

Review

Earth System Model Needs for Including the Interactive Representation of Nitrogen Deposition and Drought Effects on Forested Ecosystems

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Abstract: One of the biggest uncertainties of climate change is determining the response of vegetation to many co-occurring stressors. In particular, many forests are experiencing increased nitrogen deposition and are expected to suffer in the future from increased drought frequency and intensity. Interactions between drought and nitrogen deposition are antagonistic and non-additive, which makes predictions of vegetation response dependent on multiple factors. The tools we use (Earth system models) to evaluate the impact of climate change on the carbon cycle are ill equipped to capture the physiological feedbacks and dynamic responses of ecosystems to these types of stressors. In this manuscript, we review the observed effects of nitrogen deposition and drought on vegetation as they relate to productivity, particularly focusing on carbon uptake and partitioning. We conclude there are several areas of model development that can improve the predicted carbon uptake under increasing nitrogen deposition and drought. This includes a more flexible framework for carbon and nitrogen partitioning, dynamic carbon allocation, better representation of root form and function, age and succession dynamics, competition, and plant modeling using trait-based approaches. These areas of model development have the potential to improve the forecasting ability and reduce the uncertainty of climate models.

Keywords: nitrogen deposition; drought; carbon cycle; stress; models

1. Introduction

Earth system models (ESMs) have been used to predict the climate's response to increased CO₂ emissions (or concentrations), but uncertainty in land carbon (C) feedbacks results in a wide spread of uncertainty in model results [1]. Part of this uncertainty lies in a general lack of knowledge of the physical processes responsible for the land feedbacks on the C cycle, which makes estimating the land C sink difficult. Adding to this uncertainty is the response of ecosystems in the face of multiple stressors, the impacts of which may be non-additive and will certainly be highly variable across ecosystems. One prime example is the current increase in nitrogen (N) deposition and the predicted increase in drought [2]. Most field studies isolate one environmental component (e.g., drought, elevated CO₂, N deposition) to study plant behavior. This results in an incomplete knowledge of an ecosystem's reaction to multiple stressors, which limits our forecasting capability. Vegetation responses have a strong influence on C storage. As plants adjust their partitioning strategy for C and other nutrients to optimize uptake while limiting costs to ensure survival, the quantity and quality of C stored and the way nutrients are recycled will change.

Anthropogenic production of reactive N from fossil fuel combustion and fertilizer synthesis has led to an increased availability of reactive N in ecosystems, and this has become a global problem [3].

The current N deposition rate in some systems is over $10 \text{ kg ha}^{-1} \text{ year}^{-1}$ [4], which is well over the deposition rate from natural sources at $0.5 \text{ kg ha}^{-1} \text{ year}^{-1}$ [5]. Nitrogen deposits from industrial and agriculture activities have led to significant N loading in soils, particularly in regions of Europe and the eastern United States [6,7]. These N additions are within the critical load of N for sensitive ecosystems [8,9]. This N loading may be further exacerbated by increases in N availability from climate influences (i.e., warming and elevated CO_2) on internal N cycling, which can increase decomposition, mineralization, and biological nitrogen fixation (BNF) [10–12]. The consequences of N loading are well known and include changes in biodiversity [7,13,14], composition [15,16], productivity [17], leaching [18,19], and possibly nitrification [17]. Since N is strongly tied to C, understanding the impact of increased N availability in ecosystems in the context of climate change is crucial if we are to understand whether increased N availability will strengthen or weaken the land's C sink capacity.

Understanding the vegetative response to N deposition is increasingly difficult due a wide variability of responses between and within species and across climate and soil regimes, as well as contrasting behavior when faced with other elements of climate change (e.g., elevated CO_2 or drought). For example, increased N availability generally results in an increase in aboveground woody biomass and a decrease in root biomass, but experiments with drought indicate an increase in root biomass at the expense of aboveground tissue [20–23]. This has led to the conclusion that N deposition may increase ecosystem vulnerability to drought [24], but some studies find that N deposition may enhance the recovery of some species post drought [25]. Therefore, a large uncertainty exists for vegetation response to increased N deposition under drought, especially because many of these antagonistic responses exhibit nonlinear behavior.

Predictions of climate change indicate an increase in the frequency and severity of drought [2] in many regions that are already water stressed. For example, in the Amazon, the dry season is expected to lengthen and intensify, and the area affected by seasonal drought is expected to expand by up to 0.75 million km^2 by the end of the century [26]. The southwest and central United States are forecast to experience increases in drought severity that exceed the severest mega drought events at millennial scales [27]. Areas that do not experience a change in total precipitation may still experience changes in the timing and intensity of rainfall events. Plants under drought stress can experience hydraulic failure, C starvation, and increased vulnerability to disease, pests, and fire. Drought during peak growth periods will likely be more detrimental; juvenile and shallow-rooted plants are most susceptible to drought, whereas plants that are able to modify biogeochemical feedbacks will increase their chance of survival [28]. In general, drought results in decreased stomatal conductance and decreased net primary productivity [27]. In the past, drought events over the Amazon have reduced C storage through mortality and slowed growth [29]; increased events in the future could result in a weaker C sink of boreal, temperate, and tropical biomes across the globe [30]. This would contrast with the increased productivity that can result from high N deposition. Most ecosystems have experienced an extreme drought in the past, but extreme drought in combination with other climate impacts such as N deposition can put unprecedented amounts of stress on ecosystems. Given that the co-occurrence of drought and increased N availability are highly probable, these climate effects must be considered together to predict ecosystem behavior.

To answer questions about the future of the terrestrial C sink, we need to understand the behavior of ecosystems under long-term chronic N deposition and drought, as well as the interactions between these phenomena. ESMs are important tools for exploring the relationships between climate and vegetation responses, but current models might not be able to capture these processes.

The ESM community has made great strides in improving the C cycle in land surface models (LSMs) due to improvements to biogeochemical and hydrological cycles. Some of these advances constrain land C sequestration by imposing N limitations on C fertilization [31], water table, and inundation dynamics [32] and even hydraulic redistribution [33]. However, these models still cannot capture mortality in trees from drought, changes in biomass partitioning due to nutrient limitations, or even acclimation [34]. For example, Ukkola et al. [35] found that 14 LSMs overestimate seasonal

drought, due partly to how models handle soil hydrology and plant moisture stress. De Kauwe et al. [36] also found that LSMs exaggerate drought effects because most models assume the same drought sensitivity for all vegetation types. Adding the N cycle to LSMs results in productivity decreases that range from 7% to 64% [37], but the feedbacks between C and N are weak once a steady state is reached [38]. This suggests that ESMs still lack key processes. In order to simulate N deposition-drought interactions, we hypothesize that additional model developments are necessary to mimic ecosystem stress responses, particularly if ESMs are to represent the C cycle accurately.

This review seeks to determine whether the current ESM framework of the C cycle is sufficient to capture the vegetation response to the combined effects of drought and growing N loading in ecosystems. To that end, this paper will review the observed impacts on C uptake and allocation due to increased N availability, drought, and their combined effects. Next will be a review of how current ESMs represent the coupled carbon-nitrogen model for C uptake and partitioning. We will present recent developments in several state-of-the-art LSMs, including the limitations of the representations for capturing interactions from N deposition and drought stress. Finally, we will discuss which additional processes should be the focus of future model developments to reduce uncertainty and improve predictive power.

2. Observations of N Impacts

Nitrogen is a critical component in ecosystems; it drives productivity through photosynthesis processes [39]. Increased N deposition results in increased production because N is generally the most limiting nutrient for growth [37,40]. Bala et al. [41] estimate that an additional 175 PgC has been stored since the pre-industrial period due to increased N deposition. This increase results mostly from changes in photosynthesis (i.e., increase in foliar N) or shifts in C allocation to increase light availability (Figure 1 and Table S1). Several mechanisms will allow plants to respond to changes in N such as the ability to increase photosynthetic capacity, plasticity to alter C partitioning of resources, and the presence or absence of other limiting factors in the system (e.g., water, P, mycorrhizal associations, etc.). An overview of some of the consequences of N deposition in ecosystems is included in Figure 1.

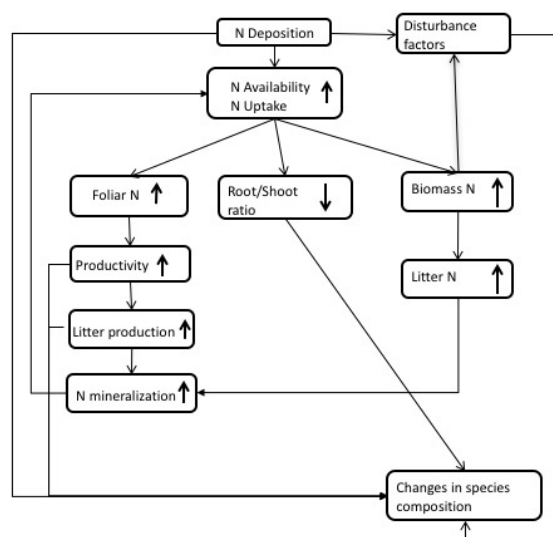


Figure 1. Effects of N deposition on ecosystems, based on the concepts of Bobbink et al. [7]. Up arrows represent an increase, and down arrows represent a decrease. Three main pathways exist: changes in foliar or leaf N, changes to biomass partitioning, and increases in biomass N. Changes in leaf or plant N generally lead to a positive feedback by increasing N in the litter pool. Changes in the partitioning of biomass can lead to changes in competition for resources that will ultimately affect species distribution. In general, the impacts of N deposition occur over short timescales (<5 years), while changes to species composition and disturbance occur over longer timescales [7].

Nitrogen deposition studies frequently find an increase in foliar N that results in decreased C:N ratios of leaves [42–44]. This relationship between N deposition and foliar N content has even been used to estimate critical loads of N in Europe [45]. Pregitzer et al. [42] suggested that the increase in foliar N is responsible for the increase in aboveground net primary productivity (ANPP) that is found under elevated N availability, considering the relationship N plays in photosynthetic capacity and C assimilation [39,46]. However, reductions in N use efficiency and C allocation shifts away from mycorrhizae may also result in increases in ANPP [47]. Increases in productivity can also lead to increases in litter production that can ultimately lead to increased N in soils.

Gains in productivity can be the result of changes in patterns of C partitioning within the plant, and they often seem to be correlated with increases in above ground biomass [42,48,49]. Most increases in aboveground biomass from increased N deposition are allocated to stems [42,50,51], particularly for small-diameter trees [52]. This response results in faster biomass accumulation, which produces taller, skinnier trees [52]. Although this is more likely to affect young trees or seedlings exposed to elevated N, Du and Fang [53] also found weak growth in a mature forest. This may increase the mortality of young trees as a result of light limitation or the respiratory costs of early rapid growth [52]. However, the increase in growth is not consistent or linear for all species. For example, de Vries et al. [50] found that tropical forests had the least response to N deposition compared to temperate and boreal forests, and in some cases a negative growth relationship exists at high N inputs [49]. Herbaceous plants also experience biomass increases from N deposition [48,54], and under low levels of N deposition they can increase aboveground biomass more than trees [51].

The increase in aboveground biomass is expected to come at the expense of belowground inputs [48]. However, it is unclear how roots respond to increased N availability; this response can include increases in productivity, even though decreases in biomass occur [55]. This occurs when increases in root turnover with N availability result in root biomass decreases over long time scales, even though C allocated to the roots likely increases. The root response is strongly associated with root sensitivity [56]; the heterogeneity of the soil, substrate, and climate can result in different root responses that will increase root vulnerability to damage or mortality.

Finally, increases in N deposition can increase N in forest biomass [57]. This increase in biomass will lead to changes in N cycling as biomass eventually flows from the canopy into the litter pool. The enhanced amount of N in the litter pool can cause faster decomposition [57] and increase N mineralization on the forest floor.

Nitrogen deposition can also increase susceptibility to disturbance factors. An increase in biomass N can lead to lowered resistance to pathogen infection or herbivory [58]. This increased vulnerability to pests can result in increased wildfires [59]. Ultimately, these changing conditions could lead to changes in species composition and biodiversity as a result of shifts in nutrient availability or toxicity, environment favorability, and competition [7].

3. Observations of Drought Impacts

Under drought conditions, plants typically undergo C starvation or hydraulic failure [60] (Figure 2 and Table S1). Either condition can be fatal. Carbon starvation occurs when stomata close to constrain water loss, resulting in significantly lower C assimilation that will not only halt growth, but also risk insufficient reserves to sustain plant maintenance requirements. Hydraulic failure occurs when xylems become damaged or collapse, limiting a plant's ability to extract water. The timing of drought and phenology will play a key role that drives plant response [61]. For example, a drought event that coincides with the peak growth period will result in higher plant mortality than drought during a less active growth period. Another important consideration is drought intensity versus drought frequency [62]. A severe drought with a long duration will have a different impact on plant response and survival than short, frequent droughts. The length of time a plant has been exposed to drought cycles is an important driver of trait changes that increase drought tolerance. Over short time scales, stomata regulate water loss, but, over longer time scales, changes in allometry will occur to

optimize hydraulic conductance [22]. Plant traits may change similarly across short and long drought intervals; for example, leaf area may decrease with decreasing precipitation, while other processes may be delayed (i.e., partitioning changes between the leaf and roots) or homeostatic (e.g., xylem vulnerability) [22]. Figure 2 shows some of the effects forests may experience under drought.

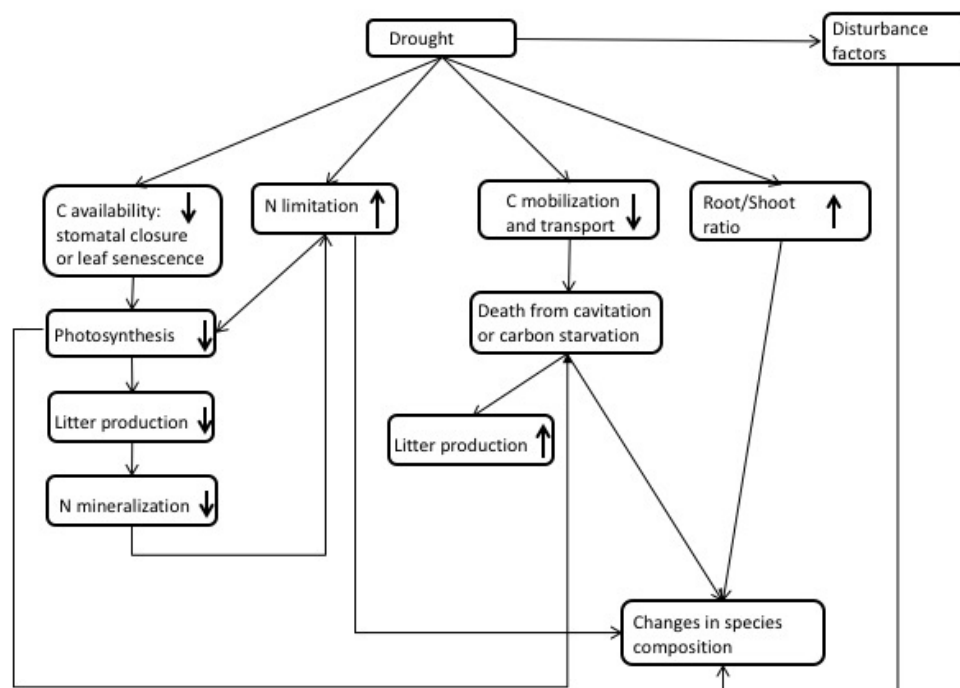


Figure 2. Effects of drought on ecosystems. Up arrows represent an increase, and down arrows represent a decrease. Four main pathways exist: changes in C availability, increases in N limitation, changes to C mobilization and transport, and changes to biomass partitioning (i.e., root:shoot). Changes in C availability and N limitation both lead to decreases in photosynthesis, which has a positive feedback on N limitation when less biomass is contributing N to litter pools. Changes in C availability and a lack of C mobilization can lead to death from carbon starvation. Several pathways result in altered species composition from shifts in nutrient availability and competition. In general, the impacts from drought occur over short timescales (<5 years), while changes to species composition and disturbance occur over longer timescales.

There are many ecological traits that can make a system more or less tolerant to drought, thereby leading to improved water use efficiency, including control over stomatal conductance, allometric plasticity, hydraulic redistribution [63], or even long-term acclimation. To survive drought, plants may also reduce C demand, which can be achieved by leaf senescence and the down-regulation of respiration [64].

Many field studies have observed increased stomatal closure [20,28,65] and increased water use efficiency during droughts [20]. However, observations also found species that have less stomatal control and may continue to transpire well into a drought event [65]. This may provide an advantage during short-term droughts but not necessarily during longer, more intense drought events. The ability to moderate water uptake and growth may be absent in the tropics; Rowland et al. [66] found no change in the growth rate of trees in the Amazon under a long-term drought.

Stomata closure will reduce photosynthesis and, over long periods, lead to lower biomass accumulation, litter production, and ultimately N mineralization in the soil [67]. Additional nutrient limitations can occur during drought because of low soil moisture levels, which act to reduce nutrient flow and diffusion in soils. These N limitations can exacerbate the effects of drought by limiting photosynthesis further.

Since plants continue to demand C for metabolic respiration, when stomata close during drought, plants rely on reserves to meet C requirements. The ability to mobilize and transport stored C may be impaired by drought but is critical for species survival [64]. Carbon reserves can help trees avoid C starvation. As these reserves are depleted, a tree may suffer from C starvation. Although this theory lacks testing, McDowell et al. [60] suspects that C starvation may result in the mortality of isohydric species under drought conditions.

Another adaptation to drought is through increases in the root-to-shoot ratio to maintain respiration during the early stages of drought, as suggested by the optimal partitioning theory. Hertel et al. [21] found a doubling of root production and an increase in root-to-leaf biomass and production under drought in a mature beech forest. Even under significant decreases in a plant's relative growth rate, its root growth may remain constant [68]. The ability to re-translocate biomass from leaves and stems or utilize stored nonstructural carbohydrates can increase survival chances [62]. Furthermore, altering the morphological characteristics of roots (e.g., length and surface area) can also aid in fulfilling water demands [69].

The ability to extend root systems to deep soil layers [70] or move water through the soil column from depth via hydraulic redistribution can also increase a plant's chance of surviving a drought. Not only can this effect transfer water upward into dry soils, allowing plants to maintain transpiration and photosynthesis during dry seasons or at night, it can move water downward to be protected from evaporation or competition. The obvious benefit of hydraulic redistribution is maintaining water potential below hydraulic failure limits, but neighboring plants can also take advantage of the new water that is available [71]. The quantity of water hydraulically transferred ranges from 0.04 mm H₂O d⁻¹ up to 1.3 mm H₂O d⁻¹ and may be as much as 80% of the water that the plant transpires [72].

Several other mechanisms can also play a role in drought mortality such as increased vulnerability to pests or fungal infection and fire [30,73]. These disturbances can have a devastating impact on forest mortality and the C cycle. Similar to N deposition impacts on vegetation, changes in biomass, composition, mortality, and nutrient cycling can lead to shifts in species competition and distribution [60] and the impairment of the mobilization and transport of stored C [64,73].

4. Interactions between N and Drought

The interactions between N and drought are difficult to determine because (1) the effects can depend on the timing of N deposition relative to drought; (2) most experiments are done with young trees or herbaceous plants and not with mature vegetation; (3) many studies impose only weak drought conditions that might not result in drought–N feedbacks [74]; and (4) the impacts vary with ecosystem and plant traits. However, in general, the effects from drought and N deposition are interdependent [24] and not always additive [75,76]. A list of studies that have examined N deposition-drought interactions is included in Table S1.

Drought seems to negate the increase in productivity observed from increased N deposition [77,78], although the effects of N addition may alleviate some of the impacts of drought on growth [78]. This can be partially attributed to the countering effects of N and drought on photosynthesis; in particular, N deposition tends to increase photosynthetic capacity, while drought limits photosynthesis. Other interactions between these two types of stress also occur. For example, N deposition tends to increase water use efficiency (WUE), but, during a severe drought, plants may lose the ability to utilize N, leading to a loss of biomass [77]. Some ecosystems experience a decline in above- and belowground biomass [24,79] and a loss of root functionality [79]. In some cases, changes in allocation between above- and belowground biomass result in higher root-to-shoot ratios [76].

The timing of a drought event is also an important factor considering N level effects. Plants are more susceptible to drought when N availability increases before drought because it leads to higher productivity, thereby increasing evaporative demands [24]. This can even result in a loss of N allocation control and adaptive strategies to mitigate drought effects [24]. Finally, increased N availability can

lower concentrations of compounds that are important for stress tolerance, which could also increase mortality under more severe drought conditions [80].

Plant age also plays a role in determining the response of N deposition combined with drought. Palátová [81] found that the reduction in root biomass due to combined N deposition and drought was more severe for young seedlings than older trees. Trees tend to allocate more biomass to roots as they age, so younger trees are more susceptible to drought, and drought following N deposition further increases sensitivity to drought [76].

However, N deposition during drought may not always be detrimental. For example, drought can lock nutrients in an immobilized state by reducing the soil water available for decomposition [28], but N deposition can increase available nutrients. Increased N deposition can also aid the recovery after drought of some species [25]. For trees that preferentially shift allocations to stems under N deposition and drought [82], water stress may be alleviated by the extra water storage in the tree. In desert systems, N deposition relieved some of the negative effects of water stress through increases in root weight, leaf number, leaf area, biomass, and decreased root-to-shoot ratios [80,83].

5. Earth System Models

ESMs are designed to predict the climate state by integrating feedback between the atmosphere, land, and ocean. One goal of these models is to capture biosphere-atmosphere interactions in order to understand what will be the vegetation response to changing environmental conditions. The land component has undergone considerable growth over the last decade and now has complexity that rivals atmospheric models. This growth has greatly improved the climate forecasting ability of ESMs, but these models still fall short of providing a good estimate of the land C sink. The following section and Table 1 details some important processes already included in many LSMs that are necessary to capture vegetation responses to increased N and drought. The limitations of these model advances are also highlighted.

Table 1. Representation of key model features from a subset of terrestrial ecosystem models.

Process	Model			
	CLM4.5	CABLE	CTEM	LM3
Reference	[84]	[85]	[86,87]	[38,88]
Time step	30 min to one hour	30 min	30 min to one day	30 min
Plant Functional Type (PFTs)	14 natural and two generic crop types	15 natural and one crop type	seven natural and two crop types (C3 and C4)	five natural
Dynamic vegetation	Dependent on climate or prescribed	NA	Dependent on climate or prescribed	Dependent on climate and light
Photosynthesis	[89,90]	<i>Plant C</i> [89]	[89,90]	[89,90]
Phenology	Evergreen, stress deciduous, seasonal deciduous, and crop	Biome dependent, four states, input from remote sensing	Four leaf states: maximum growth, normal growth, leaf fall, and dormancy	Drought and cold deciduous seasonal
Allocation	Fixed fraction	Fixed fraction	Dependent on light, water, phenological status	Functional balance to maintain root-to-shoot ratio
<i>Plant N</i>				
Uptake	Dependent on N pool size, plant demand	Dependent on N pool size, plant demand	NA	Michaelis-Menten kinetics, dependent on N pool size and root biomass; priority given to immobilization
Fixation	Function of Net Primary Productivity (NPP)	External input	NA	Dependent on plant N demand, NPP, and light availability; C cost paid for biological nitrogen fixation (BNF)
Stoichiometry (C:N)	Flexible (within 0.8 N:C)	Fixed (PFT dependent)	NA	Fixed (PFT dependent)

Table 1. Cont.

Process	Model			
	CLM4.5	CABLE	CTEM	LM3
Uptake	Dependent on plant demand, root profile, and soil matric potential	<i>Plant water</i> Dependent on plant demand, root fraction, and soil water content	Dependent on soil moisture content	NA
Root architecture	Double exponential for water uptake [91]; single exponential for soil C/N cycling [92]	Exponential [86]	Prescribed maximum rooting depth, root distribution dependent on time and PFT [93]	NA
Process	Model			
	ORCHIDEE	O-CN	JULES	LPJ-GUESS
Reference	[94]	[94,95]	[96,97]	[98,99]
Time step	30 min to one day	30 min to one day	30 min to one day	1 day
PFTs	10 natural and two agricultural grasses	10 natural and two agricultural grasses	5 natural	11 natural
Dynamic vegetation	Dependent on climate, stand structure, and light	Dependent on climate, stand structure, and light	Dependent on NPP and tree-shrub-grass hierarchy from the Lotka-Volterra competition approach	Dependent on climate, stand structure, light and soil resources, disturbance, and succession
Photosynthesis	[89,90]	<i>Plant C</i> [100]	[90,101]	[90,101]
Phenology	Drought and cold deciduous seasonal	Drought and cold deciduous seasonal	Cold deciduous	Evergreen, drought, and cold deciduous
Allocation	Rule-based response to external limits; dependent on light, water, and N	Pipe model to maintain root-to-shoot ratio	Fixed fraction	Functional balance to maintain root-to-shoot ratio
Uptake	Implicit, dependent on soil humidity and soil temperature	<i>Plant N</i> Michaelis-Menten kinetics, dependent on fine root biomass, plant N status, N pool size, and soil temperature	NA	Dependent on N pool size, plant demand, root mass, and soil temperature
Fixation	NA	Calculate potential N fixation from evapotranspiration	NA	Calculate potential N fixation from evapotranspiration
Stoichiometry (C:N)	Prescribed	Flexible (provided range)	Fixed fraction	Flexible (provided range)
Uptake	Dependent on plant demand, root fraction, and soil water content	<i>Plant water</i> Dependent on plant demand, root fraction, and soil water content	Dependent on plant demand, root fraction, and available soil moisture	Dependent on plant demand and soil water in root zone
Root architecture	Exponential root profile	Exponential root profile	Double exponential	Two soil layers; more roots in lower layer (except grass)

5.1. Nitrogen

An obvious and crucial component for capturing N deposition impacts on plants is the treatment of N, but early versions ESMs only considered the C cycle and neglected the N cycle completely. Carbon-only models miss a significant N deficit and therefore overestimate C sequestration by ecosystems under climate change [102,103]. Many of the latest versions of ESMs now include N (and a rare few include phosphorus). However, because N is often a limiting nutrient in ecosystems, the focus is on plant response under limited N conditions and on the effects of the progressive N limitation [104] that is expected under elevated CO₂. Although some models offer prescribed N, more sophisticated ones employ an N pool (bulk or speciated) that is available to both plants and decomposers. Nitrogen additions come from sources including lightning, deposition, mineralization, and biological fixation. Losses are from plant uptake, immobilization, leaching, and

nitrification/denitrification processes. Models can represent N limitation in different ways, including using N to scale photosynthesis [105,106], downscaling potential gross primary productivity (GPP) to reflect N availability [38,84,85,107], defining a C cost of N uptake [108], optimizing N allocation for leaf processes [109], or adapting a flexible C:N ratio for N allocation [106]. Nitrogen uptake is scaled depending on demand, based on stoichiometry (see Section 5.2) and availability, where photosynthesis and decomposition may be downscaled. More recent developments have led to the development of the Fixation and Uptake of Nitrogen (FUN) model [108], which expands N acquisition to include processes of passive uptake, active uptake, re-translocation, and symbiotic N fixation through a C cost. Other advances in the Community Land Model (CLM) expand N uptake to include methods using Michaelis-Menten equations [106,110] or equilibrium chemistry approximation [111,112]. Additional processes such as abiotic (i.e., mineral surface) competition for soil nutrients (Nutrient COMpetition model, [111]) are anticipated for the next generation of the CLM and the Accelerated Climate Model for Energy (ACME).

5.2. Allometry

ESMs rarely include dynamic responses to changes in resource availability. The most common allocation approach assigns C to each plant component (usually leaf, stem, and root) via fixed ratios that vary with plant functional type (PFT), but not spatially or temporally [38,85,88,95,107,113–115]. For models that include N (and less often P), N uptake plays a strong role in governing C assimilation and drives competition between plants and decomposers. In these cases, C allocation requires an additional constraint of fulfilling C:N:P ratios. Nitrogen uptake is controlled by plant demand and decomposition requirements determined from fixed C partitioning and C:N stoichiometry. When N and P demands to maintain stoichiometric C:N:P are unmet, photosynthesis is downscaled [116,117]. This simple approach works well for regions that have relatively stable environments, but it does not permit plant plasticity responses to changing nutrients. This method of C allocation has been highlighted as a weakness of these models [118,119] and has resulted in some models swapping to more dynamic allocation schemes that allow responses to stress, as in Friedlingstein et al. [120]. Carbon allocation in two ESMs (CTEM [86,87] and ORCHIDEE [94]) is governed by the most limiting resource; light limitation results in more biomass being allocated to the stem, and water and N limitations result in more biomass being allocated to the roots. However, because N is not explicit in these models, the N limitation is parameterized.

The simple representation of plant allometry in ESMs can have a significant influence on biogeochemistry since the allocation of biomass in the form of C to woody versus non-woody (or photosynthetic versus non-photosynthetic) plant components drives biogeochemical cycling, the quality and quantity of litter, and the duration of C storage. Our ability to model C uptake and subsequent storage therefore depends on including C allocation relationships and their responses under changes in resource availability.

5.3. Roots

Another component of ESMs that is oversimplified is root forms and function. For example, most root algorithms in ESMs consist of a fixed rooting depth and distribution [93]. This constrains water uptake to the root zone (weighted by effective root fraction in each layer) and does not allow differential water uptake from soil layers due to changes in root kinetics and morphology, nor does it allow changes in root distribution or depth to increase the water available to the plant. Water uptake is generally a function of plant demand (for evapotranspiration needs), root distribution, and soil water content [121]. The most common model approach to determine water limitation is to calculate a water stress scalar, which can be a function of soil water matric potential, matric potential when stomata are open or closed, or soil water content [121]. That water stress scalar is then multiplied by physiological variables such as transpiration, stomatal conductance, photosynthetic capacity, and maintenance respiration to capture water stress on plants. One approach to improve the evapotranspiration in the

CLM is to add root hydraulic redistribution [122], which can transport water either up or down the soil column. Hydraulic redistribution does not influence root growth or distribution, but it does enhance water uptake by shifting the water distribution in the root zone.

Nitrogen uptake (when included) is often less complex in ESMs; most N uptake is from a bulk N mineralization pool that depends on supply and demand rather than root biomass or profile, although some recent work has focused on uptake as a function of root biomass [106]. Essentially, plants are given every opportunity to extract all available N necessary for growth. Although this allows an implicit metric for allowing roots an opportunity to adjust their uptake, it is not realistic and lacks feedbacks on the biogeochemistry from changes in the root profile.

Recently, studies focused on modeling root growth to maximize various plant traits have been conducted. For example, Sivandran and Bras [123] used optimization techniques for root growth in the TIN-based Real-Time Integrated Basin Simulator coupled to the Vegetation Generator for Interactive Evolution (tRIBS + VEGGIE) model to maximize plant transpiration. The improved root parameterizations allowed more root C to be allocated to soil layers with high soil moisture, increased water uptake, and decreased plant water stress. Another study by McMurtrie et al. [124] altered the vertical distribution of root mass to maximize N uptake. However, the underlying limitation in all studies is that they focus on maximizing only one limiting resource, namely, water or N. This limits the studies' relevance to environments that share those resource limitations so they may not reflect the future state of those regions or be suitable for global application.

6. Models Development Priorities

While ESMs have advanced considerably, there are several processes that still require attention if we are to capture the effects from N deposition and drought as shown in the pathways in Figures 1 and 2. Future model development should focus on the following goals (see Table 2 for summary): (1) allow a more flexible coupling of C and N in models; (2) integrate a dynamic C partitioning algorithm; (3) improve the structure and function of roots; (4) include succession and age classes; (5) include intra-plant competition; and (6) develop methods of trait-based modeling rather than the traditional PFT approach. Some of these developments are being addressed, at least in part, for the next generation of models. For others, support needs to come from observation and the empirical community to develop robust methodology for inclusion in models.

Table 2. Summary of recommendations for model development.

Recommendation	Description	Impact	Example(s)
Flexibility of CN coupling	- Allows C:N ratios in the leaf to vary with N availability - Dynamic partitioning of N in the plant	Effects N in the leaf with influences on photosynthesis	Fixation and Uptake of Nitrogen (FUN) model [108] Leaf Utilization of Nitrogen for Assimilation (LUNA) [109] Community Land Model (CLM)/ Accelerated Climate Model for Energy (ACME) [106]
Adaptive dynamics approach to C partitioning	Flexibility in C allocation to account for plant plasticity across environmental conditions	- Optimize nutrient uptake - Increase tissue allocation to respond to limiting resource	CLM/ACME [106]
Improve form and function of roots	- Time varying root structure (depth and distribution) - Variable root depth, traits, plasticity, and hydraulics that scale across space and time	- Adapt to heterogeneity of water and nutrients in soil - Optimizes below ground resource uptake	Dynamic root depth [125] Maximize N [124] Maximize evapotranspiration (ET) [123]
Succession	- Representing age class - Variable growth dynamics and response to stress with age	- Capture disturbance and recovery - Heterogeneity in plant distribution, improved canopy light dynamics	Ecosystem Demography (ED) model [126]

Table 2. Cont.

Recommendation	Description	Impact	Example(s)
Competition	• Inter- and intra-species competition for resources (e.g., light, water, N, etc.) • Allows competition both within and between PFTs	• Alters allocation of resources to outcompete neighbors • Possibly altering productivity or shift vegetation distribution	Triple Tragedy of Commons [127] Competition with consumers [111]
Trait-based modeling	• Varying morphology, physiology, or phenology characteristics of individuals across an environmental gradient • Environment acts as filter for trait composition	• Adaptation and evolution of species to environmental conditions • Dynamic vegetation moves beyond simple rules of existence and/or establishment	Adaptive Dynamic Global Vegetation Model (aDGVM) [128] Jena Diversity-Dynamic Global Vegetation Model (JeDi-DGVM) [129] CSIRO Atmospheric Biosphere Land Exchange (CABLE) [130]

6.1. Flexibility of C:N Coupling in Models

Given the increase in foliar N under increased N, allowing adaptations in the stoichiometry of C and N would improve model responses [118]. The main impact of this will be to decrease C:N in leaves, driving increases in productivity and changes to soil and litter N content that would be present under increasing N deposition. Changes in C:N ratios occur not just over the lifecycle of the plant, but also in response to changes in nutrient availability, which are not captured in models. Changes in resource availability will result in changes to plant C allocation and partitioning. Furthermore, plant responses will be limited under fixed C:N ratios, which in turn drive changes in belowground biogeochemistry and ultimately C uptake and storage. However, our understanding of how C:N ratios change with plant age and resource status is limited. Therefore, more observations of how C:N is partitioned within the plant over optimal conditions and under climate change are needed.

6.2. Adaptive Dynamics Approach to C Allocation

Possibly the most challenging improvement that would likely provide the most benefit for models predicting C uptake would be to address how C is partitioned within the plant and how that varies over time and with changes to the environment. According to Franklin et al. [114], the difficulty is that C allocation is the result of several processes, which makes a mechanistic approach to represent C allocation difficult. The most robust approach for modeling allocation is adaptive dynamics that include evolution strategies that can emerge through population dynamics and can result in an evolutionary stable strategy [114]. This type of implementation will be difficult in an ESM, given the complexity of integrating dynamic C allocation and the computational demand required to run at high resolution over global scales. However, optimization techniques such as those proposed by Lynch [131] may be an alternative; vegetation may be able to take on the form of optimal response through a cost-benefit approach or game theoretical optimization [114]. This approach allows a flexible plant response to local and regional environmental conditions and nutrient availability. In addition, this functionality would allow PFTs in models to optimize nutrient capture by focusing resources to improve the uptake of the most limiting resources. In a scenario with N deposition and drought, a PFT would be able to alter its root:shoot ratio to increase allocation to roots to increase water uptake or to the stem to increase light competition.

6.3. Improving Form and Function of Roots

In order to allow ecosystems to respond to changes in the environment such as climate change, roots must be allowed to adapt to the heterogeneity of water and nutrients in the soil. Improving the form and function of roots will allow PFTs the opportunity to respond to the heterogeneity of resources, thus increasing the potential for N and/or water uptake. Increasing root depth alone is not sufficient to improve modeled water uptake in water-stressed systems; models also need to consider root distribution, plasticity, and hydraulics [132]. At a minimum, root profiles should include time-varying structures as leaves and stems. Although models tend to have homogeneous soil horizontally (in a grid cell), the vertical structure of resources is dynamic. Allowing roots to proliferate in soil layers where

resources are concentrated gives PFTs the chance to adapt to changes in environment and can further change the vertical distribution of C and N. Baker et al. [63] improved the modeled Net Ecosystem Exchange cycle in the Simple Biosphere Model compared with observations in the Amazon by adding hydraulic redistribution and soil depth to 10 m. Other elements of root systems that should be included in models are root order and classification (which will differ in respiration, uptake, turnover, and storage capacity), root phenology and turnover, and resource uptake response to heterogeneity of resources [133]. Warren et al. [121] provided additional suggestions for improving root representation in models, including scaling root function across temporal and spatial scales and including root traits that inform function and hydraulic redistribution. Although most work in ESM development has focused on improving aboveground productivity, some effort has targeted belowground activities. For example, recent work used optimization techniques to modify root growth to maximize plant transpiration [123] and N uptake [124]. Arora and Boer [93] developed a method to represent root distribution as a function of root biomass, which is a proxy for plant age, to allow root depth to increase when plants are young but grow horizontally when plants are mature. This was implemented in the Integrated Science Assessment Model [125] to capture seasonal leaf area index and GPP in northern high-latitude ecosystems. These methods should be expanded to optimize the most limiting resource, rather than focusing on only one limiting resource.

6.4. Succession

Most models do not consider succession or stand age, despite the evidence that old-growth forests do not respond as strongly as young trees to short-term changes in soil moisture or N availability [134]. This results in a homogeneous distribution of vegetation rather than the heterogeneous plant cover that occurs due to the variation of soils and climate across landscapes. This also limits a model's ability to capture disturbance and recovery events, which are major drivers of C and nutrient cycling. Including succession could help models capture different responses to N and drought stress as a result of tree age by, for example, simulating the higher mortality of young trees. A method to capture succession was implemented by Fisher et al. [135] in the Community Land Model by separating vegetation into cohorts of age, PFT, and height; this method was tested against deciduous–evergreen forest boundaries [126]. These techniques can capture the variability of individual PFTs within a grid cell, adding large-scale heterogeneity in plant distribution, and can be the first step toward a more trait-based modeling approach (see Section 6.6).

6.5. Competition

In many LSMs, plants compete for resources such as light, water, and nutrients within a grid cell based on their weight on the grid cell. In these cases, the competition is between different PFTs and not within a PFT. Dynamic vegetation models can force one PFT to replace another when climate conditions are favorable [136]. A few LSMs have adopted Lotka-Volterra predator/prey equations [137] to represent colonization rates. However, no model currently implements a game-theoretic approach to the competition for resources that can produce an overabundance of biomass for resource uptake to outcompete neighbors. This method has the potential to improve estimates of plant production, respond to changing resources, and lead to an evolutionary stable strategy [138]. PFTs would have the opportunity to alter biomass allocation (i.e., shifts in the root:shoot ratio) to outcompete neighbors for limiting resources, which would lead to shifts in productivity and vegetation species distribution. Although it is hindered by the current model's resolution, as continuously expanding computational capabilities move toward high-resolution models [139], game theory is an achievable target.

6.6. Trait-Based Modeling

The current PFT approach to modeling vegetation is limited to feedback that results from changes in species distribution since most models assume that attributes within a PFT do not change with climate [140]. To capture the adaptation and evolution of vegetation, the concept of trait-based

modeling was introduced by Lavorel and Garnier [141]. Trait-based modeling links plant traits that act as plant responses to the environment with plant traits that represent the effect of plants on the ecosystem in order to capture the plant assemblage of a region. A trait can be defined as a feature that describes the morphology, physiology, or phenology characteristics of an individual, which can vary across an environmental gradient [142]. Trait based modeling allows dynamic vegetation to move beyond simple climate based temperature controls on vegetation existence and establishment. Therefore, species distribution would be a response to N and drought in the ecosystem. This approach has been used to improve two dynamic vegetation models (aDGVM, [128]; JeDi-DGVM, [129]). The Jedi-DGVM outperformed other leading dynamic vegetation models for Leaf Area Index (LAI), NPP, CO₂ seasonality, C fluxes, and, in some regions, C stocks [129]. Incorporating plant traits in the CSIRO Atmospheric Biosphere Land Exchange (CABLE) model improved the biogeographical distribution of major forests that have multiple dominant PFTs [130]. Using plant traits to capture whole-plant hydraulics has even been suggested to improve C and water use responses to drought [143]. The benefit of trait-based modeling is that the environment acts as a filter for trait composition, analogous to evolutionary selection processes [140], and is not limited by climate and geography. This is particularly important considering that McNeil et al. [144] found that species' foliar N responses to N deposition were dependent on two main plant traits, leaf mass area and shade tolerance. Matheny et al. [136] also suggested several plant traits that could influence the availability of water to a plant that span across leaves, stems, and roots. The challenge is finding data to support the choice of traits and how different traits co-vary.

7. Conclusions

We have provided a review of the impacts of N and drought on ecosystems and a list of future model recommendations that serves to address the missing processes needed in LSMs to capture those interactions. While this list is extensive, it is by no means exhaustive. Our suggestions target two co-occurring stressors, but additional stresses will also be present that should be considered such as warming, elevated CO₂, and herbivory. For example, herbivory could reduce the N benefits of elevated productivity from consumption [145] or be a source of N deposition. Effects from elevated CO₂ can vary; CO₂ fertilization can help mitigate extreme heat and drought [146], or fertilization effects on productivity may be eliminated during drought and nutrient limitation [147]. These additional impacts on ecosystems are important, considering that CO₂ fertilization currently plays a larger role than N deposition in increasing productivity [148].

Another example is the interactions that exist between N availability, drought, and air temperature. It is thought that forest productivity should increase with temperature at the global scale, but droughts often associated with increases in temperature have lowered the NPP potential in some regions [149]. For instance, tropical forests can increase Net Ecosystem Exchange (NEE) with modest increases in air temperature, and drought effects could be ameliorated with increases in atmospheric CO₂ [150]. The interactions of temperature with drought and N can also affect the surface properties of forests beyond evapotranspiration. Drought sensitive forests (deciduous forests) tend to have a higher surface albedo than drought resistant ones (e.g., conifer forests), affecting the regional energy balance [151]. Further, increases in temperature can increase decomposition and N mineralization rates in the absence of drought, but N mineralization will not respond to temperature if moisture is the limiting factor [152]. These biophysical properties are important in understanding the global net effect of drought and N deposition on biosphere climate interactions [153] and are not the focus of this work. It is important to note that, in most elevated temperature ecosystem experiments, drought is a secondary effect caused by elevated temperature treatments [154,155], making it difficult to distinguish primary from integrated responses of forests to drought and temperature on biogeochemical and biophysical processes.

This study only focused on two stressors to ecosystems, N and drought. Although some of the identified processes targeted by this manuscript may help models to capture impacts from other climate-related effects, additional ecosystem processes will need to be addressed in the future. As the

community integrates additional processes in models to capture vegetation responses to N inputs, we can revisit the resulting C uptake to evaluate the sink capacity of the terrestrial surface. However, special care should be taken when implementing additional parameters and processes into models, particularly so that models are not over-parameterized and so that the resulting C cycle response is not constrained by incomplete observational data. In the near term, model sensitivity studies can be used to determine the most sensitive parameters and processes that drive changes in C and nutrient cycles. More research on the structural uncertainty of models can provide insight on those processes that have strong feedbacks or introduce instability. Finally, when rigorous model testing through benchmarking is complete, we can focus on additional questions related to the fate of C in the land.

Improving estimates of the global terrestrial C sink is a priority for ESM development. In order to improve the predictions and reduce uncertainty, model development should focus on the processes that will be affected by multiple co-occurring stressors such as N deposition and drought. We have suggested avenues of model improvement that are possible in the near future with hopes that future generations of models can benefit and capture the response to increased N availability and drought.

Supplementary Materials: The following are available online at www.mdpi.com/1999-4907/8/8/267/s1, Table S1, Summary of previous studies that have investigated N deposition, drought, and the interactions of ecosystems.

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