Invest now, get paid later? Growth strategies to cope with environmental stress and benefit from extended growing seasons in a future climate

Frederik Baumgarten[1,2], Yann Vitasse[2], Sally?, Rob?, EM Wolkovich[1]

May 24, 2024

[1] Department of Forest and Conservation, Faculty of Forestry, University of British Columbia, 2424 Main Mall Vancouver, BC Canada V6T 1Z4.

[2] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstr. 111, Birmensdorf 8903, Switzerland

Corresponding Author: Frederik Baumgarten; frederik.baumgarten@ubc.ca

Abstract

With increasing latitude, plants are confined to a shrinking 'time window of opportunity' set by low temperatures (frost) and water restrictions (drought). In trees, the question of when and how much growth occurs within this window, received recently considerable attention. Thanks to high temporal resolution data of dendrometers we know that cambial cell division and differentiation occurs only within a fraction of days of the potential climatic growing season and mainly at night when cell turgor is sufficiently high. These studies contributed a lot to identify the environmental drivers and their thresholds that control growth.
Yet, environmental conditions do not solely explain if a plant during the active season is growing or not. An often-overlooked factor is the phenological sequence – the developmental stages and transitions set by the genetic programming of a plant that manifests in species-specific growth patterns/habits. This internal schedule has the power to impose switches in physiological activity e.g. from structural vegetative growth to reproduction (such as fruit ripening), storage accumulation and inducing senescence despite growth-promoting conditions.
Here, we revise the old concept of (in-)determinism: the ability of trees to preform tissue as an investment for next year's growth that will overwinter in buds vs. a strategy that additionally relies on the continuous activity of the apical meristem throughout the growing season (neo formed tissue). We propose that 1) determinate species may be more resistant and resilient to environmental stressors (e.g. drought) and 2) the higher the degree of indeterminacy in a species, the greater its capacity/potential to profit from extended growing seasons. Consequently, the question of how much carbon will be sequestered in a future climate might depend not only on abiotic factors like water availability, temperature extremes and the length of the growing season, but also on the degree of determinacy set by a species' intrinsic genetic programming.

Keywords: plant growth, tree phenology, shoot extension, indeterminate growers, carbon sequestration, growing season length, drought, genetic programming, phenotypic plasticity

Introduction

Investment by trees

Investing at the right time is of crucial importance for the survival and fitness of plants. While in tropical ecosystems a continued production of tissue can be both possible and advantageous, in most other regions strategies that rely on growth from stored reserves and pre-build tissue are widely common.

Introduce seasonality

The further one travels from the equator towards the poles, the tighter plants are confined to a shrinking 'time window of opportunity' set by low temperatures. Below 5°C metabolic activity slows down to an extend where growth and development comes to a halt. More importantly, freezing temperatures can cause severe damages to plant tissue if exposed at the wrong time of development, e.g. after leaf unfolding or prior to fruit maturation. While annual plant species accommodate their entire life cycle within this window, seasonal climates urge perennials to split their growing phase into annual chunks with periods of activity alternating with a period of rest (dormancy). This is referred to as intermittent or rhythmic (as opposed to continuous) growth.

During the active growing season also high temperatures can reduce plant activity and development, ultimately to the point where meristems fail to produce new cells and protein degradation damage the photosynthesis apparatus if species-specific thresholds are exceeded (REF). Along with higher temperatures, the vapour pressure deficit rises, which in turn drives the evaporative demand of plants. High evaporation and limited soil water availablilty, decrease the water potential in the soil and along the entire root-to-shoot-continuum. Since mitosis and differentiation requires sufficient turgor (cell pressure), decreasing water status of plants in such a drought scenario limits any further meristematic activity. Figure 1 shows these temperature and soil moisture limitations as "environmental filters".

Given our developed physiological understanding on how growth is controlled by environmental factors, namely temperature and soil water availability, one could think that predictions about when and how much trees are growing in a current and future climate should be fairly simple to make. However, this is not the case (REF), although many studies currently tackle this research field and estimate the potential of carbon sequestration. It seems that environmental variables alone are not sufficient to capture the dynamic and extend of biomass production/carbon sequestration. Here we propose the framework for an additional factor to consider: internal growth control - the genetically fixed developmental program that can dictate not to grow despite of favourable environmental conditions.

While plants have evolved many mechanism to tolerate or avoid such potentially harmful conditions by specialized morphological adaptations, most species, even in the tropics cope with fluctuating temperature and moisture regimes by temporally escaping these conditions. This involves the progression of a dormancy cycle and the timing and prioritization of life history events (phenology). Plants outside the agricultural context rarely maximize biomass production (KörnerXXX). Rather they are selected for survival to increase their fitness which is tightly linked to their intrinsic programming (or phenological sequence) which imposes abrupt switches in resource allocation from vegetative growth to reproduction (flowering, fruit maturation) and storage (REF). Figure 1 shows these additional "internal filters" eventually narrowing down the window in which growth can effectively occur.

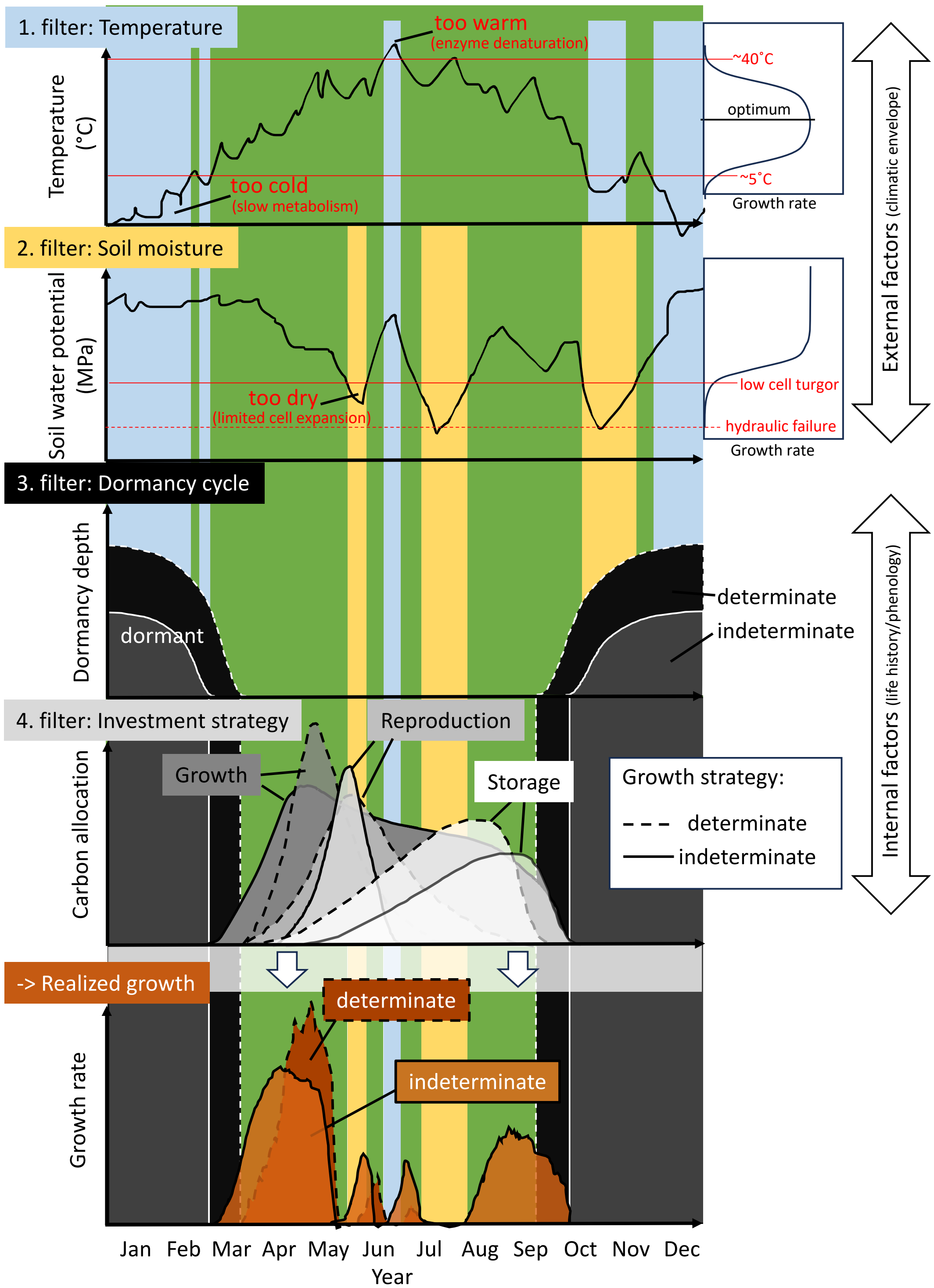

Figure 1: Schematic overview of the discrepancy between the potential growing season and the effectively realized vegetative growth. Environmental factors like temperature and soil moisture, exceeding growth-promoting thresholds can be seen as filters that narrow the window of opportunity available for vegetative growth. The species-specific life history cycle (phenology) can further impose another filter by imposing a dormancy cycle and prioritizing developmental processes other than vegetative growth (e.g. flowering, fruit maturation and storage).

The concept of (in)determinate growth

Most of our understanding on growth strategies or habits in trees dates back to a period in the mid 1900s. Since then many different terms have entered the literature along with various definitions spanning the fields of genomics, physiology and ecology across the animal and plant kingdom. All plants add to their primary bodies as long as they live and can therefore be considered 'indeterminate growers' like mollusks, fish and reptiles (Ejsmond *et al.*, 2010). However, in trees the concept of determinacy refers to the ability to:
a) preform tissue (i.e. structural growth) as a future investment that is ready to be deployed in spring with sustained growth thereafter (determinate strategy)
b) maintain a somewhat constant growth activity by forming new tissue during the growing season (indeterminate strategy)

history , old poplar in 70ies, many terms what is it? fig 1 sentence represented as dichotomous but intermediate examples exist
Figure 2 shows an example figure.
. However,

Control mechanisms/What controls/drivers of determinism

Altough a century of studying growth habits has passed we still have very little understanding of when and why trees exhibit a certain degree of (in)determinsm in their growth strategy. To a large extend this is probably due to the variable environmental condtions within and between years as well as among sites and individuals that complicates the separation of factors influencing or driving shoot elongation and for that matter other meristematic activity.
Indeed there is some evidence, that under favourable conditions, particularly soil moisture availability, stretching into the growing season prolongs the period of shoot elongation or permitting a second flush, also known as lammas growth or "Johannitrieb" (see Figure 1). This indicates that shoot growth may come to a halt because the demand for water, supporting a growing leave area, cannot be met. Since above and belowground meristem experience large differences in temperature, the higher growth rate of shoots may soon result in an imbalanced root-shoot-ratio that can only be overcome by sustaining growth of the apical meristems until root growth has caught up to reach the supply capacity. High vapour pressure deficits and the resulting water transpiration or a drying soil might have the same effect. Such a "stop and go" behaviour of the apical meristem as a consequence of lower growth rates in roots could explain the polycyclic flushing patterns observed in some species (REF).

This theory is also supported by experimental data. Artificial reduction of the leaf area caused terminal buds to keep growing until the original leaf area was re-established (REF). Similarly many species produce new shoots after a damaging spring frost or after substantial herbivory to rebuild their canopy. However, this perspective suggests that the environment can completely flip a species' strategy – but this is not the case. While manipulations on root:shoot ratios proof a certain plasticity of the apical shoot meristem to adjust the LAI after disturbance, we still observe distinct patterns when environmental conditions remain favourable. Hence, there must be an underlying internal program that sets the general pattern of how trees grow and explain the variation of growth habits among species we observe in the same environmental conditions (see Table XX for a list of species and their main growth strategy).
c) these are fundamental trade-offs - both successful and co -occur in communities successional stage, ontogeny, life span, evolution
...but will both still be successful with CC?

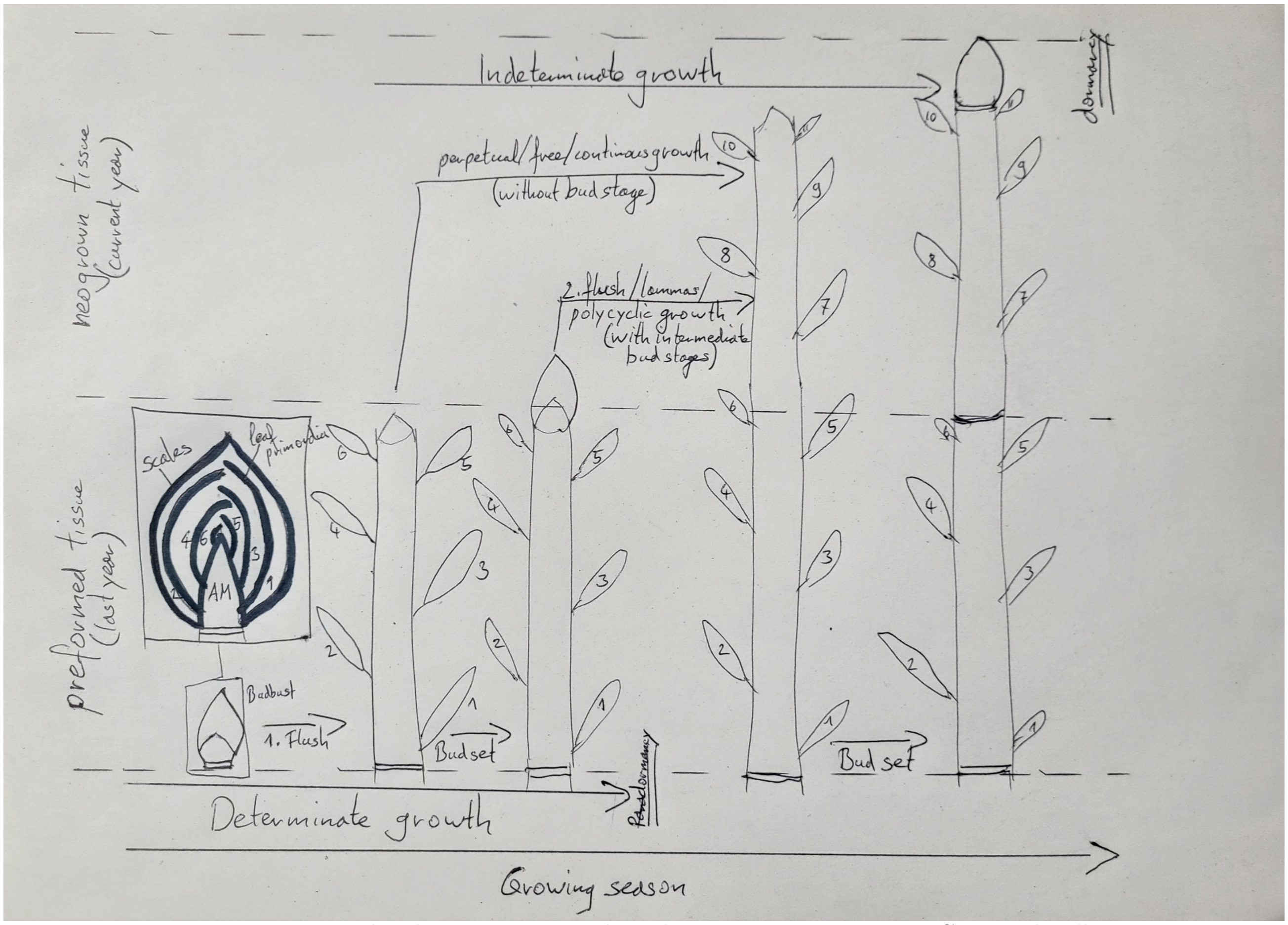

Figure 2: Determinate and indeterminate growth within one growing season. Commonly all tree species deploy buds during their first spring flush from prebuild and overwintering leaf primordia (A-B). Determinate growing species set bud that are under hormonal suppression (paradormancy) to sustain any further activity of the shoot apical meristem (C). Indeterminate growing species continue to produce new tissue directly (D) or through one or several intermediate bud stage(s) (E). Finally all species set their bud and enter endodormancy. Apical meristem (AM); Bud scale (BS); leaf primordia (LP).

The role of determinism with climate change

Climate changes is extending the growing season length while at the same time increasing the risk for severe drought (REF) and presumably also late spring frost events in many regions worldwide (REF). How are these potential benefits and threads linked to a species strategy, specifically to the degree of determinism? Which strategy profits most from an extended growing season length and which one is flexible enough to rearrange their phenological cycle to withstand increased environmental stress. And which one comes with more biomass production and C sequestration?

We propose that the degree of determinism is an important trait largely controlling the responses of trees in a future climate illustrated in Figure 4. We hypothesize that the conservative strategy of determinate growing species largely escapes their growth period from by placing it between the last spring frost and the increasing water shortages in summer, with relatively large safety margins. While this continues to be the case presumably in a future climate through an observed phenological shift (REF), increased drought risk in summer will pose a severe thread to those species with symptoms of desiccation following hydraulic failure. Even if leaves are shed to prevent further damage, the loss of the canopy, which is rarely replaced in determinate species after summer, will contribute to a lower fitness and reserve pools.

In contrast, indeterminate species will benefit from an extended growing season by extending their growth period at both ends. Although a substantial part of their growth might fall together with drought conditions, indeterminate growth may allow to 1) produce tissue better adapted to harsh environmental conditions as it is formed under the current conditions - even if that means no additional growth and 2) catch up and compensate later in the season by another productivity boost.

We therefore think that new opportunities and challenges with climate change will increasingly disrupt the phenological cycle of trees, favouring those who are more plastic in rearranging their activities by resuming growth, reproduction and/or storage filling later in the year, thereby recovering from and compensating for some stress-induced damages and losses.

This might increase competition among co-occurring species and might change species and community assemblages in the future with more indeterminate species most likely gaining ground because they might be plastic enough to fill this niche.

Figure 3 shows an example figure.

Future directions

Questions critical forcasting now to larger evolution questions

a) (1-2 paragraphfs) how much does dezerminism predict bufferin vs. exploitation of env. change? explain this in simple words experiment phaenoflex

b) How flexible are spp. in determinism? need an answer to get anywhere but must approach from several fields

bi) Physiology: universal across meristmes? linked to xylogenesis? universal across allocation? (reproduction, storage and growth?) gene/hormones (1-2 para) bii) Evol. history (end on metric fortshadowing)

c) better metricx opening....its treated dichotomy by 1 field, flexible by a different so clearly it has variability we need to understand to move forward

we propose several metrics from best to worse, dificult to easy. (1) nleaves EOS /n leaves in buds SOS

(2) shoot elongation/dendrometers radial growth?

(3) "second flushes" in large databases? US national forest network NDVI second flushes?

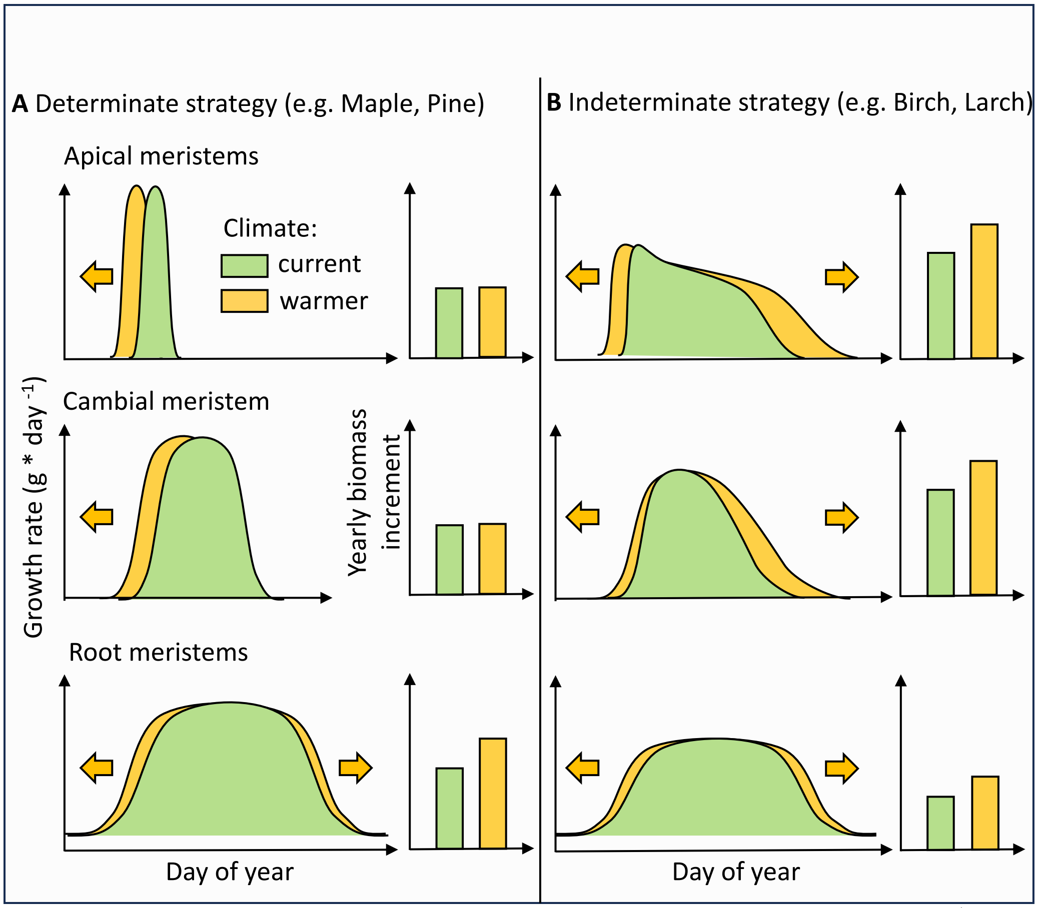

Figure 3: Hypothesized predictions of growth rates for the three major meristems (apical, cambium and root) classes of trees under current and warmer climates following an extreme determinate (A) and indeterminate (B) growth strategy. The area under the curve is summarized as yearly biomass increment in the respective bar-plot. Arrows indicate the shift of growth phenology under warmer climate conditions. Root meristems appear to be purely temperature-opportunistic for both strategies, even growing during warm winter spells. The indicated genera were observed to showcase the illustrated trends. The responses of these two contrasting growth strategy might apply not only to different tree species but also within a population (e.g. along environmental gradients) and even within an individuum as it transitions from the junvenile to the adult stage (ontogeny).

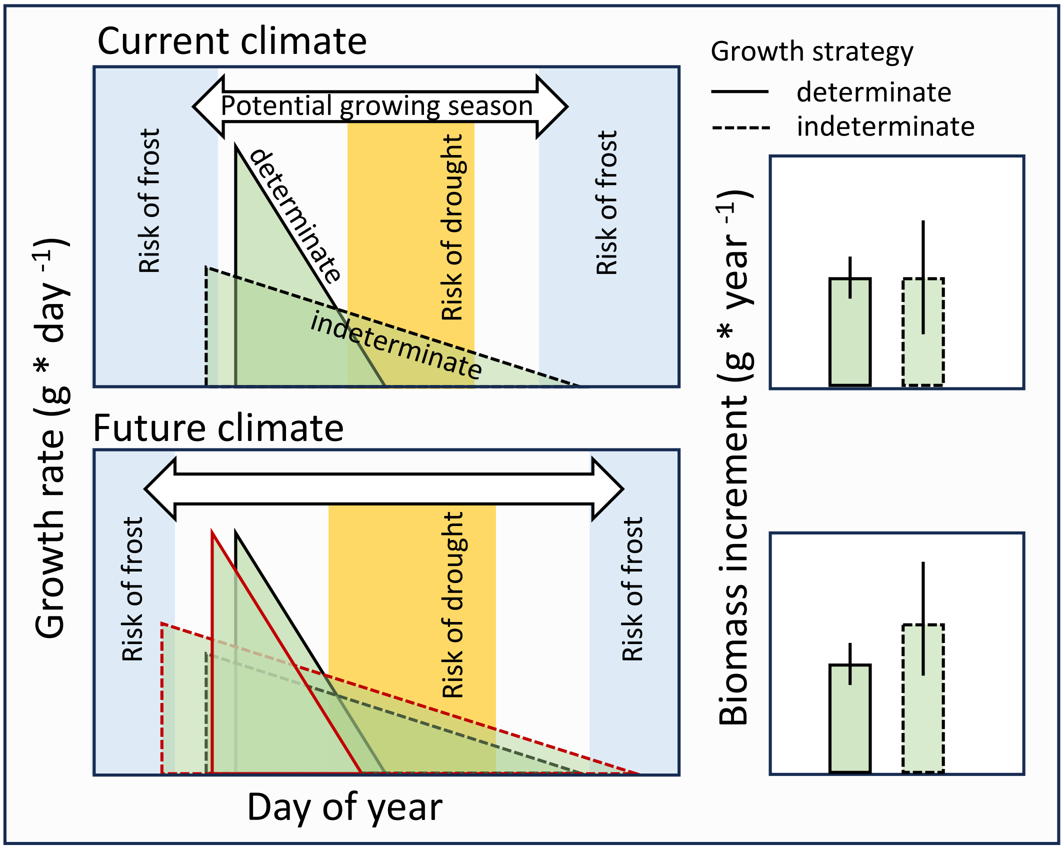

Figure 4: Hypothesized predictions of growth rates under current and future climate for determinate and indeterminate growing species. Note that the indeterminate strategy is more exposed to the risk of frost and drought events while the determinate strategy condenses most growth within a rather safe period. In the current climate the indeterminate strategy is in balance with benefiting from the full climatic growing season in some years with some drawback in other years, resulting in the same mean yearly biomass increment, but with a higher variation; right box). In a future climate the indeterminate strategy might benefit exceedingly from longer growing seasons, resulting in an overall higher mean annual biomass increment compared to determinate growers.

Bibliography

Ejsmond, M.J., Czarnołeski, M., Kapustka, F. & Kozłowski, J. (2010). How to Time Growth and Reproduction during the Vegetative Season: An Evolutionary Choice for Indeterminate Growers in Seasonal Environments. *The American Naturalist*, 175, 551–563.