

# Semiarid Vegetation Modelling Report

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## 1 Introduction

In this project we consider a process-based model of semiarid vegetation and aim to understand its mathematical properties and behaviour. To this end, we produce a simpler version of the model for analysis, which can be extended to the full model using the simplified structure.

## 2 Stewart et al. Model Summary

Stewart et al. [1] model a semiarid region in the American Southwest using discrete, annual time steps and discrete, metre-squared, spatial cells. It models the effects of three vectors, water flow downslope, wind, and movement of grazers, to move resources and propagules of two species, black grama grass, and creosotebush shrubs.

Resources are carried down-vector through connected cells until they reach a disconnected cell, where resources are then distributed locally to the  $3 \times 3$  Moore neighbourhood surrounding a the disconnected cell. Connectivity depends on the vector. Water flow and wind are connected by unvegetated cells, but are disconnected by vegetated cells which interrupt flow

with their roots and wind by above-ground biomass. On the other hand, vegetated cells are connected for grazers, as they spend time there accumulating nitrogen and propagules, which then are distributed locally once the grazers leave the vegetated area and reach an unvegetated cell.

Multiple soil layers exist in the model (top, middle, and deep), which accounts for the differences in the structure of the roots of the two species, as well as channelling effects. Creosotebushes have more roots reaching the deep layer, and their roots can quickly channel water and nitrogen down into the middle layer, unlike black grama, whose roots are higher up on average. Unused resources are kept in the soil layers, allowing both species to survive droughts where top layer water is insufficient to sustain biomass.

Growth is limited by both resources, as well as the biomass in the cell, since plants can only grow so much in a year. Plants with sufficient resources to sustain themselves use more to produce propagules, which increase biomass in that cell, as well as others by vector transport. Plants with insufficient resources produce no propagules and lose biomass to approach a maintainable amount, although drought resilience means that this is not an immediate reduction to the biomass which can be maintained by current resources. Biomass also decreases by an overall mortality, due to disease or damage, as well as grazers consuming grass.

### 3 Reduced Water-Grass Model

To translate the Stewart et al. model into a more mathematical form, we first simplified the model to only include the water vector, the black grama grass species, and only one layer of soil to hold resources (since these layers only become relevant when considering the properties of different plant species).

We continue to use annual time steps and an  $N \times N$  region of cells, however we will represent our cells as an  $N^2 \times 1$  vector, so that transport can be represented by an  $N^2 \times N^2$  matrix acting on our  $N^2 \times 1$  resource vectors. Any matrices are written in bold and are  $N^2 \times N^2$ , while any vectors are written in underlined bold with dimension  $N^2$ . As seen in Table 1, we require biomass and soil resources as initial conditions, as well as yearly rainfall and nitrogen deposition, which is outlined in Table 2.

The motion of resources ultimately depends on local transport which we will represent by the  $N^2 \times N^2$  matrix  $\sigma(\underline{\mathbf{B}}_t)$ . We can compute  $\sigma(\underline{\mathbf{B}}_t)$  at each time step using two constant  $N^2 \times N^2$  matrices  $\mathbf{U}$  and  $\mathbf{V}$ , for unvegetated and vegetated transport, which themselves can be computed from  $3 \times 3$  input matrices describing how available resources and propagules move from a given cell. We use the matrices from Stewart et al., adjusted to account for the available resource removed from the central cell, shown in Table 3.

Variable	Dependence	Description
$t$	N/A	Year of simulation.
$R_t$	N/A	Annual rainfall in year $t$ .
$D_t$	N/A	Annual nitrogen deposited in year $t$ .
$B_t$	$B_{t-1}, DW_{t-1}, DN_{t-1}$	Biomass at the start of year $t$ .
$DW_t$	$DW_{t-1}, W_{t-1}, B_{t-1}$	Underground water distribution in year $t$ .
$DN_t$	$DN_{t-1}, N_{t-1}, B_{t-1}$	Underground water distribution in year $t$ .
$WA_t$	$B_t$	Water available to be moved locally.
$NA_t$	$B_t$	Nitrogen available to be moved locally.
$PA_t$	$B_t, P_t$	Propagules available to be moved locally.
$W_t$	$B_t$	Final surface water distribution in year $t$ .
$N_t$	$B_t$	Final surface nitrogen distribution in year $t$ .
$P_t$	$B_t, W_t, N_t, DW_t, DN_t$	Potential new biomass from propagules produced in year $t$ .
$WR_t$	$B_t, W_t, DW_t$	Water resource value in year $t$ (non-physical).
$NR_t$	$B_t, N_t, DN_t$	Nitrogen resource value in year $t$ (non-physical).
$L_t$	$B_t, WR_t, NR_t$	Limiting value for growth in year $t$ (non-physical).

Table 1: Key

$$\mathbf{U} = \begin{pmatrix} -1 & 1 & & \\ & -1 & 1 & \\ & & -1 & 1 \\ & & & \ddots \\ 1 & & & & -1 \end{pmatrix} \otimes \mathbb{I}_{N \times N} \quad (1)$$

$$\mathbf{V} = \begin{pmatrix} -0.5 & 0.1 & & 0.1 \\ 0.1 & -0.5 & 0.1 & \\ & 0.1 & -0.5 & 0.1 \\ & & \ddots & \\ 0.1 & & 0.1 & -0.5 \end{pmatrix} \otimes \mathbb{I}_{N \times N} \quad (2)$$

$$+ \begin{pmatrix} 0.1 & & & 0.05 \\ 0.05 & 0.1 & & \\ & 0.05 & 0.1 & \\ & & \ddots & \\ & & 0.05 & 0.1 \end{pmatrix} \otimes \begin{pmatrix} 0 & 1 & & 1 \\ 1 & 0 & 1 & \\ & 1 & 0 & 1 \\ & & \ddots & \\ 1 & & & 0 \end{pmatrix}$$

Type	Rainfall ( $R_t$ )	Deposition ( $D_t$ )
Historical	Estimated rainfall for years 1658 to 1970	N/A
Average	$243 \text{ gm}^{-2}$	$1.5 \text{ gm}^{-2}$
Stochastic	TBC	TBC

Table 2: Resource Inputs

Black Grama	Unvegetated
$\begin{pmatrix} 0 & 0.1 & 0 \\ 0.1 & -0.5 & 0.1 \\ 0.05 & 0.1 & 0.05 \end{pmatrix}$	$\begin{pmatrix} 0 & 0 & 0 \\ 0 & -1 & 0 \\ 0 & 1 & 0 \end{pmatrix}$

Table 3: Transport Matrices

Using these constants, we can construct the movement of resources at a given time step using the current biomass distribution. Here, we multiply each column of the matrices  $\mathbf{U}$  and  $\mathbf{V}$  by the value in the column of the transposed Heaviside vector. So, for each cell, we use the  $\mathbf{U}$  redistribution if it is insufficiently vegetated, and use  $\mathbf{V}$  if it is sufficiently vegetated.

$$\boldsymbol{\sigma}(\underline{\mathbf{B}}_t) = \mathbf{U} + (\mathbf{V} - \mathbf{U}) * \text{diag} [\Theta(\underline{\mathbf{B}}_t - \underline{\mathbf{0.1}} B_{max})]^\top \quad (3)$$

Given the local movement, we can express the non-local, or accumulated downslope movement of resources. The total resources available to be redistributed locally from a given cell is equal to the sum of the resources flowing downslope from all of the cells above our given cell. Since cells only receive this contribution from cells in their own column, the total matrix is reducible to action on subspaces of dimension  $N$ , represented by lower-diagonal matrices  $\mathbf{A}_k$ . The matrix for column 1 is given below, with the larger block-diagonal total action  $\mathbf{A}_{tot}$  given below.

$$\mathbf{A}_1(\underline{\mathbf{B}}_t) = \begin{pmatrix} 1 & & & & & \\ \sigma_{1,2} & 1 & & & & \\ \sigma_{1,2}\sigma_{2,3} & \sigma_{2,3} & 1 & & & \\ \sigma_{1,2}\sigma_{2,3}\sigma_{3,4} & \sigma_{2,3}\sigma_{3,4} & \sigma_{3,4} & 1 & & \\ & & & & \ddots & \\ \sigma_{1,2} \dots \sigma_{N-1,N} & \dots & \dots & \dots & \sigma_{N-1,N} & 1 \end{pmatrix} \quad (4)$$

$$\mathbf{A}_{tot}(\underline{\mathbf{B}}_t) = \begin{pmatrix} \mathbf{A}_1 & & & & \\ & \mathbf{A}_2 & & & \\ & & \ddots & & \\ & & & \mathbf{A}_N & \end{pmatrix} \quad (5)$$

This flow carries a certain amount of the water or nitrogen deposited annually downslope, with the amount taken from each cell decreasing linearly with cell biomass, since more vegetated cells are able to trap more resources. Then the water and nitrogen available to be locally redistributed are given by equations (6) and (7), respectively.

$$\underline{\mathbf{WA}}_t = R_t \mathbf{A}_{tot}(\underline{\mathbf{B}}_t) \left[ \underline{\mathbf{1}} - \frac{1}{B_{max}} \underline{\mathbf{B}}_t \right] \quad (6)$$

$$\underline{\mathbf{NA}}_t = D_t \mathbf{A}_{tot}(\underline{\mathbf{B}}_t) \left[ \underline{\mathbf{1}} - \frac{1}{B_{max}} \underline{\mathbf{B}}_t \right] \quad (7)$$

These now give very simple expressions for our surface water and nitrogen.

$$\begin{aligned} \underline{\mathbf{W}}_t &= \underline{\mathbf{R}}_t + \boldsymbol{\sigma}(\underline{\mathbf{B}}_t) \underline{\mathbf{WA}}_t \\ &= R_t \left( \underline{\mathbf{1}} + \boldsymbol{\sigma}(\underline{\mathbf{B}}_t) \mathbf{A}_{tot}(\underline{\mathbf{B}}_t) \left[ \underline{\mathbf{1}} - \frac{1}{B_{max}} \underline{\mathbf{B}}_t \right] \right) \end{aligned} \quad (8)$$

$$\begin{aligned} \underline{\mathbf{N}}_t &= \underline{\mathbf{D}}_t + \boldsymbol{\sigma}(\underline{\mathbf{B}}_t) \underline{\mathbf{NA}}_t \\ &= D_t \left( \underline{\mathbf{1}} + \boldsymbol{\sigma}(\underline{\mathbf{B}}_t) \mathbf{A}_{tot}(\underline{\mathbf{B}}_t) \left[ \underline{\mathbf{1}} - \frac{1}{B_{max}} \underline{\mathbf{B}}_t \right] \right) \end{aligned} \quad (9)$$

To make the following equations more, readable we introduce non-physical algebraic expressions. These are proportional to the difference between the resources in a cell and the resources required to maintain the current biomass in that cell, so can be positive or negative, depending on whether resources allow for growth or are insufficient and lead to loss of biomass.

$$\underline{\mathbf{WR}}_t = \frac{1}{E_W} [\underline{\mathbf{W}}_t + \underline{\mathbf{DW}}_t - M_W \underline{\mathbf{B}}_t] \quad (10)$$

$$\underline{\mathbf{NR}}_t = \frac{1}{E_N} [\underline{\mathbf{N}}_t + \underline{\mathbf{DN}}_t - M_N \underline{\mathbf{B}}_t] \quad (11)$$

These are used to find how plant growth is limited: growth is limited by one of the resource expressions  $WR_t$  and  $NR_t$ , or by a proportional (physical) limit which the grass cannot outgrow in a year. If this limiting value is greater than or equal to zero, we have new mass,  $\underline{\mathbf{P}}_t$ , produced as propagules. If the limiting value is negative, that is, there is insufficient resources to maintain the existing biomass of a cell, no propagules are produced.

$$[\underline{\mathbf{L}}_t]^i = \min \begin{cases} WR_t^i, \\ NR_t^i, \\ g_{max} B_t^i \end{cases} \quad (12)$$

$$\underline{\mathbf{P}}_t = \text{diag}(\Theta(\underline{\mathbf{L}}_t)) \underline{\mathbf{L}}_t \quad (13)$$

Our previous definitions relied on the underground resources. These are given by difference equations, where unused resources are accumulated in the soil beneath plants.

$$\begin{aligned} \underline{\mathbf{DW}}_t &= E_W [\underline{\mathbf{WR}}_{t-1} - \underline{\mathbf{L}}_{t-1}] \\ &= \underline{\mathbf{W}}_{t-1} + \underline{\mathbf{DW}}_{t-1} - M_W \underline{\mathbf{B}}_{t-1} - E_W \underline{\mathbf{L}}_{t-1} \end{aligned} \quad (14)$$

$$\begin{aligned} \underline{\mathbf{DN}}_t &= E_N [\underline{\mathbf{NR}}_{t-1} - \underline{\mathbf{L}}_{t-1}] \\ &= \underline{\mathbf{N}}_{t-1} + \underline{\mathbf{DN}}_{t-1} - M_N \underline{\mathbf{B}}_{t-1} - E_N \underline{\mathbf{L}}_{t-1} \end{aligned} \quad (15)$$

Note that these soil values cannot become negative, since the most insufficient resource will set soil to zero (all of the accumulated soil resources are used up). A simple proof is given for water, which applies to nitrogen as well. We have equality when a resource is the minimum or most limiting.

$$\begin{aligned} L_{t-1}^i &\leq WR_{t-1}^i \text{ (by definition as minimum)} \\ \implies DW_t^i &= E_W [WR_{t-1}^i - L_{t-1}^i] \\ &\geq E_W [WR_{t-1}^i - WR_{t-1}^i] = 0. \end{aligned}$$

Finally we approach a difference equation for biomass. Our propagules are spread downslope, although the contribution from each cell is now *proportional* to the cell's biomass, rather than decreasing linearly with biomass. This means that propagules tend to spread away from biomass, rather than being accumulated by it. We note also that, unlike rainfall and nitrogen deposits, propagules produced vary spatially, so we have propagules in a diagonal matrix applied before the downslope movement  $\mathbf{A}_{tot}$ .

$$\underline{\mathbf{PA}}_t = \mathbf{A}_{tot} \text{diag}(\underline{\mathbf{P}}_t) \left[ \frac{1}{B_{max}} \underline{\mathbf{B}}_t \right] \quad (16)$$

We can express biomass in multiple ways. The first equation, (17) is fairly compact but is not very intuitive, whereas the second, (18) is more intuitive. The first line of both has carried-over biomass, as well as new growth given by propagules using local movement, similar to our surface resource equations. The following lines account for biomass loss due to insufficient resources, which is detected by the diagonal matrix containing  $\Theta(\underline{\mathbf{L}}_{t-1})$ . We then further distinguish between nitrogen and water insufficiency with another pair of Heaviside functions. The carried-over biomass is set to whatever biomass can be maintained by the resources, which is more clearly shown in the second equation. Note that our biomass can increase above the maximum allowed by maintenance, since our propagules can establish themselves for the next time step independent of the resources in the current time step.

$$\begin{aligned} \underline{\mathbf{B}}_t &= (1-k)\underline{\mathbf{B}}_{t-1} + (1-f) [\underline{\mathbf{P}}_{t-1} + \sigma(\underline{\mathbf{B}}_{t-1})\underline{\mathbf{PA}}_{t-1}] \\ &\quad + (1-k)\text{diag}[\mathbf{1} - \underline{\Theta}(\underline{\mathbf{L}}_{t-1})] \left( \frac{E_W}{M_W} \text{diag}[\underline{\Theta}(\underline{\mathbf{NR}}_{t-1} - \underline{\mathbf{WR}}_{t-1})] \underline{\mathbf{L}}_{t-1} \right. \\ &\quad \left. + \frac{E_N}{M_N} \text{diag}[\underline{\Theta}(\underline{\mathbf{WR}}_{t-1} - \underline{\mathbf{NR}}_{t-1})] \underline{\mathbf{L}}_{t-1} \right) \end{aligned} \quad (17)$$

$$\begin{aligned} \underline{\mathbf{B}}_t &= (1-k)\underline{\mathbf{B}}_{t-1} + (1-f) [\underline{\mathbf{P}}_{t-1} + \sigma(\underline{\mathbf{B}}_{t-1})\underline{\mathbf{PA}}_{t-1}] \\ &\quad + (1-k)\text{diag}[\mathbf{1} - \underline{\Theta}(\underline{\mathbf{L}}_{t-1})] \left( \text{diag}[\underline{\Theta}(\underline{\mathbf{NR}}_{t-1} - \underline{\mathbf{WR}}_{t-1})] \frac{\underline{\mathbf{W}}_{t-1} + \underline{\mathbf{DW}}_{t-1}}{M_W} \right. \\ &\quad \left. + \text{diag}[\underline{\Theta}(\underline{\mathbf{WR}}_{t-1} - \underline{\mathbf{NR}}_{t-1})] \frac{\underline{\mathbf{N}}_{t-1} + \underline{\mathbf{DN}}_{t-1}}{M_N} - \underline{\mathbf{B}}_{t-1} \right) \end{aligned} \quad (18)$$

Having an insufficient resource means that the soil of that resource becomes zero for the next time step, per our previous proof, which then shows the equivalence of the expressions for insufficient resources.

$$\begin{aligned} DW_t^i &= W_{t-1}^i + DW_{t-1}^i - M_W B_{t-1}^i - E_W L_{t-1}^i = 0 \\ \implies \frac{W_{t-1}^i + DW_{t-1}^i}{M_W} - B_{t-1}^i &= \frac{E_W}{M_W} L_{t-1}^i \end{aligned}$$

Constant	Value	Description
$E_W$	17.5	Water efficiency; how much water is used to produce a gram of new biomass.
$M_W$	3.5	Water maintenance; how much water is used to maintain a gram of existing biomass.
$E_N$	0.0273	Nitrogen efficiency.
$M_N$	0.0273	Nitrogen maintenance.
$k$	0.1	Mortality rate, independent of resource insufficiency.
$f$	0.05	Failure rate for propagules to establish.
$g_{max}$	1.125	Maximum growth rate.

Table 4: Grass Constants

## 4 Reduced Model Findings

### 4.1 General Behaviour

Using a uniform initial biomass of  $60\text{gm}^{-2}$  and a constant annual rainfall of  $243\text{gm}^{-2}$ , we see that the biomass quickly settles to a spatially homogeneous equilibrium of  $45.4877\text{gm}^{-2}$ , save for some tiny variation due to the imperfect periodic boundary conditions. However, if we lower the annual rainfall to around  $171\text{gm}^{-2}$  (about 70% of the Stewart et al. average), we start to see bands along the field, giving a simple bifurcation point between uniform and striped biomass distributions.

We continue to find settled bands of vegetation for lower constant rainfalls, shown in Figure 3, with the distance between bands increasing as rainfall decreases, since more empty cells are required to build up enough downslope water flow to maintain a vegetation band. These settled into their patterns in a few hundred years (600 for 3a down to 200 for 3c), and then continued to stay as they were for many hundreds more. The settled patterns did *not* migrate upslope, as we have observed, and as partial differential equation models predict. However, the constant rainfall and uniform initial conditions are not at all realistic, so a break from observations may not be too worrying here.

Spatially homogeneous extinction is harder to determine than our previous homogeneous equilibrium, as low rainfalls give larger distances of empty space, which can appear to be boundary effects as we saw in Figure 1b. For example, an annual rainfall of  $30\text{gm}^{-2}$  gives

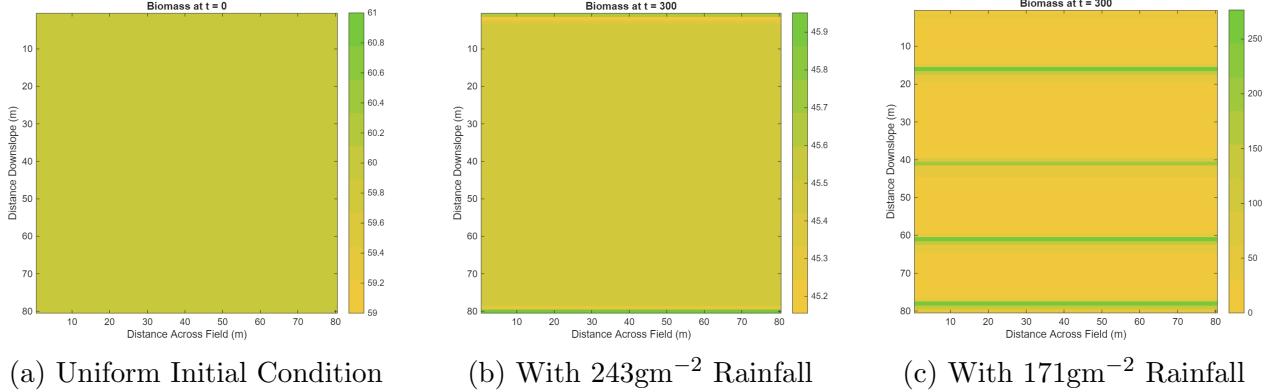


Figure 1: Field Biomass for Uniform Initial Conditions and Constant Rainfall

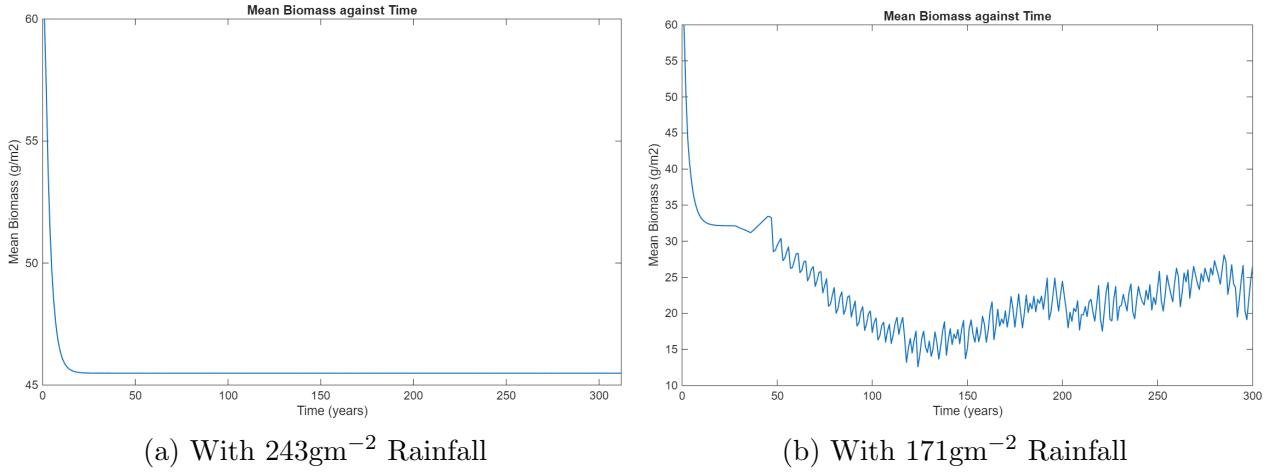


Figure 2: Mean Biomass for Uniform Initial Conditions and Constant Rainfall

a 'reversed' version of 1b for that field size, but doubling the field size makes another band appear halfway down, suggesting that the distance between bands was close to the field size of 80m. It is possible to find rainfall values which may only have biomass as a boundary effect for larger field sizes, but these are for exceptionally low values below  $5\text{gm}^{-2}$  per year.

Moving on from our simplest simulations, we now consider noisy initial conditions for biomass with constant rainfall. This can have different outcomes, depending on rainfall, as seen by Figure 4. A very low rainfall (4a) gives sparse vegetation which does not appear to have any particular pattern, ignoring the boundary effect at the top and bottom of the field. A low rainfall (4b) gives a number of small 'patchy' stripes. The average rainfall (4c) gives a fairly well vegetated field with many gaps, not unlike a mixture of a labyrinth and striped pattern. Finally, a high rainfall (4d) gives a mostly vegetated field with a few bare patches which are not clearly organised. Repeated simulations using random initial conditions give qualitatively similar results, so the position of the small gaps or patches is likely due to the initial conditions, although they are stable for many hundreds of years.

Next we consider the noisy initial biomass along with the repeated historical record, shown in Figure 5. Repeating this record provides variance in the rainfall which is more realistic than a simple stochastic rainfall.

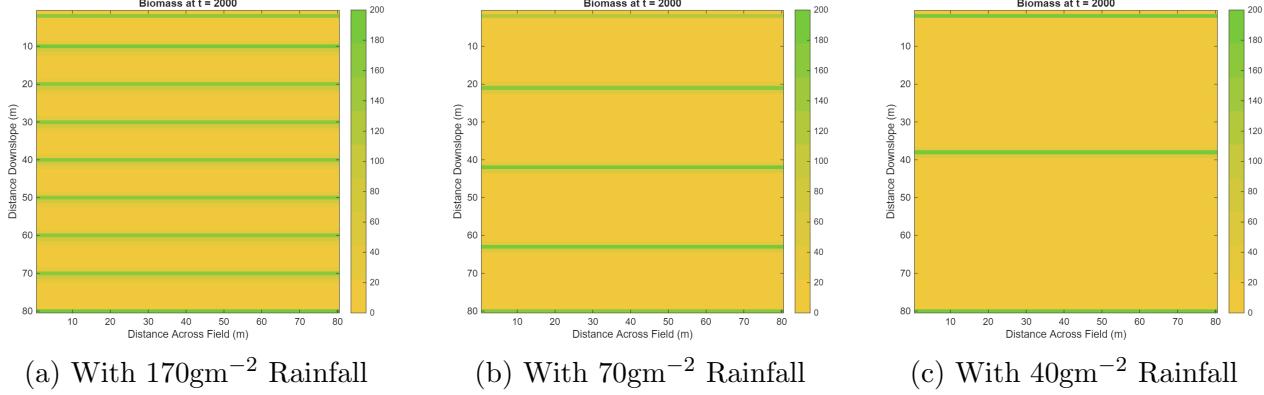


Figure 3: Striped Biomasses for Uniform Initial Conditions and Constant Rainfall

With historical rainfall, the model quickly transitions from an uniformly noisy initial biomass to bands of vegetation, which gradually move up the slope (Figure 6. This is the sort of behaviour we hope to see from the model, with clear bands of vegetation which do not straighten out for the 312-year time scale the Stewart et al. model aimed to work for.

Over very long time periods, the bands in the top half of the field straighten out, as we might expect given that resources move downhill far more than across it. However, this is not permanent, and occasional waves of 'imperfect' bands will appear from a point near the top of the field and spread downward. These continue to appear for many thousands of years, and spread very slowly over hundreds of years, seen in Figure 7. I hypothesise that this is due to the visible inhomogeneity in the very top band of vegetation (e.g. in 7a), which itself may come from the imperfect bands at the bottom of the field via periodicity. It is possible that this imperfection widening as it moves downslope allows the bottom half of the field to stay in imperfect bands, while the imperfection is shorter-lived in the top half, as we see the perfect bands correcting themselves in 7c and 7d. This wave behaviour is not seen when simulating uniform initial conditions, which form stable bands of vegetation which remain undisturbed for many thousands of years.

## 4.2 Comparing with Stewart et al.

The reduced model is compared to the Stewart et al. model using the same values for grass behaviour, given by Table 4, as well as the same estimated historical rainfall data, shown in Figure 5. For initial conditions, a random grass biomass distribution of  $60\text{gm}^{-2}$  multiplied by the random seed included in the Stewart et al. model was used, along with uniform initial mid layer soil water of  $25\text{gm}^{-2}$  and mid layer soil nitrogen of  $0.5\text{gm}^{-2}$ . The wind and grazer vectors were still used in the Stewart et al. model simulations, though both were moving only nitrogen downslope, so would only make a small difference to the outputs.

To compare the behaviour of grass more directly, initial shrub biomass was set to zero everywhere, as were deep soil layer resources, since these are accumulated by resources unused by the shrubs in the Stewart et al. model. Since these remain at zero throughout the simulation, they are omitted from the output graphs of the Stewart et al. model shown.

The two models produce a similar pattern of mean annual biomass over time, although the reduced model has a slightly larger biomass density throughout. Both also closely resemble

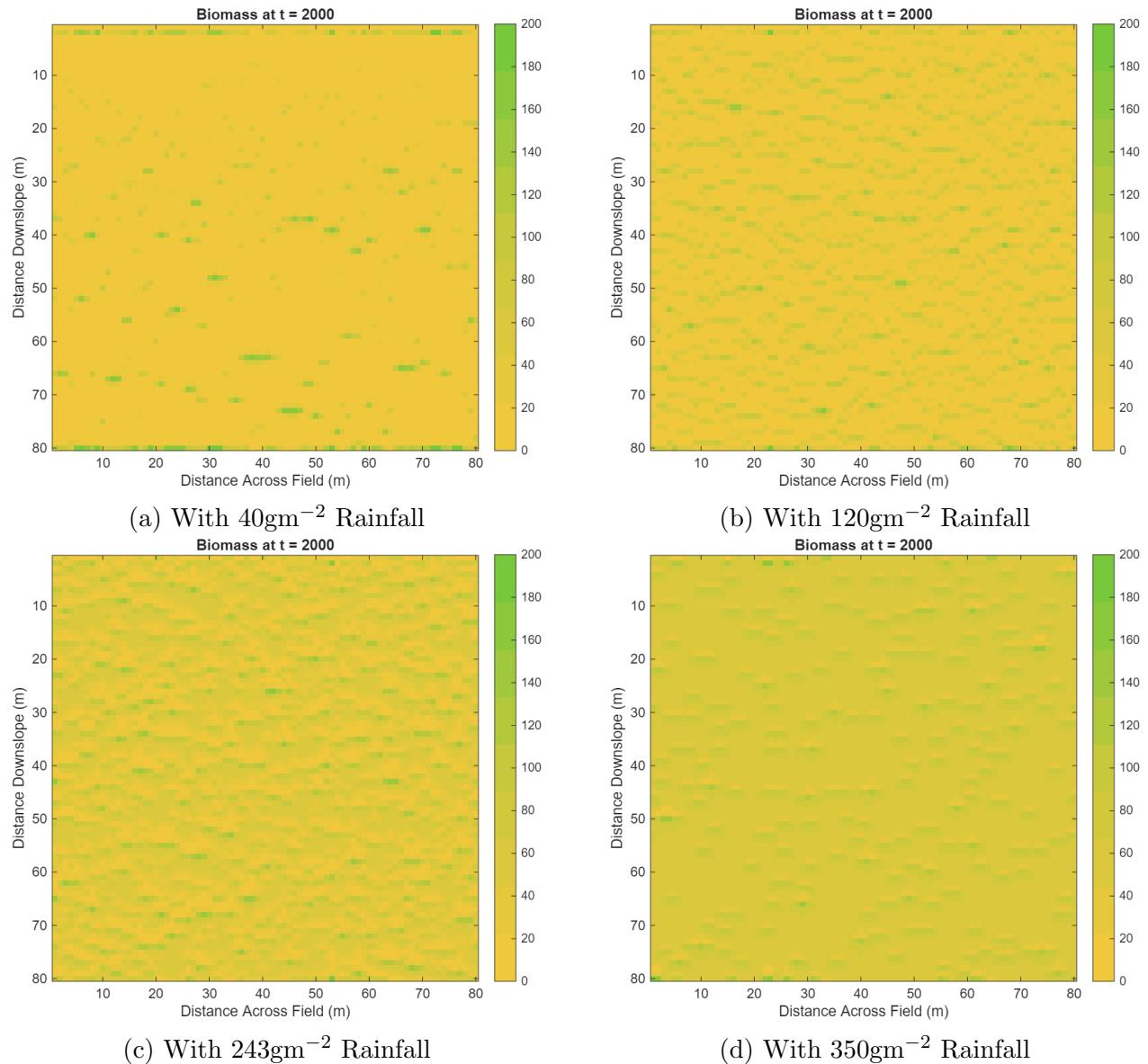


Figure 4: Field Biomass for Random Initial Condition and Constant Rainfalls

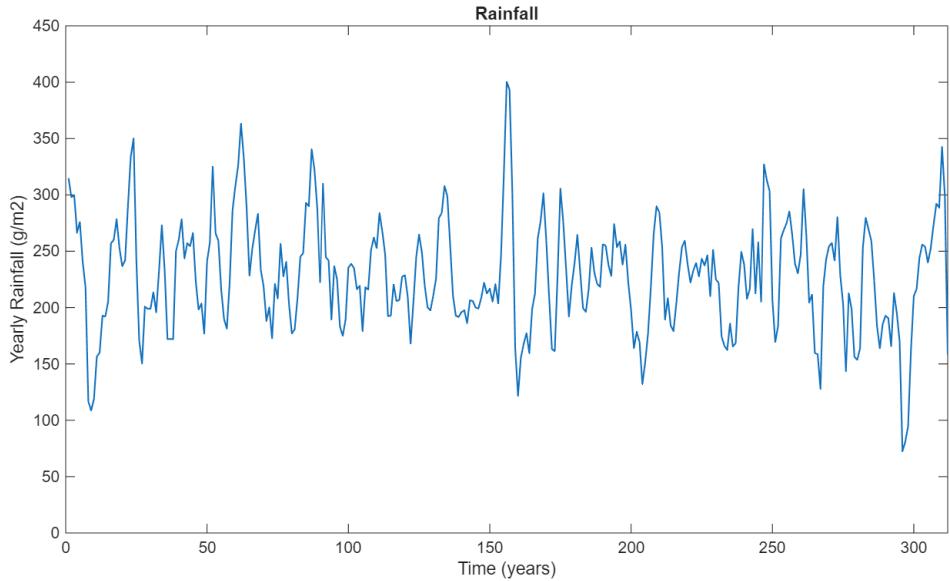


Figure 5: Historical Rainfall Data

the historical rainfall data, as expected given that water is the limiting resource in both models. This is good news, and suggests that the formulae given above can reproduce the behaviour of the Stewart et al. process-based model with some accuracy.

A more significant divergence from the Stewart et al. model is in the soil resources, shown in Figure 9. The reduced model stores very little water in the soil, and has more consistently large stores of soil nitrogen, while the Stewart et al. model more frequent spikes in soil water, along with an mostly increasing accumulation of soil nitrogen over the simulation time. We can note that the mean water stored in the Stewart et al. model is still below  $5\text{gm}^{-2}$  once we move past the large initial value, which is quite small compared to the historical annual rainfall, which has a mean of  $227.7\text{gm}^{-2}$ , so both models predict that a large majority of the water will be used each year. This may be caused by the consistent difference in mean biomass between the simulations. The reduced model having larger biomass means that it uses up more of the available water each time step than the Stewart et al. simulation, which may explain why the former ends up with less soil water than the latter when using the same historical rainfall data.

One explanation for the difference in nitrogen is the action of the wind and grazer vectors. The wind vector distributes nitrogen around vegetated cells, similar to the water vector, however it distributes slightly less further downwind, and slightly more perpendicular to the wind direction. Since wind was moving downslope in this simulation, slightly less nitrogen

Statistical Measure on Mean Biomass	Reduced Model	Stewart et al. Model
Minimum ( $\text{g}/\text{m}^2$ )	15.05	11.3
Maximum ( $\text{g}/\text{m}^2$ )	60.18	53.26
Mean ( $\text{g}/\text{m}^2$ )	41.17	35.03
Standard Deviation ( $\text{g}/\text{m}^2$ )	6.578	6.655

Table 5: Data for Annual Mean Biomass

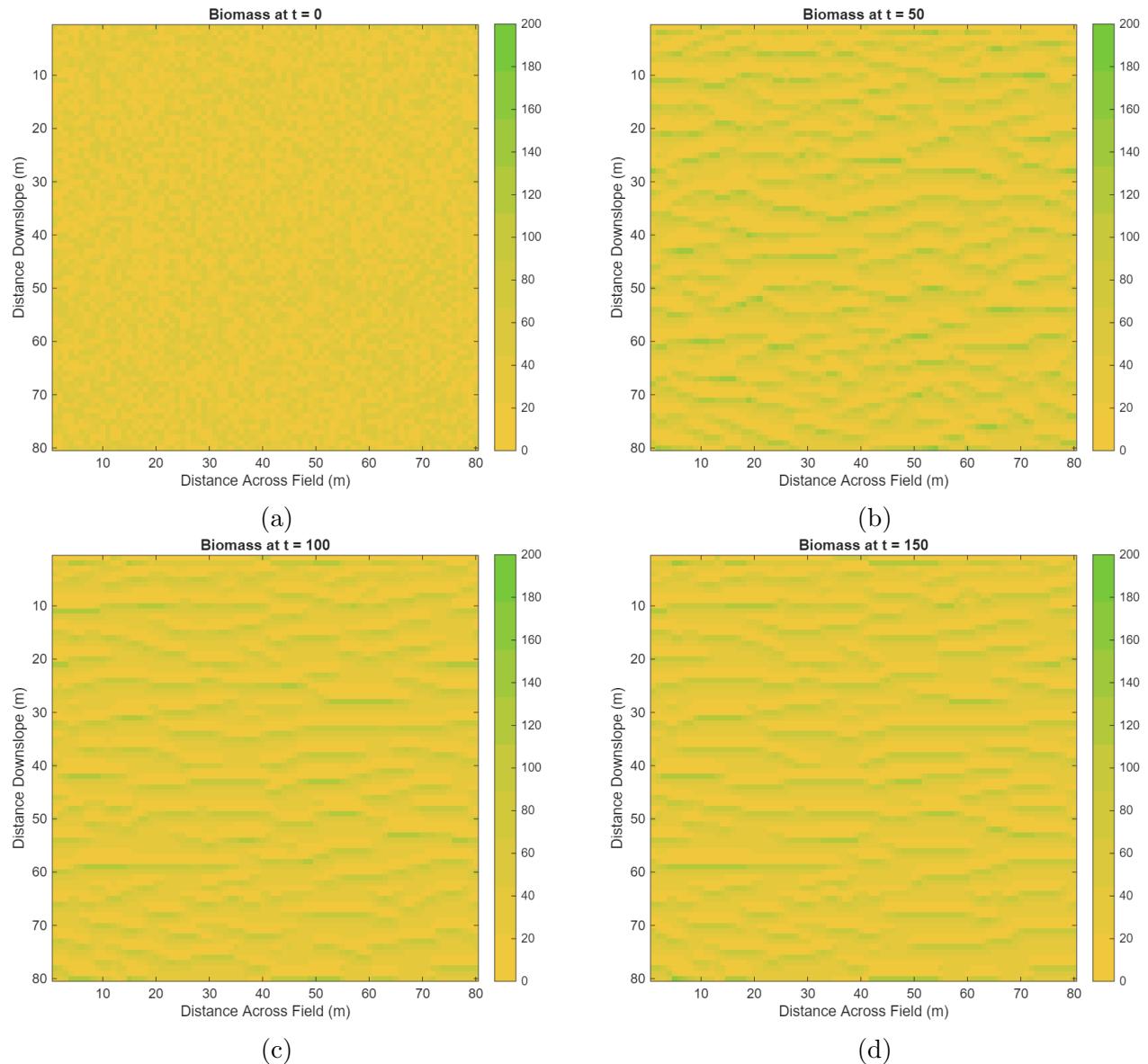


Figure 6: Field Biomass for Random Initial Condition and Historical Rainfall

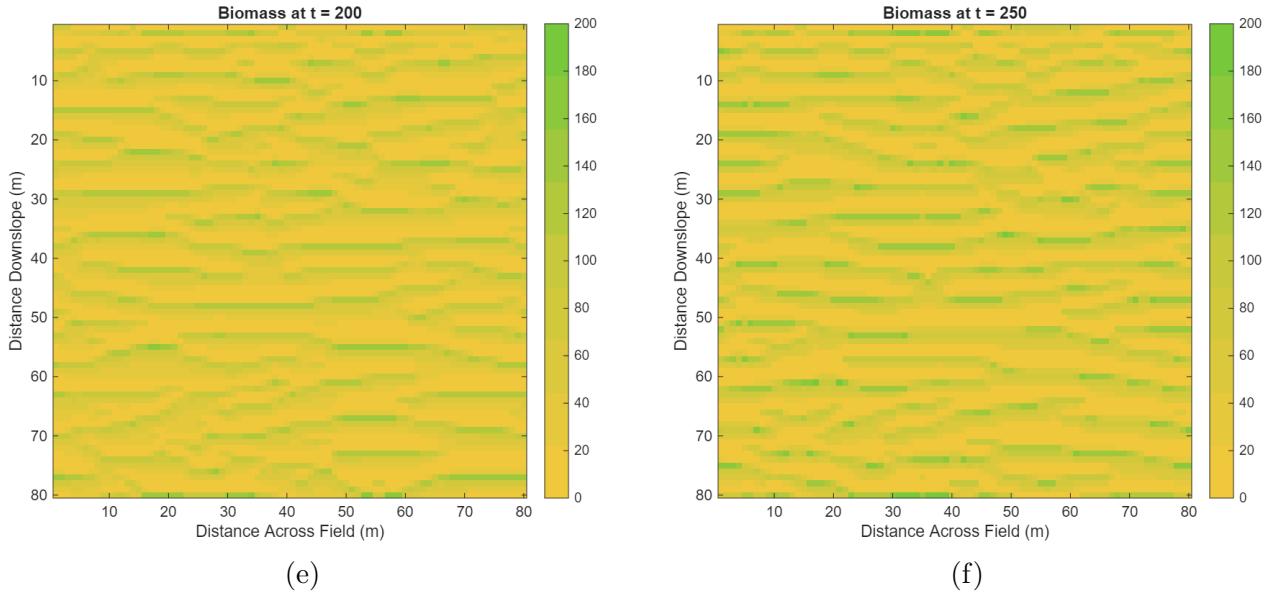


Figure 6: Field Biomass for Random Initial Condition

was carried downslope in the Stewart et al. model simulation than in the reduced model simulation, where it moves exactly the same way as water. On the other hand, the grazer vector distributes nitrogen once it reaches an unvegetated cell, so it leads to more nitrogen ending up in unvegetated cells. Both models remove 95% of soil resources from unvegetated cells each time step to prevent over-accumulation, and this likely leads to the mean soil nitrogen being lower in the Stewart et al. model compared to the reduced model. This may explain the difference in nitrogen accumulation during the first half of the simulation.

The sudden decreases in nitrogen in the reduced model appear to correspond to droughts in rainfall, where grass has insufficient water and dies out. This can be seen quite clearly when comparing the decreases in nitrogen in Figure 9 to the increases in connected (i.e. unvegetated) cells in Figure 10. The Stewart et al. model handles water insufficiency specially: all of the water but none of the nitrogen is used, and the drought resilience of the plant species means that more grass survives a time step than the maintenance values would suggest. In the reduced model, nitrogen is still used up during these years, and the faster loss of vegetation means that more cells would become unvegetated, and hence have their soil resources greatly reduced. These factors seem to be a good explanation for the presence of the sudden drops in soil nitrogen in one model but not the other.

As seen in the field outputs, Figure 11, both models produce thin bands of vegetation perpendicular to the downslope flow of water, with occasional forks joining two bands together. These have very similar spacing, with around 2-5 unvegetated cells between bands of grass which are 1-3 cells thick, save for forked areas which can be thicker.

We can also see the band of vegetation appearing at the top of the slope in the Stewart et al. model due to the downslope flow of resources being 'dumped' back to the top by the local transport's periodicity. This is not present in the reduced model, which averages resources at this boundary.

A key difference between the models is that of speed. The reduced model has a signif-

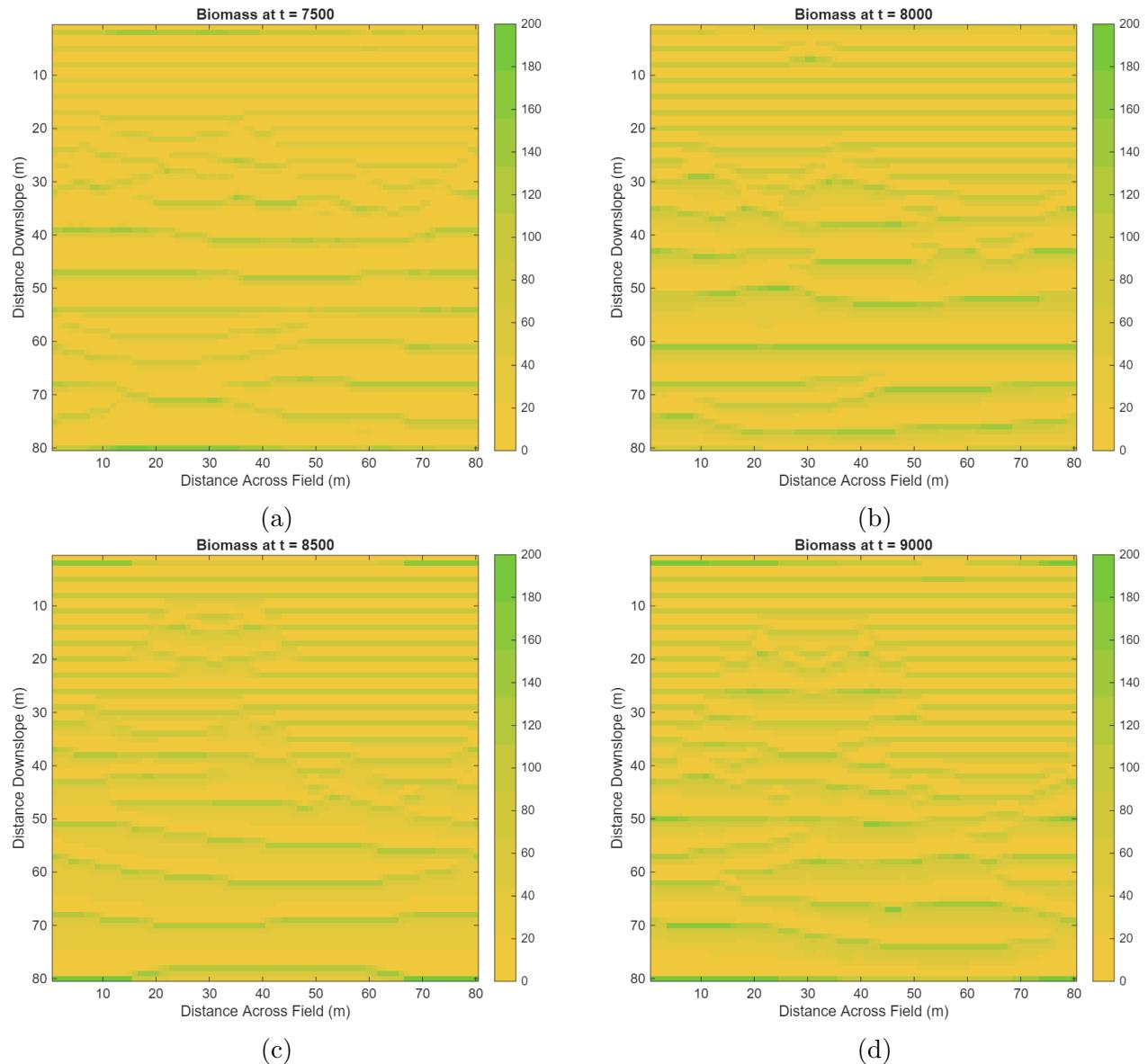


Figure 7: Long-Term Wave Behaviour

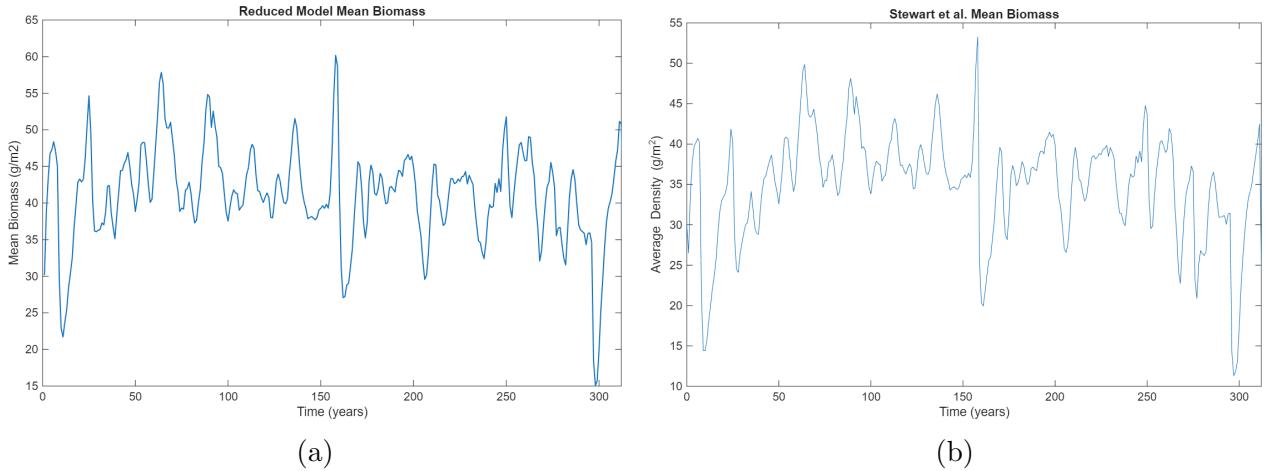


Figure 8: Mean Biomass

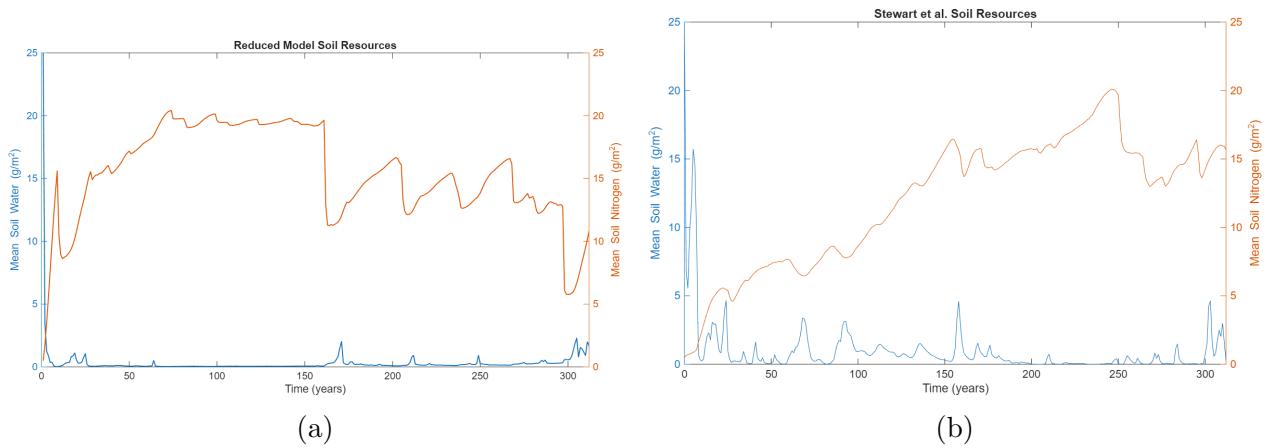


Figure 9: Mean Soil Resources

icantly faster runtime than the Stewart et al. model, as seen in Figures 12 and 13. Both models scale linearly with simulation length  $T$  for a fixed field size  $N$ , which is to be expected since  $T$  is only used to determine the length of the main for loop the simulations run through, as well as some outputs.

The reduced model appears to scale with  $N^2$ , the total number of cells we simulate, although there is a sudden jump at  $N = 362$  which is likely due to cache memory on the machine the runtimes were recorded on. The two halves closely match quadratic growth in  $N$ , save for some bumpiness in the first half where simulation times are short and MATLAB rendering takes a more significant proportion of time. The Stewart et al. model also closely matches quadratic growth, albeit with a much larger quadratic coefficient. Details are shown in Table 6.

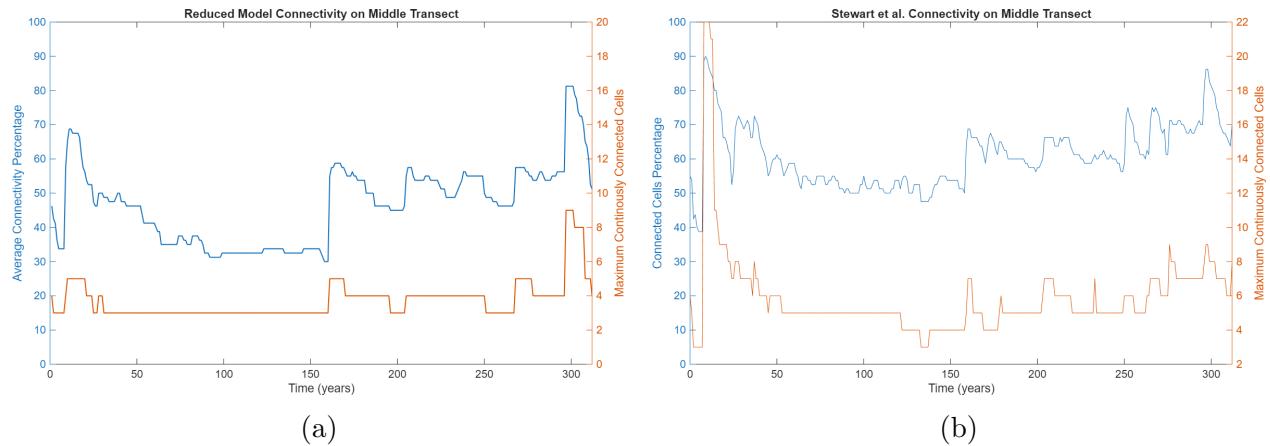
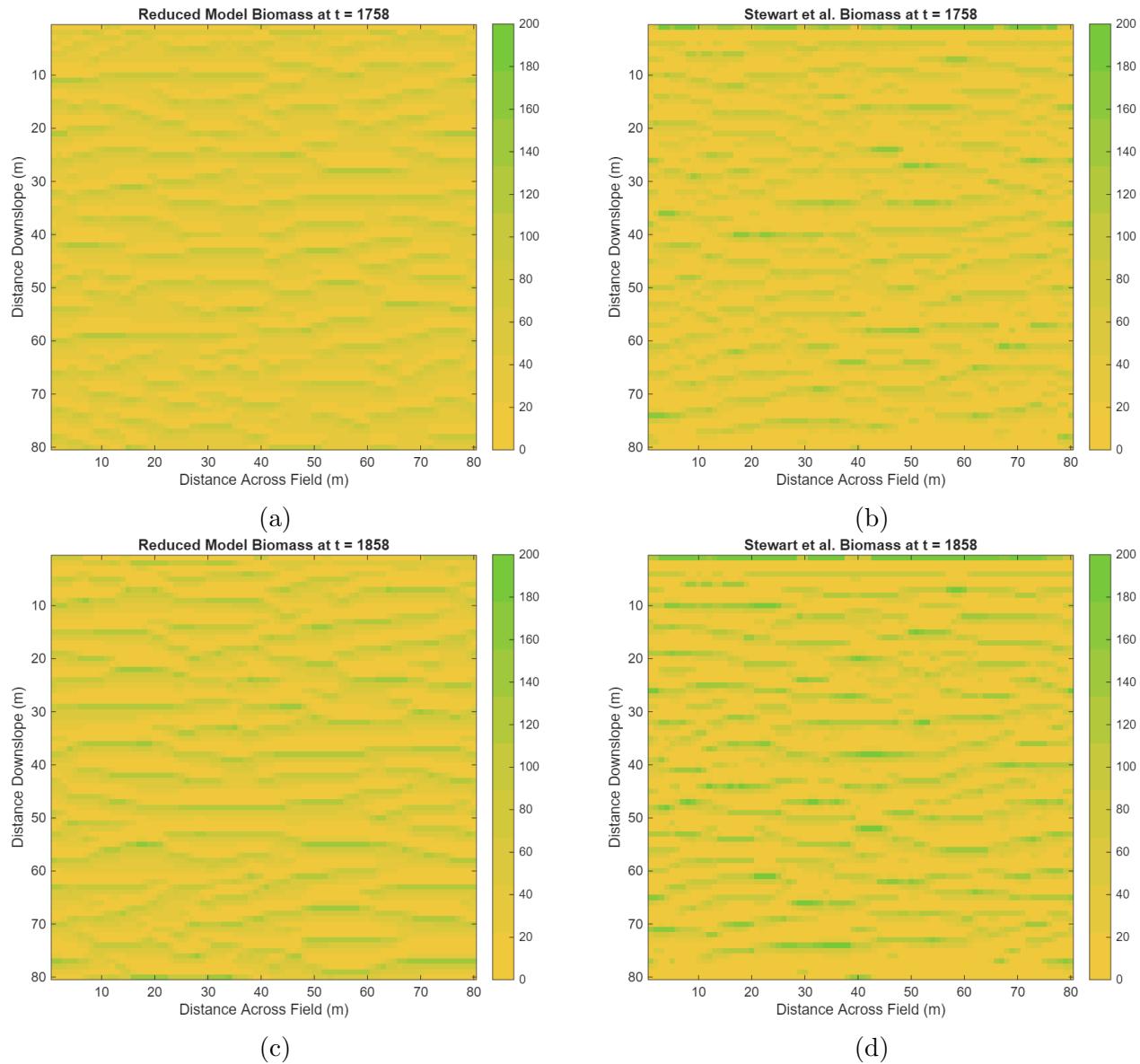


Figure 10: Connectivity Measures



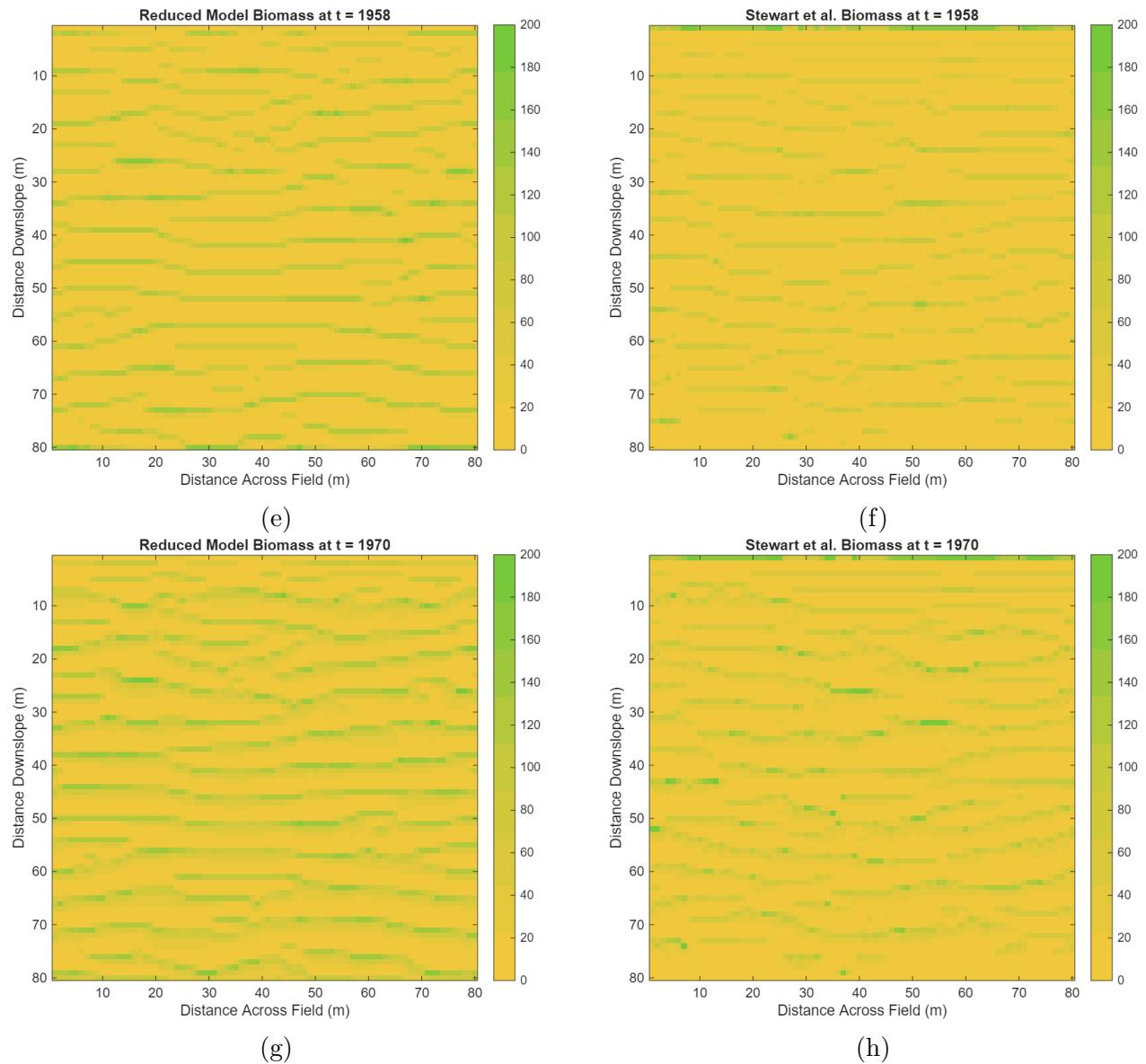


Figure 11: Field Biomass Comparison

Measure (4 s.f.)	Reduced Model First Part	Reduced Model Second Part	Stewart et al. Model
$R^2$	0.9990	0.9999	1.000
Quadratic Coefficient	1.038e-4	8.833e-5	3.927e-2

Table 6: Regression Values from MATLAB

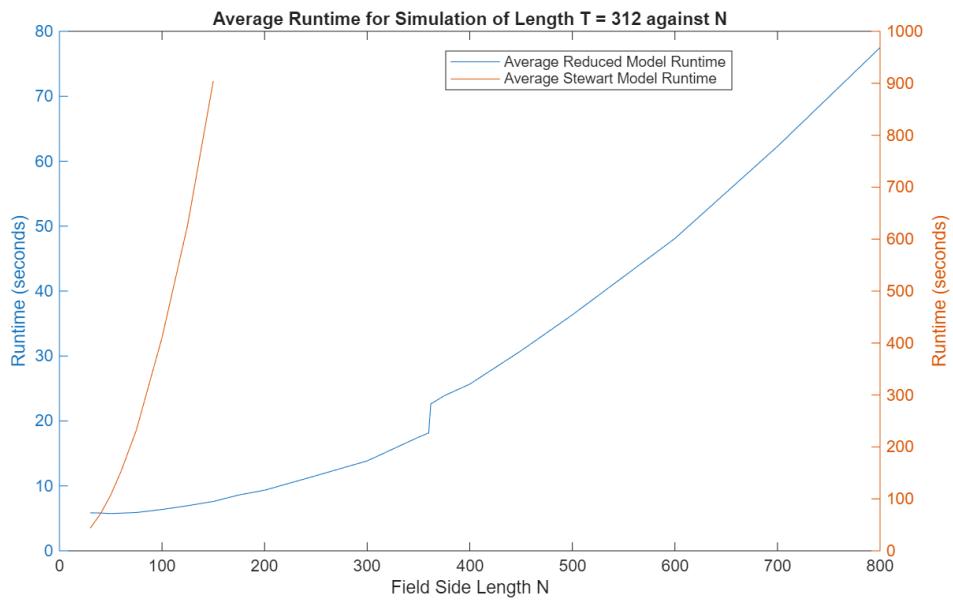


Figure 12: Runtime against Field Size  $N$

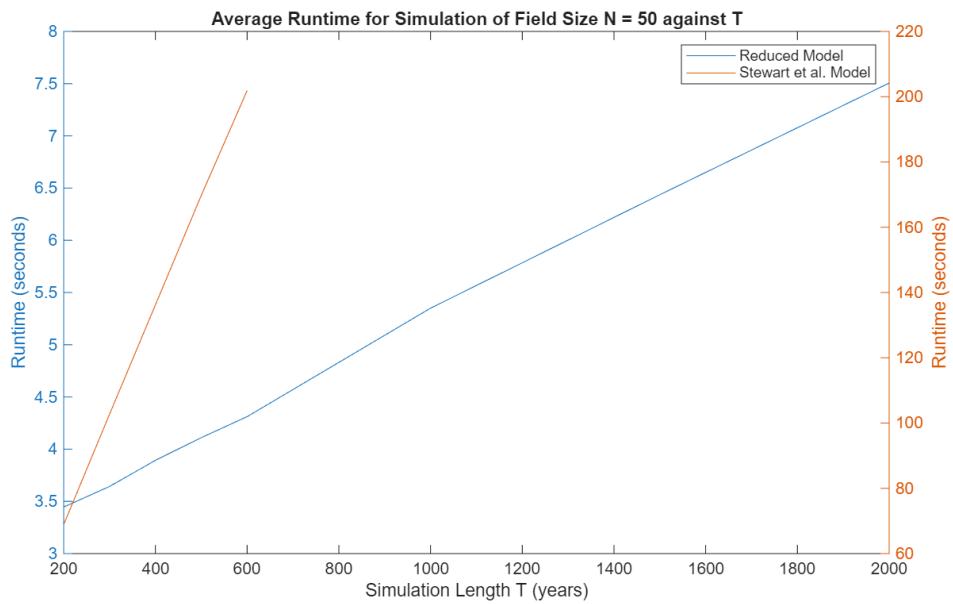


Figure 13: Runtime against Simulation Length  $T$

## 5 Conclusion

Overall, the reduced model produces similar patterns in growth to the full Stewart et al. model, albeit with some differences in soil resources. This suggests that the mathematical framework used for the reduced model can be applied successfully to recreate the Stewart et al. model, with the benefit of significantly faster runtimes, as well as the ability to better analyse the mathematical properties of the model since a full set of equations would then exist.

Adding additional plant species and additional vectors would involve generating equivalents of the  $\sigma$  matrix and updating this each time step for the current biomass distribution. This would increase runtimes, but should not change the order of complexity from  $N^2$ . Given how much faster the matrix model is compared to the original Stewart et al. code, this should still be a significant improvement to runtimes.

Additional species require the implementation of another soil layer to properly differentiate root depths, as well as balancing the distribution of resources between multiple species in a cell. The formulae for this would not be nearly as pleasant as the ones used above, but are possible to implement if one is careful about division by zero in unvegetated cells.

Other minor features of the Stewart et al. model should also be fairly straightforward to implement. Grazers would consume a certain proportion of grass each time step, which can simply be another factor added to the  $\underline{\mathbf{B}}_{t-1}$  term in the biomass equations (17) and (18). Drought resilience can also be implemented easily to (18) by adding multiplying the water insufficiency term by a constant, just as is done in the Stewart et al. code. Having the model not remove nitrogen would be slightly harder, but should be possible by adding a Heaviside term to equation (15) to only apply the maintenance removal when water resources are positive.

## 6 Bibliography

### References

- [1] J. Stewart et al. “Modeling emergent patterns of dynamic desert ecosystems”. In: *Ecological Monographs* 84 (3 2014), pp. 373–410. DOI: <https://doi.org/10.1890/12-1253.1>. URL: <https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/12-1253.1>.