Evolutionary Ecology Research, 2016, **17**: 75–93

Why do mosses have height? Moss production as a tragedy of the commons game

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ABSTRACT

Question: Why do mosses produce stem-like structures that allow them to grow above their neighbours? Does answering this question help us understand patterns in moss production under environmental change?

Hypothesis: Light competition leads to an evolutionary struggle for height that enhances the ability of mosses to acquire light relative to their neighbours.

Method: We use evolutionary game theory and develop a foraging game for carbon and nitrogen. The game seeks evolutionarily stable strategies for leaf bract and stem production in moss.

Key assumptions: Water is available in sufficient quantities so as not to limit moss growth. There is no nutrient toxicity. Resource harvest as a function of tissue production occurs with diminishing returns, and the costs of tissue production increase linearly with tissue production.

Conclusions: The model predicts that moss production should increase dramatically under carbon fertilization, but not respond to nitrogen fertilization. The struggle for height means that mosses should favour the production of stem-like structures over leaf-like structures. The empirical results in the literature are broadly consistent with these predictions.

Keywords: evolutionarily stable strategy, evolutionary game theory, moss, peatlands, tragedy of the commons.

INTRODUCTION

Why do mosses have stem-like structures that allow them to grow above the surface of the ground? Indeed, mosses are somewhat unique among Bryophytes in that they have stem-like structures that allow them to lift their photosynthetic organs above the surface of the ground (During, 1979; Cox *et al.*, 2010). This ability to grow taller than their bryophyte sister groups means that moss-dominated systems (e.g. peatlands) often have organic layers of moss tissue that can be several metres deep (Gorham, 1991; Clymo *et al.*, 1998; Gauthier *et al.*, 2015). In contrast, sister groups to mosses, such as liverworts or hornworts, do not dominate any systems, or create large amounts of organic litter. We could take it for granted that this is simply

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how mosses 'are', but it might be interesting to approach the problem from a Darwinian perspective and ask: why do mosses have these stem-like structures (hereafter stems) that allow them to be slightly tall? Answering this question might serve several purposes, chief among them is that it could advance our understanding of carbon accumulation in peatlands, which are estimated to be a global pool of >400 petagrams of stored carbon, and the fate of this carbon pool is critically important in the context of global climate change (Gorham, 1991; Clymo *et al.*, 1998).

Stems are ubiquitous in the modern landscape, but they are not a necessary condition of being a primary producer, nor have they been a constant feature in the history of terrestrial vegetation; algae, liverworts, and hornworts survive perfectly well with only leaf-like photosynthetic organs (hereafter leaves). The value of leaf-like bracts possessed by mosses are clear: leaves forage for carbon, and this foraging produces valuable photosynthates that can be catabolized to fuel respiration, anabolized to construct more leaves, invested into future survival, or invested into reproductive output. Indeed, in some sense, leaf-like photosynthetic structures are what define primary producers as primary producers. In this foraging context, the value of stems is less clear. Stems do not harvest any resources, and any allocation to stems diverts photosynthate from important processes related to survival and reproduction. We return to the question: what is the function of these stem-like structures in mosses? Here, we suggest that the reason why mosses have stems is purely competitive and requires an understanding of competition for light as an evolutionary game (Givnish, 1982; Falster and Westoby, 2003).

To understand this competitive nature of height among primary producers, consider the physical properties of light: light comes from the sun, in a straight line, and strikes the surface of the Earth. At masses relevant to the scale of moss bodies, light does not turn corners, and it cannot go around obstacles. When individuals compete for access to light, taller individuals possess a marked competitive advantage that is twofold: the tallest individuals not only secure their own access to light, but they simultaneously deprive their competitors of access to light. The production of stems is therefore a tragedy of the commons game (*sensu* Gersani *et al.*, 2001). If all the mosses in the world could somehow 'agree' to stop producing stems, presumably each moss individual could redirect photosynthate they currently allocate to stems towards reproduction, survival, and possibly more photosynthesis. However, even though selfish stem production comes at considerable cost, it affords a competitive advantage, and individuals without stems are at a severe competitive disadvantage. This game-theoretic aspect of plant height has long been recognized for vascular plant stem production (Givnish, 1982; Falster and Westoby, 2003), but to our knowledge the implications of such a game for moss growth and moss-dominated systems has not been explored.

Here we develop a simple game-theoretic model of moss growth based on principles that have been developed to understand vascular plant growth, but adjusted to reflect the unique functional ecology of mosses. The most important difference between vascular plants and mosses from the perspective of resource foraging is that mosses lack roots, and instead capture nutrients through their leaves. We ask: (1) how is moss leaf-bract and stem production predicted to change with resource availability in such a game-theoretic model? And (2), how do the traits of species affect tissue production in such a game?

MODEL

Lessons from vascular plant models

It is increasingly common to model vascular plant growth as a function of leaf, stem, and root production, where these three tissue production strategies are involved in a foraging game for resources (Dybzinski *et al.*, 2011; Franklin *et al.*, 2012; Chen *et al.*, 2013; Farrior *et al.*, 2013). We use the term foraging because leaves harvest carbon, and roots harvest nutrients [i.e. foraging (*sensu* Hutchings and de Kroon, 1994; Gleeson and Fry, 1997; McNickle *et al.*, 2009)], and it is a game because the tissue production strategies of individuals relative to their competitors influence their competitive ability (Givnish, 1982; Gersani *et al.*, 2001; Falster and Westoby, 2003; McNickle and Dybzinski, 2013). Such a game-theoretic model of plant growth relies on the concept of the evolutionarily stable strategy [ESS (*sensu* Brown *et al.*, 2007; McGill and Brown, 2007; Apaloo *et al.*, 2009; but see Apaloo *et al.*, 2014)] to seek strategies for production that maximize the competitive ability of individuals that once adopted are stable through evolutionary and ecological time and cannot be invaded by rare mutants possessing alternative tissue production strategies. Importantly, strategy changes may occur through plasticity in the lifetime of an organism (i.e. changes in allocation), ecological dynamics in ecological time (i.e. species replacement via population dynamics), or evolutionary dynamics in evolutionary time [i.e. micro-evolutionary adaptation (Maynard-Smith and Parker, 1976; McNickle and Dybzinski, 2013)]. Without an explicit population dynamic, it is not possible to determine which of these three possibilities will be the dominant force in achieving the ESS, but we can still make predictions about what we might observe in nature (Dybzinski *et al.*, 2011; McNickle and Dybzinski, 2013; Apaloo *et al.*, 2014).

The moss game differs in one key aspect from the foraging games played by vascular plants: mosses do not possess roots, and moreover, moss leaves serve a dual role in both nutrient and carbon foraging. Thus, extending concepts that have been applied to vascular plants, we hypothesize that a simple moss body plan that is composed of leaf-like structures (u_{il}) and stem-like structures (u_{is}) involved in a foraging game will be sufficient to predict a large proportion of observed variability in moss growth form and net primary productivity by mosses. We emphasize that this model is a hypothesis: what follows should be viewed as a set of testable and ultimately falsifiable hypotheses based on the assumptions made in the construction of our model; validation will require empirical work that is beyond the scope of this paper.

A tragedy of the commons game for moss

This moss foraging game is a vector-valued game where the strategy ($\mathbf{u}_i$) of moss individual i is made up of both leaf (u_{il}) and stem (u_{is}) production strategies given by the vector strategy, $\mathbf{u}_i = [u_{il}\ u_{is}]$. The model is envisioned to be parameterized to produce output as net primary productivity (NPP) in units of grams dry weight per square metre per year ($\text{g DW} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$), but could potentially predict absolute biomass. The model assumes that mosses forage for only carbon (C) and nitrogen (N), which are the most limiting resources for most terrestrial vegetation (Chapin *et al.*, 1986; Vitousek and Howarth, 1991). Moss leaves acquire both C and N in proportion to total leaf production, such that increased leaf production simultaneously increases the harvest of C and N but with diminishing returns. Let N_{avail} represent the total amount of nitrogen ($\text{g N} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$) available in the absence of competition. N_{avail} is commonly measured as available nitrogen mineralization rates per area per time. C_{avail} is a similar concept; it is the total amount of carbon (g $\text{C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$) available to each individual per area per time. C_{avail} is a more complex parameter, which is influenced by atmospheric CO_2 concentrations, temperature, and physiological traits of species, but C_{avail} can be thought of as the maximum theoretical gross primary productivity (GPP) of moss in the absence of competition. C_{avail} will not be the actual realized GPP, but instead is the maximum possible GPP in the absence of competition, and in the absence of nutrient limitation. We build these foraging equations from functional forms that have been shown to work well for vascular plant foraging behaviour (Gleeson and Fry, 1997; McNickle and Brown, 2012, 2014). These functional forms assume that the amount of plant-available C and N can be captured as a decelerating function of leaf production among x players given by:

$$H_C(\mathbf{u}_l) = C_{avail}\,(1 - e^{-\sum_{i=1}^{x} u_{il}}), \tag{1a}$$

$$H_N(\mathbf{u}_l) = N_{avail}\,(1 - e^{-\sum_{i=1}^{x} u_{il}}). \tag{1b}$$

This formulation assumes that depletion of each resource follows a negative exponential as a function of leaf production such that the amount that remains unharvested is given by:

$$C_{avail}e^{-\sum_{i=1}^{x} u_{il}} \quad \text{and} \quad N_{avail}e^{-\sum_{i=1}^{x} u_{il}}.$$

This formulation also ensures that maximum harvest may not exceed C_{avail} or N_{avail} (i.e. individuals obviously cannot harvest more resources than are available).

Equations (1a) and (1b) represent the total amount of C and N that is available to all individuals as a function of their foraging effort, and these resource harvests must be divided among competing individuals based on their relative strategy values. Competition is extremely well studied among vascular plants (Wilson, 1988; Casper and Jackson, 1997), less so for mosses. However, we argue that the ‘rules’ of vascular plant competition are largely dictated by the physical properties of resources, and thus we believe that it is reasonable to assume that competition among mosses can be described by similar functional relationships as competition for vascular plants. Specifically, since moss leaves harvest N, we assume that competition for N is symmetric with leaf biomass (Casper and Jackson, 1997; Schwinning and Weiner, 1998) such that small increases in leaf production lead to proportionally small increases in N harvest. Size symmetry in nutrient competition occurs because of the physical properties of nutrient movement: nutrients may come from many directions and can move in three dimensions through the substrate. This means that mosses with the greatest investment into leaves will gain the most access to N, but it is not possible for any one competitor to physically block access to N by competitors since nutrients can simply diffuse around obstacles. This assumption is typically modelled by hypothesizing that the amount of N captured by individual i is simply proportional to its relative leaf production (O’Brien *et al.*, 2007; McNickle and Brown, 2012) given by:

$$f(u_{il}, \mathbf{u}_l) = \frac{u_{il}}{\sum_{j=1}^{x} u_{jl}}. \tag{2}$$

When x competitors have the same leaf production strategy (i.e. $u_{1l} = u_{2l} = \ldots = u_{xl}$), then the function f takes on a value of $1/x$ and $\Sigma f = 1$ across all players in the game. This means that when there is no competition (i.e. a one-player game), $f = 1$, and the entire focus of tissue production is on resource foraging, but when there is competition (i.e. more than a one-player game), tissue production becomes partially about resource foraging and partially about resource pre-emption from neighbours (Gersani *et al.*, 2001). From equation (2), the individual with the highest leaf production gets the largest share of nitrogen, which is linearly proportional to its relative leaf production. Since this works well for vascular plants, we feel it can provide a first approximation for mosses.

Competition for C is quite different, and is well known to be asymmetric with both height (i.e. stem production) and leaf production in vascular plants (Givnish, 1982; Schwinning and Weiner, 1998; Falster and Westoby, 2003; Murphy and Dudley, 2007) such that small increases in stem or leaf production produce disproportionately large increases in competitive ability and C harvest. Size asymmetry in carbon competition happens again because of the physical properties of photosynthetically active radiation that is necessary to fix carbon. Unlike nutrients, the majority of usable light comes almost exclusively from one direction (travelling in a straight line from the sun to the surface of the Earth), moves along a one-dimensional plane and, unlike nutrients, cannot diffuse around obstacles. This means that it is relatively easy to block competitors' ability to photosynthesize by simply being taller and/or leafier than one's neighbours and thus blocking their access to light. Mathematically, we can adjust equation (2) to include both stems and leaves, and make the relationship non-linear by weighting leaf and stem production by an exponent. This size asymmetry in competitive ability can be captured for individual i by:

$$z(u_{il}, u_{is}, \mathbf{u}_l, \mathbf{u}_s) = \frac{u_{il}^{z_{il}} u_{is}^{z_{is}}}{\sum_{j=1}^{x} u_{jl}^{z_{jl}} u_{js}^{z_{js}}}. \tag{3}$$

Here, the function z is similar to the function f (eq. 2), in that it represents the proportion of available carbon captured by individual i within the community as a function of their stem and leaf production. The exponents z_{il} and z_{is} are unitless parameters that scale the degree of size asymmetry where it is assumed that $z_{il} > 1$ and $z_{is} > 1$. Again, when x competitors have the same leaf production strategy and also the same stem production strategy (i.e. $u_{1l} = u_{2l} = \ldots = u_{xl}$ and $u_{1s} = u_{2s} = \ldots = u_{xs}$), then the function z takes on a value of $1/x$ regardless of the value of the exponents z_{il} and z_{is}. However, unlike the function f, the function z gives the largest individuals a disproportionately large competitive advantage, and the degree of size asymmetry is scaled by the magnitude of the exponent z_{il} or z_{is}. Furthermore, in equation (3), u_{il} and u_{is} are multiplied so that individuals that attempt to play a value of 0 for either stems or leaves cannot fix any carbon, but because this is a ratio of the products, the multiplicative effect is erased. This multiplicative part is critical, otherwise individuals that produced 0 leaves or 0 stems could somehow parasitize the harvest of neighbours by producing only stems, or producing only leaves, and this is biologically impossible for mosses (though it could be an interesting game!).

In the final component of the model, we must combine the harvest of N and C (eq. 1a and 1b), the competitive functions (eq. 2 and 3), and link it all to fitness in order to solve for the ESS. We envision that in this foraging game, moss fitness is determined by a weighted product of the surplus carbon (π_C) and surplus nitrogen (π_N) that remains after production and maintenance of tissues. We call this surplus *resource profit*, and assume that, all else being equal, it would be invested into reproduction and survival. Under this framework, a product is employed because carbon and nitrogen have multiplicative rather than additive effects on fitness; furthermore, this product is weighted because organisms do not require C and N in the same amounts. The weights α and β appear as exponents on the resource profits and are determined such that $\alpha{:}\beta$ is the ideal $\pi_C{:}\pi_N$ ratio for moss reproductive output. That is, this is the ratio in which C and N need to be combined into the synthetic organic molecules that constitute biomass. Clearly, surplus C (or N) has no value if there is not enough N (or C) to combine to synthesize organic molecules, and α and β weight the relative importance of C and N in the creation of biomass. Thus, moss fitness as a function of leaf and stem production can be written as the following weighted product of net C and N profit:

$$G(u_{il}, u_{is}, \mathbf{u}_l, \mathbf{u}_s) = \pi_{iC}^{\alpha}\pi_{iN}^{\beta}. \tag{4}$$

Equation (4) has the form of a Cobb-Douglas production function (Cobb and Douglas, 1928; Goldberger, 1968), used by economists to optimize a single output (here fitness) that is generated from multiple inputs (here net C and N profit). The standard Cobb-Douglas theory tells us that under the condition that the total profit $\pi_C + \pi_N$ is fixed, the fitness function G will be maximized when the carbon to nitrogen profit ratio $\pi_C{:}\ \pi_N$ is equal to $\alpha{:}\beta$. More typically, the Cobb-Douglas function is used to consider the balance between labour and capital in manufacturing, but the equation has well understood properties and we believe the analogy between the production of one output from multiple inputs in manufacturing is appropriate for the production of one output from multiple foraging inputs in moss. Net profit is determined by total harvest (zH or fH) minus the costs (c) of producing and maintaining tissues, such that:

$$\pi_{iC} = z(u_{il}, u_{is}, \mathbf{u}_l, \mathbf{u}_s)\, H_C(\mathbf{u}_l) - c_{icl}u_{il} - c_{ics}u_{is}, \tag{5a}$$

$$\pi_{iN} = f(u_{il}, \mathbf{u}_l)\, H_N(\mathbf{u}_l) - c_{inl}u_{il} - c_{ins}u_{is}, \tag{5b}$$

where c_{icl} and c_{ics} represent the costs in terms of C required for tissue construction, but also maintenance and respiration (g C/g DW). Similarly, c_{inl} and c_{ins} represent the costs in terms of N required for tissue construction (g N/g DW). Costs are assumed to be linear for simplicity, but any monotonically increasing function will produce qualitatively similar results as we report here. Generally, N costs will be substantially lower than C costs because tissues are primarily composed of C, and C is also required for respiration producing a running C cost, whereas there is no running cost for N.

In this model, the ESS for all interacting individuals occurs where marginal resource harvest balances marginal costs for all individuals simultaneously. The ESS can be thought of as the most competitive strategy that simultaneously maximizes marginal benefits and competitive ability. We will call this solution an ESS, but mathematically the solution is also a Nash equilibrium, since it does not account for population dynamics (Apaloo *et al.*, 2014). The partial derivatives of equation (4) with respect to each tissue pool for player i are:

$$\frac{\partial G_i}{\partial u_{il}} = \alpha\pi_{ic}^{\alpha-1}\pi_{in}^{\beta}\frac{\partial \pi_{ic}}{\partial u_{il}} + \pi_{ic}^{\alpha}\beta\pi_{iN}^{\beta-1}\frac{\partial \pi_{in}}{\partial u_{il}}, \tag{6a}$$

$$\frac{\partial G_i}{\partial u_{is}} = \alpha\pi_{ic}^{\alpha-1}\pi_{in}^{\beta}\frac{\partial \pi_{ic}}{\partial u_{is}} + \pi_{ic}^{\alpha}\beta\pi_{iN}^{\beta-1}\frac{\partial \pi_{in}}{\partial u_{is}}. \tag{6b}$$

Table 1 gives the component derivatives required. To find the ESS for x players, equation (6a) and (6b) are evaluated at:

$$\frac{\partial G_i}{\partial u_{il}} = \frac{\partial G_i}{\partial u_{is}} = \ldots = \frac{\partial G_x}{\partial u_{xl}} = \frac{\partial G_x}{\partial u_{xs}} = 0. \tag{6}$$

Parameterization

Table 2 defines and describes the parameters and the values used. The specific values chosen were based partly on the simple fact that organic life is composed of more C than N. This leads to simple relationships that must be present to model life on Earth, for example the parameters α and β represent the C:N ratio of moss reproductive output and therefore regardless of the specific values, $\alpha \gg \beta$. For the same reason, the C cost parameters (c_{icl} and c_{ics}) should be larger than the N cost parameters (c_{inl} and c_{ins}). Our experience with the model suggests that, if these inequalities are maintained, the model is surprisingly insensitive to specific parameter values. However, we also tried to choose values based on empirical observation.

Table 1. Partial derivatives of the model

Derivative with respect to	Carbon, π_{iC}	Nitrogen, π_{iN}
Stem: $\partial\pi_{ix}/\partial u_{is}$	$\frac{\partial z(u_{il}, u_{is}, \mathbf{u}_l, \mathbf{u}_s)}{\partial u_{is}} H_c(\mathbf{u}_l) - c_{ics}$	$-c_{ins}$
Leaves: $\partial\pi_{ix}/\partial u_{il}$	$z(u_{il}, u_{is}, \mathbf{u}_l, \mathbf{u}_s)\frac{\partial H_n(\mathbf{u}_l)}{\partial u_{il}} + \frac{\partial z(u_{il}, u_{is}, \mathbf{u}_l, \mathbf{u}_s)}{\partial u_{il}} H_n(\mathbf{u}_l) - c_{icl}$	$f(u_{il}, \mathbf{u}_l)\frac{\partial H_n(\mathbf{u}_l)}{\partial u_{il}} + \frac{\partial f(u_{il}, \mathbf{u}_r)}{\partial u_{il}} H_n(\mathbf{u}_r) - c_{inl}$
Partial derivative	Equation of partial derivative	
$\frac{\partial z(u_{il}, u_{is}, \mathbf{u}_l, \mathbf{u}_s)}{\partial u_{is}}$	$\frac{u_{il}{}^{z_{il}} z_{is} u_{is}{}^{(z_{is}-1)}[(\sum_{i=1}^{x} \mathbf{u}_l{}^{\mathbf{z}_l}\, \mathbf{u}_s{}^{\mathbf{z}_s}) - u_{il}{}^{z_{il}} u_{is}{}^{z_{is}}]}{(\sum_{i=1}^{x} \mathbf{u}_l{}^{\mathbf{z}_l}\, \mathbf{u}_s{}^{\mathbf{z}_s})^2}$	
$\frac{\partial z(u_{il}, u_{is}, \mathbf{u}_l, \mathbf{u}_s)}{\partial u_{il}}$	$\frac{z_{il} u_{il}{}^{(z_{il}-1)} u_{is}{}^{z_{is}}[(\sum_{i=1}^{x} \mathbf{u}_l{}^{\mathbf{z}_l}\, \mathbf{u}_s{}^{\mathbf{z}_s}) - u_{il}{}^{z_{il}} u_{is}{}^{z_{is}}]}{(\sum_{i=1}^{x} \mathbf{u}_l{}^{\mathbf{z}_l}\, \mathbf{u}_s{}^{\mathbf{z}_s})^2}$	
$\frac{\partial f(u_{il}, \mathbf{u}_l)}{\partial u_{il}}$	$\frac{(\sum_{i=1}^{x} \mathbf{u}_l) - u_{il}}{(\sum_{i=1}^{x} \mathbf{u}_l)^2}$	
$\frac{\partial H_n(\mathbf{u}_l)}{\partial u_{il}}$	$C_{avail}\,(e^{(-\sum_{i=1}^{x} \mathbf{u}_l)})$	
$\frac{\partial H_n(\mathbf{u}_l)}{\partial u_{il}}$	$N_{avail}\,(e^{(-\sum_{i=1}^{x} \mathbf{u}_l)})$	

Note: Top rows show the partial derivatives of the profit functions (π_{iC}, π_{iN}) with respect to stem production (v_s) or leaf production (v_l), and bottom rows show the partial derivatives of the individual components of the profit functions.

Table 2. Parameter descriptions, units and values used for figures in main text

Parameter	Description	Units	Values assumed unless otherwise stated	Ranges used, Fig. 1c,d
C_{avail}	C availability: the maximum amount of carbon that can be harvested by photosynthesis in 1 year, per square metre of ground, with no competition. We envision this to be limited primarily by photoperiod and growing season length, but also influenced by atmospheric CO_2	$g\ C \cdot m^{-2} \cdot year^{-1}$	250	Varied: 10–500
N_{avail}	N availability: the maximum amount of nitrogen that can be harvested by roots in 1 year, per square metre of ground, with no competition	$g\ N \cdot m^{-2} \cdot year^{-1}$	50	10–100
α	Proportion of moss composed of C	Proportion	0.98	0.8–0.99
β	Proportion of moss composed of N	Proportion	$(1 - \alpha)$	$(1 - \alpha)$
z_{il}	Exponent for size-asymmetric competition of leaves. Larger values make size-asymmetric competition more severe. ($z_{il} = 1$ produces size-symmetric competition)	Unitless		
z_{is}	Same as z_l, but for stems	Unitless	1.5	1–1.5
c_{ics}	Carbon costs of tissue production, and	$g\ C \cdot g\ tissue^{-1} \cdot year^{-1}$	1.5	0.9–3
c_{icl}	respiration, per gram of tissue, per year	$g\ C \cdot g\ tissue^{-1} \cdot year^{-1}$	1.5	0.9–3
c_{ins}	Nitrogen costs of tissue production, per	$g\ N \cdot g\ tissue^{-1} \cdot year^{-1}$	0.03	0.01–0.3
c_{inl}	gram of tissue, per year	$g\ N \cdot g\ tissue^{-1} \cdot year^{-1}$	0.03	0.01–0.3

Note: For clarity β is also shown, but it is always equal to $1 - \alpha$. Output is sensitive to initial conditions in all numerical simulations where $u_i = [0.1\ 0.1\ 0.1]$. The parameters were estimated primarily from physiological rates observed in vascular plants.

We use observed carbon-to-nitrogen ratios in mosses as an initial estimate for α and β. For example, moss C:N ratios range from 25 to 100 (Van der Heijden *et al.*, 2000a), which translate into a range for α between 0.96 and 0.99. Since $\beta = 1 - \alpha$, the upper range for α can only approach 1, but cannot equal 1 (otherwise the moss would have zero N in its body). In our simulations, we reduced the value of α as low as 0.8 to examine the sensitivity of the model to possible values for α.

The carbon cost of tissues will primarily be the running cost of respiration required to maintain tissue. Moss respiration rates range from 4 to 13 nmol $CO_2 \cdot g^{-1}\ DW \cdot s^{-1}$ (Van der Heijden *et al.*, 2000b). Using the molecular weight of CO_2, we can convert this into grams of C per gram of tissue, although estimating this per year depends heavily on how much of the year mosses are expected to be actively respiring. For example, this range would be 1.5–4.9 g $C \cdot g^{-1}\ DW \cdot year^{-1}$ if mosses were to respire every single second of every year, but in reality most moss-dominated systems have a dormant season (e.g. winter) for at least half the year. Assuming mosses only respire for half the year changes the range to 0.75–2.45 g $\mathrm{C \cdot g^{-1}}$ $\mathrm{DW \cdot year^{-1}}$. Finally, the carbon costs will also include structural C, and must be increased slightly to account for structural C (Berendse *et al.*, 2001). Thus, we used a range for the C cost parameters ranging between 0.9 and 3 (Table 2).

The N cost of producing tissue will primarily be structural N that goes into building the tissues. The N content of dry tissues in mosses ranges between 4 and 25 $\mathrm{mg \cdot g^{-1}}$ (Van der Heijden *et al.*, 2000a, 2000b; Limpens *et al.*, 2011), which translates into N cost parameter values in the range 0.04–0.25. We increased this range slightly on either end to ensure that we captured the sensitivity of the model at the ends of the range (Table 2).

Finally, the exponents that generate size-asymmetric light competition (z_{il} and z_{is}) are abstract concepts. We were unable to find any data comparing competitive outcomes of mosses that vary in height such that we could estimate these parameters. They must necessarily be larger than 1, and we hypothesize that $z_{is} > z_{il}$; that is, being tall affords more competitive ability than being leafy. In the end, our choice of values here is somewhat arbitrary, and this is a potential source of uncertainty in the model. We use smaller values for these exponents in most of our simulations (Table 2), and then also explore a much larger range of parameter space.

RESULTS

Moss growth along resource availability gradients

Interestingly, the model predicts that moss NPP should respond strongly to factors that affect C availability, but that moss growth should have almost no response to N availability (Fig. 1a,b). This happens in the model because of the foraging aspect of the model: we assume that leaves are produced to balance marginal benefits with marginal costs for whichever resource is most limiting to fitness output (i.e. to balance $\partial zH_C/\partial u = \partial c_C/\partial u$ and $\partial fH_N/\partial u = \partial c_N/\partial u$). However, because of the dual role of moss leaves in harvesting both C and N, and because substantially more C is required relative to N to construct tissues (i.e. $\alpha > \beta$ and $c_{ic} > c_{in}$), this means that leaves are generally produced to balance $\partial zH_C/\partial u = \partial c_C/\partial u$ and, as a result, production of leaves actually exceeds what is required to harvest N such that $\partial fH_N/\partial u > \partial c_N/\partial u$. This inequality in the marginal benefits of N harvest caused by the dual foraging role of leaves and stoichiometry of moss means that mosses have excess capacity for N uptake, and therefore should respond to N availability only where they have very high C availability relative to N availability, but should respond to C availability almost regardless of N availability for both leaf (Fig. 1a) and stem (Fig. 1b) production. We highlight that the results in Fig. 1a,b are for NPP and not for fitness. Finally, the step-like breaks in the surfaces shown in Fig. 1a,b occur because of the size-asymmetric competition in the game and because $\alpha > \beta$. As more resources become available, the game favours increasingly large ESSs that jump to higher values when availability of resources permits increased allocation, and this forces all individuals to respond in kind.

The model also predicts that regardless of total NPP of mosses, stem production should typically exceed leaf production. This qualitative prediction (stems > leaves) holds because of the asymmetric nature of light competition (eq. 3) and the fact that life on Earth requires more carbon than nitrogen (i.e. $\alpha > \beta$). As parameterized (Table 2), the model predicts

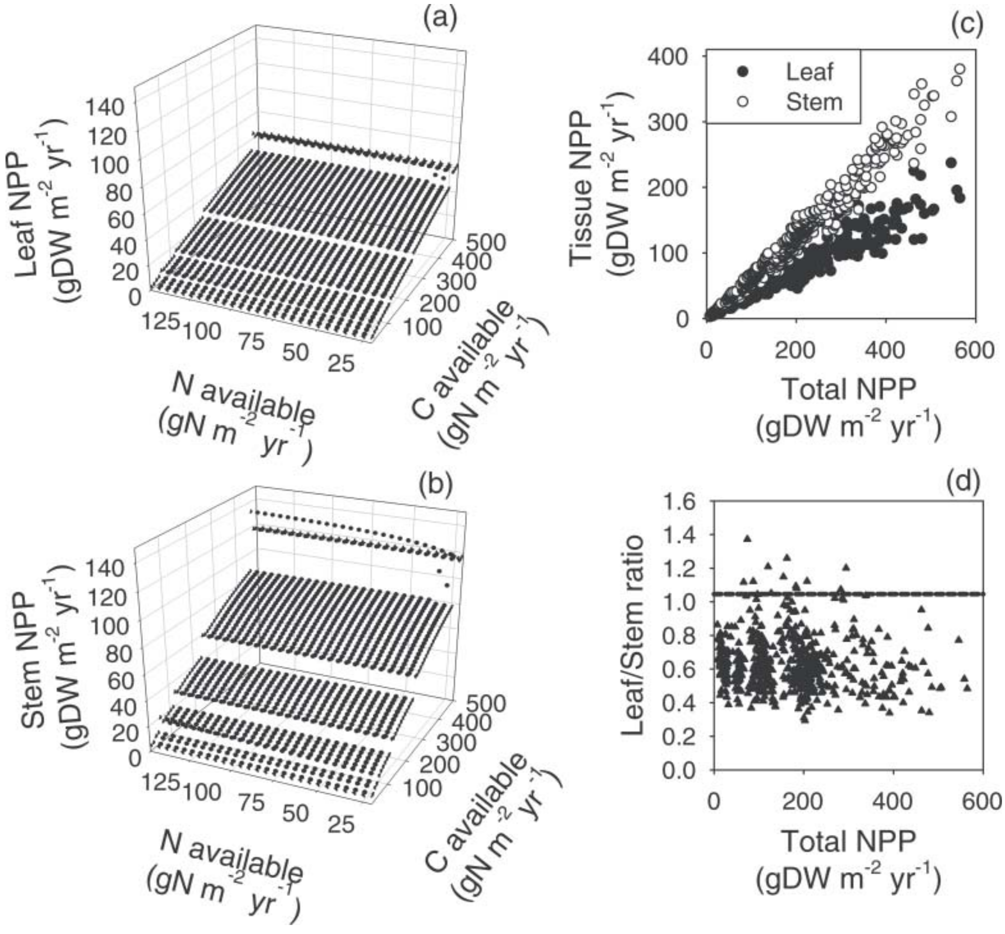

Fig. 1. Relationship between tissue production and N and C availability for moss leaves (a) and moss stems (b) for moss grown in monoculture. The general relationship between total moss productivity and (c) stem or leaf production and (d) the ratio of leaf to stem production is also shown for moss grown in interspecific competition. Parameter values are given in Table 1.

roughly a 5:3 ratio of stem to leaf production on average, with some variation around this mean (Fig. 1c,d). To examine this, we chose a range of parameter values (Table 2), randomly sampled all parameter values from this range, solved for the ESS, and then repeated this for 1000 random parameterizations. The output in Fig. 1c,d is based on these randomizations. Higher stem production relative to leaf production occurs because of the size-asymmetric nature of competition for C. As we described above, leaf production in a foraging game is about balancing marginal benefits with marginal costs. This is where the game-theoretic nature of the model is critical: in the context of foraging, stems have no value and are purely a cost, but in the context of a competitive game, being shorter than one's competitors imposes a severe disadvantage and dramatically decreases competitive ability and resource harvest. As a result, our model predicts that stem production should generally exceed leaf production because it is so important to avoid being over-topped.

A final observation is that in our randomization of species traits (Fig. 1c,d), relatively few combinations of traits were capable of producing mixed ESS solutions. Specifically, only 46.1% of the simulations had mixed ESS solutions. This implies that moss diversity may also be limited by competitive foraging games, but a full accounting of population dynamics would be necessary to explore this hypothesis, and this is beyond the scope of this paper.

Moss growth based on traits of species

Here, we explore the effects of parameters that are related to the traits of species on moss allocation. We examine how a continuous range of parameter values for costs (c_{icl}, c_{ics}, c_{inl}, c_{ins}), stoichiometry (α, β), and the degree of size-asymmetry in competition for light (z_{il}, z_{is}) alter moss production strategies for leaves and stems. It is straightforward to model such relationships; however, these parameters represent traits of species that cannot practically be manipulated. Therefore, before we discuss these results, we emphasize that these relationships could probably only be empirically examined by the use of a taxonomically diverse and, ideally, phylogenetically controlled comparison among a large number of moss species. Points on the individual curves associated with these results should therefore be viewed as individual species, and comparing two points should be viewed as comparing two species with differing traits. This analysis was designed to more completely explore parameter space, and so the ranges are increased beyond the ranges in Table 2.

Unsurprisingly for the cost parameters, higher tissue costs generally lead to declines in tissue production (Fig. 2). Here, we examine N costs over a range of 0.01–0.5 (i.e. 1–50% of dry weight), which we believe includes and also exceeds the likely range of costs for mosses (Table 1); and logically, we find it hard to imagine any organism (on Earth) that was even close to 50% N by dry weight (Lieth, 1975). N costs (i.e. the N required to construct tissue) have relatively small effects on tissue production except at very high costs (Fig. 2a,b). As for resource availability, this happens because for most resource availabilities $\partial fH_N/\partial u > \partial c_N/\partial u$, and since tissues are produced primarily such that $\partial zH_C/\partial u = \partial c_C/\partial u$, it means that most individuals will have excess capacity for N and greatly exceed their N requirements without added effort. The steps in the cost–production surface occur for the same reason that there are steps in Fig. 1: specifically, as costs decrease, there is eventually a step up in the ESS production strategies due to the size-asymmetry in aboveground competition. Finally, higher costs have a larger effect on stem production compared with leaf production because stems do not directly contribute to H.

We examined C costs over the range 0.9–3 (i.e. 90–300% of dry weight; Table 2). C costs are imagined to be higher than N costs for two reasons: first, tissues are almost entirely composed of C by dry weight; and second, these costs include respiration costs, which can be substantial (Lieth, 1975; Whittaker, 1975; Bloom *et al.*, 1985; Niklaus and Korner, 2004). Therefore, we think the range of C costs used includes and likely exceeds the likely range for mosses. As above, tissue production is hypothesized to decline with increased C costs (Fig. 2c,d). C costs have a larger effect than N costs because tissue production generally occurs to balance $\partial zH_C/\partial u = \partial c_C/\partial u$, which means that unlike N, C profit is cut directly by higher costs. As above, the C costs also have a step-like portion that occurs due to the size-asymmetric nature of C competition. Also as above, the slopes for C cost–tissue production relationships are generally steeper than for leaves because stems do not directly contribute to H. Finally, unlike for N costs, there is a discontinuity in the function at the location of the

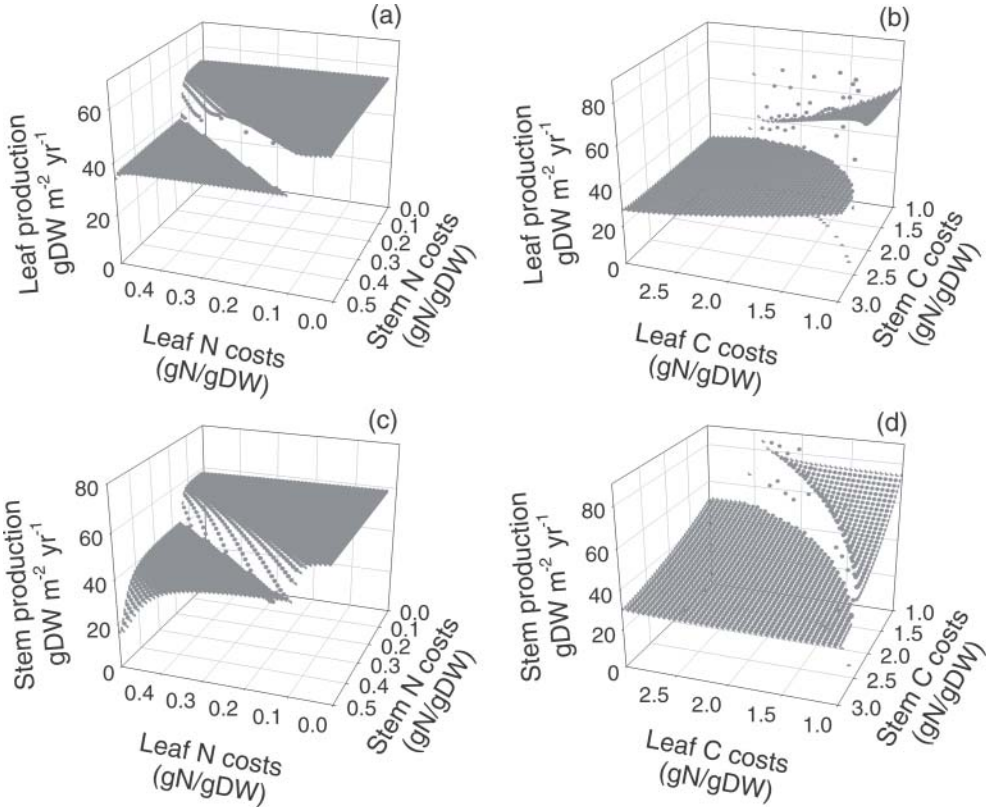

Fig. 2. Relationship between tissue production and the nitrogen costs required to construct tissues for moss leaves (a) and moss stems (c). Relationship between tissue production and the carbon costs required to both construct and maintain tissues for moss leaves (b) and moss stems (d). Parameter values are given in Table 1 unless included on a figure axis. Note that the erratic points in the C cost panels (b) and (d) are caused by a discontinuity in the function along the break point; here there is more than one unique ESS.

'step'. This means that at this exact vector of solutions, there are multiple stable solutions that can be seen by the erratic points that only occur along the edge of the surface where production steps down (Fig. 2c,d).

The stoichiometry of fitness output is determined by the parameter α. Mosses are primarily made from C by dry weight, and thus we examined a range of 0.5–1 for this parameter, though the likely range is probably closer to 0.8–1 (Table 2). This parameter has relatively little effect on either stem or leaf production in mosses (Fig. 3a). This again happens because of the dual role of leaves in both C and N foraging. As relative C demand declines, relative N demand increases concomitantly (i.e. we assume $\beta = 1 - \alpha$) and therefore tissue production increases because mosses are more likely to be N limited and less likely to be C limited (i.e. $\partial zH_C/\partial u > \partial c_C/\partial u$ and $\partial fH_N/\partial u = \partial c_N/\partial u$). Since N is less available in the environment than C on average (Chapin et al., 1986; Vitousek and Howarth, 1991), this means more tissues are required to meet foraging needs as α declines and demand for C and N is more even.

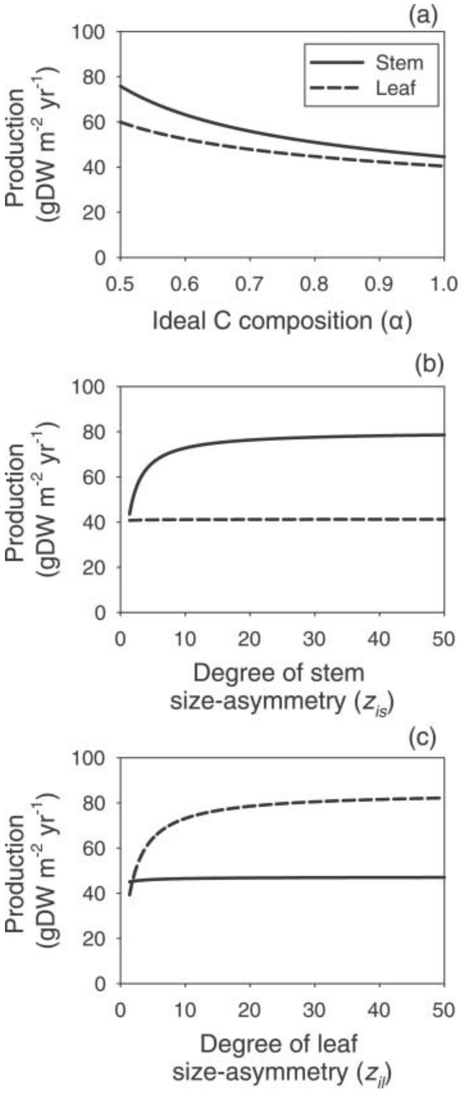

Fig. 3. (a) Relationship between tissue production and the C:N composition of moss reproductive output. Note that only α is shown because we assume that $\beta = 1 - \alpha$. Relationship between the degree of size-asymmetric competition that occurs with stem production (b) and leaf production (c). Parameter values used are given in Table 1 unless included on a figure axis. For this figure, we expanded the range defined in Table 1 to give a more complete picture of the parameter space.

Finally, the unitless exponents z_{il} and z_{is} determine the severity of size-asymmetric competition that occurs above ground. We are unsure of what values to expect for these because so little work has been done on moss competition, and thus examined the range until the effect of the exponent saturated (Fig. 3b,c). We note that as z_{il} increases so does leaf production, and as z_{is} increases so does stem production, but this effect saturates around exponent values of 50. Additionally, z_{il} increases u_{il} but not u_{is}, and z_{is} has effects on u_{is} but not u_{il}. At large z_{il} and z_{is}, production becomes limited by resource availability and the ability of plants to actually pay for increases in tissue production (i.e. to balance $\partial zH_C/\partial u = \partial c_C/\partial u$ or $\partial fH_N/\partial u = \partial c_N/\partial u$) and so the effect saturates based on the resource environment.

DISCUSSION

Moss-dominated peatlands are a critical carbon sink globally (Gorham, 1991; Clymo *et al.*, 1998; Gauthier *et al.*, 2015). For example, 32% of global terrestrial carbon has been estimated to be stored in climate-sensitive peatlands (Gauthier *et al.*, 2015), and understanding peat formation could provide key insights into climate change models. Why should moss produce organic layers that are so deep and so productive? Here we have suggested that a struggle for access to light drives mosses to be as tall as they can afford to be within the context of resource acquisition (Fig. 1) and their own physiological traits (Figs. 2, 3) and within the constraints of their ability to move water through their non-vascular tissues (see below). Proving our game-theoretic interpretation is impossible, but we can attempt to falsify it by examining some simple predictions of the model to see if it is rejected based on existing empirical observations.

One simple prediction of the model is that, unlike vascular plants that respond strongly to N fertilization, the vegetative production of mosses should largely ignore N fertilization (Fig. 1a,b). Mosses should still capture N and benefit from enriched N, but the model predicts that mosses do not need to increase production of tissues to be able to capture increased N because they have excess capacity for N foraging due to the dual function of moss leaves for C and N capture. Thus a positive response of moss to N addition would be a strong rejection of the model predictions. A meta-analysis synthesized the results of 107 field studies on *Sphagnum* moss and showed that: (1) the response of *Sphagnum* moss to N addition was zero or slightly negative, while (2) the change in N concentration within the tissues of *Sphagnum* moss was mostly positive (Limpens *et al.*, 2011). Indeed, empirical studies have not reported positive responses to N fertilization, but instead a zero response or sometimes a negative response (Chapin and Shaver, 1985; Potter *et al.*, 1995; Van der Heijden *et al.*, 2000a; Pearce *et al.*, 2003; Van der Wal *et al.*, 2003; Limpens *et al.*, 2011). These studies often used large N addition rates, and attributed these negative responses to toxicity. Our model does not consider toxicity and so does not have the capacity to predict decreased NPP in response to greater concentrations of nitrogen, but we find it encouraging that the average empirical response to nitrogen is rarely positive (Limpens *et al.*, 2011; although see Jonasson, 1992; Potter *et al.*, 1995). Considering toxicity is clearly an important future direction, and could have dire implications for peatlands if N deposition increases dramatically with climate change (Pearce *et al.*, 2003; Van der Wal *et al.*, 2003). Despite the risk of toxicity from high levels of N addition, it seems clear that increasing access to N does not cause increases in the vegetative production of moss, supporting the predictions of the model.

Contrary to the predictions for N, the model predicts that moss should respond strongly to increases in C availability by increasing production of all tissues (Fig. 1a,b). Broadly speaking, the results in the literature are consistent with this hypothesis. For example, when mosses are grown in elevated CO_2 experiments, an increase in moss biomass is typically observed (Van der Heijden *et al.*, 2000b; Heijmans *et al.*, 2001; Niklaus and Korner, 2004). Similarly, Heijmans *et al.* (2001) report an increase in *Sphagnum magellanicum* height and a decrease in bulk density under elevated CO_2 that they attribute to morphological changes involving branch growth. This may reflect the predictions of our model, which suggest that mosses would allocate more resources towards stem growth than leaf growth in an environment of increased carbon availability. Experimentally manipulating light levels has the effect of manipulating C availability, and mosses also show reduced growth in shade compared with full sun (Chapin and Shaver, 1985). It is clear that increasing access to C leads to increases in vegetative production of moss, supporting the predictions of the model.

Future directions

The responses of moss to N and C fertilization are broadly consistent with our model predictions, but there are more results that can be challenged with data in an attempt to falsify our hypotheses. We briefly outline some simple tests that would further our understanding of moss production as a tragedy of the commons game.

First, our original question was, why do mosses have height? Our suggestion is that they have some stem-like structures in order to maximize competition for light. Another simple prediction of our model is that moss bodies should be primarily composed of stem-like structures relative to leaf-like structures (Fig. 1c,d). This qualitative prediction should hold for any parameterization so long as $\alpha > \beta$. Using the best parameter estimates available (Table 2), we can make a bolder, quantitative prediction that this stem-to-leaf ratio would on average be equal to 5:3 (Fig. 1c,d). We are confident in the qualitative prediction, but much less so in the quantitative prediction which we view as an empirically testable hypothesis.

Second, we have discussed the effects of resource addition (Fig. 1), but the model also makes predictions based upon the physiological traits of organisms (Figs. 2, 3). A broad phylogenetic comparison across moss species that vary in traits like respiration rate (carbon costs), and stoichiometry (C and N costs and C:N ratio) would begin to shed light on some of the relationships predicted in Figs. 2 and 3. The simplest method would be to collect a large variety of moss species from varying habitats, estimate variation in physiological and stoichiometric traits, and grow these species in a controlled environment to estimate production. It may also be possible to introduce additional costs using environmental parameters such as toxins or pH, but this may introduce externalities that the model cannot capture (see below).

Finally, as we hinted above, it is possible that some of the complexity in response to resource addition is a product of interactions between the abiotic and biotic environment. Vascular plants respond strongly to N addition by increasing aboveground biomass (Chapin *et al.*, 1986; Vitousek and Howarth, 1991; Berendse *et al.*, 2001), and this increased aboveground production of vascular plants may lead to negative feedbacks on the moss community that are independent of the response of moss to resources alone. We suggest that manipulations to minimize competition between moss and vascular plants in N addition experiments would enhance our understanding of moss production under resource addition. For example, the shoots of vascular plants can be tied down so that they do not shade the moss understorey, while still leaving their roots intact (Cahill, 2002). It might also be possible to combine existing game-theoretic models of vascular plant growth (e.g. Dybzinski *et al.*, 2011) with this moss game to generate predictions about how vascular plants might affect moss via competition.

Assumptions and caveats

As with any modelling exercise, assumptions were made which introduce some caveats when applying the model to empirical systems. Several assumptions about the mathematical structure of our model are outlined in the model derivation such as the assumption of exponential depletion of resources and linear tissue costs and we do not repeat these here. Instead, we expand on assumptions that may influence experimental tests of the model. Most importantly, our model does not include water, and our analysis assumes that there is sufficient moisture to permit moss growth, and at the same time not limit growth. Water is critically important for moss reproduction. Furthermore, mosses only grow in very moist environments and are incredibly sensitive to seasonal variation in the water table and in precipitation (Limpens *et al.*, 2011). This means that our model should only be applied to moss systems where water is controlled across all treatments. For example, in a manipulative experiment where C and N availability are manipulated but moisture levels are controlled, the model can make predictions about growth and allocation (Fig. 1). However, care must be taken when comparing across environments where moisture is not controlled. This requirement for moisture also severely limits how tall mosses can become. There are not, and have never been, ‘moss-trees’ because of the requirement that mosses remain moist and because mosses have limited mechanisms for water transport. There are many ways that one might introduce water into the model (e.g. Franklin *et al.*, 2012; Farrior *et al.*, 2013; Wullschleger *et al.*, 2014). We explored some of these at the model development phase but decided to exclude water because: (1) we feel empirical data is lacking to inform the nature of mathematical relationships; and (2) any version of the model that included water quickly became extremely complicated and we wanted to highlight the game-theoretic nature of light competition in producing stems without getting bogged down by the complexity of water. As long as the model is only applied according to these caveats, we feel it still makes useful qualitative predictions that are consistent with empirical results.

Our model also ignores the deleterious effects of N toxicity that occur when very high levels of fertilizer are added to vegetation, which was clearly important in many experiments we cited (Chapin and Shaver, 1985; Potter *et al.*, 1995; Pearce *et al.*, 2003; Van der Wal *et al.*, 2003; Limpens *et al.*, 2011). Carbon dioxide is also toxic at high enough concentrations, though none of the studies we cited observed this effect. Thus, the model can only make predictions within regions of C_{avail} or N_{avail} that are not toxic to life, and care should be taken in manipulative experiments to delineate those regions before interpreting results.

Conclusions

Why do mosses have stem-like structures that permit them to grow slightly taller than their bryophyte sister groups? We admit that this is likely not an answerable question. However, we have hypothesized that having some height allows mosses to have an enormous competitive advantage for light. This hypothesis, as we show with our model, leads to some simple predictions about moss production. For example, mosses are predicted to respond strongly to C fertilization but not to N fertilization. Qualitatively, mosses are also predicted to allocate more to stem-like structures than leaf-like structures. Understanding moss production of stems and leaves is important because peatlands represent an enormous pool of stored carbon and the fate of this carbon pool is critically important to the Earth’s climate in the face of a warming planet. Our model represents one predictive tool to understand and predict moss production as a tragedy of the commons game in a world of increasing C availability.

ACKNOWLEDGEMENTS

G.G.M. thanks the Natural Science and Engineering Research Council of Canada for a Banting Post Doctoral fellowship. We thank Merritt Turetsky for inspiration to pursue this model, and Joel S. Brown for advice on the model.

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