

Do growing season length and growth relate?
And if not, why not?
And if we're not sure, why is that?

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August 27, 2023

Abstract

Recently a growing number of studies have challenged a fundamental assumption underlying most forecasts of future climate—namely, that longer growing seasons lead to increased tree growth—which predict increased plant growth will partly offset carbon emissions. A suite of diverse hypotheses, from increased drought and high temperatures, to internal limits on plant growth each year, have generally failed to coalesce around a predictive model why longer growing seasons do not increase tree growth. Here we highlight how progress could come from rising to the interdisciplinary challenge of this topic. Working across dendrochronology, ecology, and physiology, we present a mechanistic framework for predicting when longer seasons should lead to greater growth. While persistent biases in which disciplines study which mechanisms means much of the framework remains untested, we show that critical data—currently untapped—could rapidly advance our understanding, and in turn greatly improve vegetation models.

The idea that longer growing seasons lead to increased plant growth is an intuitive tenet across multiple fields, including physiology (CITES), dendrochronology (CITES) and ecology. It is also a foundational assumption of most models of the future global carbon cycle (CITES). Most models project that future anthropogenic warming will be partly offset by increased carbon sequestration—primarily of temperate and boreal forests—as warming lengthens growing season (CITES), an assumption supported by a suite of ecosystem-scale studies (CITES). Yet recent work has called this assumption into question.

A suite of recent studies have suggested longer growing seasons do not lead to greater tree growth (CITES), with potentially large implications for future climate change. This research suggests limitations on plant growth mean forests will be limited sinks with increased warming. Such findings challenge decades of research that find growth does increase with longer seasons, from large-scale studies along natural elevational gradients (CITES) to small-scale studies of cell growth in lab settings (CITES) to previous studies of ecosystem fluxes with warming (CITES). Proposed mechanisms for the apparent disconnect are highly diverse, from previously unknown fundamental internal limits on plant growth (CITES) to effects of climate change itself, such as increased drought or temperatures too high for plant growth (CITES), as well as differences simply due to the metric of growth (GREEN KEENAN).

Here we review the connections between growing season length and plant growth across fields to identify the potential mechanisms that unite—and could disconnect—these processes. Our approach spans multiple fields to unify foundational studies with recent research related to anthropogenic warming. We find a pervasive disciplinary split between studies that limits our current ability to identify the underlying processes, and further highlight critical insights from physiology, community ecology, and life history theory that have been unexamined in recent work. Taken together, the current and past versions of fields studying connections between growing season length and growth appear primed to develop a holistic theory of when, where and how climate change may increase tree growth, with implications for both forecasts of future climate change and for fundamental science.

How warmer temperatures increase tree growth, or not

Fundamentally, temperature limits biological processes and is a dominant controller of biological time. Temperatures that are too cool (often considered to be below 5C for temperate trees) and too warm (an area of active research but maybe 30-45C for trees???, but perhaps see a figure we'll add?) slow down biological processes to near-unobservably slow and eventually can lead to tissue death (CITES). Between the upper and lower limit biological processes underpinning growth generally accelerate such that warming can have a direct effect, effectively by accelerating biological time, up until the maximum rate (Fig. 1). This maximum rate means absolute time also matters to plant growth, which provides the mechanism through which longer growing seasons—extending absolute available time—can increase total plant growth.

End this section with short part of how well do we know this based on controlled studies? (Alana)

i. Hypotheses for why GSL x growth is not found are not equally tested across fields: Constraint issues in provenance but not tree ring etc. ii. Our premise is that some hypotheses for what is going may be tractably already answered by combining data across fields/methods iii. And, you could go far by cross-field tweaking of what each field is doing

And somehow ... This is important! i. Carbon storage and climate change ii. Fundamental to physiology, species assembly

Studies that Green & Keenan say no relationship:

Most global models of future warming assume increased anthropogenic carbon will be offset by increased carbon sequestration in forests as growing seasons lengthen.

The proposed mechanisms for this, however, are highly diverse—and most studies measure different aspects of growth across widely varying spatial and temporal scales.

Yet the proposed mechanisms for this are highly diverse, as are the temporal and spatial scales of st

each with varying hypothesis for why.

A positive link between longer growing seasons and increased carbon sequestration

A suite of recent studies have called into question this fundamental assumption failed to find a link between longer seasons and increased tree growth

This assumption appeared well supported by several large-scale studies of ecosystem fluxes

1 Figures

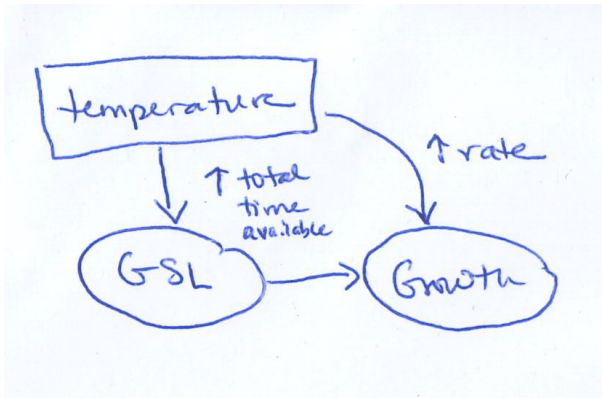


Figure 1: Idealized simplified version of the world, where resources (including water, N etc.) are abundant and temperatures are never too cool or too hot. In this world, temperature can increase growth directly (through increasing the speed of biological processes, up to some limit) and indirectly, but increasing the absolute available time for those processes to happen and lead to more growth.

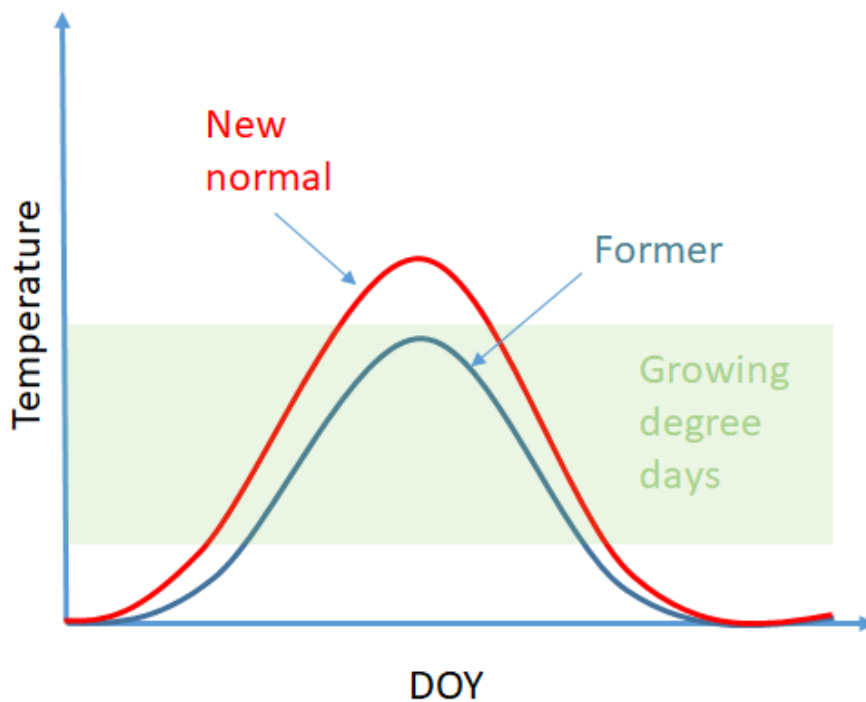


Figure 2: Simplified version of how GDD works before and after climate change.

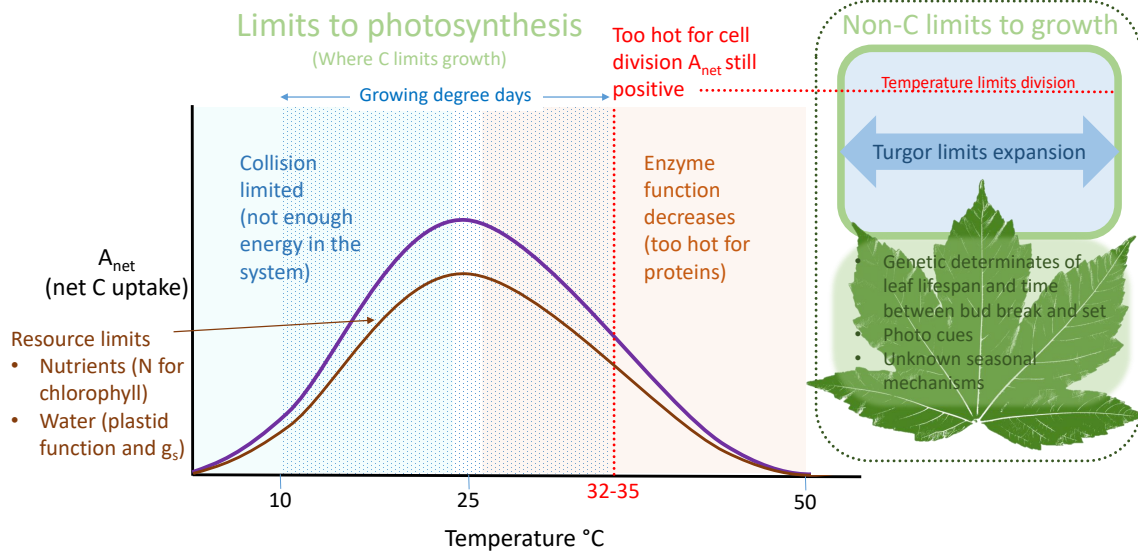


Figure 3: Less simplified version of how temperature works.

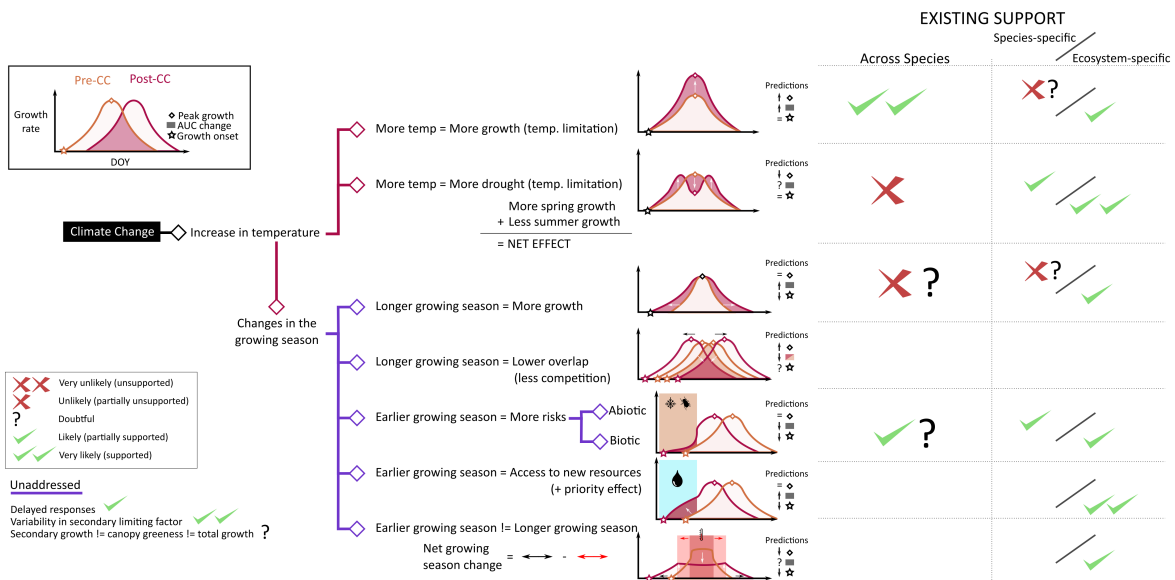


Figure 4: Pathways through which climate change could alter growing season length and growth.

2 Old take home results from table

Warnings & disclaimers: *I flip between counting papers at the start to looking more at rows, so you were forewarned on that.*

Out of 37 papers (we have currently 60 rows of data).

3 Getting back to writing our paper

Reminder of what we expected the table we worked on since April to help us with ...

1. Section: Review three reasons for not growing

(a) Overview paragraph of three reasons

- i. Measurement – see box/figure (include measurement only here or briefly so we move through it fast)
- ii. Resource limitation
- iii. Constraints

(b) Resource limitation, evidence for an against _____

- i. Nutrients
- ii. Water
- iii. Is this more species-specific?

Table will help us with this

(c) Constraints, evidence for an against _____

- i. Leaf life span
- ii. Budset stuff ... (Zohner, Sool.)
- iii. Evidence across species? Or which is species-specific

Table will help us with this

2. What do do next (The future! Is there a framework to our future directions? It would be nice if we found one) _____

So, we hoped these studies would help with the prevalence of evidence for external and endogenous factors. I haven't got as far on this (and we did not consistently enter whether growth or GSL or both was limiting) but here's a quick look at the 28 papers that found evidence of external factors and 15 that found evidence of endogenous (in contrast to 12 papers that looked but did not find evidence of external or 25 endogenous factors).

For those that did, they looked at these GSL metrics:

```
> table(exoyes$gsl)
```

This needs a total overhaul after the table; figure out the section headers

	date	not measured
	1	11
plant vegetative phenology		satellite derived
	20	2
temperature or snow metric		wood phenology
	5	5

```
> table(endoyes$gsl)
```

	not measured	plant vegetative phenology
	10	11
satellite derived		wood phenology
	2	5

And specifically:

```
> table(exoyes$gs_metric_used)
```

	end metric only
	8
	none
	1
	start metric only
	9
	start to end
	12
	start to end (I think for SFGCC)
	1
	suitable days
	4
time with growth estimated (from mar-may temperature records)	
	1
	time with growth observed
	2
	unsure
	2

```
> table(endoyes$gs_metric_used)
```

	end metric only	none	start metric only
	7	1	6
	start to end	time with growth observed	unsure
	10	2	2

And these growth metrics (seems a bias towards annual core studies looking at external; we have 14 annual core results):

```
> table(exoyes$growth)
```

NDVI/greenness	annual core
2	11
biomass height stems	dendrometer/circumference
8	3
ecosystem fluxes	intra-annual core (xylogeneis)
7	5
not measured	photosynthesis
1	7
root:shoot ratio	
1	

```
> table(endoyes$growth)
```

NDVI/greenness	annual core
1	2
biomass height stems	dendrometer/circumference
6	4
ecosystem fluxes	intra-annual core (xylogeneis)
8	2
photosynthesis	root:shoot ratio
5	1

4 Next steps

- How to finalize the table cleaning?
 - I would prefer this all documented over github than being done over email
 - Not sure how to resolve Richardson study
 - And there are likely more
- How do we want to analyze the table?
 - One idea is to break out what parts of the paper people are working on and then they do their own analysis – but built off one set of shared cleaning code or such.
 - Work on analysis using the table is centralized in one person
- Do we want to make a figure that reviews the path diagram from GSL to growth and somehow summarizes what we have found?
- Do we want to re-analyze any of the studies that have the data but did not test our definition? (Dow2022, Finzi2020, Stridbeck2022, zani2020, chen1998, ren2019)
- What else?