



Forest productivity under climate change: a checklist for evaluating model studies

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Climate change is highly likely to impact on forest productivity over the next century. The direction and magnitude of change are uncertain because many factors are changing simultaneously, such as atmospheric composition, temperature, rainfall, and land use. Simulation models have been widely used to estimate how these interacting factors might combine to alter forest productivity. Such studies have used many different types of models with different underlying assumptions. To evaluate predictions made by such studies, it is essential to understand the type of model and the assumptions used. In this article, we provide a checklist for use when evaluating modeled estimates of climate change impacts on forest productivity. The checklist highlights the assumptions that we believe are critical in determining model outcomes. Models are classified into different general types, and assumptions relating to effects of atmospheric CO₂ concentration, temperature, water availability, nutrient cycling, and disturbance are discussed. Our main aim is to provide a guide to enable correct interpretation of model projections. The article also challenges modelers to improve the quality of information provided about their model assumptions. © 2011 John Wiley & Sons, Ltd. *WIREs Clim Change* 2011 DOI: 10.1002/wcc.108

INTRODUCTION

Climate change presents significant threats and opportunities for forests around the globe.^{1,2} Rising atmospheric CO₂ concentration, rising temperatures, changes in amount and timing of rainfall, changes in atmospheric humidity, and altered storm and drought frequency directly impact forest productivity.³ Climate change will also impact forest productivity through changes in fire frequency, severity of pest attacks, and the distribution of tree species. At the same time, these changes interact strongly with other aspects of global change that affect productivity, such as nitrogen deposition and land-use change.

It is not straightforward to estimate the combined effects of these changes on forest productivity. Directly measuring forest response to change in a

single environmental factor is challenging owing to the large spatial and temporal scales involved, and the many plant and ecosystem processes affected. Understanding and predicting the impacts of many interacting factors on forest productivity is more complex still, and is only really possible through the use of simulation models that quantify and integrate the major response processes.

Models have an important role to play in predicting likely impacts of climate change on forest productivity. A plethora of models have been used for this purpose, and there is a significant body of literature describing model studies of climatic impacts on forests. However, navigating this literature is not straightforward, as the model applications vary considerably in nature, with different model structures, process representations, input scenarios, species, locations, and scales of application. Some of these differences among model studies will be relatively unimportant, but others have a major impact on model predictions and determine the degree of confidence that we can assign to those predictions. If a reader wishes to correctly interpret the outcomes of a given study, it is essential that they understand these key differences among model studies and identify

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how they are treated in that specific study. It is also important to be aware that models are not static and thus different studies may include different features because they use a different version of the same model.

The aim of this review is to provide the background necessary to evaluate modeling studies of climate impacts on forests. To achieve this aim, we provide a checklist of what we see as the most important factors determining study outcomes. We explain how these factors determine model predictions, and we review the experimental evidence for and against different assumptions. We apply our checklist to some individual model studies to illustrate how different assumptions are implemented and how they affect model outcomes. We specifically focus on model studies of the impact of climate change on forest growth, net primary productivity (NPP), and carbon sequestration over the next 100 years.

The checklist is also intended to challenge modelers to improve the quality of information that they

provide about their study. It is clearly infeasible to provide all details of a model study in any given article. However, enough information should be provided for the reader to move beyond the 'black box': to understand the major assumptions underlying a study and hence correctly interpret the outcomes. We argue that at least the points raised below should be clearly answered in any modeling study.

QUESTION 1: WHAT TYPE OF MODEL IS USED?

Many different modeling approaches have been used to predict climate impacts on forest productivity. These approaches have generally been used for different purposes and their outputs should be interpreted accordingly. Here, we have classified these models into six broad categories. Some examples of models in each category are listed in Table 1. The key distinctions among the categories are: (1) the spatial scale at

TABLE 1 | The Different Classes of Model Used to Predict Climatic Impacts on Forest Productivity

Type	Spatial Scale	Level of Empiricism	Species Change Predicted	Example Models	Reference	Example Applications
(1) Process-based stand models	Forest stand	Process-based	No	GDAY	10	16
				CENW	11	17
				CENTURY	12	18
				PnET	13	19
				CABALA	9	20
				GOTILWA+	14	21
ecosys	15	22				
(2) Terrestrial biogeochemical models	Regions to global	Process-based	No	BIOME-BGC	23	27
				TEM	24	28
				HRBM	25	29
				TRIPLEX	26	30
(3) Hybrid models	Forest stand	Hybrid	No	MELA	31	34
				FVS-BGC	32	
				FULLCAM	33	
(4) Carbon accounting models	Regions	Hybrid	No	CBM-CFS	35	38,39
				GORCAM	36	40,41
				EFISCEN	37	
(5) Gap models	Patches to regions	Process-based	Yes	SIMA	42	46
				FORSKA	43	47
				FORCLIM	44	48
				PICUS	45	49
(6) Dynamic Global vegetation models (DGVMs)	Regions to global	Process-based	Yes	LPJ	50	55
				CLM-DGVM	51	56
				Orchidee	52	57
				MC1-DGVM	53	
				SDGVM	54	

Some examples of each class of model are given, but note that this is a far-from-comprehensive list, nor are these classifications definitive, as some models have versions that could fit into other classifications (for example, the terrestrial biogeochemistry model TEM has recently been developed into a dynamic vegetation model;⁵⁸ LPJ-GUESS is a 'gap model' version of the LPJ DGVM suited to landscape or regional applications⁵⁹). The references in the left-hand column refer to articles that contain original model descriptions; the references on the right refer to articles that contain model applications to climate change issues.

which the model is applied (stand vs region or globe); (2) the level of process representation; and (3) whether or not changes in species distribution are predicted.

A large group of models can be classified as ‘stand-scale process-based models’. These models represent a homogeneous stand of forest, such as an even-aged plantation, and attempt to simulate the key physiological processes that determine growth rate, and their dependence on environmental conditions (see reviews of this class of model by Ryan et al.,⁴ Battaglia and Sands,⁵ and Mäkelä et al.⁶). Typically the models simulate the uptake of carbon through photosynthesis, losses of carbon to respiration and mortality, and allocation of carbon to growth of different tissues (foliage, stemwood, and roots). These processes are represented as functions of environmental conditions such as incoming radiation, temperature, atmospheric CO₂ concentration (C_a), and humidity. Most of the stand-scale models also calculate soil moisture storage, using a water budget approach, and the effect of low soil moisture on growth. Additionally, many of the stand scale models simulate the nutrient cycle, and reduce growth when soil nutrient availability is low.

The level of detail used to describe these processes varies considerably among models, with some models simulating leaf-scale biochemical processes on an hourly time step⁷ and other models simulating whole-canopy carbon gain on a monthly time-step.⁸ Models with high levels of detail do not necessarily perform better than models with lower resolution, because the more detailed models require more parameterization, and parameter values may be difficult to determine, introducing error. Different levels of detail are appropriate for different purposes; for example, decision support tools for forestry⁹ require more detail in order to be able to simulate specific plantations, compared to models developed as research tools¹⁰ to investigate general features of forest climate sensitivity.

The second class of model is the ‘regional biogeochemistry models’. These models are similar in nature to the stand-scale process-based models but employ simplifications to enable their application at larger scales, from region to globe. The processes represented are similar, but the process representations are simplified to make them computationally tractable. It is also necessary to simplify the parameterization of the vegetation. In a stand-scale model, it is possible to directly measure parameters of the vegetation being modeled; these parameters may be highly specific to the species present in the stand. At regional scale, individual species can rarely be modeled. Instead, vegetation is classified into plant functional types (PFTs; for example, broadleaf deciduous forest or

C₃ grass) and average parameters used to represent each PFT. Morales et al.⁶⁰ compared the performance of two such models against two dynamic global vegetation models (DGVMs) using eddy covariance data as a benchmark.

In contrast to these process-based models, foresters have used empirical growth and yield models for many decades to predict forest growth^{61–63} going back more than 200 years to the use of yield tables to predict wood volume growth.⁶⁴ The empirical models are commonly based on forest inventory data but may also use tree-ring records.^{65,66} The empirical models typically assume the ‘site quality’ is an unchanging state, so they are unable to predict how changing climate or other environmental change might affect future growth. There have been several attempts to develop ‘hybrid’ models that build on the empirical growth and yield models by adding in climate and C_a modifiers that have been developed from process-based models.

This approach can be applied for individual stands (which we call ‘hybrid models’) or at regional scale (which we call ‘carbon accounting models’). Typically, these models have been developed in close collaboration with the forestry industry and have direct practical applications. For example, the EFI (European Forest Institute) scenario analysis model (EFISCEN^{37,40}) interfaces regional forest inventory data with multiple process-based models that predict effects of climate change on forest productivity. The emphasis of this approach is on wood volume growth, growing stock, and interactions with forest management.⁴⁰ This approach is also commonly used in carbon accounting studies where net carbon balance of regional forestry industry can be estimated.^{33,67}

In the above four types of models, it is assumed that the type of vegetation present at a given location is static and that the vegetation parameters do not change. However, climate change may also alter species composition at a given site. A further two classes of models attempt to represent changes in species composition following changes in climate. ‘Gap models’ represent these changes for individual stands. These models were originally developed to study forest succession following disturbance⁶⁸ and generally simulate establishment, growth, and mortality of competing species. With the inclusion of climatic impacts on these processes, the models can be used to simulate dynamics of species composition as well as productivity. An alternative approach with a similar outcome was taken by Chiang et al.,⁶⁹ who used bioclimatic analysis of current species distributions⁷⁰ to estimate future species distribution. Forest productivity was then modeled given this species distribution

using the process-based stand-scale model PnET-II. Taylor et al.⁷¹ provide a recent review of this class of models.

'DGVMs' are similar to gap models in some ways. They are applicable at larger scales and simulate changes in PFT, rather than species, with climate. The dynamic vegetation models simulate plant productivity in a similar fashion to the regional biochemistry models, but they also simulate competition between different vegetation types and hence can predict the distribution of vegetation across the globe. These models can be coupled with global climate models (GCMs); such coupled models capture feedbacks to climate due to changes in global vegetation. Sitch et al.⁷² compare the performance of five such coupled DGVMs.

A further class of model not discussed here contains the equilibrium vegetation models. These simulate the distribution and productivity of vegetation, similar to the DGVMs, but only at equilibrium: a long-term mean climate is used as the basis for predictions. This class of models includes several well-known models including BIOME4⁷³ and MAPSS.⁷⁴ We do not specifically consider such models here because we focus on predictions of forest productivity over the next 100 years: given the long lifespans and slow dynamics of forest vegetation, it is unlikely that equilibrium responses to climate change will be reached in the next 100 years, and these models are therefore not appropriate for this purpose. However, we do note that the assumptions of such models are consistent with DGVMs in many ways (for example, the logic for forest productivity and water use is shared between BIOME4 and LPJ⁵⁰), so our checklist could nonetheless be applied to these models.

We consider, therefore, six major types of models that can be used to predict climate impacts on forest productivity over the next century. These models differ in a great many ways, but some of these differences are relatively unimportant, whereas others have a major impact on model predictions. In this article we provide a 'checklist' of what we see as the key model assumptions that determine model outcomes. The checklist is largely based on personal experience of model sensitivities, informed by published sensitivity analyses^{20,75–77} and model comparisons.^{4,72,78,79} However, the checklist is not exhaustive, and we suggest that an aim of future model comparison exercises should be to update this checklist with additional questions, if other model assumptions are shown to have a major impact on predicted productivity responses to climate change.

We illustrate how the checklist can be used to interpret model predictions by using it to compare

some example applications of each of the major model types, listed in Table 2. (Note, model type 4 was omitted from this table because the features of type 4 models depend on the process-based models from which their response surfaces are derived.) The examples considered in Table 2 were chosen at random from the literature and are not intended to represent particularly 'good' or 'bad' studies; all of the model studies are valuable *as long as the assumptions underpinning them are clearly understood*. The checklist should help readers to identify these key assumptions in any given modeling study.

The example studies examined in Table 2 predict effects on forest productivity at different locations over the next century that range from a decrease of 40% to an increase of 70%. Two models applied at the scale of the globe, LPJ⁵⁵ and TEM,²⁸ predicted overall increases in NPP of the order of 15–30%. There was regional variation; the sign of the response differed among tropical and sub-tropical ecosystems due to uncertainty in simulated precipitation patterns. Increases in NPP were also predicted in Alaska²⁷ and Finland.³⁴ In other studies, NPP was predicted to be reduced because of lower water availability, for example, in Canada,⁸¹ France,⁸² and Australia.⁸⁰ Using the checklist, we can identify the key differences among these model studies, and other studies in the literature, that drive such differences in model predictions.

QUESTION 2: HOW ARE THE EFFECTS OF INCREASING ATMOSPHERIC CO₂ CONCENTRATION REPRESENTED?

The Evidence Base

The atmospheric CO₂ concentration (C_a) has already increased from 280 to 380 ppm since the pre-industrial period, and is currently rising at an average rate of 1.9 ppm per year.⁸⁷ There is clear evidence that elevated C_a affects forest productivity.^{3,88,89} Studies of the photosynthetic process demonstrate clearly that rising C_a increases leaf photosynthetic rate (Figure 1; Ref 90); in forest trees, which are C₃ plants, the increase is linear at the current C_a but begins to saturate at concentrations above 600 ppm.⁹¹ Early pot, seedling, and open-top chamber experiments on the impacts of increasing C_a demonstrated that the increase in photosynthetic rate leads consistently to an increase in tree productivity.^{92,93} However, in many cases, the short-term increase in photosynthetic rate at elevated C_a was reduced or 'downregulated' over time.⁹⁴ This downregulation is commonly associated with low nutrient availability⁹⁴ and it has been shown

TABLE 2 | A Comparison of Nine Model Studies of Impacts of Climate Change on Forest Productivity over the Next 100 Years

Model Name	GenW	ecosys	TEM	BIOME-BGC	3-PG	MELA	FORCLIM	LPJ	Orchidee
Reference (application)	80	22	28	27	81	34	48	55	82
Reference (technical model description)	11	15	24,83	84	85	31	86	50	52
Q1 Model type	Types 1–6	1	2	2	3	3	5	6	6
Q2 CO ₂									
CO ₂ effect on photosynthesis	Y/N	Y	Y	Y	N	Y	N	Y	Y
CO ₂ effect on <i>g_s</i> included	Y/N	Y	Y	N	N	N	n/a	Y	Y
Downregulation photosynthetic capacity	Y/N	Y	Y	Y	N	N	N	N	N
Q3 Temperature									
Empirical (E)/ process-based (P)	E/P	P	P	P	E	E	E	P	P
Acclimation	Y/N	N	Y	N	N	N	N	Y	N
Optimum temperature at current CO ₂	Parameter and value	whole-plant C gain: 15–20°C	GPP: optimum between mean air <i>T</i> of month with max leaf area, and <i>T</i> _{max} – 1°	n/d	NPP: plateau above approx 20°C	Volume growth increment: no peak for Scots pine/silver birch; above optimum for Norway spruce	Varies by species; parameters not published	n/d	<i>A</i> _{max} : 25°C
Interaction between temperature and CO ₂ ?	Y/N	N	N	Y	N	Y	N	Y	N
Q4 Water availability									
Water balance simulated?	Y/N	Y	Y	Y	Y	N	N	Y	Y

TABLE 2 | Continued

Model Name	CenW	ecosys	TEM	BIOME-BGC	3-PG	MELA	FORCLIM	LPJ	Orchidee
Soil water holding capacity	mm	42	n/d	>500	10–260 (average 80)	n/a	n/a	150–450	90–180
Threshold soil water potential	Value and units	n/d	n/d	–0.63 MPa	50–80% depending on soil texture	n/a	n/a	n/d	50% of relative extractable water
How is soil moisture threshold parameterized?	Empirical (E)/ Complex (C)/ Simple index (S)	C	S	E	E	n/a	S	E	E
Processes affected by drought	g_s (E)/ growth (G)/ mortality (M)/ allocation (A)/ senescence (S)	ESM	E	E	EGA	n/a	G	EM	EASM
Q5 Nutrient cycling									
Nutrient cycling included?	Y/N	Y	Y	Y	N	N	N	N	N
How many soil organic matter pools?	3	4	1	1	n/a	n/a	n/a	n/a	n/a
Q6 Other global change effects	Nitrogen deposition (N)/ Fire (F)/ Pests (P)/ Land-use change (L)	—	—	N	—	M	—	F	F
Q7 Scenarios used	WRE450,WRE 550, SRES mean, SRES A2	SRES A1B (ca $T + 3^\circ\text{C}$, $P + 2.5\%$ after 100 years)	3 scenarios with T of 1.6°C , 2.6°C , 3.1°C by 2100	SRES A1B for $[\text{CO}_2]$: $T + 5^\circ\text{C}$; Precip $+ 30\%$	SRES A2; CGCM2 ensemble GCM predictions to 2080	$[\text{CO}_2] + 350 \text{ ppm}$; $T + 4^\circ\text{C}$; either slow (over 100 yr) or rapid (immediate)	SRES A2, HADCM3 GCM	IS92a scenario, 5 GCMs ($T + 3.7$ to $+6.2^\circ\text{C}$ by 2100)	SRES B2, ARPEGE GCM

TABLE 2 | Continued

Model Name	CenW	ecosys	TEM	BIOME-BGC	3-PG	MELA	FORCLIM	LPJ	Orchidee
Location and species of application	Radiata pine, SW Australia	Boreal jack pine stands, Canada	Global softwood and hardwood stocks	Black spruce, Alaska, U.S.A.	Douglas fir, British Columbia, Canada	All forests, Karelia, Finland	All forests, Switzerland	All vegetation, Global	Temperate needleleaf forests, France
Projected impact on forest productivity	Little change in wood production in three scenarios; reduction of 20–40% under extreme scenario (SRES A2)	Initial increase of forest woody biomass growth, but after 100 years T-induced dieback due to increased autotrophic respiration	Always increase in growth, but regional variation. Range 0–20% increase in NPP by 2040	Increase in NPP of 30%	10–40% growth increase in most areas due to increased T, but decreases of 10–40% where drought severity increased	By 2030, increase in annual increment of +15% under slow climate change and +70% under rapid climate change	Significant changes in species composition (productivity not predicted)	By 2100, Increase in global NPP of 16–32% depending on GCM	By 2090, NPP increase up to 25% in the East, but up to 40% decrease in the drier West, due to increased drought frequency

These example studies were chosen randomly from the literature and are used to illustrate the use of the checklist in evaluating and comparing model studies. We compiled this table using published literature only. Note that the table entries refer to the particular model applications given in the top row of the study; other applications of the same models could have different features if different model versions are used. GCM, global climate model; GDP, gross primary productivity; n/a, not applicable; n/d, not able to be determined from the published information; NEP, net ecosystem productivity; NPP, net primary productivity.

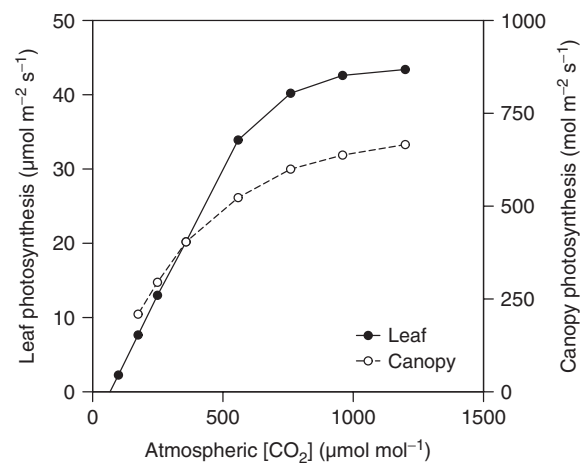


FIGURE 1 | Comparison of the effects of increasing atmospheric CO₂ concentration on instantaneous leaf photosynthesis (filled symbols) and annual canopy photosynthesis (open symbols). Leaf photosynthesis data were measured by Jeff Warren at the Oak Ridge National Laboratories (ORNL) FACE (free air CO₂ enrichment) experiment. Annual canopy photosynthesis was estimated using the MAESTRA canopy photosynthesis model (www.bio.mq.edu.au/maestra) parameterized for the ambient treatment at ORNL FACE, with only atmospheric CO₂ concentration varying. The y-axes are scaled so that points overlap at current ambient CO₂ (360 μmol mol⁻¹).

that increases in tree productivity were lower in experiments where nutrient availability was low.⁹⁵ It has been hypothesized that this nutrient feedback will dominate C_a responses at the forest stand scale.⁹⁶ In the last 15 years, free air CO₂ enrichment (FACE) experiments have been established to examine the C_a response at the scale of forest stands.⁸⁸

Five large-scale forest FACE experiments have been carried out to date. Two experiments were in young, rapidly expanding poplar and poplar-birch stands;^{97,98} two in closed-canopy plantations^{99,100} and the fifth in a mature beech forest.¹⁰¹ Stem productivity increased by 20–60% under elevated C_a in three of these experiments. In the fourth experiment in a *Liquidambar* plantation, total NPP increased in the first six years of exposure, but this increase was allocated to fine roots with small, statistically insignificant increases in wood production.⁹⁹ In this experiment, declining nutrient availability over time reduced the effect of elevated C_a on total NPP to less than 10%.¹⁰² Similar to this experiment, a Web-FACE experiment in a 35-m forest at the Swiss Canopy Crane facility reported that there was no overall above-ground growth stimulation under elevated C_a.¹⁰¹

Are C_a Effects Included in the Model?

It is clear from experiments, then, that increasing C_a can affect forest productivity, although the magnitude

of the effect will depend on nutrient availability. In some model applications, however, particularly those based on empirical data such as the hybrid models, the effects of elevated C_a are not incorporated. These model applications will yield lower estimates of forest productivity over the next century than models that do include the CO_2 fertilization effect, and their predictions are likely to be underestimates. For example, studies based on the 3-PG model, which does not include CO_2 fertilization, predict effects of climate change on Canadian forest productivity of the order of -30 to $+30\%$ ^{66,81} (Table 2), whereas predictions for similar forests using the CENTURY model, which does incorporate CO_2 fertilization, are considerably higher, of the order of $+30$ to $+50\%$.¹⁰³

Is the Effect of Increased C_a of the Correct Order of Magnitude?

In the absence of downregulation, we can estimate with some certainty the magnitude of the C_a effect on productivity in closed-canopy forests. We can express NPP as the product of two factors:

$$NPP = LUE \times APAR, \quad (1)$$

where LUE is the light-use efficiency ($g\ MJ^{-1}$) and APAR ($MJ\ m^{-2}\ year^{-1}$) is the photosynthetically active radiation absorbed by the canopy.¹⁰⁴ For closed canopies, in the absence of downregulation, an increase in C_a from ambient to 550 ppm should lead to an increase of approximately 25% in light-use efficiency (Figure 1; Ref 105). There is a limit to the potential increase in absorbed PAR because it cannot exceed the incident PAR, and closed canopies typically already absorb much of the incident PAR. For example, assuming an extreme response, a doubling of leaf area index (LAI) (the leaf area per unit ground area) from 2 to 4, APAR increases by approximately 36%. This gives an upper limit to the potential C_a effect on productivity of approximately 70% (because $1.25 \times 1.36 = 1.7$). Predicted C_a responses exceeding this level are likely to be overestimates and may result from inappropriate scaling of leaf-level responses to the canopy.

For example, Ollinger et al.,¹⁹ using the PnET-CN model, estimated potential C_a effects on productivity of north-eastern US forests in the range of 40–80%. This effect appears high, particularly for forests which have high LAI under current C_a . This model assumes that the canopy photosynthetic response to increased C_a is the same as the response of a light-saturated leaf.¹³ This assumption is incorrect, because shaded leaves are light-limited and have lower

[CO_2] responses than sunlit leaves (Figure 1; Ref 90). Hence, C_a responses estimated in this study are likely to be overestimates.

Is Stomatal Conductance Reduced at Elevated C_a ?

Elevated C_a has also been shown to directly affect stomatal conductance in many plant species including trees.⁹¹ In theory, if stomatal closure occurs at elevated C_a , plant water status will be improved and productivity could be increased if water availability is low. This effect has been demonstrated in grasses¹⁰⁶ but the evidence for such a water-saving effect is currently equivocal for forests.^{89,134} Models incorporating this effect are likely to predict higher C_a effects on productivity in dry conditions,¹⁰⁷ and less severe impacts of drought on productivity. For example, Tatarinov and Cienciala¹⁰⁸ applied the BIOME-BGC model, which does not include this effect, to central European forests and highlighted the predicted negative impact of drought on productivity. In contrast, Zaehle et al.,¹⁰⁹ using the LPJ model, which does include this effect, found that increases in water-use efficiency with rising CO_2 largely counteracted the effect of reduced precipitation on European forests.

Is There Downregulation of Photosynthesis?

The major uncertainty about the C_a response of productivity is the extent to which downregulation will moderate the initial stimulation of photosynthesis. In some modeling studies, this effect is simulated by including nutrient cycling in the model (see Table 2); we discuss this approach below. In other studies, this uncertainty is dealt with by running simulations with alternative assumptions about the effects of elevated C_a on photosynthesis.^{19,20} This approach is helpful because it provides upper and lower limits to the potential response of productivity. However, the range indicated in such studies is very wide, indicating that resolving this uncertainty is one of the key research issues in this area.

QUESTION 3: HOW ARE THE EFFECTS OF INCREASING TEMPERATURES REPRESENTED?

Although predictions of temperatures over the coming century are variable, there is consensus that almost all land areas are facing a mean annual warming in the range of 1–5°C.² There are several major challenges in quantifying the impacts of such warming on plants. Firstly, changes in temperature affect many

plant ecosystem processes simultaneously, including photosynthesis, respiration, phenology, allocation, turnover, and litter decomposition. The overall effect of warming on growth represents the integration of all these processes, making it complex to identify causes of temperature effects on ecosystem productivity. In particular, many studies focus on the effects of rising temperature on plant processes such as photosynthesis and respiration. However, warming of the soil is likely to have a large impact on nutrient cycling, enhancing soil nutrient availability,¹¹⁰ and it has been suggested that this effect could be more important than the direct effects on plant processes.¹¹¹ This issue is discussed further under Question 5.

Secondly, plants have a remarkable ability to acclimate and adapt to changes in temperature, with the result that long-term responses to warming may differ strongly from the observed short-term responses.¹¹² For example, although growth rates generally peak at an optimum temperature for a given species, a global study of the effects of temperature on forest NPP found no evidence of a peak, but rather a monotonic increase,¹¹³ indicating long-term adaptation of plants to their growth environment. This ability to acclimate and adapt means that timescale must be carefully considered when interpreting any experimental data looking at effects of temperature on forest growth. Manipulative experiments, where temperatures are artificially increased, either in greenhouses or in the field, may capture only short-term responses to temperature. On the other hand, studies of growth processes across natural temperature gradients may be dominated by plant adaptive responses to temperature. Unfortunately, neither can be directly extrapolated to predict effects of temperature on the 100-year timescale.

Thirdly, temperature responses are nonlinear. The influence of temperature on forest productivity thus critically depends on the initial climatic conditions of each site.^{99,114,115} A meta-analysis of warming experiments showed that the response of ANPP to increased temperature decreased with the mean annual temperature of the site.^{115,116} It is therefore not appropriate to generalize from individual warming experiments across the globe; initial climatic conditions must be considered, and different processes may be important in different regions.

Finally, there are strong interactions between temperature and water availability. Increasing temperatures generally increase evaporative demand, causing increased water stress, which may impact on plants more strongly than the increase in temperature alone.¹¹⁷ Unraveling these effects experimentally is difficult. Studies of growth processes in relation

to naturally occurring variation in temperature are confounded by variation in humidity and radiation. Experimental manipulations of temperature are also likely to modify humidity but, unfortunately, this effect is rarely measured, let alone accounted for, in such experiments.¹¹⁸ Disentangling this confounding effect is particularly important because the correlation between temperature and evaporative demand is likely to change with global warming.¹¹⁹ Overall, it is fair to say that the evidence base for effects of temperature on forest growth must be interpreted with great care. Consequently, model predictions also need to be examined with care.

Empirical or Process-based?

A key difference in the way that models simulate temperature effects on productivity is whether they are parameterized with empirical observations of growth response to temperature, or simulate growth as the outcome of a number of temperature-dependent processes. Currently, process-based representations dominate in model applications. The hybrid-type models, although based on empirical yield databases, often take their temperature response functions from process-based models.^{34,41} The major class of models using empirical temperature–growth relationships is the forest gap models, where the temperature dependence of growth is parameterized individually for different species.⁴⁵ In theory, the two approaches, empirical and process-based, should give similar predictions; the process-based representations of temperature dependences should integrate to give a response similar to the observed temperature dependence of growth. However, different temperature responses could easily be obtained for a given species at a given site, because the types of data used for parameterization of the two approaches are quite different: tissue-level gas exchange data compared to tree- or stand-level growth data.

What Is the Optimal Temperature for Carbon Gain?

In boreal and temperate regions where growth is temperature limited, the effects of temperature on phenology dominate the overall temperature response.¹²⁰ The link between temperature and growing season length is well quantified, giving us confidence in predicted impacts of temperatures on growth in these regions. However, where temperatures are approaching or above optimum, the temperature effects on productivity will depend on the optimum itself. We suggest that it would be useful for model studies to quantify the approximate optimum temperature for

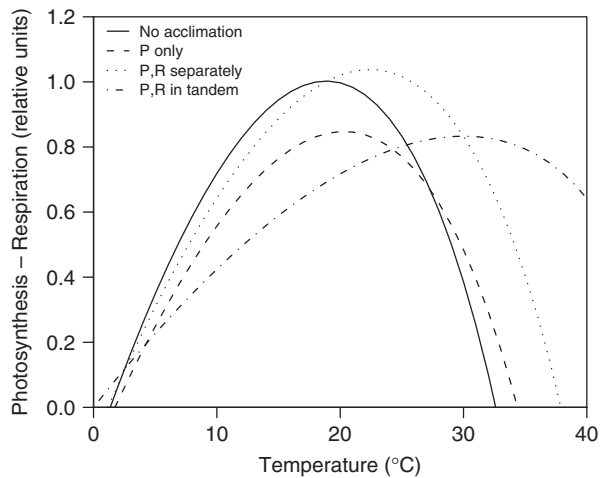


FIGURE 2 | Effect of different assumptions about acclimation to temperature on predicted net leaf carbon uptake (= photosynthesis – respiration). Photosynthesis is assumed to have a peaked response to temperature, with an optimum at 25°C; respiration is assumed to increase exponentially with temperature. The thick solid line shows net leaf carbon uptake at ambient growth conditions (optimum at 19°C). The dashed line is generated by assuming that optimum and maximum temperatures for photosynthesis increase by 5°C but respiration rates do not change (acclimation of photosynthesis only; optimum at 20°C). The dotted line is generated by assuming that optimum and maximum temperatures for photosynthesis and the reference temperature for respiration all increase by 5°C (independent acclimation of photosynthesis and respiration; optimum at 22°C). The dot-dash line is generated by assuming that optimum and maximum temperatures for photosynthesis increase by 5°C, and that respiration at the reference temperature of 20°C is a constant proportion of photosynthesis (acclimation of photosynthesis and respiration in tandem; optimum at 30°C).

carbon gain arising from their model assumptions, and to indicate the source of data used for parameterization of this response. Such information would demonstrate how close the study species is assumed to be to its optimum temperature, allowing readers to better evaluate and compare studies. For example, Simioni et al.⁸⁰ (see Table 2) simulated growth of *Pinus radiata* in south-west Western Australia, at sites where mean annual temperature ranges from 15 to 17°C. The optimum temperature for leaf photosynthesis was assumed to be in the range 15–20°C.¹²¹ Thus, in this study, *Pinus radiata* is likely above optimum temperature for NPP for considerable parts of the year in the current climate, which may partially explain why zero or negative growth responses were predicted.

For models that are parameterized with empirical growth responses, this optimum is generally a parameter to the model. For example, Coops et al.⁸¹ (see Table 2) used an explicit temperature modifier for growth which plateaus at a maximum daily

temperature of approximately 20°C. For process-based models, the optimum temperature for NPP depends on the balance between the temperature effects on photosynthesis and respiration, and whether acclimation is included or not (see below). The resulting optimum temperature for NPP is rarely indicated in studies using process-based models, although it would be extremely useful for model evaluation. Many studies do indicate the optimum temperature for light-saturated leaf photosynthesis. The optimum temperature for NPP will be several degrees below this value, once effects of light-limited photosynthesis and respiration are taken into account¹²² (see also Figure 2).

Is There an Interaction between Rising CO₂ and Temperature?

Physiological studies of leaf photosynthesis find a strong interaction between temperature and CO₂ responses,¹²³ with the temperature optimum for photosynthesis increasing with increasing C_a. When this interaction is included, negative effects of rising temperature on plant carbon balance are delayed, occurring at higher temperatures. About half of the models in Table 2 incorporate this interaction. We observed that negative effects of climate change only occur in the models that do not make this assumption. This observation suggests that this model assumption has an important role to play in determining model outcomes.

Is There Acclimation to Temperature?

Plant processes such as photosynthesis and respiration can acclimate strongly to temperature on a range of timescales.^{124,125} Models using empirical responses of growth to temperature effectively incorporate acclimation, because they are based on long-term growth rates across temperature gradients. Some process-based models do attempt to capture acclimation by modifying photosynthetic and respiration rates depending on growth temperature.⁹ Process-based models that are parameterized and tested only against short-term (diurnal, seasonal) temperature changes¹²⁶ do not capture acclimation and are more likely to predict strongly negative long-term temperature effects on plant productivity. For example, Grant et al.²² (see Table 2), who assumed no acclimation, predicted dieback of Canadian forests as rising autotrophic respiration outpaces temperature effects on GPP. Similarly, Sitch et al.⁷² show that boreal forest dieback occurs in the LPJ DGVM, which does not include photosynthetic temperature acclimation, but does not occur in the Orchidee

DGVM, which does simulate acclimation. Unfortunately, process acclimation is not straightforward to parameterize because different species appear to vary in their capacity for acclimation.¹²⁷ Different assumptions about acclimation strongly affect predicted responses to temperature, particularly at the upper end of the temperature response (Figure 2). There is a clear need for better quantitative information on acclimation that can be incorporated into models.¹²⁸ Model studies also need to clearly state whether and how acclimation is represented.

QUESTION 4: HOW IS THE EFFECT OF WATER AVAILABILITY REPRESENTED?

The Evidence Base

Climate change is expected to result in significant changes in rainfall patterns and extreme weather events such as drought and flooding.² Increased temperature may affect forest water balance by increasing evaporative demand,¹²⁹ exemplified by the extremely hot and dry summer of 2003 across parts of Europe,¹¹⁷ whereas changes in precipitation are spatially variable and highly uncertain. On regional scales, water availability exerts a strong influence on plant productivity as shown by correlations between NPP and annual precipitation,¹³⁰ while experimental studies have shown that the timing and variability of rainfall are equally important.^{131,132} If drought stress increases with climate change, it seems inevitable that forest productivity will decline.¹³³ Elevated C_a is often thought to remedy soil water stress by reducing transpiration rate and increasing water-use efficiency, but this effect is rarely demonstrated in field experiments on trees.^{89,134}

The short-term response of forests to moderate water stress involves a number of plant processes that are generally well understood,¹³⁵ in contrast to the long-term effects including acclimation of plant leaf area, phenology, species composition, mortality, seedling establishment, interaction with nutrient mobilization and mineralization, etc.^{133,136–139} A number of throughfall exclusion experiments are in operation to study such long-term responses,¹⁴⁰ while further evidence comes from comparative studies across rainfall gradients.^{137,141} Long-term reduction in throughfall in such experiments typically leads to reduced NPP, as well as a number of other processes,¹⁴² including mortality of larger trees.¹⁴³

Modeling effects of drought on productivity generally proceeds in two steps: first, the soil water storage dynamics is simulated, and subsequently the effects of a 'water deficit' on forest productivity. For both of

these sub-models, a range of approaches exist that vary widely in their complexity and data needs.¹⁴⁴

Is the Water Balance Simulated?

While it is possible to simulate drought effects through use of a dryness ratio, such as precipitation to potential evapotranspiration, such an approach does not allow for the effects of temporal variation in rainfall. Instead, most models of forest productivity simulate the soil water balance, including at least transpiration (soil water uptake), canopy interception, and drainage. The latter can be estimated simply, using a 'bucket model' where excess water drains immediately (e.g., in 3-PG⁸⁵), or using a detailed multilayered soil model where drainage is calculated from soil hydraulic conductivity (e.g., in ecosys¹⁵), and root water uptake is estimated for each soil layer depending on fine root density, water content, and soil properties. Models that do not simulate the soil water balance include some large-scale models (e.g., MELA³¹) or early versions of models to which water balance has since been added (e.g., TEM²⁴ and ForClim⁸⁶), another reason to clearly point out which version of the model was used in a particular application.

What Is the Total Soil Water Storage?

The total soil water storage is important in modeling the water balance because it determines the buffering capacity of the forest to droughts, but it is unfortunately very difficult to estimate. Although a wealth of data exists which describe rooting distributions across the globe,¹⁴⁵ the depth of the deepest roots is much more variable and uncertain.¹⁴⁶ It is these deep roots that have a profound influence on forest water balance as well as water uptake during intense droughts,^{138,147,148} and can cause a decoupling of forest water balance from precipitation through groundwater uptake.^{149,150}

For example, contrast the studies by Simioni et al.,⁸⁰ in SW Australia, and Loustau et al.⁸², in France, in Table 2. The effects of increasing drought stress on productivity are similar in both studies (ca 30% reduction) but the rainfall reductions driving these decreases are quite different: a 45% reduction in SW Australia compared to a ca 10% reduction in France (from similar initial rainfall). The effects of drought in SW Australia are buffered by a much larger soil moisture holding capacity, of the order of 600 mm,¹⁷ compared to values of the order of 100–150 mm in France. Similarly, the study by Coops et al.⁸¹ (Table 2) predicted strong reductions in productivity due to increasing drought in parts of British Columbia, despite relatively small changes in rainfall.

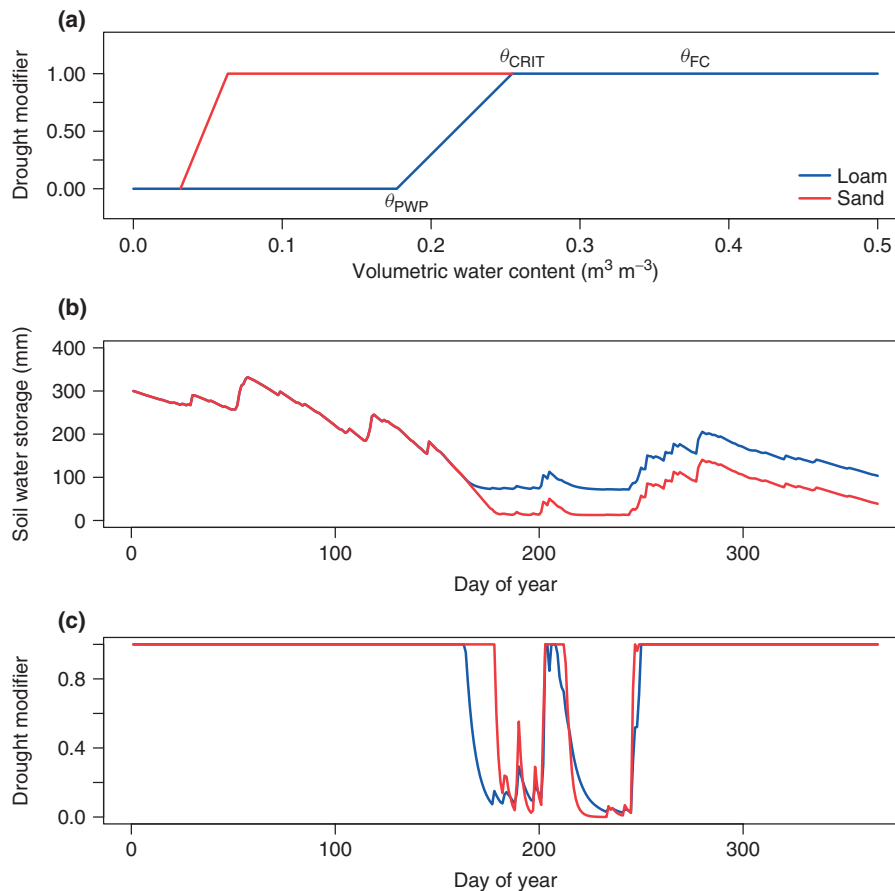


FIGURE 3 | Illustration of the importance of the threshold for drought effects on forest transpiration, simulated with a typical simple bucket model. (a) The 'drought modifier', i.e., the relative effect of water availability on transpiration for two soil types of different texture, as a function of the soil volumetric water content. Three important water contents are marked for the loam soil type: θ_{FC} is the water content at 'field capacity', θ_{CRIT} the 'critical' water content and θ_{PWP} the 'permanent wilting point' (PWP). The critical water content is much lower for the sand soil type, but the decline to the PWP is much steeper. (b) Example simulation of the water balance for 1 year with a simple bucket model for the two soil types. Soil moisture storage reaches lower values in the sand soil type because transpiration is not reduced until a lower soil water content. (c) Simulated drought stress for the two soil types over the year. Drought stress is shown to depend strongly on the critical water content and PWP, with a much later onset of drought in the sandy soil, but a much steeper decline.

However, soil water holding capacity averaged just 80 mm. Thus, the strongest effects of drought are likely to be seen in model studies where soil water storage is low.

How Is the Soil Moisture Threshold Parameterized?

The response of water use and productivity to soil water availability is highly nonlinear, with no effect of water availability until a critical threshold is reached (θ_{CRIT}), after which the response is very steep (Figure 3).¹⁵¹ The response of forest productivity to precipitation is very sensitive to the value of this threshold. For example, there are two model studies examining the reduction in forest carbon uptake during drought measured using eddy covariance at

Tumbarumba, NSW, Australia.¹⁵² Pepper et al.¹⁵³ attributed the reduction to a direct effect of soil moisture and VPD on photosynthetic productivity, whereas Kirschbaum et al.¹⁵⁴ concluded that the direct effects were small and that the reduction was instead due to insect pest damage to the canopy. These model studies arrived at these different conclusions because they parameterized the threshold for the impacts of soil moisture on productivity differently; Pepper et al.¹⁵³ assumed a direct linear reduction of productivity with soil moisture, whereas Kirschbaum et al.¹⁵⁴ assumed an indirect effect via stomatal conductance, resulting in this case in a much lower threshold for soil moisture to affect productivity.

Although this threshold is important, it is rarely clear from modeling studies what threshold was

assumed, and how the threshold was parameterized. Different models implement the threshold in different ways. In some models, it is an empirical parameter that must be specified by the user (e.g., CenW, Table 2). Other models define the threshold as a fraction of the relative extractable water (0 is permanent wilting point, 1 is field capacity), with estimates in the range 0.3–0.5.^{155,156} The actual drought effect then depends on soil type mainly through field capacity and permanent wilting point (Figure 3). More complex models that account for vertical variation in root density and other fine details are also available (e.g., ecosys, see Table 2). To compare the predicted impacts of drought across modeling studies, one would need to know the effective value for the threshold. We were largely unable to determine this information from the studies considered in Table 2. We challenge modelers to make this information clear, to enable their studies to be correctly evaluated and compared.

Which Processes Are Affected by Drought?

Apart from direct effects of soil water deficit on forest productivity through stomatal closure, there are a number of longer-term processes that negatively impact forest productivity after the drought has ended. These include reduction in LAI^{141,157} through increased leaf turnover and mortality,^{143,158} loss of hydraulic conductance through cavitation,¹⁵⁹ reduction in photosynthetic capacity,¹⁶⁰ effects on roots (turnover rates, distribution with depth),¹⁶¹ biomass allocation (e.g., root–shoot ratios¹⁶¹), and nitrogen mineralization rates.¹⁶² In Table 2, we indicate model studies that include long-term effects of drought on growth, allocation, and senescence. Models including such assumptions are likely to predict larger and more prolonged effects of drought.

Drought-induced mortality, in particular, is a key problem in simulating climate impacts on forest productivity. Inclusion of mortality obviously makes a large difference to predictions: if trees survive, the long-term effects of one year's drought on productivity are relatively small, whereas the effect is catastrophic when trees are killed.²⁰ However, drought mortality is difficult to model because the mechanism causing mortality has not been clearly identified: there is currently an intense debate over the role of carbon starvation versus hydraulic failure.^{163,164} In some models, mortality rates are assumed constant and unaffected by drought, whereas other models (e.g., LPJ, Orchidee, see Table 2) simulate mortality through carbon starvation, allowing extreme drought to cause mortality. Drought mortality is an area where further model-oriented research is clearly required.

QUESTION 5: HOW IS NUTRIENT CYCLING REPRESENTED?

Evidence Base

Feedbacks through soil nutrient cycling processes have the potential to significantly modify effects of climate change on forest growth. Sequestration of nutrients in litter and soil organic matter at elevated C_a could reduce nutrient availability and limit the response of productivity to increased C_a .⁹⁶ Meta-analysis of open-top chamber experiments on trees found that, across a large range of experiments, the C_a response of productivity was higher when nutrient availability was not limiting.⁹⁵ In contrast, initial results from forest FACE studies suggested that the C_a effect on forest productivity could be maintained for several years, with the trees increasing nutrient uptake to support increased productivity.¹⁶⁵ However, continuation of these experiments for a decade has clearly shown that nutrient availability can limit the C_a response of productivity. After 10 years at elevated C_a , the stimulation of NPP at the ORNL FACE site has fallen from initial heights of 20–30% to below 10%.¹⁰² On the other hand, enhanced decomposition of soil organic matter with increasing temperature could increase nutrient availability and stimulate growth, causing a positive feedback to forest growth under climate change.¹¹¹ Meta-analysis of soil warming experiments has shown a consistent increase in nitrogen mineralization and tree productivity when soils are warmed.¹¹⁰

Is Nutrient Cycling Incorporated?

Nutrient availability clearly plays an important role in determining forest productivity. Nutrient cycling feedbacks are included in many process-based stand-scale models^{11,166} and regional biochemistry models.¹⁶⁷ These feedbacks have recently been incorporated into DGVMs¹⁶⁸ and initial results^{169,170} are consistent with stand-scale studies showing that inclusion of nutrient feedbacks significantly alters the predicted responses to individual climate change drivers such as rising C_a .^{166,171,172}

Interestingly, however, there is no clear difference among predictions of the overall effect of climate change on forest productivity over the next century between models that do include nutrient feedbacks and those that do not (Table 2; see also model comparisons in Ref 4). This lack of difference occurs because there are compensating effects of nutrient feedbacks to rising C_a and temperature; responses to rising C_a are reduced under nutrient limitation, but responses to warming are increased because of enhanced decomposition of soil organic matter and consequent increases in nitrogen mineralization.

Model assumptions that are clearly important in determining responses to individual drivers also become less important when the total effect of climate change is considered. For example, McMurtrie and Comins⁷⁶ showed that one key assumption determining the response of productivity to rising C_a regards flexibility of the C:N stoichiometry of plant and soil pools with long turnover times, such as heartwood and recalcitrant soil organic matter. If C:N ratios of these pools are assumed to be conservative, then responses to increasing C_a are minimal, whereas if the ratios are assumed to vary with N availability, the effect of increased C_a on productivity is not reduced by nitrogen limitation.^{172,173} However, the flexibility in C:N stoichiometry has opposite effects on the strength of the productivity response to warming.¹⁷² That is, if the C:N ratios are assumed conservative, rising temperatures cause a large increase in nitrogen mineralization and therefore productivity. In simulations by McMurtrie et al.,¹⁷² the response of ecosystem carbon balance to simultaneous gradual increases in temperature of 3°C and in C_a of 300 ppm over a century was similar whether C:N ratios were assumed to be flexible or conservative. However, the relative contributions of temperature and C_a to the carbon uptake differed considerably, with the temperature effect dominating when soil C:N was assumed to be conservative, and both effects contributing equally when soil C:N was assumed to be flexible.

What Soil Organic Matter Pools Are Represented?

The strength of nutrient cycling feedbacks changes over time depending on the equilibration time of the soil organic matter pools. For example, warming initially stimulates decomposition and nitrogen mineralization, but as nitrogen is lost from the soil organic matter pools, they reach a new equilibrium, and nitrogen mineralization rates are no longer stimulated. Medlyn et al.¹¹¹ demonstrated this effect with a soil organic matter model comprising three pools of differing timescales, showing that the stimulation of growth by enhanced nitrogen mineralization with warming was highest on the equilibration timescale of the largest soil organic matter pool. The number, relative size, and turnover times of the soil organic matter pools therefore provide a useful indication of the timescale on which nutrient feedbacks will act. The C:N ratio and temperature sensitivity of the largest pool are also key parameters, as they will determine the amount of nitrogen that will become available from the soil to support plant growth.

QUESTION 6: WHAT OTHER GLOBAL CHANGE IMPACTS ARE ACCOUNTED FOR?

There are a range of other global change factors which may strongly impact on forest productivity. Model outcomes can differ significantly depending on whether or not these factors are considered in the study; model studies should therefore be examined to identify which, if any, of these factors are included.

Nitrogen Deposition

Nitrogen deposition from atmospheric pollution ranges up to 10 g N m⁻² year⁻¹, particularly in industrial areas such as central Europe and the north-eastern USA.³ This nitrogen deposition is likely to stimulate productivity, particularly in nitrogen-limited forests. The size of the stimulation is under debate but estimates range from 40 to 200 kg C per kg N deposited.^{174,175} Modeling studies that include nitrogen deposition generally predict considerably stronger responses of productivity to climate change.^{79,176} For example, Pepper et al.⁷⁹ found, using the G'DAY and DAYCENT models, that predicted increases in NPP were of the order of 20–40% without N deposition, and 50–100% with N deposition. However, N deposition rates must be relatively high (e.g., Pepper et al.⁷⁹ assumed 1 g N m⁻² year⁻¹) for this response to occur. Of the models in Table 2, two can include N deposition, but in the applications considered, have it set to zero or a negligible value.

Land-use Change

Changes in land use and forest management can have a significant effect on forest productivity at regional scales.³ Impacts of previous changes in land use on carbon balances have been quantified using regional biogeochemistry models and DGVMs.²⁹ It is difficult to forecast future trends in land use or forest management, but the impacts of possible alternative scenarios can be modeled. For example, Karjalainen et al.⁶⁷ compared a management-as-usual scenario with a multifunctional management scenario using the EFISCEN carbon accounting model, and found that carbon sequestration rates were similar under both scenarios. The effects of land-use change on predicted productivity will clearly be specific to the type of land-use change assumed.

Fire

Significant changes to disturbance regimes are likely to negatively impact on forest productivity.³⁹ Fire is one

of the major ecosystem disturbances, and warmer, drier conditions under climate change are likely to lead to more frequent and more severe fires,¹⁷⁷ reducing forest productivity and carbon storage. Several regional biogeochemistry models and DGVMs attempt to simulate impacts of changed fire regimes by incorporating relationships between climate, fire, and vegetation.^{18,57,178} Models including climate effects on fire predict reduced forest carbon storage in future;¹⁷⁸ however, conceptual understanding of drivers of fire is still emerging¹⁷⁹ and consequently modeled fire impacts are currently highly uncertain.

Pests

Damage from pests can have dramatic effects on forest productivity.³⁸ It is difficult to generalize impacts of pests because climatic changes affect life cycles of different pest species in different ways. Attempts to model disturbances due to pest damage therefore tend to focus on particular pest species of importance to forest productivity, for example, bark beetle in European forests¹⁸⁰ and *Mycosphaerella* leaf disease in Australian eucalypt plantations.¹⁸¹ These studies generally indicate that pest outbreaks could significantly reduce forest productivity under climate change. However, few models have the features necessary to represent pest damage in a mechanistic way.¹⁸¹ These features include, among others, photosynthetic rates which are linked to source: sink balance, allowing photosynthetic responses to defoliation to be captured, and the capacity to vary biomass allocation and leaf longevity in response to pest attack.

QUESTION 7: WHAT CLIMATE CHANGE SCENARIOS ARE USED AS INPUT?

Finally, model outcomes will clearly depend on the actual climate change scenario assumed. Here, model studies generally adopt one of two approaches: either driving the model with output from GCMs, or directly modifying climate variables such as temperature and precipitation.

What GCM Output Is Used?

For model studies employing GCM output, two questions should be asked. Firstly, which emissions scenario was used? Secondly, what is the sensitivity of the GCM used? Many recent modeling studies draw from the IPCC SRES emissions scenarios, which are based on possible alternative futures.² These scenarios can be classified as 'growth' scenarios (e.g., A1FI,

A1B, A2), representing a high-emission future or 'stable' scenarios (e.g., A1T, B2, B1) where atmospheric CO₂ concentrations are assumed to stabilize around the end of the century.

GCMs are then used to predict climate change given these emission scenarios. The degree of climate change predicted for a given scenario varies amongst GCMs. For example, Schaphoff et al.⁵⁵ (see Table 2) drive the LPJ model with output from five GCMs using the 'growth' scenario IS92a. Predicted global average surface warming from these five GCMs ranges from +3.7°C to +6.2°C by 2100. This difference in driving variables has a major effect on model predictions. The model simulation using the least sensitive GCM (CSIRO) predicts the largest positive increase in global NPP (+32%) because this level of temperature increase is beneficial. However, the model simulation using the most sensitive GCM (CGCM1) predicted just 16% increase in productivity, possibly because the LPJ model does not include acclimation of temperature, so rates of respiration would have increased dramatically under this high level of warming. Thus, information is needed about the relative climate sensitivity of the GCM used, to indicate whether the climate predictions underlying the study should be considered to be extreme or mid-range.

What Are the Actual Changes in Climate Variables?

Some model studies directly perturb driving variables by a given amount; in this case, the size of the perturbations assumed should be carefully examined. As we have just seen, the actual rise in temperature assumed is of importance, because small increases in temperature may have positive effects but large increases may have negative ones. The assumed change in precipitation is also important. It varies considerably among studies, largely because spatial patterns in rainfall are predicted to change, with some locations receiving more rainfall and others less. In Table 2, for example, rainfall is reduced by up to 45% in a study in SW Australia,⁸⁰ but increased by 30% in a study in Alaska.²⁷

Moreover, changes in seasonality of rainfall are predicted in some cases. It is important to note in modeling studies whether the climate change scenario resulted in a shift in this seasonality, because it has a strong influence on water availability and annual runoff^{182,183} as well as plant carbon and water fluxes.¹⁸⁴ For example, Loustau et al.⁸² (see Table 2) predicted relatively small changes in annual rainfall across France, but there was a distinct shift in seasonality with increases in winter and decreases in spring

and summer, with consequent large effects on drought severity.

The effects on vapor pressure deficit (VPD) should also be considered. It is as yet unclear how air humidity will be affected by rising temperature.¹⁸⁵ For a given parcel of air, the relative humidity declines as temperature increases (and the VPD increases).¹⁸⁶ Many model studies assume this increase in VPD with temperature, driving higher transpiration and exacerbating water stress. However, the global hydrological cycle is strongly affected by elevated temperature as well, which likely compensates for some of this expected increase based on temperature alone. For example, Donohue et al.¹¹⁹ found that, although temperature has been increasing across Australia in recent times, potential evaporation has declined due to compensatory effects of net radiation, wind speed, and vapor pressure. Model studies should clearly state what assumptions were made about air humidity in conjunction with the temperature scenario, and quantify the resulting increases in VPD.

SUMMARY AND CONCLUSIONS

There are many studies predicting responses of forest productivity to climate change in the literature. Some studies find that rising CO₂ and temperature will have positive effects on productivity.^{19,40,46,69,82,187–189} Other studies find negative effects of climate change, principally where drought frequency is predicted to increase as a result of increased temperature-driven potential evapotranspiration and changes in rainfall,^{19,66,82} or where other extreme events are predicted to increase in frequency and intensity such as pest occurrence^{180,190} and fire.^{189,191}

However, predictions from model studies ought not be directly compared. Different studies vary widely in how they represent critical processes, and their predictions can be better evaluated if the key assumptions are understood. In this article, we have presented a checklist of the major assumptions that differentiate among model studies. ‘Optimistic’ assumptions, which lead to predictions of increased productivity under climate change, include: increased photosynthesis and water use efficiency due to rising C_a;

high optimum temperatures for photosynthesis or growth; increased optimum temperature with rising C_a; high soil moisture holding capacity; high nitrogen deposition rates; and mild climate change scenarios. ‘Pessimistic’ assumptions, leading to predictions of decreased productivity, include downregulation of photosynthesis in response to rising C_a; low optimum temperatures for photosynthesis or growth; low soil moisture holding capacity; low thresholds for drought effects on carbon uptake; increased drought mortality; increased disturbance from fire and pests; and extreme climate change scenarios. Our checklist can be used to identify which of these assumptions have been made, allowing outcomes of model studies to be clearly interpreted and compared.

This review has highlighted many areas of uncertainty in predicting forest productivity responses to climate change. In addition to individual gaps in knowledge, we suggest that a general research priority should be to improve model predictions through a strategic, model-based approach to research. Ideally, models and experimental research should be closely integrated. A modeling framework can be used to generate research questions and identify key sets of measurements needed; experimental data need to be used critically to test model performance. In forests in particular, long-term, intensively studied experiments are needed to generate sufficient data to test alternative model hypotheses. The IUFRO report¹ stated that: ‘The vast majority of global change experiments have been conducted as single-factor studies with young temperate-zone trees and there is a need for multiple factor studies conducted in boreal, subtropical and tropical biomes. These experiments must be well-replicated, robustly designed, and run for long time periods in order to allow exposure to climatic conditions for stand dynamics and pest population cycles to operate so the role of global change drivers in predisposing trees to other biotic and abiotic factors is better understood’ (Ref 1, p. 43). We echo this statement, but add that it is imperative that such experiments be closely integrated with models if uncertainty about future forest productivity is to be reduced.

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