

1 *Type of the Paper (Article)*

2 **Can future CO₂ concentrations mitigate the negative effects of** 3 **high temperature and longer droughts on forest growth?**

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10 **Abstract:** 1) Background: Climate change may subject forests to climate conditions to which they
11 are not adapted. Elevated temperatures reduce net photosynthesis by increasing respiration rates
12 and increasingly long droughts dramatically increase morbidity. CO₂ enrichment enhances
13 productivity, but it is not clear to what extent CO₂ enrichment can offset the negative effects of
14 elevated temperatures and longer droughts. 2) Methods: We used a mechanistic landscape model
15 to conduct controlled simulation experiments manipulating CO₂ concentration, temperature,
16 drought length and soil water capacity. 3) Results: We found that elevated CO₂ stimulates
17 productivity such that it dwarfs the negative effect caused by elevated temperature. Energy
18 reserves were not as strongly mitigated by elevated CO₂, and mortality of less competitive cohorts
19 increased. Drought length had a surprisingly small effect on productivity measures, but had a
20 marked negative effect on mortality risk. 4) Conclusions: Elevated CO₂ compensated for the
21 negative effect of longer droughts in terms of productivity measures, but not survival measures.

22 **Keywords:** climate change; temperature stress; drought; elevated CO₂; soil water; forest succession;
23 mechanistic landscape model; LANDIS-II; PnET-Succession.
24

25 **1. Introduction**

26 Climate change is expected to alter temperature and precipitation patterns throughout much of
27 the world [1], subjecting forests to climate conditions to which they are not adapted. Water stress is
28 a major limiting factor on plant growth [2]. Individual trees can become water stressed because of
29 inadequate precipitation inputs and/or inferior ability to extract water from the soil compared to
30 adjacent competitors, and when water stress becomes acute, individuals can die [3]. When water
31 stress is widespread, such as during drought, forest dynamics can be impacted by increased
32 morbidity of drought intolerant species across the landscape. Temperature stress is less likely to
33 directly cause mortality, but it can reduce photosynthetic efficiency and increase respiration rates
34 such that growth can be reduced and energy reserves depleted, making individuals more susceptible
35 to mortality by other causes [4].

36 Gustafson et al [4] used a mechanistic forest landscape model (FLM) based on the PnET-II
37 ecophysiology model [5] to conduct a controlled simulation experiment to quantify the relative effect
38 of temperature, precipitation, light (cloudiness) and soil water capacity on growth and competition
39 of tree species found in temperate forests of central North America. They discovered that
40 temperature had a positive effect on growth when temperature rise was moderate (+3 °C), but a
41 negative effect when temperatures rose by 6 °C (driven by very high respiration rates). Available
42 water (precipitation and soil) had the greatest effect on growth, with more water resulting in greater
43 growth. Light had a similar effect, but the effect was much more modest. However, that study did
44 not explicitly examine the effect of CO₂ concentration on growth, and concentrations rose gradually,
45 being <510 ppm for the first half of 100 year simulations. That study also reduced precipitation as a
46 constant fraction of monthly precipitation and did not include drought events. Droughts,

47 particularly long droughts, can have an important effect on forest dynamics. Tree mortality on tens
48 of thousands of forest inventory plots in the Midwestern U.S. over 40 years was more related to the
49 length of dry periods (droughts) than to the magnitude of precipitation reduction [6,7]. However,
50 the interaction of droughts with other aspects of climate change has been little studied formally.

51 Elevated CO₂ increases plant productivity through several mechanisms that may reduce
52 temperature and water stress. Water is primarily lost from a plant when leaf stomata are opened to
53 allow CO₂ to diffuse into the leaf. At increasingly higher CO₂ concentrations, the stomata open less
54 frequently, decreasing water loss and thus increasing water use efficiency. Elevated CO₂ also
55 increases conductance of CO₂ into the leaf and produces more favorable internal leaf conditions
56 relative to CO₂ compensation point [8].

57 The objective of this study was to conduct a simulation experiment using representative
58 temperate tree species to quantify the interactions of CO₂, temperature, drought length and
59 disturbance on forest growth and competition to complement the findings of Gustafson et al [4].
60 Our expectation was that chronically elevated CO₂ concentrations (750 ppm) would increase growth
61 rates even at high temperatures. This contrasts with the findings of Gustafson et al [4] that growth
62 was reduced when temperature increased by 6 °C but CO₂ only gradually increased to 697 ppm in
63 100 years. We also expected that increased drought length (holding decadal precipitation amount
64 constant) would produce a greater negative effect on growth than Gustafson and Sturtevant [6] found
65 with just a proportional decrease in precipitation. We also surmised that there may be an interaction
66 with CO₂ such that drought effects are also mitigated by high CO₂ concentrations by reducing
67 stomatal water loss. Finally, we expected that more disturbance would increase landscape-wide
68 productivity under elevated temperature and water stress by hastening a species composition change
69 favoring species with greater heat and drought tolerance. Such composition changes may also
70 result in changes to the spatial pattern of the landscape.

71 2. Materials and Methods

72 We conducted two sets of simulation experiments: 1) a site-scale experiment to tightly control
73 the main treatment effects while minimizing the confounding effects of disturbance and
74 establishment of new competing cohorts to determine the relative effects of each factor and their
75 interactions, and 2) a landscape-scale experiment to assess how spatial processes such as seed
76 dispersal and disturbance interact with the treatment factors, to discover how CO₂ concentrations
77 may mitigate the climate drivers in forest settings. We used the mechanistic, physiological first
78 principles PnET-Succession model because it is equally suited to site and landscape scale simulations,
79 and has direct, mechanistic links between growth (photosynthesis) and the experimental factors of
80 temperature, drought and CO₂ concentration, allowing competitive outcomes to emerge from the
81 simulated growth of species with varying life history attributes.

82 PnET-Succession [9] operates within the LANDIS-II FLM [10]. It mechanistically projects tree
83 species cohort growth by simulating photosynthetic production at a monthly time step. In PnET-
84 Succession, cohorts compete for water and light on each landscape grid cell. Cohort size (biomass)
85 determines the priority of access to light, while access to soil moisture depends on each species' ability
86 to extract soil water at the water potential found on the cell. Cohort leaf biomass is sorted into
87 canopy layers based on woody biomass (a surrogate for height), and light attenuates through the
88 resulting mixed-species canopy according to the extinction coefficients of the component species.
89 Soil water is tracked at the grid-cell level using a bulk-hydrology "bucket" model where rooting
90 depth and the water holding capacity of the soil represents the size of the "bucket," with precipitation
91 providing the input, and losses result from foliage interception, evaporation, runoff and percolation
92 out of the rooting zone, and uptake by vegetation (transpiration).

93 Foliar nitrogen (FolN) is the primary determinant of maximum photosynthetic capacity (A_{max})
94 in PnET-Succession. Various limiting factors compute realized photosynthesis (A) by applying
95 individual growth reduction multipliers to A_{max} such that values of 1.0 produce no reduction and
96 values <1.0 reduce A_{max} proportionally, with a single value of 0.0 halting photosynthesis altogether
97 [9]. The light stress multiplier (fRad) reflects the light available to each cohort throughout its vertical

98 canopy profile, given its shade tolerance. The water stress multiplier (fWater) reflects soil water
99 available to the cohort, given the water potential to which it can extract water. The senescence
100 multiplier (fAge) increasingly reduces (negative exponential) photosynthesis as cohorts approach
101 their longevity age, reaching 0.0 at longevity age. The temperature multiplier (fTempPsn) equals
102 1.0 at the species-specific optimal temperature for photosynthesis and declines as temperature
103 departs (in either direction) from that value. There is an analogous CO₂ enrichment multiplier
104 (Delamax) that increases above 1.0 as atmospheric CO₂ concentration exceeds 350 ppm according to
105 the equation of Franks et al [8] [11]. Photosynthesis occurs in the months when average temperature
106 exceeds the species-specific minimum, allowing phenology to respond to variation in seasonal
107 temperature. PnET-Succession accounts for reductions in biomass accumulation due to growth and
108 maintenance respiration. The model uses a Q₁₀ relationship in which a 10 °C increase in
109 temperature results in a ten-fold increase in respiration rate [12]; foliar respiration depends on
110 temperature and moisture, and maintenance respiration depends on temperature and biomass.
111 Respiration acclimation is simulated according to Wythers et al [13]. When respiration exceeds
112 photosynthetic production (e.g., from water and/or temperature stress), non-structural carbon
113 reserves become depleted and mortality occurs when reserves are below a user-specified minimum
114 (typically 1%) at the end of a calendar year. Cohort establishment probabilities are proportional to
115 computed growth rates below the canopy for each species. Temperature, precipitation, radiation
116 and CO₂ are input to the model as monthly means, which allow growth and establishment rates to
117 vary in response to both gradual change and extreme events. For model details see De Bruijn et al
118 [9] and Gustafson et al [11].

119 Site-scale experiment

120 The site-scale experiment was conducted on a single cell using a full-factorial design with four
121 fixed treatment effects (temperature, CO₂ concentration, drought length and soil texture (available
122 water capacity)) applied to assemblages of four generic tree species with randomly generated life
123 history traits. Soil texture was included as a treatment effect because soil texture has a large effect
124 on the availability of water for tree photosynthesis for a given level of precipitation [7]. Response
125 variables represent distinct aspects of physiological response to the treatments. 1) Total annual net
126 productivity (NetPsn) of each cohort over the course of the growing season was chosen as the
127 indicator of photosynthetic response, integrating effects of temperature on photosynthesis and
128 respiration, length of growing season, and seasonal precipitation variability. 2) Total cohort woody
129 biomass production was evaluated because it integrates photosynthetic output, water use efficiency
130 and maintenance respiration. 3) Mean monthly carbon reserves (NSCfrac) are believed to be an
131 indicator of plant stress and inversely correlated with likelihood of mortality [14b, 3]. 4) The mean
132 age attained by the four cohorts on a cell was used as a measure of crowding-induced mortality
133 (competitive exclusion), with a mean age <140 indicating that at least one cohort died prior to the end
134 of the simulation. Rather than choose a single simulation year to compute response variables, we
135 used the mean value observed over the course of each simulation for biomass, net photosynthesis,
136 and NSCfrac, assuming that these averages represent the relative vigor and competitive ability of
137 each cohort (and its competitors) in response to the treatments throughout its lifetime. For cohorts
138 that died, only the years prior to death were included to represent the state of the cohort prior to
139 death.

140 Experimental parameter settings (Tables 1, 2) were applied for 100 years to even-aged (40 years
141 old) assemblages of four species competing on a single cell. When life history traits differ among
142 species in an assemblage, certain combinations of abiotic conditions will favor the growth of some
143 species while hindering the growth of others. Furthermore, these traits may interact in different
144 ways depending on the traits of competitors such that the specific combination of life history traits of
145 the species in an assemblage has a large impact on the outcome of their competition. We therefore
146 randomized the life history traits of the four hypothetical deciduous tree species in each replicate by
147 selecting (with replacement) one of three possible values for each of four specific life history traits
148 (Table 1). These life history traits were chosen because they determine growth capacity (FoIN) or

149 control the physiological response to the treatments. Each random assemblage was simulated for
 150 all combinations (N=81) of the full factorial of treatments (Table 2) and the response variables for a
 151 single species formed a single observation, along with the treatment levels and the values of the four
 152 life history traits. We simulated 250 species assemblages, resulting in 81,000 cohort observations.

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Table 1. Levels of species life history traits used to randomly create species assemblages for simulation.

| Life history trait | Parameter | Low | Mid | High |
|---------------------|---|-------------|-------------|-------------|
| Productivity | FolN (% wt.) ¹ | 2.2 | 2.5 | 2.8 |
| Shade intolerance | HalfSat ($\mu\text{mol}/\text{m}^2/\text{s}$) ² | 275 | 437.5 | 600 |
| Drought tolerance | H3/H4 (MPa) ³ | -0.98/-1.37 | -1.07/-1.47 | -1.16/-1.57 |
| Optimal temperature | PsnTOpt (°C) ⁴ | 19 | 23 | 27 |

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¹ Foliar nitrogen; determines maximum photosynthetic capacity in PnET-Succession

² Light level when photosynthesis is half of its full sunlight rate; determines shade tolerance.
 Lower values indicate more shade tolerance

³ H3 is the water potential below which photosynthesis begins to decline; H4 is the water potential below which photosynthesis stops

⁴ Optimum temperature for photosynthesis

Table 2. Levels of the experimental treatment factors.

| Treatment | Parameter | Low | Mid | High |
|-----------------|--|------|-------|-------|
| Temperature | Monthly min. and max. temperature (°C) ¹ | +0 | +3 | +6 |
| CO ₂ | Mean monthly CO ₂ concentration (ppm) | 400 | 575 | 750 |
| Drought length | Drought length (yr) | 1 | 3 | 5 |
| Soil texture | AWC (mm) ² | 60.5 | 107.5 | 150.8 |

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¹ Implemented as monthly temperature relative to the baseline climate

² Maximum available water capacity, calculated as field capacity – wilting point

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Each treatment factor had three levels (Table 2). We used the temperature treatment time series of Gustafson et al [4] to enhance comparisons with that study. This series was based on weather data from Oconto county (Wisconsin, USA) from the period 1949-2010, which was replicated to create a time series extending through the year 2205 (200 years) and the treatments were implemented by modifying the monthly temperature values by adding the number of degrees of each treatment level to the temperature values in the climate input file. We did not use the precipitation time series of Gustafson et al [4] because that time series had very few drought years and our experiment required distinct drought periods. We instead used the precipitation projections used in the landscape experiment (below) generated by the MIROC GCM [14b] under the RCP8.5 (Representative Concentration Pathways) emissions scenario because it had a steady precipitation trend with several drought events. For this purpose we used the projected precipitation of the scenario, and we implemented the drought length treatment by: 1) swapping dry and wet years to change the length of wet and dry periods without altering the total precipitation of the full weather series, and 2) intensified the droughts by reducing precipitation by 40% in drought years and increasing it by the same amount in the wet years that were swapped, to produce a strong drought signal as in Gustafson et al [7]. Droughts were arbitrarily defined as periods when annual precipitation was less than the median of the 100-year precipitation time series, and less than the 25% quantile of total growing season precipitation and of maximum monthly growing season precipitation. Sixteen years qualified as drought years by these criteria. We swapped wet for dry years to center droughts on the years 2025, 2050 and 2075 (N=3 droughts). We sought to swap years that occurred closely in

187 time as much as possible, avoiding the creation of near-drought conditions longer than one year
188 elsewhere in the time series. The CO₂ treatment used a fixed value of CO₂ set at the treatment level
189 throughout the simulations. The levels of the soil factor created a gradient of available water
190 capacity (AWC), defined as field capacity minus wilting point, using three standard soil texture
191 classes (sand, sandy loam, loam) [15] (Table 2).

192 Each replicate random assemblage was simulated on a single 30 m cell, and in each assemblage,
193 a single cohort of each of the four hypothetical species was established on an empty cell in 1970 and
194 grown for 40 years to compute starting biomass using fixed monthly averages of temperature,
195 precipitation and PAR and constant CO₂ (385 ppm). The treatments were applied beginning in 2010
196 and run for 100 years. Establishment of new cohorts was not simulated to avoid confounding the
197 experiment. The complete set of PnET-Succession input parameters is provided in the online
198 Supplement.

199 **Analysis**

200 Our primary objective was to assess the relative magnitude of impact of each of the main effects
201 on the dynamics of species responses under different competitive environments. We used a least-
202 squares means procedure to compute mean responses to individual experimental effects by holding
203 all covariates to their mean level [16]. Our expectation was that these effects might potentially
204 interact to produce non-intuitive dynamics. We focused on the relative magnitude of effects and
205 intentionally avoided making inferences about the significance of differences because our model
206 generated different populations for each combination of inputs, and differences in response variables
207 could always achieve statistical significance with enough replicates [17]. Readers can draw their
208 own conclusions about significance by comparing 99% confidence intervals among treatment means.

209 **Landscape-scale experiment**

210 A similar factorial simulation experiment was conducted at the landscape scale using PnET-
211 Succession to incorporate the effects of spatial processes such as dispersal and contagious
212 disturbances that typically structure forested landscapes. The experiment featured the real
213 assemblages of species (Table 3) found on a 104,471 ha sub-boreal mixed forest landscape in northern
214 Wisconsin (USA) (Figure 1) that was used by Gustafson et al [4], to enhance comparisons with those
215 results. Topographic relief is minimal, so climate was assumed to be homogeneous across the study
216 area. Variation in soil type was included in the land type map, which was produced by assigning
217 all SSURGO [18] soil map polygons to the most similar of the three soil types used in the local
218 experiment (Figure 1). The initial forest conditions (species and age cohorts) were those used by
219 Janowiak et al. [19], created using the methods of Wilson et al. [20]. Cell size was 30 m. The main
220 effects were Emission scenario, with the associated CO₂, temperature and precipitation levels,
221 drought length (Table 4), with AWC not a fixed treatment effect, but varying across the landscape
222 according to the landtype input map.

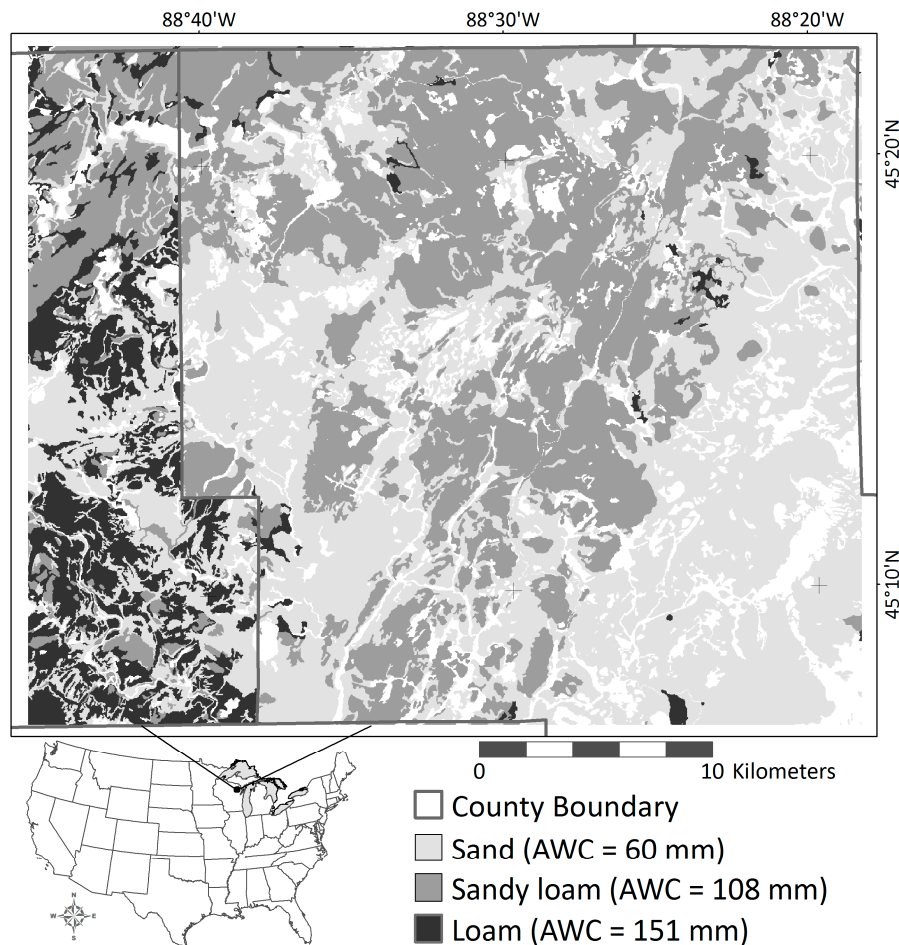


Figure 1. Soil types used in the study area in Oconto county (Wisconsin, USA). Unshaded areas are non-forested and not included in the simulation.

Table 3. Selected life history attributes of species used in the landscape experiment.

| Species | Longevity (years) | FoIN (%) | Drought tolerance class1 | Shade tolerance class1 | PsnT Opt (°C) | Forest Type |
|------------------------------|-------------------|----------|--------------------------|------------------------|---------------|-------------------|
| <i>Abies balsamea</i> | 150 | 0.9 | S-intol | S-tol | 19 | SpruceFir |
| <i>Acer rubrum</i> | 200 | 2.2 | S-tol | S-tol | 26 | RedMaple |
| <i>Acer saccharum</i> | 300 | 2.1 | S-intol | Tol | 23 | SmapBchBassYbirch |
| <i>Betula alleghaniensis</i> | 300 | 2.2 | S-intol | S-tol | 21 | SmapBchBassYbirch |
| <i>Betula papyrifera</i> | 130 | 2.4 | Intol | S-intol | 21 | Aspen-birch |
| <i>Carya corda</i> | 200 | 2.5 | S-intol | S-intol | 25 | Rare |
| <i>Fagus grandifolia</i> | 250 | 2.0 | S-tol | Tol | 23 | SmapBchBassYbirch |
| <i>Fraxinus americana</i> | 200 | 2.5 | S-tol | Interm. | 25 | CherryAsh |
| <i>F. nigra</i> | 150 | 2.6 | Intol | S-intol | 23 | Rare |
| <i>F. pennsylvanica</i> | 200 | 2.5 | S-tol | Interm. | 25 | CherryAsh |
| <i>Picea glauca</i> | 200 | 1.1 | S-tol | Interm. | 21 | SpruceFir |
| <i>P. mariana</i> | 200 | 1.0 | S-tol | Interm. | 20 | MxdSwampConif |
| <i>Pinus banksiana</i> | 100 | 1.3 | Tol | Intol | 20 | JackPine |
| <i>P. resinosa</i> | 250 | 1.5 | Tol | S-intol | 21 | PineOakHemlock |
| <i>P. strobus</i> | 300 | 1.8 | S-tol | Interm. | 21 | PineOakHemlock |
| <i>P. balsamifera</i> | 150 | 2.4 | Intol | Intol | 19 | Aspen-birch |
| <i>P. grandidentata</i> | 90 | 2.5 | Intol | Intol | 22 | Aspen-birch |
| <i>P. tremuloides</i> | 90 | 2.5 | Intol | Intol | 21 | Aspen-birch |

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|---------------------------|-----|-----|---------|---------|----|-------------------|
| <i>Prunus serotina</i> | 150 | 2.5 | S-tol | S-intol | 25 | CherryAsh |
| <i>Quercus alba</i> | 300 | 2.7 | Tol | S-intol | 26 | MixedOak |
| <i>Q. ellipsoidalis</i> | 200 | 2.6 | Tol | S-intol | 21 | MixedOak |
| <i>Q. macrocarpa</i> | 300 | 2.7 | Tol | Interm. | 23 | MixedOak |
| <i>Q. rubra</i> | 210 | 2.6 | S-tol | Interm. | 24 | PineOakHemlock |
| <i>Q. velutina</i> | 200 | 2.3 | S-tol | Interm. | 24 | MixedOak |
| <i>Thuja occidentalis</i> | 400 | 1.0 | S-intol | Interm. | 20 | MxdSwampConif |
| <i>Tilia americana</i> | 200 | 2.5 | S-tol | S-tol | 23 | SmabBchBassYbirch |
| <i>Tsuga canadensis</i> | 450 | 1.4 | S-intol | Tol | 21 | PineOakHemlock |

¹ Classes: Tolerant, Somewhat tolerant, Intermediate, Somewhat intolerant, Intolerant

Table 4. Levels of the landscape-scale experimental treatment factors, resulting in 4 combinations of levels.

| Treatment factor | Low | High |
|--------------------------------|---------|----------|
| Emission scenario | RCP3.0 | RCP8.5 |
| CO ₂ (ppm)* | 381-443 | 381-1962 |
| Approx. temperature rise (°C)* | +1.5 | +8 |
| Length of droughts (yrs) | 3 | 5 |

* CO₂ and temperature are not separate treatment factors, but are derived from the emissions scenario, varying monthly through time.

We linked the CO₂ and temperature treatments by using GCM projections of temperature driven by two RCP emissions (CO₂) scenarios developed for the Intergovernmental Panel on Climate Change Fifth Assessment Report [1] for the period 2006-2100. We chose the Model for Interdisciplinary Research on Climate earth system model (MIROC-ESM r1i1p1) [14b] to generate the temperature and base precipitation weather stream for the RCP emission scenarios because it predicts a very warm future in our study area under the RCP8.5 scenario. For both climate scenarios, we used future monthly values of solar irradiation from the Vegetation-Ecosystem Modeling and Analysis Project (VEMAP 2; https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=567) [21]. The RCP3.0 scenario projects CO₂ atmospheric concentrations to peak at 443 ppm around the year 2050 and decline thereafter, while the RCP8.5 scenario projects concentrations to rise throughout this century and stabilize around the year 2250 at over 1900 ppm. Because the climate projections end at the year 2100, we duplicated the precipitation series (negligible temporal trend) for an additional three centuries to produce a time series through the year 2405 (400 years). A stochastic background disturbance regime was simulated in all factorial combinations that included fire, windthrow and timber harvest. Fires were simulated using the Base Fire extension [22], parameterized based on data in [23]. Microburst wind events were simulated using the Base Wind extension [24], parameterized based on data in Rich et al [25]. Tornadoes and derechos were simulated using the Linear Wind extension [26], parameterized based on data in Hjelmfelt [27] and online sources (<http://www.wunderground.com/resources/education/tornadoFAQ.asp?MR=1>). Timber harvest was simulated using the Biomass Harvest extension [28], using generic harvest prescriptions based loosely on those used in another study in the region [23]. Prescriptions included a mix of clearcut (various rotation intervals), shelterwood and selection cutting methods. Input files for all LANDIS-II extensions are included in the online Supplement.

Three replicates of each factorial combination were simulated for 400 years. Because of the longevity of some species, we found that 400 years was required to erase the legacy of the starting conditions. The response variable was mean biomass through time of sets of functional groups defined by: drought tolerance, PsnTOpt, forest type (consistent with Gustafson et al [4]). We plotted the temporal trends in the response variable under each treatment combination in side-by-side panels to allow visualization of the treatment effects. We also computed mean measures of diversity

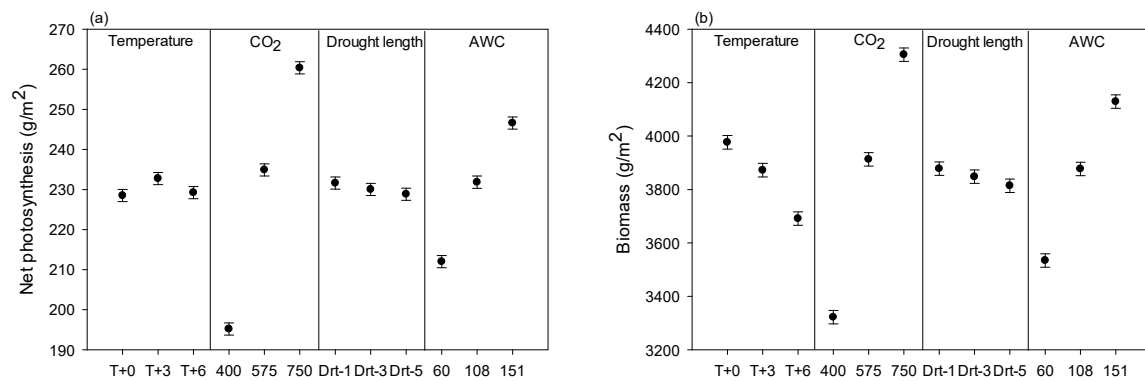
264 (species and age class richness) for all forested cells and an index of landscape fragmentation
 265 (Aggregation Index [29]).

266 3. Results

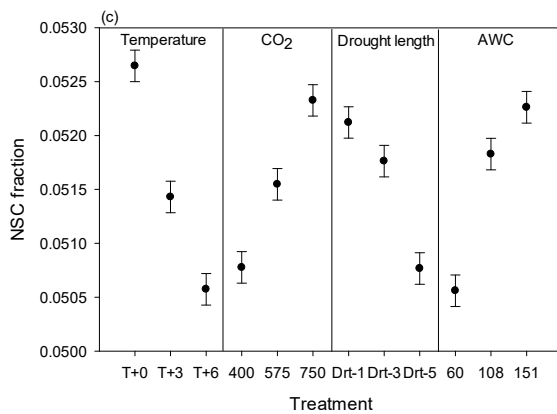
267 Site-scale experiment

268 The CO₂ treatment factor had the greatest effect on all of the response variables except NSCfrac
 269 (carbon reserves). Its positive effect on growth (Figure 2a,b) dwarfed the negative effects of elevated
 270 temperature and longer droughts, and approximately compensated those negative effects for carbon
 271 reserves (Figure 2c). All four factors had a negative effect on mean age attained by cohorts (Figure
 272 2d). Elevated CO₂ and increasing AWC had an indirect negative effect on mean age attained by
 273 cohorts by enhancing the competitive advantage of rapidly growing cohorts, allowing them to
 274 competitively exclude slower growing cohorts. Elevated temperature and longer droughts also had
 275 direct negative effects by increasing respiration costs and reducing reserves, promoting mortality of
 276 cohorts. The magnitude of the positive effect of CO₂ relative to the negative effect of temperature
 277 and drought length is clearly seen in Figures 3 and 4.

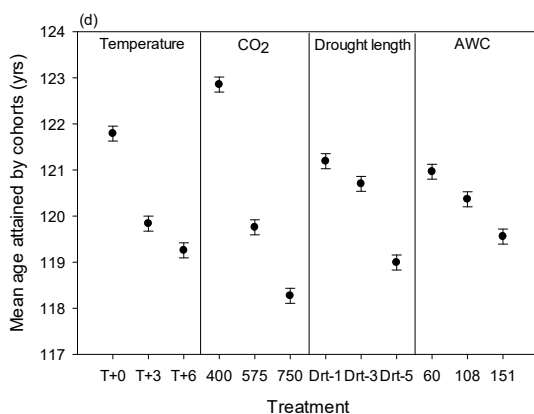
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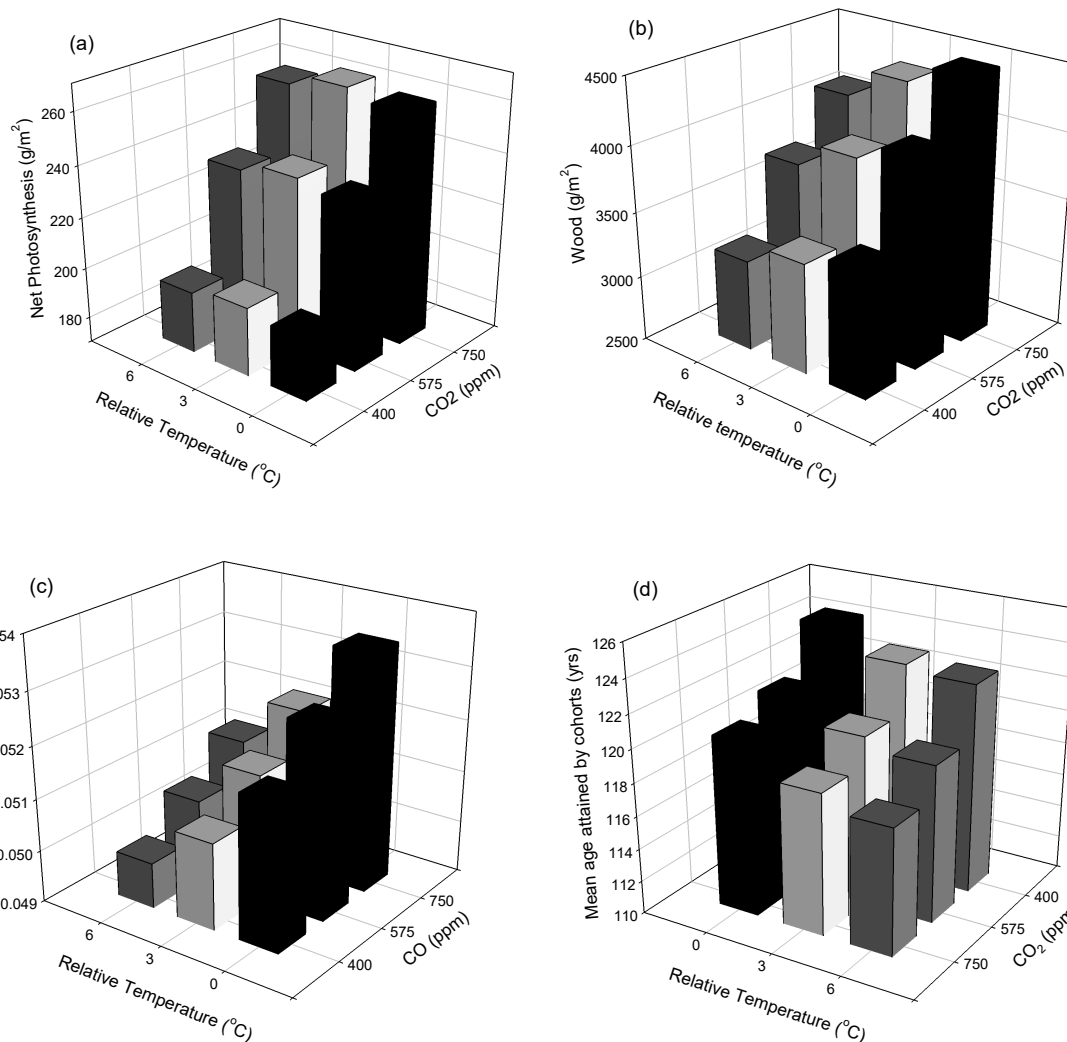
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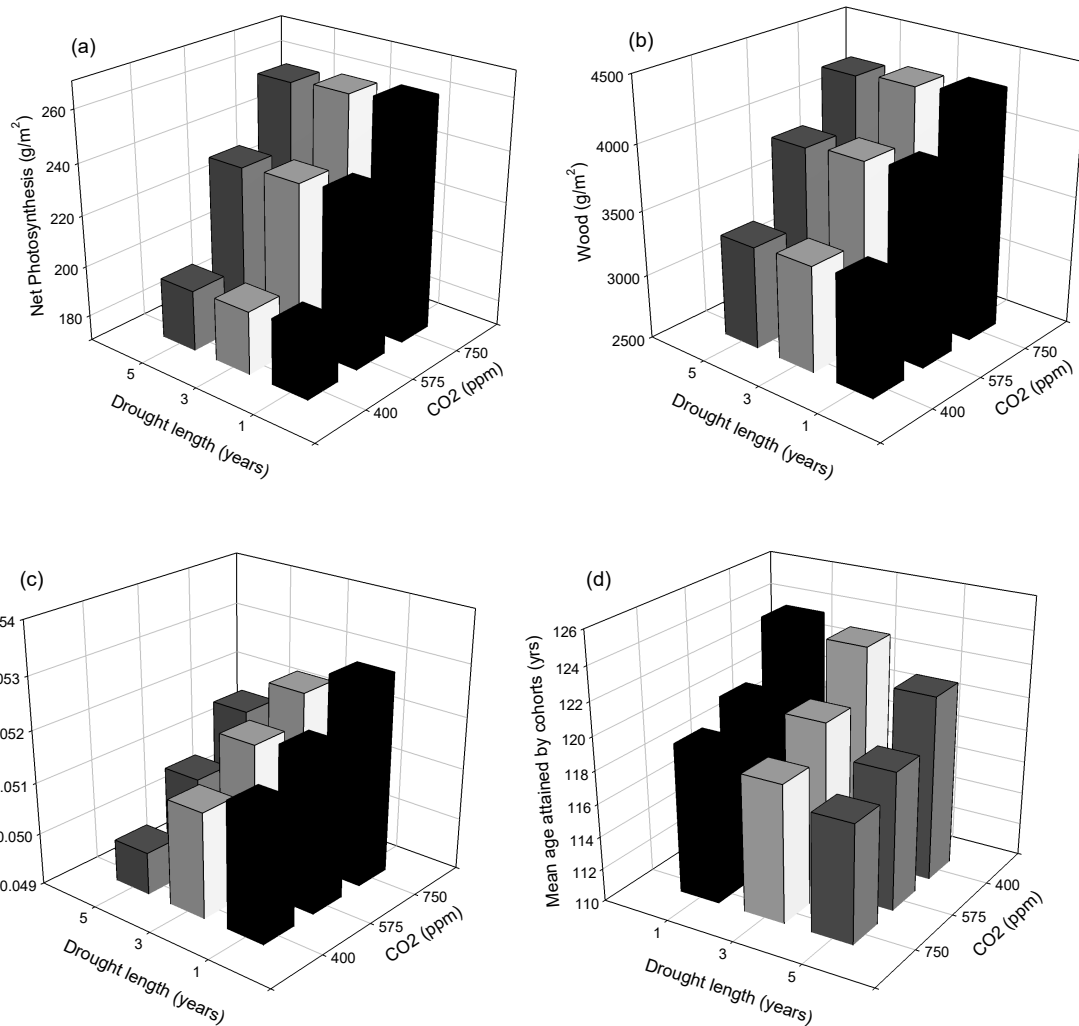
281 **Figure 2.** Mean and 99% confidence intervals (error bars) of (a) average annual net
 282 photosynthesis ($R^2=0.015$), (b) woody biomass ($R^2=0.014$), (c) cohort energy reserves ($R^2=0.003$) and
 283 (d) competitive exclusion ($R^2=0.008$) of cohorts over the 100 simulated years in response to the
 284 treatment levels, adjusted using least squares techniques. There was no evidence of important
 285 interactions except perhaps between temperature and AWC and drought and AWC in (d).



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Figure 3. Mitigating effect of CO₂ on the negative temperature effect. Note axis inversion in (d).



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Figure 4. Mitigating effect of CO₂ on the negative drought length effect. Note axes inversions in (d).

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Landscape-scale experiment

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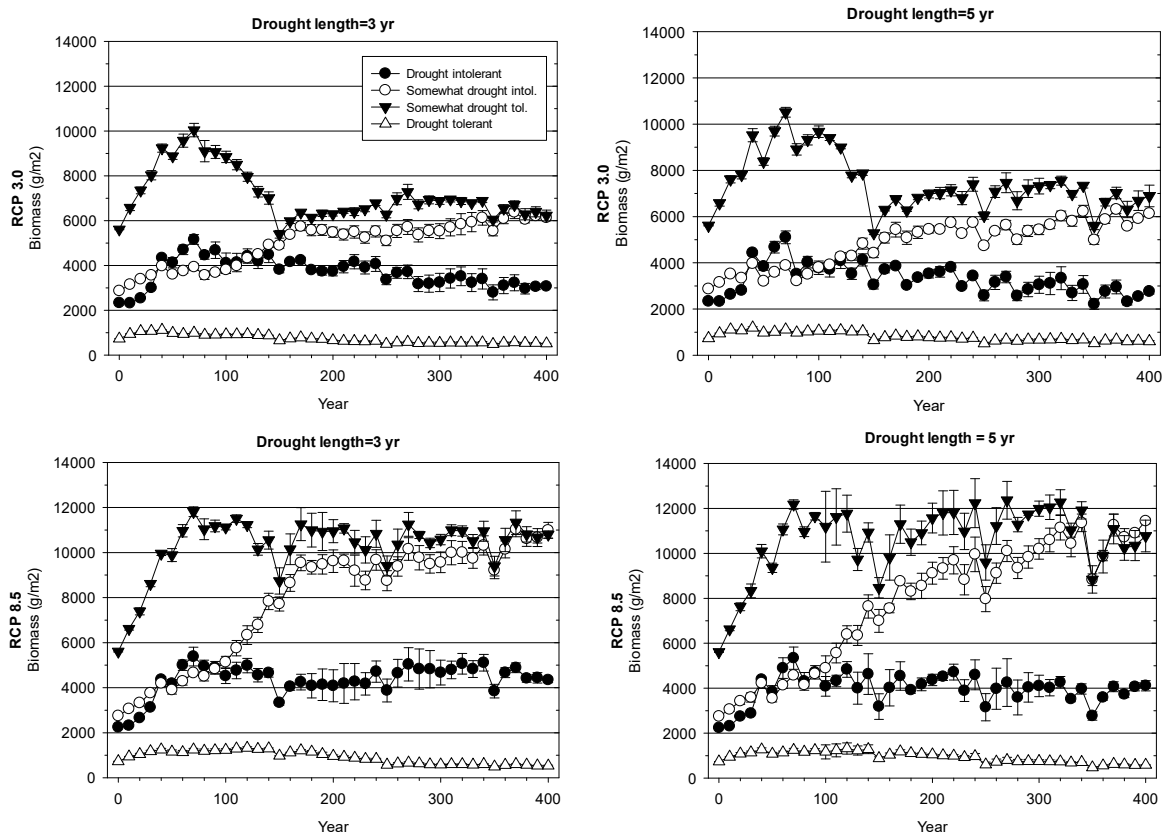
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At the landscape scale, productivity was impacted by climate scenario to a much greater extent than drought length (Figures 5, 6, 7). Under both climate change scenarios, longer droughts increased variability around the long-term trend, and generally, less drought-tolerant species (H4=-1.37, -1.40) had somewhat lower biomass and more drought-tolerant species (H4=-1.44, -1.50) had somewhat higher biomass (Figure 5). Higher CO₂ concentrations and warmer temperatures (RCP8.5) generally increased the biomass of all drought-tolerance groups, and only marginally mitigated the effect of drought length. The most drought-tolerant group (H4=-1.50) showed almost no response to drought length, although such species were very uncommon and may not have had enough photosynthetic machinery (foliage biomass) to take advantage of their competitive advantage under longer droughts.



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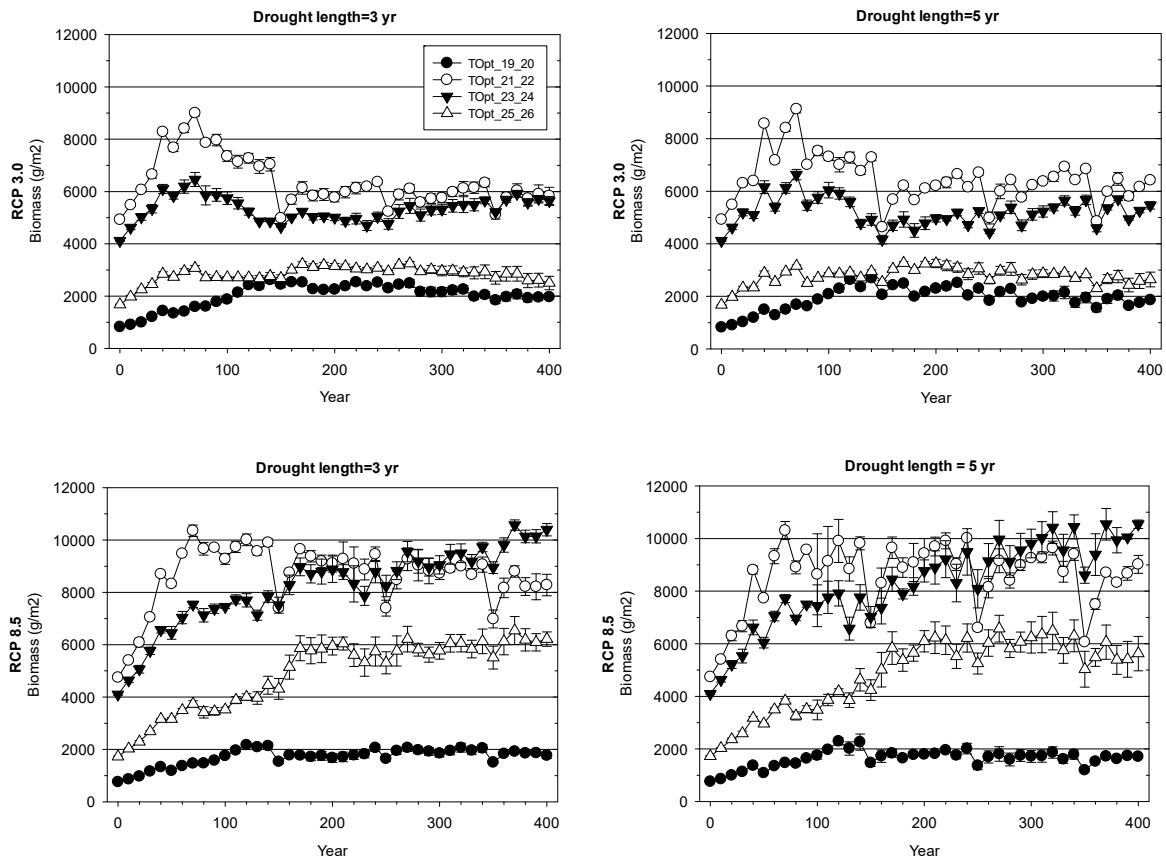
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Figure 5. The effect of climate (rows) and drought length (columns) on productivity (mean species biomass) by drought tolerance groups. Error bars show one standard deviation.

Species productivity (biomass growth) was enhanced by warmer temperatures and elevated CO₂ for all but the most cold-adapted group (T_{Opt}=19-20 °C) (Figure 6). Drought length did not greatly affect the biomass of optimal temperature groups, suggesting that drought-tolerance is not correlated with optimal temperature for the species studied.

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Figure 6. The effect of climate (rows) and drought length (columns) on productivity (mean species biomass) by optimal temperature groups. Error bars show one standard deviation.

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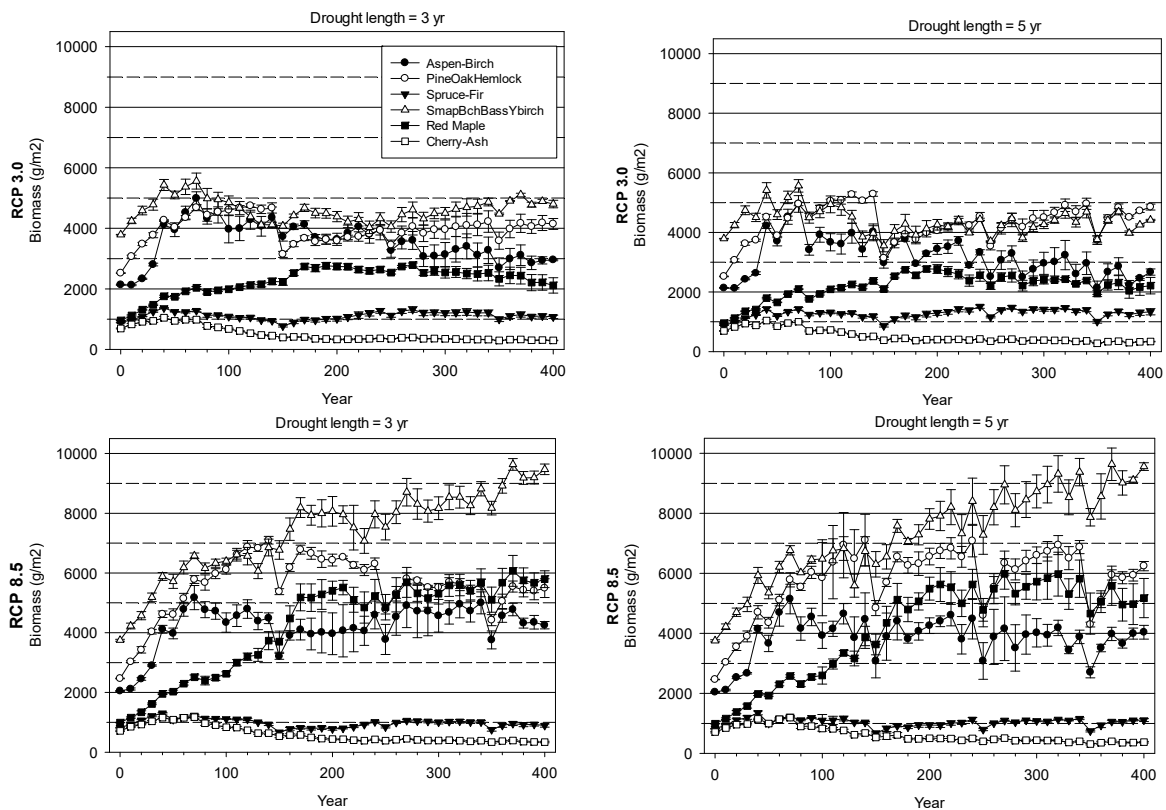
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The growth response (biomass) of forest type groups often responded dramatically to climate scenario, while the response to drought length was more subtle (Figure 7). Specific responses depended on many life history attributes, with optimal temperature and drought-tolerance being the most directly linked to the treatments. For example, aspen-birch responded negatively to both extreme climate (RCP8.5) and longer droughts. Red maple responded positively to extreme climate and negatively to longer droughts. The pine-oak-hemlock group responded positively to both extreme climate and longer droughts.



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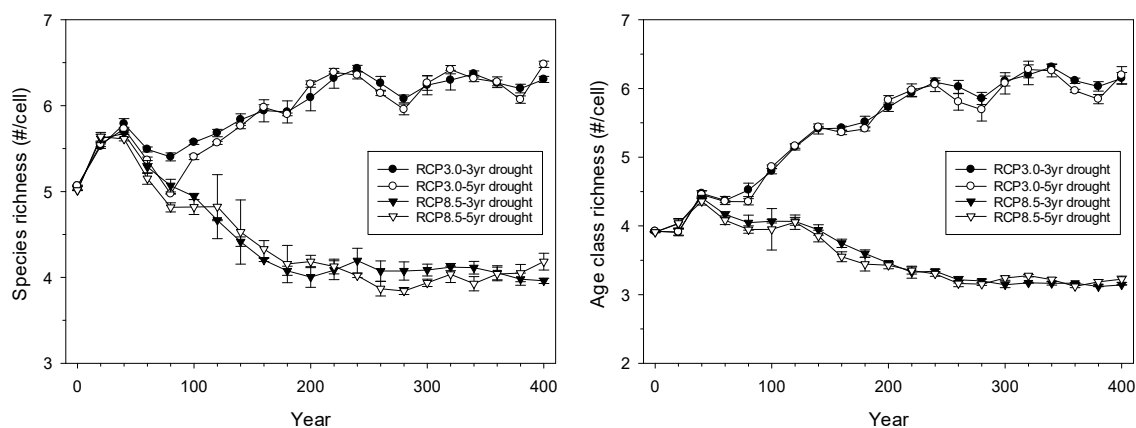
328

329 **Figure 7.** The effect of climate (rows) and drought length (columns) on productivity (mean
 330 species biomass) by forest type groups. Mixed swamp conifers and mixed oaks were very
 331 uncommon and are not shown. Error bars show one standard deviation.

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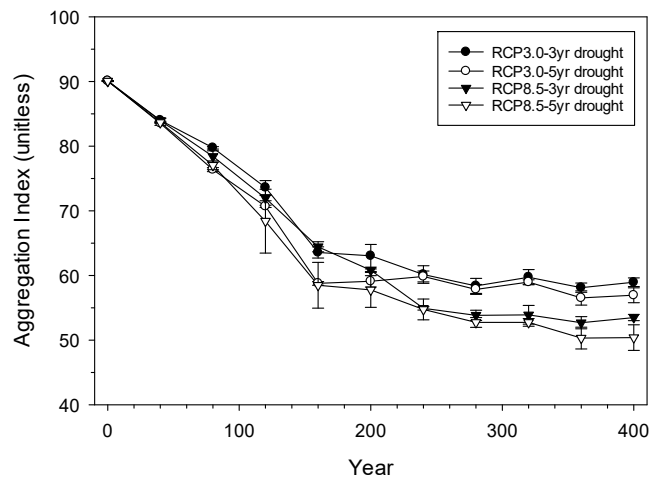
334 Climate had a pronounced effect on species and age class diversity (richness) while drought
 335 length did not (Figure 8). Mild climate change (RCP3.0) increased diversity, and severe climate
 336 change reduced it. Disturbances had a strong fragmenting effect on forest as defined by forest type
 337 over the first 80 years, and harsh climate change increased fragmentation somewhat in the long term
 compared to mild climate change (Figure 9). The effect of drought length was less pronounced,
 with longer droughts having a greater fragmenting effect.



338

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Figure 8. Change in mean richness measures on forested cells through simulated time.



340
341 **Figure 9.** Change in Aggregation Index (measure of clumpiness) through simulated time on
342 maps classified by forest type.

343 4. Discussion

344 Site-scale experiment

345 Our results clearly show that greatly elevated CO₂ stimulates productivity (NetPsn and biomass
346 production) to such an extent that it dwarfs the negative effect of higher respiration rates caused by
347 elevated temperature (Figure 2a,b). In Figure 3a,c, productivity measures for the next highest
348 temperature and CO₂ level are always higher than at the lower levels, indicating that a 175 ppm
349 increase in CO₂ more than compensates for the increased respiration caused by a 3 °C temperature
350 increase. This result clarifies the results of Gustafson et al. [4] that showed a negative effect on
351 growth of a 6 degree (C) temperature increase without the concomitant CO₂ concentration that would
352 accompany such a temperature increase. This result is consistent with empirical findings of large
353 CO₂ enrichment effects. Charney et al [30] used continent-wide empirical observations of tree
354 sensitivity to climate and CO₂ to predict increases in growth across much of North America of up to
355 60% under the RCP8.5 emissions scenario. In a test of the ability of PnET-Succession to simulate the
356 effects of CO₂ enrichment on tree growth and competition in the Aspen-FACE experiment in northern
357 Wisconsin, USA [31], Gustafson et al [11] found good agreement with empirical CO₂ effects with no
358 calibration required. Giardin et al [32] found a negative temperature effect (attributed to
359 respiration) on the growth of trees across Canada in the last half of the 20th century, which was not
360 completely mitigated by the CO₂ concentrations of that period (<400 ppm). It is important to note
361 that our model does account for CO₂ acclimation effects on growth as described by Franks et al [8],
362 and to maintenance respiration acclimation as temperature rises [12,33], so these results can be
363 considered robust at the CO₂ and temperature levels simulated. Conversely, carbon reserves
364 (NSCfrac) were not as strongly mitigated by elevated CO₂. Increased temperature reduced carbon
365 reserves while increased CO₂ concentration increased them by about the same amount (Figure 2c).
366 Although the magnitude of the differences in mean NSCfrac may appear to be small, it is not
367 uncommon for simulated cohorts to have “near misses” with death in the event of an extreme climate
368 event, typically drought. Thus, a small difference in mean carbon reserves may dramatically change
369 the likelihood of cohort survival.

370 The relationship between temperature and CO₂ was opposite for the metric of competitive
371 exclusion (mean age attained by cohorts) compared to all other response variables (Figure 2d),
372 although the mechanisms driving the response was consistent for all variables. The mean age of
373 cohorts declined when some cohorts died prematurely, reflecting competitive exclusion. Mean
374 cohort age declined when temperature increased because the increased respiration load reduced
375 carbon reserves and increased the risk of mortality. However, mean cohort age also declined when
376 CO₂ concentration increased, through the competition process. Elevated CO₂ gave dominant

377 cohorts an even greater competitive advantage over subdominant cohorts, which became more prone
378 to mortality because they were less able to maintain carbon reserves.

379 Drought length had a surprisingly small effect on productivity measures (Figure 2a,b), but a
380 marked negative effect on mortality risk (NSCfrac and mean age) (Figure 2c,d, 4c,d). In fact, the
381 trends suggest a negative exponential decline in survival measures when droughts exceed 5 years in
382 length (Figure 2c,d). The modest negative effect of drought length at each level of CO₂ for the
383 productivity measures (Figure 4a,b) suggests that surviving cohorts compensate for the lost
384 productivity of killed cohorts as competition for light and water resources is reduced, consistent with
385 the empirical results described by Gustafson and Sturtevant [6], where biomass lost to mortality on
386 US Forest Service inventory plots increased exponentially with drought length. Elevated CO₂ was
387 able to compensate for the negative effect of longer droughts in terms of productivity measures (e.g.,
388 compare 5-year drought productivity to the 1-year drought values at the next lower CO₂ level (Figure
389 4a,b)), but not for survival measures (Figure 4c,d). This suggests that elevated CO₂ may sustain or
390 even increase the productivity of forests in the face of rising temperatures or longer droughts, but it
391 may not sustain species or age class diversity.

392 Increased soil water (AWC) always increased productivity and carbon reserves, but it also
393 increased competitive exclusion (Figure 2). This reflects the fact that water is the primary limiting
394 factor as cohorts gain biomass and increase transpiration demand. Increased AWC results in
395 increased mortality of less competitive cohorts by enhancing the growth of their competitors. While
396 elevated CO₂ speeds biomass gain and therefore hastens the time when water becomes limiting,
397 greater AWC enables greater biomass gain in response to elevated CO₂. Similar to the trends for
398 drought length, NSCfrac decreased non-linearly with decreasing AWC, suggesting that chronic water
399 stress can rapidly reduce reserves and make cohorts more likely to die. Because water stress differs
400 among the species on a given cell according to their drought tolerance (i.e., H3/H4, Figure 5),
401 simulated droughts tend to kill less drought tolerant species first, potentially altering species
402 composition.

403 **Landscape scale experiment**

404 The tightly controlled site-level experiment clearly revealed the response of competing
405 assemblages of species without the confounding effects of disturbances, dispersal, establishment, and
406 the spatial pattern of soil types and existing vegetation. The landscape-scale experiment was more
407 realistic in that it featured real assemblages of species and life history traits typical of the sub-boreal
408 zone, and revealed whether the responses were altered when interacting with spatial legacies and
409 landscape structuring processes. Although the treatments mostly altered the absolute biomass of
410 most forest type groups, the rank order in biomass of forest types remained consistent, with the
411 exception of the aspen-birch group. Even under the RCP8.5 scenario, longer droughts had about
412 the same effect as under the RCP3.0 scenario (Figure 7). Based on these simple simulations on a
413 single real landscape, it appears that CO₂ enrichment can substantially mitigate the negative effects
414 of elevated temperatures on forest productivity, although its ability to mitigate drought is less
415 obvious. However, there are consequences for forest composition because there are winner and
416 loser species under climate change. It appears that forests would become less diverse (more losers
417 than winners) and less aggregated under the RCP8.5 scenario compared to the RCP3.0 scenario,
418 which may lessen their resilience [34]. Our results do not provide specific insight into how forests
419 might respond to intermediate emissions scenarios (e.g., RCP6.0), but it is reasonable to expect that
420 outcomes would be intermediate to the scenarios studied here.

421 Our landscape experiment illustrates the power of a mechanistic landscape model to scale up
422 physiological first principles that are typically derived and applied at leaf and plant scales to
423 landscape scale. All processes that structure the landscape were simulated at a scale appropriate to
424 the drivers and the mechanisms that underlie their behavior, and they each act somewhat
425 independently on the vegetation state of cells (in our case, the biomass of the extant cohorts), with
426 the interaction of all these processes across all the cells of the landscape representing the projected
427 forest dynamics. Because most processes are linked mechanistically to climate and vegetation

428 drivers, using this approach to predict the effects of environmental conditions without historical
429 analog (e.g., climate change) is notably powerful and robust [35]. Reichstein et al [36] point out that
430 climate extremes such as droughts and heat waves have the potential to negate the expected increase
431 in carbon stocks predicted by studies such as ours, and our mechanistic modeling approach is well-
432 suited to integrate such climate extremes into the simulation of ecosystem response.

433 5. Conclusions

434 Our results, combined with those of Gustafson et al [4], help suggest mechanisms for results
435 reported by others. Duveneck et al [37] and Wang et al [38] simulated increased biomass in
436 temperate US forests over the next century, attributing the increase to longer growing seasons caused
437 by warming temperatures. Our results suggest that elevated CO₂ may be an important contributing
438 cause. Giardin et al [39] simulated the effects of climate change on the growth of black spruce in
439 Canada, and found negative impacts attributed to increased maintenance respiration associated with
440 high summer temperatures and water stress that were only partially ameliorated by elevated CO₂
441 concentrations. Because black spruce is slow-growing, easily subject to water stress, and loses
442 approximately two-thirds of its gross primary productivity to respiration [40], elevated CO₂ is
443 unlikely to increase the low natural productivity of black spruce enough to offset the negative effects
444 of temperature and water stress. Sanchez-Salguero et al [41] reported a simulated decline in tree
445 productivity in Spain under various RCP emissions scenarios, including RCP8.5, which was
446 attributed to temperature and water stress effects on photosynthesis. However, their model did not
447 simulate any CO₂ effects on water use efficiency or photosynthesis, which our results suggest may
448 have compromised their findings. Nemani et al [42] used productivity efficiency models and
449 climate data to show that global climate changes (1982-1999) relaxed climatic limitations
450 (temperature, water and radiation) on plant growth globally. This result from the last century is
451 consistent with the results of Gustafson et al [4], and our current results suggest that increasing CO₂
452 concentrations can be expected to at least partially ease future climate constraints. These are but a
453 few examples of the many studies for which the findings reported here can provide insight into the
454 mechanisms behind their results.

455 Our results provided insight into our hypotheses. 1) We hypothesized that chronically
456 elevated CO₂ concentrations would increase growth rates even at high temperatures, and our results
457 clearly support this. However, it should be noted that our model assumes that soil nutrients are not
458 limited, and that actual growth rates on perhaps the majority of forested sites globally may be less
459 than we project [43]. 2) We also hypothesized that increased drought length would produce a
460 greater negative effect on growth than just a proportional decrease in precipitation. This hypothesis
461 was not supported. Gustafson et al [4] found that NSCfrac decreased by about 8% when monthly
462 precipitation was reduced by 40%, and we found that increasing drought length from 1 year to 5
463 years decreased NSCfrac by only about 2%. 3) We also thought that there may be an interaction
464 with CO₂ such that drought effects are also mitigated by high CO₂ concentrations by reducing
465 stomatal water loss. Our results (Figure 4) suggest that elevated CO₂ does not protect trees from
466 drought. 4) Finally, we hypothesized that disturbance would increase landscape-wide productivity
467 under elevated temperature and water stress and elevated CO₂ by hastening a species composition
468 change favoring species with greater heat and drought tolerance. Our results showed that drought
469 tolerant species did not increase in biomass under climate change, while that all species with an
470 optimal temperature greater than 20 °C did increase in biomass (Figure 5, 6).

471 We conclude that elevated CO₂ can indeed mitigate the decrease in net photosynthesis resulting
472 from increased respiration costs caused by increasing temperature, but the ability of CO₂ to mitigate
473 water and light stress is not as strong. Our results suggest that forest managers can expect that
474 elevated CO₂ in the future will increase forest productivity even as temperatures rise, and even if
475 droughts become more frequent and of longer duration. However, they can also expect that forests
476 will become more simplified as less competitive species experience somewhat enhanced mortality.

477 **Supplementary Materials:** The following are available online at www.mdpi.com/xxx/s1, PnET-Succession input
478 files.

479 **Author Contributions:** Conceptualization, Gustafson and Sturtevant; Methodology, Gustafson and Miranda;
480 Software, Miranda; Validation, Gustafson; Formal Analysis, Gustafson, Sturtevant and Miranda; Investigation
481 Gustafson; Resources, Gustafson; Data Curation, Gustafson; Writing-Original Draft Preparation, Gustafson;
482 Writing-Review & Editing, NA; Visualization, NA; Supervision, Gustafson; Project Administration, Gustafson;
483 Funding Acquisition, Gustafson.

484 **Funding:** This research received no external funding

485 **Acknowledgments:** This study was funded by the Northern Research Station of the USDA Forest Service. We
486 thank Meghan Graham MacLean and Yan Boulanger for critical reviews of the manuscript.

487 **Conflicts of Interest:** The authors declare no conflict of interest.

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