under growing conditions	See below (m^2/m^2)
k_{24}	Leaf area index under dry conditions	See below (m^2/m^2)
k_{25}	Leaf area index under winter conditions	See below (m^2/m^2)
k_{26}	Growth respiration fraction	0.33
k_{27}	C_4 quantum efficiency	0.055 mol electrons/Ein

* Not given, taken from BIOME3.

Table B.15
Plant type-specific parameters for DEMETER

Vegetation type	C_v	k_1	$k_{18(l)}$	$k_{18(s)}$	$k_{18(r)}$	$k_{19(l)}$	k_{23}	k_{25}	k_{27}
Tropical rain forest	20	4×10^{-6}	0.03	0.85	0.12	0.0014	7	7	7
Seasonal tropical forest	14	4×10^{-6}	0.03	0.85	0.12	0.00185	6	4	4
Temperate deciduous forest	10	3.5×10^{-6}	0.03	0.08	0.17	0.00370	5	5	2
Cool conifer forest	17	3.0×10^{-6}	0.05	0.75	0.2	0.00120	5	5	4.5
Boreal forest	9	2.5×10^{-6}	0.04	0.8	0.16	0.00350	5	5	5
Warm grass and shrub (C_4)	1.5	6×10^{-6}	0.2	0.2	0.6	0.00055	4	2	2
Cool grass and shrub	1	6×10^{-6}	0.2	0.2	0.6	0.0037	3.5	2	2
Tundra	1	5×10^{-6}	0.35	0.2	0.45	0.005	3	3	3
Desert	0.5	12×10^{-6}	0.05	0.25	0.75	0.0006	2	1.5	1.5
Generic*	15	5.5×10^{-6}	0.03	0.8	0.15	0.002	6	4	4

* Not published. Calculations here based on the values given for the forest vegetation types.

Table B.16
Parameter values used in BIOME3, Haxeltine and Prentice (1996a,b)

Parameter	Description	Value
k_1	Photosynthesis co-limitation parameter	0.7
k_2	Leaf photosynthesis efficiency parameter	See below
k_3	Molar mass of carbon	12 g/mol
k_4	Quantum efficiency adjustment	0.5
k_5	Intrinsic quantum efficiency	0.08 mol electrons/Ein
k_6	Extinction coefficient	0.5
k_7	Atmospheric oxygen concentration	20900 Pa
k_8	Low temperature inhibition parameter	0.2
k_9	Low temperature inhibition parameter	10 °C
k_{10}	Michaelis–Menton constant for CO_2 parameter	30 Pa
k_{11}	Michaelis–Menton constant for CO_2 parameter	2
k_{12}	Q_{10} function parameter	0.1
k_{13}	Q_{10} function reference temperature	25 °C
k_{14}	Michaelis–Menton constant for O_2 parameter	30000 Pa
k_{15}	Michaelis–Menton constant for O_2 parameter	1.2
k_{16}	CO_2 compensation point parameter	5200
k_{17}	CO_2 compensation point parameter	0.57
k_{18}	Ratio of respiration to Rubisco carboxylation	0.015
k_{19}	Minimum canopy conductance	See below (mol CO_2/m^2 per day)
k_{20}	Atmospheric pressure	100100 Pa
k_{21}	Maximum canopy conductance	17280 mol CO_2/m^2 per day
k_{22}	Unknown	1.4
k_{23}	Optimum ratio of internal to external leaf CO_2	0.7
k_{24}	Maximum daily transpiration rate	278 mol per day
k_{25}	Psychrometer constant	65 Pa/K
k_{26}	Evapotranspiration demand parameter	0.6
k_{27}	Evapotranspiration demand parameter	107
k_{28}	Latent heat of vaporisation of water	40660 J/mol
k_{29}	Rate of change of water vapour pressure parameter	2.5×10^6
k_{30}	Rate of change of water vapour pressure parameter	17.269
k_{31}	Rate of change of water vapour pressure parameter	237.3
k_{32}	Rate of change of water vapour pressure parameter	237.3
k_{33}	Reference sapwood respiration rate	0.0557 gC/kgC per day
k_{34}	Sapwood respiration response function	308.56 K
k_{35}	Leaf turnover rate	0.082 g/m^2 per day
k_{36}	Ratio of sapwood to leaf area index	1000 gC/m^2
k_{37}	Reference sapwood respiration temperature	10 °C
k_{38}	Minimum sapwood respiration temperature	−46.02 °C
k_{39}	Optimal ratio of internal to external CO_2 partial pressure, C_4	0.4
k_{40}	Intrinsic quantum efficiency, C_4	0.053 mol electrons/Ein
k_{41}	C_4 ratio of respiration to RuBP carboxylation rates	0.035
k_{42}	Photosynthesis low temperature inhibition parameter	0.3
k_{43}	Photosynthesis low temperature inhibition parameter	13 °C
k_{44}	Photosynthesis low temperature inhibition parameter	0.3
k_{45}	Photosynthesis low temperature inhibition parameter	36 °C

Table B.17
PFT-specific parameters for BIOME3

Vegetation type	k_2	k_{23}
Tropical broadleaved evergreen	1	1728
Tropical broadleaved seasonal	1	1728
Temperate broadleaved evergreen	1	1728
Temperate/boreal conifer	0.8	1036.8
Temperate/boreal summergreen	1	1728
Cool grass	1	1728
Warm grass	1	2764
Generic*	1	1728

* Not published. Calculations here based on the values given for the forest vegetation types.

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