'A Fine Balance': Exploring the Interplay of Reproductive Strategies and Growth Dynamics in Trees

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1 Introduction

The fundamental processes in a plant's life cycle—growth, reproduction, defense—all compete for the same resources. Plants must apply trade-offs to maximize their fitness when resources are limited. One of the most significant of these is the growth-reproduction trade-off, which is influenced by both environmental conditions and a plant's life history strategy (Grime, 1977; Stearns, 1998). In resource-rich environments, plants are able to allocate resources both to rapid growth and reproduction, while in resource-poor environments, plants often face a decision: they can either allocate resources to growth, ensuring their long-term survival, or they can invest in reproduction, which may come at the expense of growth (Bazzaz, 1997). This trade-off can lead to high variability in reproduction across years, which is manifested as mast seeding, an important reproductive strategy for many plant species (Pearse *et al.*, 2016).

Mast seeding is the phenomenon of synchronized and variable seed production within plant populations. It determines regeneration within a population and is closely related to ecosystem-level functions that influence processes such as seed dispersal, predation and plant recruitment, since seeds can be food resources for many mammals or hosts for pathogens (Davies & MacPherson, 2024; Janzen, 1971; Kelly, 1994). Mast seeding is widely observed in wind-pollinated tree species, but also occurs in *Poaceae* as well as *Dipterocarpaceae* (Kelly & Sork, 2002). Although there are several hypotheses explaining the potential mechanism selecting for mast seeding (e.g., predator satiation, resource matching, etc., discussed more in Chapter 2, Koenig, 2021), the

exact environmental factors that trigger it in different species and ecosystems are not fully understood. Current data suggest that it is mainly driven by specific climatic conditions that cause synchronized reproductive efforts of the species at population level (Pearse *et al.*, 2016).

Research on masting has often focused on its unique features, which make it distinct from annual fluctuations in seed production of non-masting species—specifically its interannual variation, synchrony, temporal autocorrelation, and frequency (Hacket-Pain & Bogdziewicz, 2021). While annual fluctuations in seed production for non-masting species are generally more closely tied to short-term environmental factors (or may appear random), interannual variation in masting is not entirely random or caused by immediate environmental conditions; instead it should be synchronous across large spatial areas (e.g., hundreds of kilometers, Kelly, 1994), and show distinct temporal autocorrelation, where a mast year is typically followed by several years of low or no seed production. Finally, mast years often occur at a certain frequency, with some species exhibiting a more fixed interval (e.g., every 2-3 years) and others a more irregular pattern (e.g., 2-5 years).

Masting plays an important ecological role by influencing seed dynamics and broader ecosystem processes. According to the predator satiation hypothesis, mast years overwhelm seed predators by producing abundant seeds, ensuring that some seeds will survive and germinate. In this way, plants can regulate predator populations and enhance seedling establishment. Mast seeding also contributes to the creation of seed banks for some species, which provide a reserve of seeds that help the population buffer against environmental variability, allowing seeds to wait for favorable conditions to germinate (Venable, 1989). This strategy not only improves seedling survival in the short term but also promotes long-term regeneration, helping to maintain a plant population over time.

Ongoing anthropogenic climate change is extending growing seasons, shifting precipitation patterns, and likely making environmental variability less predictable (Calvin *et al.*, 2023). These changes may influence the balance of the growth-reproduction trade-off through altered plant resource availability and consequently, masting behavior, which will not only affect the forest population dynamics itself, but also the seed predator community that relies on the forests. Understanding how these dynamics function, and the role that climate plays, is critical for predicting future forest composition and natural regeneration, but the complexity of masting has

slowed progress. Currently, we lack a comprehensive model to predict how climate change will affect masting that includes the relationship between growth and reproduction, and can make predictions across different species and ecosystems.

The aim of my thesis is to investigate how masting as a reproductive strategy is related to the growth dynamics of tree species and their role in forest ecosystems, particularly in the context of climate change. Using Mount Rainier as a case study, my proposed research will address three key questions: (1) Which reproductive traits are associated with masting? Addressing this will help to potentially identify what triggers masting across species, and in different environments. (2) Is there a detectable trade-off between mast seeding events and tree growth? (3) How will changing climate conditions affect seed dynamics? Answering these questions will contribute to our understanding of how masting shapes the growth and regeneration dynamics of coniferous forests in Mount Rainier, with inference on how masting dynamics might be related to growth and environmental changes in other coniferous forests.

2 Explore which reproductive traits are relevant to masting

Masting is widely observed across different plant lineages in different biomes, with several major hypotheses for how masting could yield fitness benefits, compared to reproducing every year (Koenig, 2021; Waller, 1979). The most commonly accepted hypothesis for masting is the predator satiation hypothesis, which suggests that masting overwhelms seed predators with a large seed crop in one year, then starves these predators during the following years with a low seed crop (Janzen, 1971). By manipulating the seed predator population, masting should thus increase the likelihood of seed survival and germination. Another widely accepted hypothesis focuses on the benefits of masting for pollination success—the pollination coupling hypothesis (Crone & Rapp, 2014). Under this hypothesis, highly synchronized flowering improves pollination success and results in more seeds. While both of these hypotheses focus on reproductive success, the resource matching hypothesis focuses more on resource constraints. It suggests that a fixed fraction of resources is allocated to reproduction every year (Kelly, 1994). In years when environmental conditions are favorable, plants accumulate more resources, which allows them to produce a larger seed crop during a masting event. Under this hypothesis, masting is not driven by a selective advantage per se, but rather a result of a resource availability constraint, with the

potential for increased reproductive output when resources are abundant. Thus, masting may appear as a neutral or incidental outcome of environmental conditions rather than an adaptive strategy to increase fitness (Isagi *et al.*, 1997). Closely related to this is the environmental cues hypothesis, which suggests that certain environmental events trigger masting (Pearse *et al.*, 2016). These hypotheses are not mutually exclusive and may operate for different species in different environments.

Based on these hypotheses, we can link specific traits to the phenomenon of masting. Since masting is a reproductive event, I expect the most relevant traits may be related to seed reproduction, which occurs through at least three critical stages: pollination, seed maturation and seed dispersal (Satake & Kelly, 2021). Each stage presents unique opportunities that can influence the overall success of mast seeding. During pollination, traits can be linked to the pollination coupling hypothesis, which suggests that synchronized flowering improves pollination success and then seed production. Thus whether a plant is monoecious or dioecious may impact its probability of masting, though the predicted directionality is arguable. Because dioecious plants may have lower pollination success (where separate genders for each individual plant may reduce pollination success in low-density populations, Bawa, 1980) we may predict that dioecious plants are more likely to mast in order to increase their odds of pollination. Monoecious plants, in contrast, may be more likely mast because they have similar genders across all individuals and thus may naturally be able to synchronize more easily. Another important trait is duration of flowering, where a longer flowering period might increase pollination success (Knight *et al.*, 2005) and thus increasing seed set (independent of masting). Following my predictions for monoecious versus dioecious species to mast, we may similarly predict flowering duration to be more common across species with short durations (to increase their comparatively lower odds of pollination success) or long durations (where it is potentially easier to synchronize given the longer duration). Masting species are also most likely to be wind-pollinated, so pollination is not restricted by the number of pollinators when large numbers of flowers bloom simultaneously (Bogdziewicz *et al.*, 2017, 2020), and I will test this general prediction.

After pollination, fertilized seeds enter the maturation stage, which is more related to the resource matching hypothesis. Traits such as leaf longevity and leaf and flower bud determinacy, which influence the timing of seed development and investment in reproduction, are thus likely important at this stage. Leaf determinacy (whether the leaf material is prebuilt the year before

4

or not, Lechowicz, 1984) may influence how quickly plants can shift their resource allocation into reproduction. Plants with determinate leaf growth—because they have prebuilt and thus 'ready' buds—may be able to shift resources more rapidly toward reproduction, potentially leading to higher reproductive output in response to favorable conditions. In contrast, indeterminate leaf growth could be slower to respond since new bud tissues need to be built, which could result in more prolonged resource allocation to other growth functions, possibly reducing the ability to invest heavily in a single reproductive event like masting. Our understanding of determinacy across species, however, is still poor (Hallé *et al.*, 1978; Kozlowski & Clausen, 1966; Marks, 1975) and thus an alternative prediction is also possible, where plants with determinate leaf buds must invest too far in advance to shift enough in response to favorable years, while indeterminate species can rapidly develop new buds and thus shift resources quickly to reproduction. Flower bud determinacy—how far in advance flower buds are built—should play a major role, with predictions similar to leaf determinacy. However, to my knowledge most trees that mast built buds two years in advance, suggesting there may be limited variation in this trait as it relates to masting in trees (Burns, 1990). Leaf longevity could also play a role in addition to determinacy. As greater longevity facilitates more carbon fixation and thus could enhance the resources available for reproduction (Adler *et al.*, 2014), species with greater longevity may more easily build up resources for seed production and thus be more like to mast.
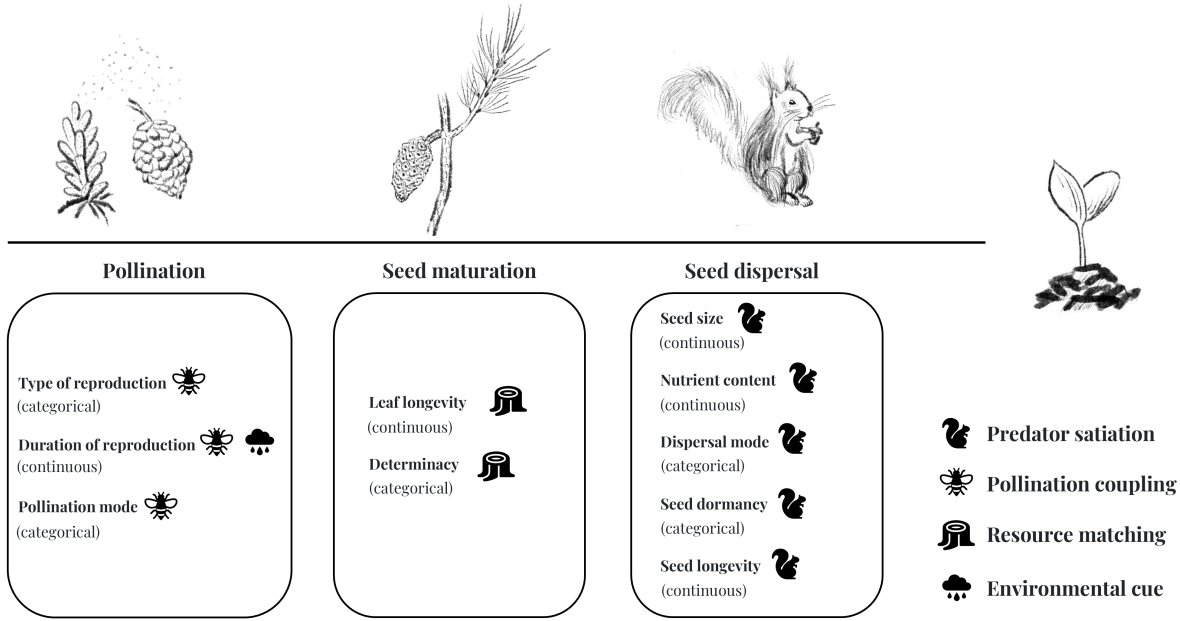
Figure 1: Conceptual framework linking reproductive traits to the phenomenon of masting across critical stages of seed reproduction. The symbols indicate different hypotheses. I include the information on whether the traits are categorical or continuous below each trait.

When seeds mature and are ready for dispersal, the role of seed predators becomes crucial. According to the predator satiation hypothesis, plants can manipulate the population of seed predators by producing large numbers of seeds in masting year and low number of seeds in following years. Masting species, however, may also rely on seed dispersers to carry seeds away from the parent tree, increasing the chances of seedling survival if they escape predation (Janzen, 1971; Silvertown, 1980). In this context, seed traits such as seed size, nutrient content, dispersal mode, seed dormancy and seed longevity all can play important roles. Larger seeds with higher nutrient content may be more attractive to seed predators, so they are more likely to benefit from masting events. Seed dormancy and seed longevity help ensure that seeds do not germinate immediately after dispersal, allowing them to wait for better conditions to establish in a more favorable environment since mast events only occur once every few years.

My proposed work advances on previous studies in this area, which have explored the relationship between a limited number of traits and interannual variability in seed production to test for

support for different hypotheses (Fernández-Martínez *et al.*, 2019; Journé *et al.*, 2023; Pearse *et al.*, 2020), but did not explain how different environmental conditions may link to which reproductive traits are more critical. In this meta-analysis, I will include more reproductive traits associated with different hypotheses (Figure 1) to investigate how these traits are related to a species' tendency to mast in different forest types and biomes.

2.1   Research Question and Objectives

Which reproductive-related traits are related to masting? Additionally, do these traits that relate to different masting hypotheses vary by species or environment?

– **Investigate trait associations:** Analyze the relationships between specific reproductive traits and masting and their frequency to determine which traits are more important in masting for different species.

– **Compare across different environments:** Compare the most critical traits across different forest types and biomes to determine if they vary.

2.2   Methods

This chapter aims to explore the relationship between reproductive traits and the tendency of a species to mast in different environments through a meta-analysis.

Data collection

Data for this meta-analysis will be primarily sourced from following resources:

– **Silvics of North America** (Burns, 1990): Provides a comprehensive database of tree species and their reproductive characteristics in North America, and will be our main dataset. It includes flowering traits, seed dispersal traits, mast cycles and forest types. For biomes, I will use the information in the distributional map provided by the book and categorized into temperate, subtropical and tropical. For forest type, I will extract information from the section of associated forest cover, and aim to categorize it according to North American forest cover types.

- **MASTREE+** (Hacket-Pain *et al.*, 2022): This is a specialized database focused on tree species' mast seeding behavior, which will be a supplemental source for identifying species tendencies for mast seeding and interannual variability.

- **Co-mast** (Nigro *et al.*, 2025): This is a specific database on harmonized seed production data for woody plants across US, which will also be a supplemental source for mast cycles.

- **Kew Seed Dataset, Worldwide Seed Mass Dataset, USDA Seed Manual** (Bonner & Karrfalt, 2008; Royal Botanic Gardens, 2007; Moles, 2015): These sources will offer supplementary information on seed mass and other reproductive traits.

Statistical Analysis and Model Development

The main analysis will involve logistic regression to determine the likelihood of mast seeding for a species based on selected reproductive traits and environmental variables. Given that there is still no clear definition of masting, this analysis will consider both a binary definition—whether a species masts or not based on whether there are descriptions of regular large crop cycles, and a continuous definition using the coefficient of variation (CV) of the mean annual seed crop, which is widely used in masting-related research to describe the high year-to-year variability in seed production. These two response variables will be analyzed separately to evaluate the occurrence and variability of mast seeding behavior (Kelly & Sork, 2002).

2.3 Significance

Studying the reproductive traits related to masting can provide valuable insights into reproductive strategies and the broader ecological impacts on forest ecosystems. First, it can help explain the potential mechanisms that drive this complex reproductive strategy, shedding light on why certain species mast while others do not in different environments. Examining traits such as seed size, nutrient content, dormancy, and longevity can yield insights into how these characteristics influence the success of seed production and dispersal during mast years, which may then relate to seed predators' population dynamics.

Additionally, understanding these relationships can help us to predict how environmental factors, such as climate change, may impact masting behavior in the future. For example, knowing which seed traits are most relevant to masting behavior in specific ecological contexts can help

us anticipate how shifts in temperature, precipitation, and other environmental cues might change masting patterns. By addressing the question of what causes masting by examining reproductive traits, we may better understand the dynamics of forest ecosystems. It is also important to understand masting in terms of its implications for the availability of seed, which plays a cruicial role in supporting restoration and reforestation processes, especially in regions affected by deforestation nad climate-related disturbances.

3   Understanding the relationship between masting and growth

The growth-reproduction trade-off suggests that increased investment in one process often comes at the expense of the other (Grime, 1977; Stearns, 1998). For trees, the decision to allocate resources to a large seed crop during a masting year can significantly affect overall growth dynamics (Hacket-Pain *et al.*, 2016a). This relationship between growth and reproduction can be complex, as the years leading up to a masting event may involve resource accumulation for reproductive efforts, while the years following masting could exhibit a different pattern, influenced by less demand for reproduction (Kelly, 1994).

With anthropogenic climate change, tree growth is generally expected to increase, as warmer temperatures increase growth rates and provide trees with more time to growth each year with extended growing seasons, assuming there is no water stress (Keenan *et al.*, 2014; Finzi *et al.*, 2020). Most climate models predict a positive relationship between temperature and growth (Friedlingstein *et al.*, 2022; Ito *et al.*, 2020). However, recent studies have questioned whether extended growing seasons due to warming has actually led to increased tree growth (Dow *et al.*, 2022; Green & Keenan, 2022). Studies have suggested that biotic factors, such as intrinsic species differences, and how plants allocate the additional carbon gained during warmer seasons, also play a significant role (Hacket-Pain *et al.*, 2016b). Further, new research suggests drought in some areas, especially persistent drought events, may limit increased growth in response to longer warmer seasons (Hajek *et al.*, 2022; Hammond *et al.*, 2022; Chen *et al.*, 2025). In the context of masting, these dynamics become even more complex, underscoring the importance of understanding how different tree species will behave in future climates.

While many studies have examined how climate influences both growth and reproduction, of-

ten comparing responses to various climate factors (Bajocco *et al.*, 2021; Koenig *et al.*, 2020; Redmond *et al.*, 2019; Sánchez-Humanes *et al.*, 2011), only a few have directly investigated the growth-reproduction trade-off in the context of masting. The majority of these studies have focused on oak and pine species. Studies on pines have emphasized on the allocation to defence, rather than looking at trade-off between growth and reproduction specifically (Larrinaga *et al.*, 2024; Redmond *et al.*, 2019). Research on oaks found little evidence of a strong, consistent trade-off between radial growth and seed production (Koenig *et al.*, 2020; Patterson *et al.*, 2023). However, this lack of evidence may be due to a large biomass allocation to roots, as oaks generally have deep root systems and tend to allocate more resources to root development from youth to maturity (Burns, 1990). In contrast, the species I will use in this study, either have shallow roots or do not develop resources-expansive taproots, thus they may exhibit a different response.
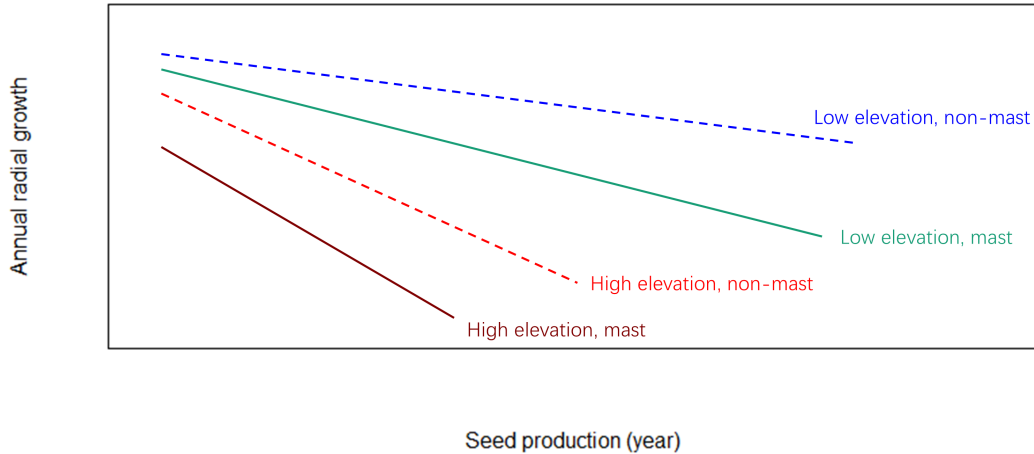

Figure 2: A conceptual figure showing the expected trend of a hypothesized growth-reproduction trade-off in masting years vs. non-masting years at different elevations. I predict that the trade-off is more pronounced in masting years compared to non-masting years in general and individuals at higher elevation stands would experience a stronger trade-off.

The relationship between masting and growth could also differ across elevations, where resource availability and environmental stresses vary. Trees at higher elevations may experience a more

pronounced trade-off between growth and reproduction due to increased resource limitation and harsher environmental conditions (Figure 2). By examining different species at varying elevations, we can gain a better understanding of the potentially complex relationship among resources, growth, and reproduction.

Combining Mount Rainier's large elevational gradient, which spans a wide range of climatic zones influenced by rain shadow effects on both the eastern and western sides of the park, with long-term tree growth data from tree rings, this chapter explores the relationships between resource availability, growth and reproduction in six common coniferous species. It emphasizes how the strength of trade-offs that shape reproductive strategies may differ across varying ecological conditions.

3.1   Research Question and Objectives

Is there a detectable trade-off between mast seeding events and growth?

- **Assess Growth Patterns:** Test for a trade-off by analyzing historical annual growth of selected tree species in relation to their masting events.

- **Compare Species Responses:** Evaluate the differences in masting and growth responses among six tree species across different elevations.

3.2   Methods

This chapter aims to examine the growth-reproduction trade-off in relation to mast seeding for six common conifer species at Mount Rainier across different elevations. To explore this relationship, I will incorporate long-term seed trap data with historical growth data derived from tree core samples, and use statistical approaches to analyze their relationship.

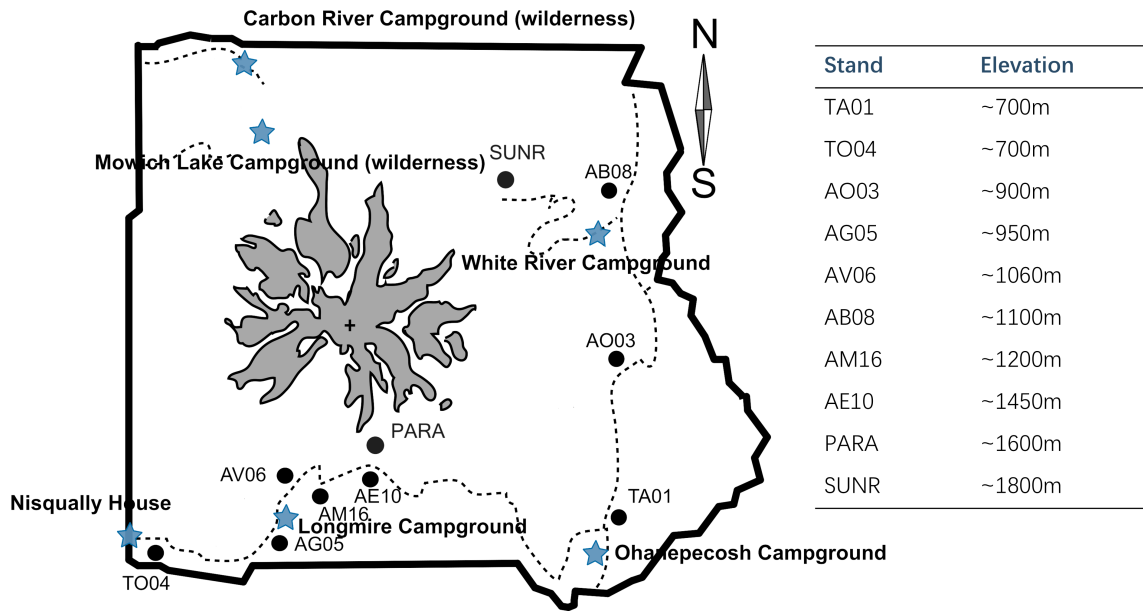| Stand	Elevation
TA01	~700m
TO04	~700m
AO03	~900m
AG05	~950m
AV06	~1060m
AB08	~1100m
AM16	~1200m
AE10	~1450m
PARA	~1600m
SUNR	~1800m

Figure 3: A map of Mount Rainier with all the sampling stands for this study and the elevation of each stand. The black dots are the stands with their elevations shown in table at right (blue stars are campgrounds).

Study site and sample collection

I will conduct this study in Mount Rainier National Park, Washington, USA, focusing on six common conifer species that exhibit varying masting behaviors and occur across different elevations in the park (Figure 3).

The data I plan to use in this chapter include two components:

– **Long-term seed data:** Our collaborator Dr. Janneke Hille Ris Lambers, has been collecting stand-level seed production data using seed traps since 2008, which will provide a valuable record of masting events across different stands and elevations at Mount Rainier (Figure 4).
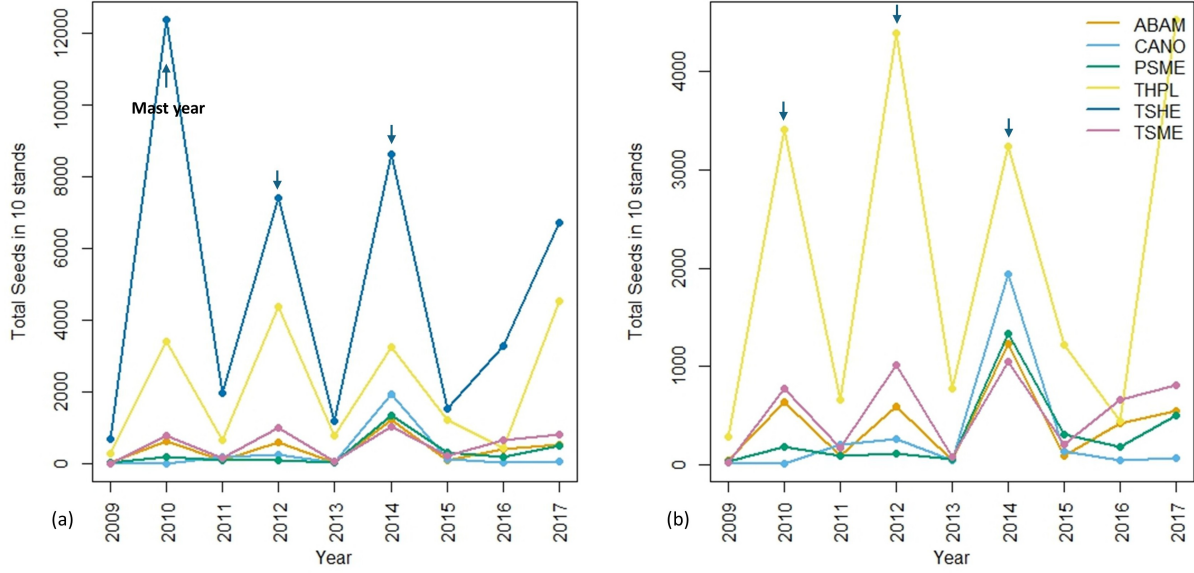
Figure 4: Seed data across all 10 stands collected by seed traps from 2009-2017 at Mount Rainier. (a) total seeds (sum of filled and empty seeds) for all six species; (b) total seeds for only five species excluding TSHE in finer resolution with different y-axis scale. Short blue arrows indicate potential masting years. ABAM: *Abies amabilis*, CANO: *Callitropsis nootkatensis*, PSME: *Pseudotsuga menziesii*, THPL: *Thuja plicata*, TSHE: *Tsuga heterophylla*, TSME: *Tsuga mertensiana*.

Table 1: Targeted species for Chapter 2-3

Tree species	Common name
Abies amabilis	Pacific silver fir
Pseudotsuga menziesii	Douglas-fir
Tsuga heterophylla	Western hemlock
Tsuga mertensiana	Mountain hemlock
Thuja plicata	Western redcedar
Callitropsis nootkatensis	Yellow cedar

– **Tree growth data:** To assess the historical growth of individual trees, I will collect cores from targeted species in Table 1 in each stand with long-term seed data. Within each stand, there are at least two targeted species, and each species appears in at least four stands. I plan to collect tree cores from 25 individuals per species per stand, covering a

size gradient. To make sure the trees we core are mature enough to reproduce at least 10 years ago to match with seed trap time window, I will only collect from trees with DBH greater than 25 cm. Additionally, I will prioritize individuals that are close to seed traps to better correlate with seed data. I will core trees at breast height using increment borers, taking two tree cores from the opposite sides of the tree while avoiding slopes. To account for at least 15 years of growth and for cross-dating purposes, I will collect long cores of 25 cm from larger trees with a DBH above 50 cm, while for smaller trees, I will core to the center if possible.

Tree core processing

I will prepare the cores for analysis by sanding them with fine grit sandpaper (up to 2000 grit depending on the visibility of rings) to ensure a smooth, clear surface. For cores with rings that are difficult to distinguish, I will use a microtome to further enhance the visibility of the rings, creating a clear surface for better quality.

After preparation, I will scan the cores using a high-resolution camera to capture detailed images of the growth rings, then I will analyze the images with CooRecorder, a software used to measure tree ring width. I will also double check the cross-dating results with COFECHA, a computer program that assesses the quality of crossdating and measurement accuracy of tree-ring series (Cook & Kairiukstis, 2013; Speer, 2010).

Statistical analysis

My proposed model investigates the trade-offs between growth (radial growth) and reproduction (seed production). It partially pools species and stands to allow for variation, while sharing information between groups to produce an overall estimate. Thus far, I have developed the model for seed production (below) and am developing the model for radial growth. This part is more complex, as it requires determining an appropriate method for removing size effects at the individual tree level, followed by scaling up to stand-level estimates. These estimates will then inform the modeling of the relationship between growth and reproduction. The full development of this model will be a key part of this chapter.

Likelihood for Seed Production

The seed count for a particular stand j, species sp, and year y follows a negative binomial

distribution with mean $\lambda_{j,sp,y}$ and dispersion term ϕ:

$$\text{Seed}_{j,sp,y} \sim \text{NegBinomial}(\lambda_{j,sp,y}, \phi)$$

The modeled seed count $(\lambda_{j,sp,y})$ for stand j, species sp, and year y is:

$$\log(\lambda_{j,sp,y}) = \alpha_0 + \alpha_{\text{sp}} + \alpha_{\text{j}} + \beta_{1,\text{sp}} \cdot \text{Growth}_{j,sp,y} + \beta_{2,\text{sp}} \cdot \text{Growth}_{j,sp,y-1} + \beta_{3,\text{sp}} \cdot \text{Elevation}_j$$

Where:

α_0 is the grand mean across all species, stands and years;

α_{sp} is the species-specific intercept for species sp;

α_{j} is the stand-specific intercept for stand j;

$\beta_{1,\text{sp}}$ is the slope for the relationship between current-year growth and seed production for species sp;

$\beta_{2,\text{sp}}$ is the slope for the relationship between previous-year growth and seed production as the lag effect for species sp;

$\beta_{3,\text{sp}}$ is the effect of elevation on seed production for species sp.

3.3   Significance

Understanding the relationship between masting and growth is important for predicting how tree species will respond to changing environmental factors, particularly in the context of extended growing seasons with climate change, where how trees allocate additional carbon can impact the global carbon cycle. By examining how these processes interact, we can gain insights into the adaptive strategies of different species and their potential resilience or vulnerability to future climate changes. This knowledge could help us make more informed predictions about future forest dynamics, including shifts in species composition, regeneration, and ecosystem health. As climate conditions continue to shift, understanding the masting behavior and growth responses will be essential for effective forest management and conservation efforts, helping us to anticipate changes and make management plans that will support the sustainability and resilience of forest ecosystems.

4 Investigate how changing climate affect masting dynamics

Plants need to assimilate sufficient resources to produce seeds, a process that depends on a combination of environmental conditions, including adequate light, water, nutrients, and suitable temperatures. These factors influence mast seeding both directly—by affecting seed development—and indirectly through their effects on flowering and vegetative growth. Importantly, these factors also play a critical role in the differentiation of reproductive buds during the year prior to seed development and dispersal, setting the stage for potential mast events. Flowering for some species, for instance, is regulated by daylength, with light influencing the production of hormones that control both flowering and growth (Lau & Deng, 2010). Light is also crucial for photosynthesis, which supports healthy plant growth. Water is another essential element for both flowering and fruiting. When water is limited, plants conserve energy, leading to fewer or smaller flowers, reduced pollination, or early flower shedding (Gallagher & Campbell, 2017). After fertilization, water continues to play an important role in the expansion and maturation of seeds. Aside from its direct effects on reproduction, water stress also inhibits growth, limiting the resources available for reproduction (Hsiao, 1973; Anjum *et al.*, 2011). Nutrients, both macronutrients and micronutrients, as well as photosynthate, are essential for both energy transfer and storage, playing a significant role in the formation of flowers and seed development. Nutrient availability influences the timing of flowering and seed formation, with well-nourished plants more likely to flower at the appropriate time and set seeds successfully. Temperature, especially spring temperature, is one of the most widely studied climatic factors linked to masting events (Bajocco *et al.*, 2021; Moreira *et al.*, 2015; Schauber *et al.*, 2002; Bogdziewicz *et al.*, 2024), as it plays a critical role in successful pollination and seed development. Temperature conditions in the year prior to masting, however, are equally important, as hot, dry summers are known to promote the differentiation of male and female reproductive buds in many conifers (Moreira *et al.*, 2015). These preconditioning effects likely contribute to the synchronization of masting events observed in conifer species at Mount Rainier.

Exploring the relationship between environmental factors and mast seeding behavior can help us to understand how climate change may impact masting events. The four main features of masting: interannual variation, synchrony, temporal autocorrelation, and frequency are all likely affected by climate change in different ways (Hacket-Pain & Bogdziewicz, 2021). Additionally,

warmer temperatures could increase the frequency of droughts, which would limit water supply. In areas with year-round snow cover, temperature changes may also alter water dynamics, affecting the timing and availability of water, which is critical for tree growth and reproduction. These shifts could have profound implications for the frequency and intensity of masting events.

Another important factor in the flowering and fruiting process is environmental 'vetoes', which occur when weather events or environmental conditions prevent plant processes, even when resources are adequate (Bogdziewicz, 2022). Environmental vetoes can take two forms: (1) a lack of weather cues, such as when specific weather conditions required to trigger flowering or fruit maturation are not met, preventing reproduction despite adequate resources; and (2) extreme weather events, such as frost, drought, or heavy rainfall, which can directly damage plant tissues, including shoots, buds, flowers and fruits, thereby preventing successful reproduction. With climate change, environmental vetoes may become more frequent, which is generally considered detrimental to plants. However, studies have shown that environmental vetoes preventing seed production in certain years can actually facilitate masting, allowing for higher regeneration success (Bogdziewicz *et al.*, 2018, 2019). Therefore, understanding how environmental vetoes influence seed production in different species and regions is critical for predicting future forest dynamics. Once we understand how various environmental factors influence different aspects of masting, we can make better predictions of masting events and thus have a better understanding of how future changing climate may shape the seed dynamics (Hacket-Pain & Bogdziewicz, 2021).

Elevation has long been used as a proxy for climate change in ecological studies, since it is closely linked to a variety of climatic factors, particularly temperature and water availability (Körner, 2007). It provides a natural system to study the long-term, large-scale effects of climate change on communities and ecosystems, which cannot be accomplished by experiments (Sundqvist *et al.*, 2013). By using elevation as a proxy for climate change, we can better understand how plant populations at different elevations respond to environmental factors and refine predictive models that incorporate shifting climatic variables at finer spatial resolutions. Although some studies have questioned the validity of the space-for-time substitution in climate change research (Perret *et al.*, 2024), this approach can still offer valuable insights—especially within relatively small geographic regions.

Mount Rainier provides an ideal location for studying how climate change may impact forest

dynamics, as it features a distinct elevation gradient with diverse snowmelt patterns. The rain shadow effect on different sides of the mountain also creates varying water availability. The climate in this region has already undergone significant changes in recent decades and, by combining historical seed data with climate data, we can explore the relationship between climatic variables and various aspects of mast seeding.

This chapter aims to understand how masting patterns are influenced by environmental factors. By investigating the large variance in interannual masting patterns, and exploring the relationship between spatial as well as temporal changes in masting across elevational gradients, we can better understand how climate change will impact seed dynamics in this area.

4.1   Research Question and Objectives

How does the changing climate affect seed dynamics at Mount Rainier?

- **Identify Environmental Influences:** Investigate how key environmental factors (e.g., temperature, precipitation) are related to masting events at Mount Rainier.

- **Climate change proxy:** Use the elevational gradient at Mount Rainier as a proxy for changing climate conditions to compare how masting behavior varies across different elevations.

- **Develop Predictive Models:** Develop predictive models of masting behavior across elevations to forecast future seed dynamics under changing climate conditions.

4.2   Methods

This chapter aims to investigate how climate change influences seed dynamics at Mount Rainier, focusing on the relationship between mast seeding patterns adapted to local climatic conditions across different elevations. By using long-term seed trap data and corresponding climate data, I will assess how seed production synchrony and variability change along the elevation, which is used as a proxy for climate change for the same set of species we used in last chapter. **Data collection**

- **Long-term seed data:** The same long-term seed trap data from last chapter.

- **Local climate data:** Our collaborator Dr. Janneke Hille Ris Lambers has data loggers in the stands recording long-term soil moisture, ambient temperature and light data.

Statistical Analysis and Model Development

- **Time series model, mixed-effect models:** I will build on the model developed in Chapter 2, which explores the growth-reproduction trade-off during mast seeding events, to create a more climate-sensitive model of mast seeding dynamics. This extended model will incorporate climate variables such as temperature and precipitation to assess how changing climatic conditions may alter the frequency, magnitude, and synchrony of mast seeding events.

- **Predictive modeling:** I will develop predictive models to forecast future trends in masting behaviours at Mount Rainier under projected climate scenarios. These models will use climate projections for this region to predict how seed dynamics might shift in response to future climate change.

4.3   Significance

Changes in masting behavior can have cascading effects on forest dynamics, including seed predator interactions and the regeneration success of tree species. Since masting events can provide a large food source drives population dynamics of lots of mammals in the forest, changes of masting patterns will alter these ecological relationships, and the overall structure of ecosystems. For example, if climate change causes masting events to be less synchronized across species or elevations, it will affect seed availability for animals that rely on them as a food source, potentially impacting their survival and reproduction.

Masting could also affect the regeneration of the studied tree species themselves. Many species rely on mast seeding years to establish successful new seedlings in the face of competition and predation. If climate change affects the frequency or intensity of mast seeding events, the successful regeneration of some tree species might be affected. Thus, understanding how these

characteristics of masting might be influenced by climate change is essential for predicting the resilience of forest ecosystems.

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