# 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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# 1 Outline

1. Introduction (what's happened in the past and where this paper goes)
   (a) Multiple fields assume longer GSL means more growth
   (b) Unexpected controversy over GSL[1] and tree growth
      i. But ... Tree ring old studies do show GSL x growth (ring width) ... this might be inferred through tree line or such.
      ii. Back when: Ecosystem scale growth (NPP?) increases with warming
      iii. New studies: New studies (all tree rings?) don't show GSL x growth (ring width)
      iv. Here, we. ...
         A. Hypotheses for why GSL x growth is not found are not equally tested across fields: Constraint issues in provenance but not tree ring etc.
         B. Our premise is that some hypotheses for what's going may be tractably already answered by combining data across fields/methods
         C. And, you could go far by cross-field tweaking of what each field is doing
   (c) How warmer temperatures increase tree growth, or not
      i. How they could ...
         A. fundamentally, temperature limits biological processes and is a dominant controller of biological time.
         B. Too cool is bad, too hot is also bad.
         C. These upper limits to rates means absolute time matters also (it's the bottom of the rate equation)
         D. temperature should thus limit growth through two major pathways
         E. Directly by increasing rates
         F. Through extending periods when development and growth are possible – extending absolute period of absolute time available (versus relative time)
         G. End this section with short part of how well do we know this based on controlled studies? (Alana) ... Maybe end on: So, if the physiological evidence is maybe not so amazing, where does this hypothesis come from?
   (d) Dendrochronology has long assumed growth decreases with factors that shorten seasons, especially: elevation and latitude
      i. Lots of elevation studies, though most assume the relationship – fewer show it (see Fig)

[1] GSL: growing season length; RL: resource limitation

ii. Many look for shifting climate correlations with elevation, more than growth shifts with elevations ... this is a hallmark of dendro – tree ring growth as a detector of climate, not other factors that limit growth (usually)

iii. Less work on latitude, but some (see refs)

iv. But dendro has never looked deeper, and the literature is really split from the phenology literature – dendro is conifers mostly and phenology is most often deciduous

v. Note to self: Don't get into complexities here – the goal is to show the relationship exists at this point in ms.

(e) Given this does seem a real thing, WTF is happening in recent studies?

i. Well, they all propose mechanisms (for the most part)

ii. Most reported is external drivers – offsetting increased growth is the latent hypothesis here (so we assume it is happening) – temperatures are too high or precipitation/drought is limiting

iii. In contrast, some also now report brand new fundamental development constraints ...

(f) Yet these hypotheses are tested in radically different ways, never together and miss a whole suite of knowledge on this topic including major possible mechanisms.

i. We know this because we systematically reviewed the literature (see Supp for methods) and found it (see FIGURE? Figure instead of text would be great....) ..

ii. The current state of this field is a mess – while recent papers herald the lack of relationship, we actually found TOTALLY split results suggesting we need a better framework.

iii. Part of that means dealing with language, which is not our focus here (but see box)

iv. So, what are they? Let us tell you ....

What really could be happening? (Full suite of mechanisms)

1. Our handy-dandy, fancy-smantzy framework of what controls the relationship between growing season length and plant growth, according to the actual literature that considers dendro, ecology, and plant phys. (I think this line should be one short paragraph). Which has both a suite of external and a suite of internal factors. We highlight what has been studied, and through which disciplinary lenses along the way maybe?

2. External

(a) External abiotic stuff, which is super well studied by the dendro world.

i. Temperature (too high or low; note to self: Save any complexity about this for paths forward)

ii. Soil moisture (mainly drought)

iii. These above two are measured a lot, because they (1) easy to measure and (2) what dendro likes to look at.

iv. Miscellaneous other (VPD etc.)

v. We found dendro basically always finds external effects ... but that is sort of the AIM of the whole field, no?

(b) Biotic external

i. Herbivory

ii. Disease

iii. Not much on the above too because they are episodic, and less on competition as it is usually considered a nuisance problem for dendro

iv. Competition

3. The world of internal programming ... (starting with what is studied, to elephants in the room that are unstudied, as best we can tell)

(a) What has been mentioned ...

i. Genetic and developmental constraints include fundamental limits through biophysical (allometry, chemical reaction limits, genetic architecture), but also includes constraints more particular to a certain species, population or individual (e.g., some developmental example – isn't there one about max photosynthesis depends on temperature early on or such?).

ii. Zohner has suggested his solstice idea ... as universal, but previous work also shows ..

iii. Local adaptation can lead to such constraints ... CITES

iv. Not mentioned, but likely super important: Evolutionary constraints. These are a legacy of historical evolutionary pressures. Reflects the selection that your ancestral lineages experienced (you're a tree here). Lead to clade differences which are, umm, NEVER discussed in this literature.

v. Phylogenetic analyses routinely suggest temperature limits show this ... and evergreen versus deciduous findings (Way & Oren 2010) also suggest it

(b) What someone really should have MENTIONED by now

i. Plant strategies! Acquisitive to conservative plant strategies (lots of words for this, but basically some species are probably set up to exploit a longer season

and some are not ... our indeterminate/determinate discussion goes here) ... This means SPECIES will differ. They also differ in their ...

ii. Growth-reproduction trade-offs, which also lead to between-year dynamics – see Hacket-Pain etal 2016

iii. The above two, plus phylogeny, mean we should really expect species-differences! Did I mention that?

iv. Actual work on elevation etc. (growth x gsl) is on very limited species list ... we really have never addressed this, perhaps in part because the dominant fields looking at this, dendro and physio, do not think much about species generally or focus on only one species forever and ever.

4. We have a problem Houston!

   (a) The lack of tests of some of the major hypothesis is a problem

   (b) And the testing of only certain hypotheses in certain disciplines means we lack coherent tests that compare multiple mechanisms.

   (c) Too much external in dendro, but endogenous folks don't look at external, so we have no idea of the relative scale of each effect

   (d) We maybe actually never nailed this in biology.... but there's no time like the present. 'Robin! To the bat mobile!'

5. Ay! So much could be happening ... How do we tackle this framework?

   (a) Without a cross-discinplinary approach, you cannot tackle this framework. (Lack of standard ways to tackle this question (even when putatively addressing the same question))

      i. People need to do things a little more similarly ...

      ii. And then we say what are the important explanatory variables, response variables, and give opinions on how they should be measured, etc? Ditto for statistical approaches...

   (b) Physiologists need to dive deeper on mechanisms so we can compare external and internal drivers better

      i. We have a fundamental lack of mechanistic understanding for when and why growth should increase with GSL and when or why it should not.

      ii. Where my physiologists at? We are mostly measuring this growth/phenology stuff without digging deep into mechanisms, we need more interdisciplinary work/cross talk to figure out what is going on when we either do or don't find a link between growing season and growth. Carbohydrate and cell division/expansion dynamics are especially promising.

iii. Most ideas are focused on external (dendro), but need to bridge to include and test for constraints

iv. this is particularly important if we are going to use these relationships and any constraints we find to project - extrapolating is particularly dangerous when you have the underlying models wrong.

(c) This bridge means bridging timescales, from usually short physio to super long dendro

i. Both teams need to include lag effects of growth, as a nod to the complexity of storage in trees

ii. And bring in some new ways to bridge this timescale divide: Measure GSL and tree rings in other ones: FACE, Phynwald, Rainout things, SPRUCE

(d) Dendro needs to embrace internal drivers and blow up its statistical approaches

i. Tree rings are the answer! These folks have so much to offer, but ...

ii. they don't have much phenology data, because they love conifers ...

iii. Maybe here: PEP725 x ITRB plot – sampling overlap; sample more places/species withe phenology data

iv. Dendro is designed to see growth through the eyes of climate, looking for other drivers, requires a new outlook, and ...

v. they need to figure out the transfer f(x) that really separates out growth and climate

vi. So they need a new sampling design and ...

vii. New stats (see de Sauvage 2022 and probably others where the detrending can really remove stuff)

viii. They should more consistently figure out key disturbances throughout the growing season: VPD, baby, and 'Yes, maybe the season starts earlier and ends later, but what's happening in the middle? Are there droughts, false springs, intense heat waves?'

(e) From these shifts in dendro and physio, it's time to get into comparative numbers folks! (See Box perhaps?)

i. What actual effect sizes do we expect for GSL versus external drivers? They are actually mushed in the elevation studies ... as is species.

ii. Scale of GSL effect (interannual) versus variation across sites versus species versus drought ...

iii. How do we tell apart high temperatures that accelerate growth from ones that stall it out? Physiologists need to provide some answers here!

iv. VPD x temperature curves – figure those out, include more xylogenesis here

v. They probably also need to thoughtfully include species variation (and include phylogeny in meta-analyses)

(f) Both fields need to accept species level variation as variation in growth strategies is a hallmark finding of both life history theory and community ecology

i. But it's not just 'species differ' there are some obvious ways to tackle this

ii. Theory suggests aquisitive versus cons trade-off, and reproduction matters – find variation in this when picking species

iii. Take a phylogenetic perspective – sample thoughtfully across clades when doing the above

(g) We need to get a handle on species-level variation because we need to understand the scale of it versus other levels of variation and drivers ...

i. Species variation

ii. Population within species variation

iii. Interannual variation (where a LOT of work has jumped)

iv. What do we know so far? Some studies on this ... deSauvage 2022 Soolanakanay has phenology x growth but not tree ring; Knott et al. 2022 'Phenological response to climate variation in a northern red oak plantation: Links to survival and productivity' has survival and phenological sensitivity but no growth ... (and King 2013?)

v. And massive opportunity here through common gardens! So core common gardens and estimate this, especially on a yearly basis (not every 5 years) across spp.

vi. Which species to target? Go for ones at the ends of acquitistive conservative ... so Populus, and Oak, for example

(h) What we really need to know ... likely means to merge experimental and observational results

i. Effect of increased growth due to warmth VERSUS due to longer season – scaling from experiments to forests

ii. Experiments testing the effect of GS expansion (at both sides) on growth increments over 2 GS (because autumn warming might increase growth only in the next year if at al). This should be done under favourable conditions (e.g. fully watered conditions) as we already know that drought will stop growth processes.

iii. Effect of fruiting (start recording that?)

iv. local adaptation vs plasticity in growth strategies

v. We probably need models to do this, with latent effects to help go from experiment to observational versus using small-scale or other non-realistic experiments to try to set hard bounds on temperature limits etc.

6. Conclusions
   (a) Climate change as rediscovering dusty, old fundamentals, but also possibly things we maybe never figured out
   (b) Close on why this is important to get right

**Box for measurement** Currently not very organized notes, some repetitive

1. We're not discussing it here in part because it has been discussed elsewhere, and in part because the issue is clearly bigger than measurement ..
   (a) While our lit review found a lot of different terms, there was no systematic bias in what was found with what terms (in contrast with suggestion by Koerner)
   (b) Ref a table in supp?
2. Very difficult to compare studies as terms are defined differently (e.g., growing season length) ... could compare what the terms mean across fields
   (a) Semantic issues make it difficult to know what is or has been tested
   (b) Everyone is measuring stuff in a slightly different way makes it really hard to compare (especially when everyone is doing only part of the diagram (see figure idea below))
   (c) Briefly about growing season length: Which to measure? Actual growth end/start as growth (but which growth) or phenological start/end ...
   (d) Maybe they are growing and you measured the wrong thing
   (e) What scale of effect can we detect (and do we expect)?
   (f) Maybe we are measuring the wrong species ...

**Box for suggested models?**

1. If you want to resolve this debate, you need comparable estimates – you have to report similar models
2. Here's what we suggest?

**Where are we submitting?**

*Nature Climate Change* (3-4K, 4-6 figures), *Global Change Biology*, *New Phytologist* ... thinking of places where we will get an interdisciplinary audience.

**Methods**: Found 33 refs through ISI search on 12 April 2023: "growing season length" AND "tree ring*" (ALL FIELDS). We then looked through citations within and cited since, as well

as incidental during the review process.

## 2 Figure ideas

1. Ruben's figure
2. Alana's rate x temperature (x limitations) figure: maybe add in agriculture
3. Conceptual of connections (sort of path diagram figure)
    (a) Start simple: temp → GSL → growth (this was NEP x growth studies from a while ago; and the tree ring people go backwards along this diagram)
    (b) Next: Just the conceptual: temp → GSL → growth PLUS resource bubble
    (c) Supp figure on measurements? Figure with methods layered on, maybe do just for start and end of GSL or such
    (d) Layer onto this figure: What each fields offer – size of arrow is the number of studies that do it
    (e) Layer onto this figure: What each field could offer if they did x, y, z – FUTURE directions also
    (f) We need relative magnitude of these arrows
    (g) Message here: Full path diagram of what is happening is more complicated than perhaps is being let on, and no one has tested it fully
        i. The provenance people have a lot to offer but they don't measure annual growth ... they have the constraint information, but asking it for a different reason.
        ii. Could they manipulate temp and resource?
        iii. Or we need the tree ring people to work on this: tree rings across distribution → response + variability of response
        iv. Greenhouse/growth chamber folks can do the full figure
4. ISI cross-pollination currently across fields or see `https://www.connectedpapers.com/`
    (a) tree rings in climatology
    (b) tree rings in ecology
    (c) constraint folks
    (d) forestry plots (provenance trials)
    (e) experiments ...
5. PEP725 x ITRB plot
6. Figure for future part?

7. Table/figure on advantages/limitations for each approach? Key places where interdisciplinary opportunities (leverage)

**Stuff in need of a home in outline, maybe**

1. This is important!
   (a) Carbon storage and climate change
   (b) Fundamental to physiology, species assembly
2. Basics: GDD model of growth suggests GSL x growth (with some base temperature for GDD)
3. Test for possible endogenous drivers with flux towers? (To bridge some of the current method x endo/evo divide)
4. atitude or altitude vs growth. Would be cool to actually demonstrate this
5. The amount of growth that is happening at each point in the growing season and how is it related to GSL. The question I have here is if earlier GS means that peak growth will happen early, then if maybe poor conditions later in the GS don't matter as much, or maybe they do? Or if there are endogenous constraints on the peaking of growth then shifts to earlier GS wouldn't really help at all
6. We've talked about this before but collecting cores from places where phenology has been already recorded and is continuing to be recorded would be really important for examining long term changes and trends. It seems to me like collecting cores would be more feasible than collecting phenology data (which you'd need to visit every location multiple times)
7. Also still really curious about where the carbon goes. How much of it goes to growth vs maintenance or reproduction or whatever else. Would be cool to track it in flux tower areas where they can detect the CO2 drawdown across the season showing that photosynthesis is happening earlier but if we're not detecting radial growth then what is the consequence of this earlier photosynthesis start. Another way to look at this could be an experiment where we would tag CO2 (can you tag CO2? maybe isotopes) and then destructively sample the plants at different points along the growing season to find out where the CO2 went? Of course the caveat being that it would likely be juveniles, or model organisms so how much would we really be able to extrapolate?

**Things that need a home**

1. Conifers (tree ring data) versus deciduous (phenology data)
2. Conifers: Does leafout matter in conifers or would it be much more related to when they start photosynthesizing with old leaves?
3. Species diversity in tree ring studies ... maybe make table on whether the studies with tree rings and growth have looked at dominant canopy species
4. Maybe ... which species have budset constraints been shown in?

add to Janneke's table?

## 3 The table is done in late June!

*Remember what our main new aims for the paper:* We're interested in constraints, resource limitations, species and interdisciplinarity; we should stay focused on this. Species too...

*What we have found overall (3 July 2023 meeting):*

1. Lizzie reported out on the question of which studies do or don't find relationships. Seems like of the common growth metrics, annual cores do not find our definition and they don't always find their definition either. No relationships with country or biome jump out (pretty biased towards certain places though). We need to do some more work to look at species as that looks complicated, but nothing jumped out in which species do or do not show relationships.
2. Team external: lots of tree ring studies look at external and they all find a relationship. Not many experiments do and whether they find a relationship or not is more mixed than for tree rings. Next steps for this could be that the experimental and forest-scale results need to connect better: maybe this means looking at better metrics than temp and precip (such as PET) or looking at interactions or TBD.
3. Team endogenous found three major types of effects: provenance, species (and functional types) and 'growing early' (Zohner paper bolus; though Frederik only mentioned Zani paper: 'Greater GPP, higher Photosynthesis, earlier growing season leads to earlier senescence (Zani 2020)'). Very few studies mechanistically try to understand what causes provenance, species effects. (Of the 56 rows in our table 23 indicate that authors have looked and 21 found evidence for endogenous factors. These are mostly provenance / experimental studies, hardly any tree ring studies. )
    (a) Maybe we (or physiologists) need to review what the mechanisms could be? Ideas are...
        i. Leaf life span
        ii. Tade-offs between reproduction and growth
        iii. budset programming
        iv. Proportion of determinate vs. indeterminate buds. Can we get info on that?
        v. Maybe group species by CSR or shade tolerance?
        vi. Check out Silvics manual (`https://www.srs.fs.usda.gov/pubs/misc/ag_654/table_of_contents.htm`)
        vii. It could be nice to discuss the tradeoffs involved of a tree's growing season ending. Potential gains in growth, fruit production and reserve allocation vs. Tissue damages and fitness loss (unripened fruits, dieback), loss of nutrients in foliage due to delayed senescence.
    (b) Whatever it is, we need to somehow see it scale up to latitudinal variation (provenance effects); this reality seems to be missing from Zohner and other work

4. Next steps from Frederik: It seems there is not much to get out of the table regarding endogenous factors. If we would like to include a section in the paper about this I suggest we gather and discuss the current hypothesis around this topic. What comes into my mind is: amortization time, reach a certain reserve level, distinguish between determinate and indeterminate growth, photoperiodic constraints and induction of bud set, senescence and dormancy. I would be interested to do that!

Also, Lizzie checked out Rossi *et al.* 2013 (cited in Korner paper from 2023) and it does not appear relevant to our table. See `https://link.springer.com/article/10.1007/s00442-006-0625-7` if you want to check for yourself.

# 4 Where to find other notes

`grephon/notes/2023SpringLucidEtc/Grephon_Lucid board notes - Google Docs.pdf` is a file extracting the main take-homes from our Lucidboard work (December 2022 until sometime in early 2023). You can also see the Lucid board in PDF file: Grephon December 2022 brainstorm

See treeringnotes.pdf for our notes from reading papers in fall 2022.

In August 2023, Lizzie reviewed this doc and the Lucid board (again) and a little the notes from last year, she pulled out the following:

Stuff to probably work into ms ...

- Biophysical constraints
  - To what extent can the internal phenological program constrain C uptake/additional growth and influence the fate of C?
  - Do phenological shifts push the growing season into periods of low VPD? This should enhance growth if turgor is the limit, but might lead to more regional variation in response. Can we test this with treeNet data?
- How much local adaptation is there in G x P?
- Show PEP725 + ITRB overlay (w/ Rubén) and highlight potential of this data in understanding growth-phenology
- Stuff we critically need to know
  - When does growth happen for different species (early versus late season) and how flexible is this pattern?
  - How photoperiod matters (or doesn't and why folks get it wrong in dendro so much)
  - Better understanding of NSCs and phenology - are we seeing differences across wood anatomy or is it even more species specific or population specific
  - Differences in patterns across space/species/source populations?
- It may not be a long-term stable strategy to try to adjust growth dramatically year-to-year, so should we really expect this correlation?
- Cite Knott et al. 2022 'Phenological response to climate variation in a northernred oak plantation: Links to survival and productivity' – no growth data, we really need more common garden studies

Especially cool ideas to do someday (but maybe not in this paper)

- What does the flux tower data tell us about the availability of photosynthate for growth? Can we use this to make assumptions about the sugars going elsewhere, like to heartwood?
- Compare numbers: ring growth across elevations/across time/in dendro studies/dendrometers

- What is the regional variation like in the growth phenology relationship? Are there places where growth is clearly increasing? If so, what is the climate like? Where would we expect growth to increase with a longer GS? Where would we not?
- Statistical issues