

AN ABSTRACT OF THE THESIS OF

Claudio Andres Guevara Diaz for the degree of Master of Science in Sustainable Forest Management presented on November 29, 2021.

Title: Modelling Early-Seral Vegetation Dynamics Using Climate and Soil Moisture

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Forest plantations in the Pacific Northwest are highly productive and have been intensively managed to maximize tree growth with practices such as Forest Vegetation Management (FVM). Different FVM regimes have been shown to enhance forest establishment by reducing the competition between the planted seedlings and early-seral vegetation. To better understand these interactions, it is important to study early-seral vegetation growth and their seasonal dynamics.

Vegetation biomass is commonly measured through destructive sampling, but this method is time-consuming and is not applicable for certain studies. Therefore, it is necessary to find reliable methods to estimate vegetation biomass indirectly. This study developed models to estimate early-seral vegetation biomass using vegetation cover,

height, or a combination of the two for different growth forms (ferns, forbs, graminoids, brambles, and shrubs) and environments (wet and dry) in reforested timber stands in Western Oregon, USA. Six different linear and non-linear regression models were tested using cover or the product of cover and height as the only predicting variable, and two additional models tested the use of cover and height as independent variables. Generalized models tested the combination of all growth habits (total vegetation) and sites (pooled data set). Power models were used to estimate early-seral vegetation biomass for most of the growth habits, at both sites, and for the pooled data set. Furthermore, when power models were preferred, most of the growth habits used vegetation cover and height separately as predicting variables. Selecting generalized models for predicting early-seral vegetation biomass across different growth habits and environments is a good option and does not involve an important trade-off by losing accuracy and/or precision. The presented models offer an efficient and non-destructive method for foresters and scientists to estimate vegetation biomass from simple field or aerial measurement of cover and height. Depending on the objectives and availability of input data, users may select which model to apply.

Vegetation dynamics of cover and height were assessed periodically during the first years after seedling establishment, and vegetation biomass was estimated for each study site and measurement time. The observed dynamics of vegetation cover, height, and biomass differed across growth forms (ferns, forbs, graminoids, and brambles) and for the total vegetation due to differences in plant morphology and biomass distribution. Four different non-linear models were tested to characterize these dynamics using the

Julian day of the year as the predicting variable. The Gaussian model was found to better represent the observed data and the parameters of the equation offered a straightforward interpretation. Parameters a , b , and c represented the maximum abundance (asymptote), the day when the maximum was reached, and the slope of the increment, respectively. Multiple regression models estimated these parameters using different weather and soil variables such as; rainfall, potential evapotranspiration, water deficit, minimum, maximum, and mean air temperatures, degree days, vapor pressure deficit, solar radiation, air relative humidity, soil moisture, and soil bulk density. The Gaussian-Environment model allowed the different vegetation traits and growth forms to select the environmental variables better associated with their growth dynamics. Both the Gaussian and Gaussian-Environment models provided adequate estimations of vegetation cover, height, and biomass dynamics, allowing the user to select a model based on their research objective and data input availability. Different environmental variables were selected for each combination of vegetation traits (cover, height, and biomass) and growth forms. Out of the 81 environmental variables selected by the multiple regression models, the most widely selected was soil moisture (44 times; 54.3%), followed by relative humidity (11 times; 13.6%), minimum temperature (7 times; 8.6%), and solar radiation (4 times; 4.9%). The least selected variables were rainfall, water deficit, maximum temperature, potential evapotranspiration, degree days, bulk density, and vapor pressure deficit. Only the mean temperature was never selected by the regression models.

These non-destructive methods can be easily applied by professionals and scientists from a variety of fields to efficiently estimate vegetation abundance at any given time during the growing season. Understanding and quantifying vegetation growth dynamics is important and can be used on the assessment of carbon storage, fire load accumulation, water balance, wildlife habitat, biodiversity change, sustainable energy generation, invasive species management, among other ecological applications.

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Modelling Early-Seral Vegetation Dynamics Using Climate and Soil Moisture

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Claudio Andres Guevara Diaz, Author

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1. Introduction and Literature Review

1.1 Reforestation in the Pacific Northwest

In the U.S. Pacific Northwest (PNW), forests are characterized by their intrinsic high productivity. These forests, mostly dominated by conifer species, vary in composition depending on site conditions such as temperature and humidity (Franklin & Dyrness, 1973). In the PNW, Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) (DF) is the most planted tree due to its adaptability to multiple environments. It succeeds in full exposure to sunlight as well as partial shade. Even though DF prefers moist and well-drained soils, it can tolerate sustained drought periods, which makes it well suited for the Mediterranean and Temperate areas with hot summers and cold winters (Lavender & Hermann, 2014). Another important tree species in the PNW is western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (WH), which is normally associated with DF forests and can become dominant in climax stages. WH is dominant in temperate rainforests close to the coast where rain and fog events during the growing season are more frequent (Burns & Honkala, 1990). DF and WH are the most important sources of timber in Oregon. During 2013 and 2014, DF and WH accounted for 70% and 11% of the total timber harvested, respectively (Simmons et al., 2016).

1.2 Forest Vegetation Management to Reduce Competition for Site Resources

In natural ecosystems, major stand disturbances such as landslides, windstorms, or wildfires, allow site resources to be available for early-seral species. In managed forests, large harvest operations such as clearcutting have a similar effect, but site resources are

shared between the newly planted trees and the surrounding vegetation that emerge spontaneously around them. This surrounding vegetation consists of opportunistic, fast-growing species, both herbaceous and woody, either native or exotic to the area, and it is considered competitive because they capture growth-limiting site resources such as soil water, nutrients, or light at the expense of crop trees (Davies, 1987; Goldberg, 1990; Halpern, 1989). This competition process is considered one of the most important drivers influencing tree establishment and growth in the region (Thompson & Pitt, 2003), and have the potential of shifting community composition from native to introduced species (Dinger & Rose, 2009), and in extreme circumstances, competitively superior species become dominant and may drive subordinates to extinction (Brown & Sax, 2004).

As site resources are limited, particularly in water-limited sites or areas with poor and shallow soils, it is crucial to control competing early-seral vegetation to better allocate the resources to the desired trees. In the case of the PNW, and especially after a clearcut harvest, vegetation is comprised of very competitive species, such as the graminoids *Carex geyeri* and *Calamagrostis rubescens* (Riegel et al., 1995). These highly competitive species make seedling establishment nearly impossible without vegetation control (Balandier et al., 2006). Forest vegetation management (FVM) arose decades ago as a fundamental practice to reduce competition and ensure a successful forest establishment in multiple parts of the world (Newton & Preest, 1988; Wagner et al., 2006).

There are several vegetation management methods and silvicultural operations that can control competing vegetation development by inducing changes in both, plant cover and species composition, which at the end may affect the overall competitive dynamics of the stand (Balandier et al., 2006). In forest plantations, where the trees are planted several meters from one another, there is a high amount of bare soil exposed that can be potentially colonized by competitors (Roberts & Dong, 1991). Forest managers have the opportunity to balance different techniques to ensure sustainable management. For example, focusing on the nearest 0.5 to 2 m from the planted seedlings will minimize herbicide use (Richardson et al., 1996) while allowing species diversity (Hartley, 2002; Miller et al., 2003), as well as wildlife habitat, and food for forage animals (Miller & Miller, 2004). Similarly, the presence of shrubs and tree sprouts can suppress graminoids and forbs preventing the rapid depletion of soil moisture (Balandier et al., 2006), although this process takes effect approximately 3 to 5 years after the disturbance event.

In the PNW, the preferred FVM method corresponds to site-specific herbicide regimes that consist of a fall site preparation (pre-planting) and a spring release (post-planting) to be applied during seedling dormancy on successive years as required (Dinger & Rose, 2009; Maguire et al., 2009; Wagner et al., 1996). Herbicides have been shown to increase seedling growth and survival (e.g. Dimock et al., 1983; Harrington et al., 1995; Ketchum et al., 1999; Maguire et al., 2009; Miller et al., 2003; Rose et al., 2006; Vargas et al., 2018; Wagner et al., 2006) through temporarily reducing the amount

of unwanted vegetation, even when applied in low to moderate amounts (1 or 2 applications) (Dinger & Rose, 2009, 2010; Lauer et al., 1993; Richardson et al., 1996; Zutter et al., 1986). Although herbicides are highly cost-effective, the suppressing effect is temporary and early-seral vegetation might regenerate during the same year the treatment was applied. Depending on pre-treatment site's richness and the residual activity of the herbicide chosen, early-seral vegetation cover after a year of treatment can get up to 80% (Cain, 1999; Dreyfus, 1984; Miller et al., 2003; Zutter et al., 1986). Maguire et al. (2009) found that the competing vegetation cover ranged between 4 and 11% during the first five years after establishment in the plots that received sustained vegetation control, while in the no post-planting herbicide application plots it ranged between 124 and 151%.

Ammer et al. (2011) explain that in Europe, herbicides are viewed by the public as a threat to forest functions, so non-chemical methods are preferred. Nilsson and Örlander (1999) found that mechanical site preparation (mounding) was as effective as herbicide treatments for planted Norway spruce (*Picea abies*) seedlings. Shelterwood and group selection harvesting systems allow overstory trees to be retained for longer periods. Some species, such as European beech and Norway spruce in Europe or WH in the PNW, can suppress early-seral vegetation by casting a deep shade (Maguire et al., 2009; Waring, 1987) or can even lead to niche complementarity between two naturally coexisting functional groups (Frivold & Frank, 2002).

1.3 Benefits of FVM regimes

There is widespread evidence of the benefits of applying FVM methods to enhance crop tree growth and survival. Additionally, some studies have reported an increase in soil moisture availability (Cole & Newton, 2020; e.g. Dinger & Rose, 2009, 2010; Gonzalez-Benecke & Dinger, 2018; Petersen et al., 1988; Powers & Reynolds, 1999; Rose & Ketchum, 2002; Zutter et al., 1986), and a decrease in seedling water stress (e.g. Cleary, 1971; Dinger & Rose, 2009; Nambiar & Sands, 1993; Petersen et al., 1988). However, the interaction between the trees and the surrounding vegetation is variable in time, especially during the first years after planting during forest establishment (Wagner et al., 1999). Furthermore, the response to FVM often depends on the target tree species, vegetation composition, weather conditions, site quality, stand age, resource availability, the timing of application, and (or) silvicultural treatment (Ammer et al., 2011; Balandier et al., 2006; Dinger & Rose, 2010; Flamenco et al., 2019; William et al., 1994). Having these multiple factors interacting, forest managers need to better understand the relationships between competing vegetation, soil moisture dynamics, and seedling growth and mortality during the first years after planting (Dinger & Rose, 2009).

Additionally, in studies about the long-term effects of FVM, Aernouts et al. (2018) found that DF and WH increased ring, earlywood, and latewood areas with vegetation management treatments. These growth gains were achieved without compromising wood quality. Similarly, Flamenco et al. (2019) and Gonzalez-Benecke et al. (2018)

concluded that reducing competition with unwanted vegetation during the early years of stand establishment would have a positive impact on tree biomass growth, having no effect of stem biomass allometry.

In terms of intrinsic water use efficiency (iWUE), Aernouts et al. (2018) reported that DF and WH trees growing under sustained vegetation control showed a reduction in iWUE because the trees were able to keep their stomata open for longer periods. Furthermore, at the same study site, Flamenco et al. (2019) found, at age 16 years, a higher leaf area index (LAI) on plots with sustained control of competing vegetation during the first five years after planting. This reflects that surviving trees that grew free of competition had increased access to site resources as LAI is positively correlated to water (Grier & Running, 1977) and nutrient availability (Velazquez-Martinez et al., 1992), factors controlling site quality.

Old-growth forests in the PNW have high biomass storage, far more than any other region in the United States. In the 1990s, 22.6 billion tons of carbon were found in PNW forests, accounting for 39% of the total carbon stored in U.S. forests (Birdsey, 1992). This total is equivalent to the sum of carbon stored in the Rocky Mountains, Southeast, and Northeastern forests. Nevertheless, young forests can accumulate biomass at higher rates on an area basis (Gray et al., 2016), which could also increase with silvicultural treatments that increase forest productivity, such as FVM (Flamenco et al., 2019; Fox et al., 2007; Martin & Jokela, 2004; Wagner et al., 2006). Allocating site resources into the desired trees not only enhances timber production but also improves forest

restoration and carbon sequestration. Flamenco et al. (2019) reported that sustained vegetation control using herbicides during the first 5 years after plantation allowed crop trees to increase their biomass stock 11 years after the treatment application ended. From a nutrient content perspective, Cannon (2020) found that vegetation control increases the total plant-derived masses of Ca, C, Cu, P, and B and the nutrient use efficiency of N, P, Mg, S, and Cu for four conifer species growing at two sites in the PNW. On a later report, Cannon et al. (2021) found little effect of FVM treatment on soil and foliar nutrient concentrations across species and sites. These studies also indicate that total soil reserves were generally unaffected by sustained vegetation control, implying that there is a low probability of an adverse effect on soil nutrient storage. These studies are one of the few of their kind in the PNW, proving the long-term benefits of controlling competing vegetation. However, the authors suggested that these effects may be site- or species-specific and may depend on the number of hardwoods that get established in the midstory.

Overall, sustained vegetation control during the first years after plantation can significantly reduce the time needed to ensure seedling establishment (Lauer et al., 1993; Wagner et al., 1999), enhance the feedback loop between resource availability and seedling growth, and even minimize the necessity of further herbicide applications (Dinger & Rose, 2010). Understanding the dynamics of competing vegetation development may allow us to anticipate their effect on site resources, as well as on seedling growth and survival.

1.4 Early-Seral Vegetation Growth Forms

There is a relationship between vegetation traits and their competitive potential, generally associated with the species' efficiency for acquiring and using site resources, or tolerating low levels of such resources. However, it is difficult to isolate the competition effect of a single species on the planted trees. For this reason, we are interested in vegetation groups determined by growth form, taxonomy, morphological and/or physiological attributes as suggested by Goldberg (1996), and similar to those used by Chen (2004) and Dinger and Rose (2009). These growth forms are graminoids, forbs, ferns, brambles, and shrubs.

- Graminoids correspond to a wide variety of grasses of different heights, growth rates, below-ground root density, and the ability to form continuous canopies (Balandier et al., 2006). This group is possibly the most serious competitor and their effects on tree seedling growth and survival have been widely reported (e.g. Davies, 1987; Mitchell et al., 1999; Morris et al., 1993; Nilsson & Örlander, 1999; Otsamo et al., 1997).

Graminoids have an advantage over tree species; they can grow numerous long and thin roots (Ludovici & Morris, 1997; Zutter et al., 1999), which allows them to explore and colonize new soil volume and rapidly capture available resources. Although the extensive root system of graminoid species may cause high seedling mortality during the first years after planting, once the seedling's root

system grows into deeper soil layers, the competition level of graminoids decreases progressively (Miller et al., 2003).

- Forbs consist of herbaceous annual and perennial broad-leaved plants with a high aerial growth rate that rapidly colonize open spaces and can form a dense cover due to the prevalent presence of forb seeds in the soil seed bank (Balandier et al., 2006; MacDougall & Turkington, 2005). Compared to graminoids, forbs are less competitive for soil resources (nutrients and water) (Coll et al., 2003) because their root system grows slower than those of grasses, limiting forb's ability to colonize new soil volumes. Nevertheless, forbs can cause stronger competition for light (Frochot et al., 2002) when growing around small seedlings.
- Ferns are one of the oldest groups of vascular plants on Earth and the second-most diverse after flowering plants, from which they differ in reproducing by spores instead of seeds. Ferns can be classified into two categories; those that grow in clumps (like sword-fern) and those that grow rhizomes (underground stems) and send out single leaves (like bracken-fern). Clump ferns grow slowly and cast little shade on the forest floor as their leaves grow vertically, while single-leave ferns cast dense shade that can inhibit seedling establishment (Jackson & Finley, 2016). Some tall ferns can overtop small seedlings, but the negative effect only lasts the first years after forest establishment and can be reduced by allowing light to pass through the fern canopy (Horsley, 1993). When

the surviving seedlings grow taller shoots and deeper roots, they can overcome competition.

- Brambles correspond to rough and prickly shrubs with rambling or mounding growth habits, mostly from the *Rubus* genus. These plants grow long shoots that can root easily in contact with soil, allowing them to rapidly colonize the aboveground surface. The root system is less dense than those of grasses but can grow much deeper and can capture high volumes of soil water and nutrients (Fotelli et al., 2001, 2002; Thevathasan et al., 2000), severely impacting seedling growth and survival in the early years after establishment. Nevertheless, brambles also compete for light with their thorny, broad leaves and stem that can reach up to 2 m in height, which easily overtop smaller seedlings.
- Shrubs are either small or tall woody species, whose competitive effect depends on their origin (from seeds, stumps, or rootstocks), phenology (perennial or deciduous), and abundance. In the PNW, shrub competition ranges from minor to severe (Dinger & Rose, 2009; Harrington et al., 1995; Rose et al., 1999) and their main competitive ability is via light interception (Jobidon, 2000; Küßner et al., 2000; Rose et al., 1999). Shrubs differ from other growth forms in that they can survive the drastic changes in environmental conditions after the planted seedlings reach canopy closure. Therefore, they might become a permanent component of the midstory and have long-term competitive effects.

In different water-limited zones of the world, vegetation has adapted both morphological and physiological traits to optimize water uptake and reduce water loss (i.e. leaf morphological adaptations, low leaf transpiration, low stomatal conductance, low xylem hydraulic conductivity, and high resistance to xylem cavitation) (Balandier et al., 2006). These adaptations are related to a resource conservation strategy, allowing plants to survive and grow with low resources available (Goldberg, 1990). On the other hand, in environments with high resource availability, plant species that adopted a different competition strategy can maximize resource acquisition and grow rapidly, often depleting site resources before other plants could access them. This is a common strategy for highly competitive species such as perennial graminoids and forbs (Balandier et al., 2006). Knowing which competition strategy is used by the competing vegetation is essential to develop efficient FVM regimes that could improve the effectiveness of silvicultural treatments applied on reforestation sites (Dinger & Rose, 2009).

1.5 Next Chapters: Vegetation Biomass Functions and Dynamics

To better understand the competitive abilities of different early-seral vegetation growth forms, we are aiming to quantify the abundance and the seasonal dynamics of early-seral vegetation biomass, tasks that I am going to cover in chapters 2 and 3, respectively.

Vegetation biomass is commonly measured through destructive sampling, but this method is time-consuming and is not applicable for certain studies. Therefore, it is

necessary to find reliable methods to estimate vegetation biomass indirectly. In our study, functions to estimate early-seral vegetation biomass using vegetation cover, height, or a combination of the two were developed for different growth forms (ferns, forbs, graminoids, brambles, and shrubs) and environments (wet and dry) in western Oregon. Six different linear and non-linear regression models were tested using cover or the product of cover and height as the only predicting variable, and two additional models tested the use of cover and height as independent variables. Generalized models combining all the growth forms (total vegetation) as well as combining sites (pooled data set) were also developed. The presented equations offer an efficient method for foresters and scientists to estimate vegetation biomass from simple field or aerial measurements of cover and height. Depending on the objectives and availability of input data, users may select which model to apply.

Vegetation abundance naturally fluctuates throughout time, starting low at the beginning of the growing season, reaching a peak at some point during the summer, and dropping again as senescence occurs. These dynamics differ across environments, years, and growth forms, especially between herbaceous and woody vegetation. I assessed vegetation dynamics on two study sites managed by the Vegetation Management Research Cooperative (VMRC) on plots that did not receive vegetation control to better understand the natural growth patterns of early-seral vegetation. To characterize these dynamics, four different non-linear models were tested using time (the Julian day of the year) as the predicting variable. The Gaussian model was found to better represent the

observed data and the parameters of the equation offered a straightforward interpretation. Parameters a , b , and c of the Gaussian model represented the maximum abundance (asymptote), the day when the maximum was reached, and the slope of the increment, respectively. The analyses proceeded by developing multiple regression models that estimated these parameters using 13 different weather and soil variables; rainfall, potential evapotranspiration, water deficit, minimum, maximum, and mean air temperatures, degree days, vapor pressure deficit, solar radiation, air relative humidity, soil moisture, and soil bulk density. The models were developed for early-seral vegetation cover, height, and biomass for four different growth forms (ferns, forbs, graminoids, and brambles), and the total vegetation. The presented equations have the potential to estimate early-seral vegetation dynamics across the PNW based on weather and soil data.

1.6 Objectives and Hypotheses

The goal of this research is to quantify early-seral vegetation abundance (in terms of cover or biomass) and model its seasonal dynamics during the first years after a disturbance event such as a clearcutting harvest operation. The first objective is to generate a set of equations to estimate early-seral vegetation biomass for different growth forms, using vegetation cover or a combination of cover and height. Samples were gathered from different years and study sites. The second objective is to model the seasonal dynamics of early-seral vegetation cover, height, and biomass for different growth habits, utilizing weather and soil variables. These models will be independent

of site and year, as these factors are reflected in the weather and soil variables, to use them on different years and sites across the PNW.

We hypothesize that equations including both vegetation cover and height will better estimate early-seral vegetation biomass across growth forms and sites. We anticipate that vegetation cover alone will still be a strong predictor for early-seral vegetation biomass. We also hypothesize that early-seral vegetation cover, height, and biomass dynamics will differ across growth forms and that the models will select different weather and soil variables for their estimations. We anticipate that the variables that better explain such dynamics will be the air mean temperature, air relative humidity, and available soil moisture during the spring months.

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GROUND COVER - BIOMASS FUNCTIONS FOR EARLY-SERAL VEGETATION

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2. Ground Cover - Biomass Functions for Early-Seral Vegetation

2.1 Introduction

The characterization of vegetation community biomass has been widely studied for decades due to its importance in applied ecology. Vegetation biomass has been used to characterize biomes and ecosystems (e.g. Ji et al., 2012), to predict fire behavior (e.g. Gonzalez-Benecke et al., 2015), to estimate carbon stocks (e.g. García et al., 2010), as an indicator of ecological functioning and site productivity (e.g. Eisfelder et al., 2017; Gonzalez-Benecke et al., 2014), and as a surrogate of species richness and composition of plant communities, among other uses (Catchpole & Wheeler, 1992; Grime, 1979). The most common method of measuring vegetation biomass in the field is through destructive sampling, but this method is time-consuming and requires multiple repetitions to accurately represent the morphological diversity within a species or a vegetation community. Destructive sampling is also not applicable for permanent plot studies, susceptible environments, or protected areas. Due to this, researchers have sought to estimate vegetation biomass with indirect techniques (Catchpole & Wheeler, 1992; Jonasson, 1988; Somogyi et al., 2007).

Current indirect methods of estimating vegetation biomass are oriented to analyze macro-scale patterns and utilize equipment such as LiDAR (e.g. Dubayah et al., 2010; García et al., 2010; Ji et al., 2012; Kronseder et al., 2012) or remote-sensing techniques based on satellite images of normalized difference vegetation index (NDVI) (e.g. Bendig et al., 2015; Thenkabail et al., 2004). Oftentimes, these methods have reduced

accuracy in ecosystems with scarce vegetation, are site- and time-specific (Eisfelder et al., 2012), and still require destructive sampling for validation. In order to develop biomass models derived from other vegetation attributes, numerous studies have found good correlations between vegetation cover and biomass for individual species (e.g. Guevara et al., 2002; Heinrichs et al., 2010; Röttgermann et al., 2000; Yarie, 1980), or vegetation formations such as grasslands, herbaceous layers, and shrublands (e.g. Chiarucci et al., 1999; Gilliam & Turrill, 1993; Hermy, 1988; Muukkonen et al., 2006).

The benefit of estimating vegetation biomass from cover is that cover measurements are easy to repeat and are, generally, well correlated to biomass (Axmanová et al., 2012; Chiarucci et al., 1999; Ferrari, 2013; Flombaum & Sala, 2007; Mueller-Dombois & Ellenberg, 1974; Muukkonen et al., 2006; Röttgermann et al., 2000). Mueller-Dombois and Ellenberg (1974) found that other measures of vegetation abundance such as density and frequency provided poor correlation with biomass. Estimations of vegetation biomass using vegetation cover as the only predictor variable can provide a good fit for some species and growth forms (Flombaum & Sala, 2007; Guevara et al., 2002), but can produce misleading results in more complex types of ecosystems such as wetlands or stratified forests. For instance, not accounting for vegetation height can make a single-layer canopy having similar biomass to a multi-layer canopy, or shorter plants having similar biomass to taller plants for any given vegetation cover. Additionally, as some studies set a maximum vegetation cover to 100%, it is difficult to account for species overlap in highly productive ecosystems.

Axmanová et al. (2012) tested multiple variables as predictors of vegetation biomass in different ecosystem types in Central Europe. In this study, the authors developed linear relationships for aboveground biomass to: a) total cover of the herbaceous layer; b) the sum of species cover multiplied by their heights; c) an adjusted estimate of the latter to account for species overlap; and d) the total cover of the herbaceous layer multiplied by the median of plant heights. Even though the cover of the herbaceous layer had a robust correlation with herbaceous biomass in all the ecosystems tested, the biomass estimate that used the median of the heights proved to have a stronger correlation. Likewise, in a study on perennial grasses in Argentina, Guevara et al. (2002) used vegetation cover (in area units), and height to develop biomass functions. They concluded that models that included height as an independent variable improved model fit for some species, while other species had a better fit when vegetation cover was the only independent variable. However, these models were developed using data from only one growing season, making them susceptible to year-to-year variability, as observed by Johnson et al. (1988) in a different study.

This study was carried out as part of the Competition and Site Interactions Experiment (CoSInE) being conducted by the Vegetation Management Research Cooperative (VMRC) at Oregon State University. The CoSInE project is a large long-term study designed to investigate the mechanisms driving planted conifer seedling responses to forest vegetation management treatments (Guevara et al., 2019). Developing indirect methods for estimating vegetation biomass is an important

component of the study as vegetation biomass is a more comprehensive measure of competing vegetation abundance than cover or height. Destructive vegetation sampling would also not be appropriate inside of the permanent plots used to monitor seedling response as such sampling would alter competition dynamics.

Different vegetation types differ in their allometric relationships and, for this reason, we separated the vegetation community into five growth forms including graminoids, forbs, ferns, brambles, and shrubs. In this study, cover, height, and biomass of early-seral vegetation were measured during two consecutive growing seasons after planting at two different sites in western Oregon, United States. The objective was to develop biomass functions of early-seral vegetation using cover or a combination of cover and height as predicting variables. Functions were developed for each vegetation growth form and for each site. We analyzed the differences between sites for the same growth form, aiming to have one function that works well across different sites, whenever possible.

2.2 Materials and Methods

2.2.1 *Study Sites Description*

Two study sites located in western Oregon were selected to represent contrasting climatic conditions of forestlands in the PNW. The Coastal – Wet (CW) study site is located at 45°07'15" N, 123°54'15" W in the Coast Range near Pacific City, OR. Soils are characterized by the Tolovana-Templeton series defined as a silt loam with a water holding capacity (WHC) of 282 mm in the top 1 m of soil (Soil Survey Staff, 2019).

The elevation is about 120 m and the study area sits on a south-west-facing ridge within 6.5 km of the Pacific Ocean. The average annual rainfall is 2,610 mm and the mean annual temperature is 9.9° C (Wang et al., 2012). Plots were installed in early September 2016, after a clear-cut harvest operation was carried out during the previous summer, in August 2015. The most common species observed at the site were *Digitalis purpurea*, *Polystichum munitum*, *Stachys rigida*, *Hypochaeris radicata*, *Rubus ursinus*, and grasses in the *Agrostis* genus.

The Inland – Dry (ID) study site is located at 43°35'35" N, 123°08'25" W near Yoncalla, OR. Soils are defined as silt loam from the Windygap series and have a WHC of 171 mm in the top 1 m of soil (Soil Survey Staff, 2019). The site has an elevation of 100 m, the average annual rainfall is 1,299 mm, and the mean annual temperature is 10.8° C (Wang et al., 2012). Plots were installed in early September 2017, after the unit was harvested in August 2017. Both study sites were established and managed by the VMRC. The most common species observed at the site were *Rumex acetosella*, *Cirsium* species, *Senecio sylvaticus*, *Polystichum munitum*, *Rubus ursinus*, *Holcus lanatus*, and grasses in the *Agrostis* genus.

Inter-annual climatic variation was observed across sites during the first two summers (June-August) after seedling establishment (Table 2.1). During 2017 and 2018 at the CW site, there were 27 and 39 rainy days, respectively, while at the ID site there were 6 and 14 rainy days during 2018 and 2019, respectively. The total rain associated with those days was 53.8 and 29.9 mm at the CW site, and 37.0 and 39.3 mm at the ID

site. The average daily vapor pressure deficit (VPD) was 0.56 and 0.39 kPa at the CW site, and 1.42 and 1.28 kPa at the ID site. When averaging both years at each site, the daily maximum VPD and temperature were 0.87 kPa and 19.1° C, respectively at the CW site and 2.46 kPa and 26.8° C, respectively at the ID site, demonstrating clear differences in growing conditions between the two sites.

Table 2.1 Number of days with rainfall (Rainy days), total rainfall, mean daily maximum temperature (T max), mean daily temperature (T mean), mean daily daylight hour relative humidity (RH), mean daily maximum vapor pressure deficit (VPD max), and mean daily daylight hour vapor pressure deficit (VPD mean) for the first two summers (June-August) at the Coastal – Wet (CW) and Inland – Dry (ID) sites in western Oregon.

	CW		ID	
	2017	2018	2018	2019
Rainy days	27	39	6	14
Total Rain (mm)	53.8	29.9	37.0	39.3
T max (°C)	19.1	19.1	27.2	26.3
T mean (°C)	14.6	14.6	18.4	18.2
RH (%)	74.7	81.1	54.8	57.3
VPD max (kPa)	0.95	0.80	2.60	2.31
VPD mean (kPa)	0.56	0.39	1.42	1.28

Field measurements of the top 20 cm of soil determined that soil bulk density ranged from 0.298 to 0.541 g cm⁻³ at the CW site with an average of 0.445 g cm⁻³. At the ID site, bulk density ranged from 0.638 to 1.255 g cm⁻³ with an average of 0.984 g cm⁻³. Both sites had no signs of soil compaction, are rich in organic matter (coming from the harvesting operations), and have a high water holding capacity.

2.2.2 *Study Design*

At both study sites, seedlings were planted at a 3 x 3 m spacing. The CW site was planted with western hemlock using styro-10 container stock on March 2017 while the ID site was planted using bareroot Douglas-fir Plug + 1 stock on January 2018. The planted location of all seedlings was previously marked using pin flags to ensure proper spacing.

The CoSInE study series includes eight unique treatments representing different combinations of pre-planting and post-planting herbicide applications during the first two growing seasons (Guevara et al., 2019). Each treatment is replicated in four blocks. The destructive sampling of vegetation within the permanent plots that receive these treatments was not considered to be appropriate and, due to this, one 18 x 18 m biomass plot was installed within each block for destructive sampling of vegetation and remained unsprayed with herbicides throughout the study. Inside each biomass plot, two 1 m² clip plots were randomly assigned to previously numbered locations in front of a seedling every month during the growing season (April to October). In accordance with the biomass sampling method shown by Gilliam & Turrill (1993), clip plots were used to destructively sample all aboveground biomass of the vegetation found inside the plot, after estimating vegetation cover (%) and height (cm) by growth form, following the methods of Samuelson and Stokes (2011). All biomass samples were brought to the laboratory to be oven-dried at 65°C for a minimum of 72 hours until the weight remained constant. The measurements were carried out during the first three years after

conifer seedling planting (2017-2019) at the CW site, and the first two years (2018-2019) at the ID site.

We identified two fern species; sword fern (clump) and bracken fern (rhizome). Due to their different morphology, the species were differentiated during the development of the biomass functions to better represent their allometric relationships. Additionally, another function was developed to estimate biomass from the vegetation of all growth forms combined (total) for each site. Total vegetation cover was calculated as the summed cover of all growth forms found inside a clip plot and could therefore exceed 100% cover. Total vegetation height was calculated as the average of the heights of all growth forms found inside a clip plot.

Biomass functions were developed for both study sites separately. A third data set was created by pooling the data from both sites to test if the same biomass function could be used across sites for any given growth form.

2.2.3 Model description

The software CurveExpert Professional version 2.6 (Hyams Development, Chattanooga, TN, USA) was used to explore compatible linear and non-linear regression models to estimate early-seral vegetation biomass depending on cover and height data. Following similar procedures to those reported in Gonzalez-Benecke et al. (2014), biomass models were described, fitted, and evaluated. Six functions were selected to be tested; 1) linear, 2) power, 3) logistic, 4) logistic power, 5) shifted power, and 6) exponential association (Seber & Wild, 2003).

$$B_v = a + b \cdot x + \varepsilon_i \quad (\text{eqn 2.1})$$

$$B_v = a \cdot x^b + \varepsilon_i \quad (\text{eqn 2.2})$$

$$B_v = a / (1 + b \cdot \exp^{-c \cdot x}) + \varepsilon_i \quad (\text{eqn 2.3})$$

$$B_v = a / (1 + (x/b)^c) + \varepsilon_i \quad (\text{eqn 2.4})$$

$$B_v = a \cdot (x - b)^c + \varepsilon_i \quad (\text{eqn 2.5})$$

$$B_v = a \cdot (1 - \exp^{-b \cdot x}) + \varepsilon_i \quad (\text{eqn 2.6})$$

where B_v is the biomass (Mg ha^{-1}) for each vegetation growth form (including total); a , b , and c are curve fit parameter estimates; \exp is the base of natural logarithm; ε_i is the error term, with $\varepsilon_i \sim N(0, \sigma_i^2)$; and the variable x can be either vegetation cover, or the product of cover and height (C·H, cover in percent; height in cm). Additionally, cover and height were also tested as independent variables for a modified version of equations 2.1 and 2.2, as follows:

$$B_v = a + b \cdot \text{Cover} + c \cdot \text{Height} + \varepsilon_i \quad (\text{eqn 2.7})$$

$$B_v = a \cdot \text{Cover}^b \cdot \text{Height}^c + \varepsilon_i \quad (\text{eqn 2.8})$$

where B_v is the biomass (Mg ha^{-1}) for each vegetation growth form (including total); a , b , and c are curve fit parameter estimates, and ε_i is the error term, with $\varepsilon_i \sim N(0, \sigma_i^2)$.

2.2.4 Model fitting and evaluation

The Statistical Analysis Software version 9.4 (SAS Institute Inc. Cary, NC, USA) was used for all statistical analyses. Non-linear model fitting was conducted using the procedure `proc nlin` for all parameter estimates reported. Within each growth form, the model with the highest coefficient of determination (R^2) and the lowest Akaike

information criterion (AIC) was selected. When two or more models had similar R^2 and AIC, we selected the model that had a combination of good biological meaning, simplicity, and that could be used across sites and growth forms. As non-linear model fitting was carried out, an empirical R^2 (Myers, 2000) and AIC (Akaike, 1974) were determined as:

$$R^2 = 1 - \frac{SSE/df_e}{SST/df_t} \quad (\text{eqn 2.9})$$

where SSE and SST are the sum of squares of residuals and total, respectively, and df_e and df_t are the degrees of freedom of error and total, respectively.

$$AIC = -2 \cdot \ln(L) + 2 \cdot k \quad (\text{eqn 2.10})$$

where L is the value of the maximum likelihood and k is the number of independently adjusted parameters.

The predictive ability of the selected models was evaluated by using a 10-fold cross validation (Neter et al., 1996), splitting the data set randomly into ten subsets with an approximately equal number of observations. To evaluate the goodness-of-fit between the observed and predicted values for each growth form, the root mean square error (RMSE) and the coefficient of variation (CV, $100 \cdot \text{RMSE}/\text{mean}$) were used. Normality and heteroskedasticity were checked using the Shapiro-Wilk and the White tests, respectively. All figures were produced using SigmaPlot version 14 (Systat Software, Inc. San Jose, CA, USA).

2.3 Results

Table 2.2 provides a summary of the sample size, mean, and range of cover (%), height (cm), and biomass (Mg ha^{-1}) by growth form of the samples measured at both study sites (and for the pooled data set) during the first two growing seasons after seedling conifer planting. At the ID site, no bracken fern or shrubs were found on sampled clip-plots.

Table 2.2 Summary statistics of cover, height, and biomass measured by growth form for the Coastal-Wet (CW) and Inland-Dry (ID) sites in western Oregon. Data from both sites were combined to create a pooled data set.

Site	Growth form	n	Cover (%)			n	Height (cm)			Biomass (Mg ha^{-1})		
			Mean	Min	Max		Mean	Min	Max	Mean	Min	Max
CW	Bf	32	26.8	1	100	19	49.6	12	100	0.8	0.01	3.1
	Sf	18	20.4	2	90	18	39.3	20	72	1.4	0.04	7.3
	F	90	27.4	1	90	65	32.5	5	150	1.1	0.03	3.4
	G	76	14.1	1	98	54	28.8	5	148	0.7	0.002	7.4
	B	47	7.4	1	35	36	17.9	4	60	0.2	0.001	1.5
	S	18	4.6	1	25	16	23.1	9	50	0.1	0.002	1.3
ID	Sf	19	16.7	1	65	19	37.6	5	68	1.8	0.01	9.2
	F	47	35.6	3	90	47	28.6	5	80	1.4	0.04	5.3
	G	29	30.7	1	95	29	39.9	7	86	1.4	0.02	6.5
	B	30	18.2	1	95	30	21.5	5	50	0.6	0.001	4.1
Pooled	Sf	37	18.5	1	90	37	38.4	5	72	1.6	0.01	9.2
	F	137	30.2	1	90	112	30.9	5	150	1.2	0.03	5.3
	G	105	18.7	1	98	83	32.7	5	148	0.9	0.002	7.4
	B	77	11.6	1	95	66	19.5	4	60	0.4	0.001	4.1

Bf: Bracken fern; Sf: Sword fern; F: Forbs; G: Graminoids; B: Brambles; S: Shrubs. The sample size for biomass is the same sample size of cover.

Mean cover, height, and biomass of sword fern did not differ across sites ($P>0.440$) and averaged 18.5%, 38.4 cm, and 1.6 Mg ha^{-1} , respectively. For forbs, mean cover was 8.2% higher at the ID site compared to the CW site ($P=0.022$). Although no significant

differences were found for forb height across sites ($P=0.915$), mean forb biomass was 0.3 Mg ha^{-1} higher at the ID site ($P=0.031$). Mean graminoid cover at the ID site was more than twice that of the CW site (30.7% vs 14.1%, respectively, $P=0.002$), while mean graminoid height did not significantly differ across sites ($P=0.083$) and averaged 32.7 cm. Mean graminoid biomass at the ID site also doubled that of the CW site (1.4 vs 0.7 Mg ha^{-1} , $P=0.022$). For brambles, mean cover and height did not significantly differ across sites ($P>0.056$) but mean bramble biomass was three times higher at the ID site compared to the CW site (0.6 vs 0.2 Mg ha^{-1} , $P=0.022$).

A comparison among growth forms and study sites for the relationships between cover and biomass is presented in Fig. 2.1. Most growth forms had samples within the whole range of cover (0-100%), except by shrubs, which only had a maximum cover of 25% at the CW site. Graminoids and ferns had the widest ranges of biomass sampled going up to 7.4 and 9.2 Mg ha^{-1} , respectively, while we found a maximum biomass of 5.3 , 4.1 , and 1.3 Mg ha^{-1} for forbs, brambles, and shrubs, respectively (Fig. 2.1).

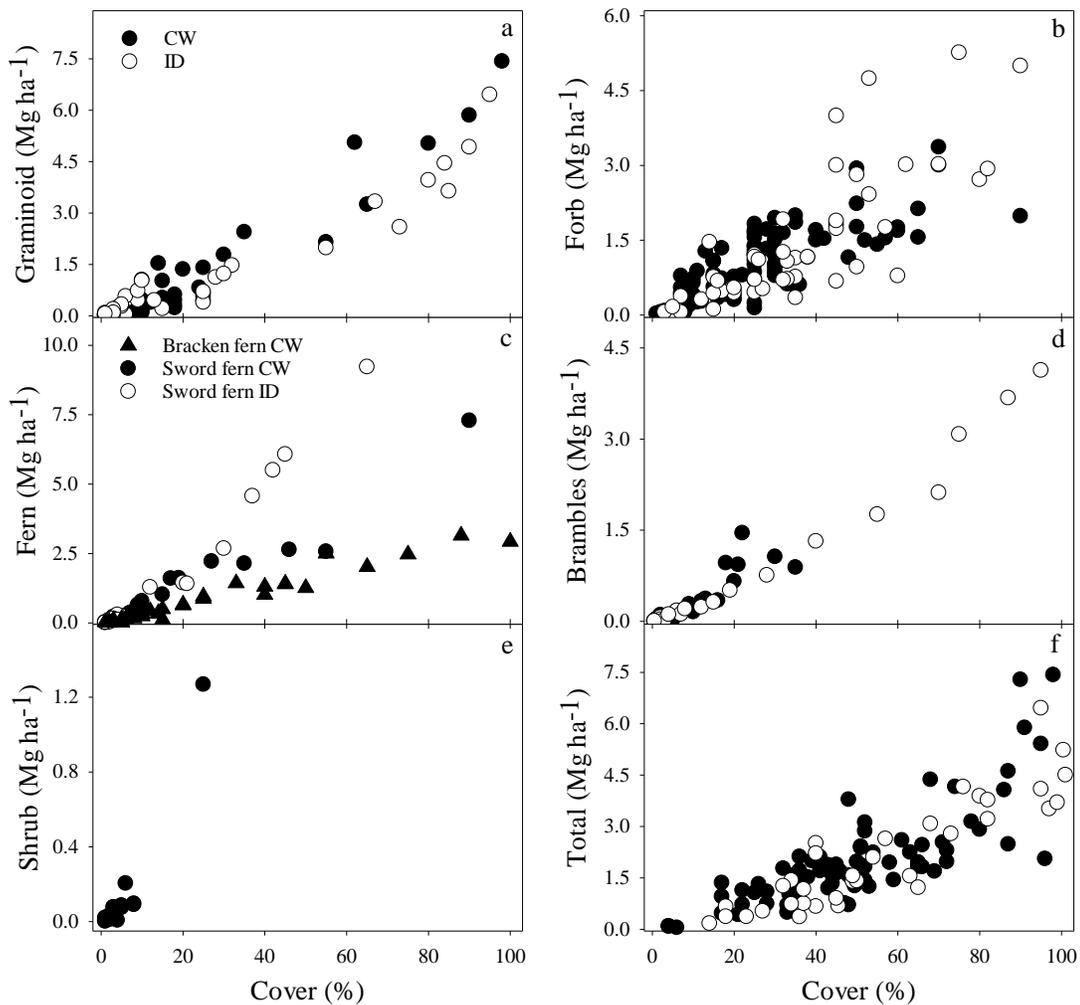


Figure 2.1 Relationship between cover (%) and biomass (Mg ha^{-1}) for a) graminoids, b) forbs, c) ferns, d) brambles, e) shrubs, and f) total for early-seral vegetation growing at the Coastal-Wet (CW, filled circle) and Inland-Dry (ID, open circle) sites in western Oregon. The fern graph (c) includes bracken fern found at the CW site (filled triangle) and the shrub graph (e) does not include data from the ID site due to a lack of samples found.

2.3.1 Model selection

Goodness of fit indexes of the eight functions tested to estimate biomass for each growth form present at the CW and ID sites, as well as for the pooled data set, are displayed in Tables 2.3, 2.4, and 2.5, respectively. At the CW site, five different growth

forms were found: ferns, forbs, graminoids, brambles, and shrubs. When only using cover as a predictor variable, the power function (equation 2.2) provided the best estimates of biomass for all the species and growth forms except for brambles which were better estimated with the logistic function (equation 2.3). When height was included, bracken fern, graminoids, and brambles had a slight reduction of R^2 and/or an increment in AIC, so the model using only cover was still preferred. Other growth forms had a considerable improvement in the estimation of biomass when including height as an independent predictor variable (equation 2.8). Such is the case of forbs and total, whose R^2 increased from 0.88 to 0.92 and from 0.90 to 0.94, respectively (Table 2.3).

The power function using cover and height independently as the predictor variables (equation 2.8) provided a better estimation of vegetation biomass for sword fern, forbs, shrubs, and the total. Using a power function to estimate the biomass of brambles would have been ideal to keep consistency within the site, and while there was no difference in R^2 , the AIC decreased from -177.6 to -207.4 when using a logistic function (equation 2.3) with cover as the only predictor variable. Consequently, the logistic function was selected to estimate bramble biomass at the CW site.

Table 2.3 Goodness of fit of the functions tested to estimate biomass for each growth form of early-seral vegetation growing at a Costal-Wet (CW) site in western Oregon.

Predictor	Model	Bracken fern		Sword fern		Forbs		Graminoids		Brambles		Shrubs		Total	
		R ²	AIC	R ²	AIC	R ²	AIC	R ²	AIC	R ²	AIC	R ²	AIC	R ²	AIC
C	1	0.95	-97.30	0.93	-25.10	0.59	-140.73	0.92	-140.13	0.81	-177.36	0.90	-80.58	0.60	-54.16
C·H	1	0.76	-23.50	0.94	-28.52	0.55	-92.53	0.80	-48.19	0.85	-135.40	0.99	-98.31	0.50	-27.62
C	2	0.97	-98.81	0.96	-27.40	0.88	-145.13	0.95	-167.15	0.85	-177.59	0.98	-114.07	0.90	-54.49
C·H	2	0.94	-34.51	0.97	-36.62	0.88	-104.71	0.88	-61.32	0.92	-146.24	0.98	-139.48	0.91	-39.54
C	3	0.97	-91.90	0.95	-24.22	0.88	-141.60	0.94	-143.78	0.92	-207.37	0.98	-113.09	0.89	-52.63
C·H	3	0.96	-42.03	0.94	-20.36	0.86	-92.79	0.89	-61.68	0.92	-148.43	0.99	-129.16	0.90	-34.46
C	4	0.97	-99.46	0.96	-25.40	0.88	-144.21	0.95	-165.15	0.91	-198.12	0.98	-112.07	0.89	-52.49
C·H	4	0.96	-42.23	0.97	-34.62	0.88	-102.71	0.89	-62.75	0.92	-148.64	0.96	-86.19	0.91	-37.89
C	5	0.97	-93.82	0.96	-28.10	0.88	-143.56	0.95	-165.40	0.84	-173.10	0.98	-114.24	0.90	-53.34
C·H	5	0.94	-32.90	0.97	-35.88	0.88	-103.40	0.88	-59.35	0.91	-144.51	0.98	-142.61	0.91	-37.95
C	6	0.97	-98.77	0.95	-25.21	0.88	-146.27	0.92	-121.63	0.84	-173.93	0.82	-71.72	0.89	-53.48
C·H	6	0.96	-42.69	0.97	-34.01	0.85	-89.00	0.89	-65.23	0.93	-151.24	0.98	-95.63	0.89	-30.83
C and H	7	0.93	-45.19	0.94	-27.25	0.74	-127.28	0.90	-85.52	0.88	-142.86	0.90	-68.15	0.73	-60.45
C and H	8	0.97	-48.00	0.98	-38.68	0.92	-129.77	0.94	-100.67	0.91	-144.24	0.99	-137.88	0.94	-63.50

C: vegetation cover (%); H: vegetation height (cm); 1: linear; 2: Power; 3: Logistic; 4: Logistic Power; 5: Shifter Power; 6: Exponential Association; 7: Linear with independent variables; 8: Power with independent variables; Total: includes all vegetation; R²: coefficient of determination; AIC: Akaike Information Criterion; Background shading indicate the best model for each species or growth form.

At the ID site, when using cover as the only predictor variable, the power function (equation 2.2) was preferred for forbs, brambles, and the total, while the logistic function (equation 2.3) was preferred for sword fern and graminoids. No bracken fern or shrubs were found at the ID study site. When height was included as a predictor variable, the power function using both variables independently (equation 2.8) provided the best estimations of vegetation biomass for all growth forms as indicated by an increase in R^2 and/or decrease in AIC. In the case of forbs and graminoids, using C·H resulted in a slightly lower AIC, but this difference was considered negligible and the function using cover and height independently was selected to keep consistency within and across sites. The biomass of sword fern, forbs, and the total was better predicted using the same function and predicting variables as those used at the CW site. In contrast, at this site, the estimations of graminoid biomass were improved when height was included as a predictor. This is reflected in the R^2 , which increased from 0.96 to 0.99, and in the AIC, which decreased from -44.6 to -80.7. Similarly, at this site, bramble biomass was better estimated using a power function and including height as an independent variable (equation 2.8).

Table 2.4 Goodness of fit of the functions tested to estimate biomass for each growth form of early-seral vegetation growing at an Inland-Dry (ID) site in western Oregon.

Predictor	Model	Sword fern		Forbs		Graminoids		Brambles		Total	
		R ²	AIC	R ²	AIC	R ²	AIC	R ²	AIC	R ²	AIC
C	1	0.96	-21.97	0.63	-17.26	0.91	-34.61	0.97	-95.20	0.80	-21.42
C·H	1	0.95	-18.49	0.94	-101.88	0.98	-84.60	0.98	-104.95	0.48	10.62
C	2	0.99	-45.45	0.83	-17.55	0.96	-44.58	0.99	-127.79	0.93	-23.15
C·H	2	0.97	-22.87	0.97	-100.64	0.99	-82.67	0.98	-107.70	0.87	-1.57
C	3	0.99	-52.50	0.82	-15.37	0.97	-53.93	0.98	-103.28	0.93	-21.82
C·H	3	0.96	-13.95	0.97	-100.46	0.98	-61.98	0.96	-81.27	0.86	1.29
C	4	0.99	-50.50	0.82	-15.56	0.96	-42.58	0.99	-125.79	0.93	-23.15
C·H	4	0.97	-20.87	0.97	-98.64	0.99	-80.67	0.98	-105.70	0.88	-3.33
C	5	0.99	-45.64	0.82	-15.56	0.97	-53.70	0.99	-127.88	0.93	-21.16
C·H	5	0.97	-20.44	0.97	-103.16	0.99	-84.75	0.98	-105.79	0.88	-1.94
C	6	0.96	-15.29	0.82	-14.96	0.94	-33.60	0.97	-91.50	0.91	-12.22
C·H	6	0.96	-17.03	0.97	-100.27	0.99	-79.61	0.98	-107.64	0.88	-3.90
C and H	7	0.96	-21.54	0.85	-57.86	0.93	-42.17	0.97	-93.22	0.87	-34.55
C and H	8	0.99	-55.83	0.97	-99.68	0.99	-80.68	0.99	-159.72	0.96	-39.28

C: vegetation cover (%). H: vegetation height (cm). 1: linear; 2: Power; 3: Logistic; 4: Logistic Power; 5: Shifter Power; 6: Exponential Association; 7: Linear with independent variables; 8: Power with independent variables; Total: includes all vegetation; R²: coefficient of determination; AIC: Akaike Information Criterion; Background shading indicate the best model for each species or growth form.

As shrubs were not present at the ID site, the pooled data set includes functions for sword fern, forbs, graminoids, and brambles and for the sum of all (total). When using only cover as a predictor variable, the power function (equation 2.2) provided the best estimations of biomass for all the growth forms. However, when height was included, the power function including both variables independently (equation 2.8) provided more accurate estimations of biomass for all growth forms, except for sword fern, which was better estimated using a logistic function (equation 2.3) with $C \cdot H$ as the predicting variable. This is reflected in its improved R^2 (from 0.89 to 0.93) and the decreased AIC (from -6.0 to -22.9), compared to the power function using cover and height independently as predictor variables (equation 2.8). Including height as an independent predictor variable improved the R^2 of all growth forms, increasing from 0.84 to 0.91 for forbs, from 0.94 to 0.95 for graminoids, from 0.97 to 0.98 for brambles, and from 0.91 to 0.95 for total (Table 2.5).

Table 2.5 Goodness of fit of the functions tested to estimate biomass for each growth form of early-seral vegetation for the pooled data set.

Predictor	Model	Sword fern		Forbs		Graminoids		Brambles		Total	
		R ²	AIC	R ²	AIC	R ²	AIC	R ²	AIC	R ²	AIC
C	1	0.83	-4.52	0.60	-127.77	0.90	-155.77	0.96	-276.05	0.69	-74.37
C·H	1	0.80	0.41	0.69	-119.96	0.85	-84.70	0.97	-244.96	0.48	-10.47
C	2	0.88	-3.10	0.84	-127.70	0.94	-177.52	0.97	-293.06	0.91	-77.73
C·H	2	0.89	-5.93	0.88	-128.53	0.92	-108.10	0.97	-246.59	0.89	-39.63
C	3	0.88	-1.77	0.83	-123.13	0.93	-162.31	0.94	-236.37	0.91	-76.65
C·H	3	0.93	-22.89	0.88	-132.72	0.93	-114.41	0.94	-195.23	0.88	-32.45
C	4	0.89	-3.58	0.84	-127.70	0.94	-175.52	0.97	-291.06	0.91	-75.73
C·H	4	0.92	-18.05	0.88	-126.55	0.93	-114.92	0.97	-244.59	0.90	-40.90
C	5	0.88	-1.34	0.84	-125.81	0.94	-179.52	0.97	-291.07	0.91	-77.26
C·H	5	0.89	-4.08	0.88	-126.78	0.92	-106.16	0.97	-245.79	0.89	-39.31
C	6	0.88	-2.80	0.84	-127.69	0.92	-145.22	0.96	-262.58	0.90	-68.27
C·H	6	0.91	-14.20	0.87	-122.36	0.93	-119.19	0.97	-246.11	0.88	-33.04
C and H	7	0.83	-4.22	0.73	-135.60	0.91	-124.11	0.96	-228.62	0.80	-92.90
C and H	8	0.89	-5.99	0.91	-163.29	0.95	-149.43	0.98	-272.42	0.95	-100.54

C: vegetation cover (%). H: vegetation height (cm). 1: linear; 2: Power; 3: Logistic; 4: Logistic Power; 5: Shifter Power; 6: Exponential Association; 7: Linear with independent variables; 8: Power with independent variables; Total: includes all vegetation; R²: coefficient of determination; AIC: Akaike Information Criterion; Background shading indicate the best model for each species or growth form.

2.3.2 *Model fitting*

Parameter estimates for the selected functions to estimate biomass for each growth form, at the CW and ID sites, as well as for the pooled data set, are reported in Table 2.6 when using only cover as the predictor variable, and in Table 2.7 when height was included. All parameter estimates were significant at $P < 0.05$. When using only vegetation cover as the predictor variable, the selected models to estimate early-seral vegetation biomass provided good estimations, with R^2 , RMSE, and CV ranging between 0.83 to 0.99, 0.04 to 0.81 Mg ha⁻¹, and 12.8 to 56.2%, respectively (Table 2.6). When pooling the data sets, goodness of fit was improved, with a trend of reducing RMSE and CV. For example, for brambles, the CV of the CW and ID sites was 51.2 and 39.7%, respectively, whereas for the pooled data set the CV was 18.4%.

Table 2.6 Parameter estimates and fit statistics of the selected functions to estimate biomass using cover for each growth form of early-seral vegetation growing in Western Oregon.

Site	Growth form	Model	Param	Parameter Estimate	SE	R ²	RMSE	CV	
CW	Bf	$= a \cdot Cover^b$	a	0.030351	0.007426	0.972	0.21	24.4	
			b	1.016627	0.058688				
	Sf	$= a \cdot Cover^b$	a	0.039499	0.017128	0.958	0.44	32.3	
			b	1.139870	0.104380				
	F	$= a \cdot Cover^b$	a	0.093137	0.025081	0.881	0.44	41.4	
			b	0.751169	0.072756				
	G	$= a \cdot Cover^b$	a	0.013234	0.003293	0.954	0.33	48.3	
			b	1.366124	0.057796				
	B	$= \frac{a}{1 + b \cdot exp^{-c \cdot Cover}}$	a	1.095629	0.066066	0.924	0.11	51.2	
			b	70.709855	30.877161				
			c	0.285186	0.032782				
	S	$= a \cdot Cover^b$	a	0.003051	0.001236	0.983	0.04	35.0	
			b	1.872408	0.127451				
	T	$= a \cdot Cover^b$	a	0.024005	0.012096	0.896	0.70	37.5	
b			1.119684	0.121707					
ID	Sf	$= \frac{a}{1 + b \cdot exp^{-c \cdot Cover}}$	a	9.965688	0.373641	0.994	0.23	12.8	
			b	45.279774	6.867032				
			c	0.096193	0.005173				
	F	$= a \cdot Cover^b$	a	0.040084	0.012863	0.838	0.62	52.0	
			b	0.996012	0.082203				
	G	$= \frac{a}{1 + b \cdot exp^{-c \cdot Cover}}$	a	663843166	$7.28 \cdot 10^{12}$	0.972	0.38	26.2	
			b	1932462172	$2.12 \cdot 10^{13}$				
			c	0.030093	0.001911				
	B	$= a \cdot Cover^b$	a	0.015168	0.002712	0.971	0.15	39.7	
			b	1.220071	0.042044				
	T	$= a \cdot Cover^b$	a	0.012402	0.004927	0.908	0.70	36.2	
			b	1.279081	0.093410				
	Pooled	Sf	$= a \cdot Cover^b$	a	0.023319	0.005501	0.992	0.29	15.8
				b	1.440794	0.060425			
F		$= a \cdot Cover^b$	a	0.014729	0.010594	0.829	0.81	56.2	
			b	1.266369	0.175836				
G		$= a \cdot Cover^b$	a	0.005639	0.004692	0.960	0.45	31.2	
			b	1.502171	0.189706				
B		$= a \cdot Cover^b$	a	0.005966	0.001728	0.992	0.11	18.4	
			b	1.432098	0.066262				
T		$= a \cdot Cover^b$	a	0.004544	0.003300	0.931	0.70	32.6	
			b	1.509432	0.164803				

CW: Coastal - Wet site; ID: Inland - Dry site; Pooled: Pooled data set combining both sites; Bf: Bracken fern; Sf: Sword fern; F: Forbs; G: Graminoids; B: Brambles; S: Shrubs; T: Total vegetation; Cover: vegetation ground cover (%); Height: vegetation height (cm); SE: standard error; R²: coefficient of determination; RMSE: root mean square error (Mg ha⁻¹); CV: coefficient of variation (%). For all parameter estimates $P < 0.05$.

At the CW site, the selected functions to estimate biomass from cover and height (Table 2.7) provided accurate and precise estimations for early-seral vegetation of the different growth forms, with R² values from 0.92 to 0.99, RMSE from 0.01 to 0.55 Mg

ha⁻¹, and CV from 10.8 to 56.3%. At the ID study site, the functions to estimate early-seral vegetation biomass had a better fit, with R² ranging from 0.96 to 0.99, RMSE ranging from 0.07 to 0.55 Mg ha⁻¹, and CV ranging from 10.7 to 25.6%. Lastly, the pooled data set showed intermediate estimations of early-seral vegetation biomass, with R² ranging from 0.91 to 0.98, RMSE from 0.12 to 0.71 Mg ha⁻¹, and CV ranging from 28.9 to 44.9%.

Table 2.7 Parameter estimates and fit statistics of the selected functions to estimate biomass from cover and height for each growth form of early-seral vegetation growing in Western Oregon.

Site	Growth form	Model	Param	Parameter Estimate	SE	R ²	RMSE	CV
CW	Bf	$= a \cdot Cover^b \cdot Height^c$	a	0.050765	0.030871	0.971	0.26	31.0
			b	1.141709	0.140055			
			c	-0.25019	0.202383			
	Sf	$= a \cdot Cover^b \cdot Height^c$	a	0.013492	0.005656	0.979	0.32	23.1
			b	0.907455	0.078963			
			c	0.511214	0.137416			
	F	$= a \cdot Cover^b \cdot Height^c$	a	0.043841	0.012741	0.920	0.36	33.8
			b	0.76563	0.073362			
			c	0.224945	0.050597			
	G	$= a \cdot Cover^b \cdot Height^c$	a	0.01224	0.003973	0.945	0.38	56.3
			b	1.299804	0.095254			
			c	0.085844	0.07546			
B	$= \frac{a}{1 + b \cdot \exp^{-c \cdot C \cdot H}}$	a	1.132271	0.078635	0.923	0.12	33.0	
		b	15.110096	4.215749				
		c	0.520423	0.07042				
S	$= a \cdot Cover^b \cdot Height^c$	a	0.000120887	0.000045629	0.994	0.01	10.8	
		b	1.255475	0.038010				
		c	1.333292	0.111233				
	T	$= a \cdot Cover^b \cdot Height^c$	a	0.029662	0.012457	0.941	0.55	29.3
			b	0.949564	0.110260			
			c	0.241096	0.054032			
ID	Sf	$= a \cdot Cover^b \cdot Height^c$	a	0.004689	0.002191	0.993	0.21	11.7
			b	1.436381	0.048306			
			c	0.407966	0.105510			
	F	$= a \cdot Cover^b \cdot Height^c$	a	0.001469	0.000615	0.971	0.34	23.2
			b	1.021933	0.076051			
			c	0.918408	0.072488			
	G	$= a \cdot Cover^b \cdot Height^c$	a	0.001849	0.000762	0.989	0.24	16.5
			b	0.906781	0.064931			
			c	0.919863	0.107180			
	B	$= a \cdot Cover^b \cdot Height^c$	a	0.002623	0.000539	0.994	0.07	10.7
			b	1.278391	0.038965			
			c	0.400863	0.054239			
T			a	0.006148	0.003314	0.958	0.55	25.6

Pooled	Sf	$= \frac{a \cdot Cover^b \cdot Height^c}{1 + b \cdot \exp^{-c \cdot C \cdot H}}$	b	1.30716	0.129175	0.932	0.71	44.0
			c	0.225179	0.045990			
			a	7.990414	0.588840			
			b	20.53199	5.062166			
	F	$= a \cdot Cover^b \cdot Height^c$	a	0.011322	0.003521	0.911	0.48	39.8
			b	0.95861	0.067395			
			c	0.418276	0.049445			
	G	$= a \cdot Cover^b \cdot Height^c$	a	0.008294	0.002681	0.954	0.40	44.9
			b	1.09882	0.075305			
			c	0.352346	0.057777			
	B	$= a \cdot Cover^b \cdot Height^c$	a	0.004285	0.001250	0.982	0.12	33.5
			b	1.082031	0.038280			
c			0.49964	0.081455				
T	$= a \cdot Cover^b \cdot Height^c$	a	0.016582	0.005320	0.946	0.56	28.9	
		b	1.089033	0.081624				
		c	0.225714	0.035750				

CW: Coastal - Wet site; ID: Inland - Dry site; Pooled: Pooled data set combining both sites; Bf: Bracken fern; Sf: Sword fern; F: Forbs; G: Graminoids; B: Brambles; S: Shrubs; T: Total vegetation; Cover: vegetation ground cover (%); Height: vegetation height (cm); C·H: product of cover and height; SE: standard error; R²: coefficient of determination; RMSE: root mean square error (Mg ha⁻¹); CV: coefficient of variation (%). For all parameter estimates $P < 0.05$.

Focusing on each growth form, it is worth noticing that only sword fern, forbs, graminoids, and total used the same type of function (power; equation 2.8) and predictor variables (cover and height, independently) to estimate biomass at each site. However, when both sites were pooled, sword fern biomass was better predicted using a logistic function (equation 2.3) and C·H as the predictor variable. Brambles used different predicting variables and even different functions across sites.

The values of the parameter estimates of height were generally smaller than the parameter estimates of cover, indicating that the estimations of biomass are mostly explained by the changes in vegetation cover. For example, the ratio of the parameter estimate of cover to the parameter estimate of height ($b:c$) for sword fern was 1.78 and 3.52 for the CW and the ID study sites, respectively. Similarly, for the total, the $b:c$

ratio was 3.94 and 5.80 for the CW and ID sites, respectively. Only shrubs at the CW site and forbs and graminoids at the ID site had a $b:c$ ratio close to 1.

2.3.3 *Model evaluation*

Figure 2.2 shows the graphical evaluation of the vegetation biomass functions selected when using cover (from Table 2.6) or cover and height (from Table 2.7) for each growth form for the pooled data set and show no signs of heteroscedasticity. For a clearer display of the results, each graph has its own X and Y scales, and the Y-axis (residuals) was centered around zero (0). Residuals from the functions that use cover and height (open circles) showed a reduced variability compared to those from functions using only cover (filled circles), as the values are closer to zero (Fig. 2.2).

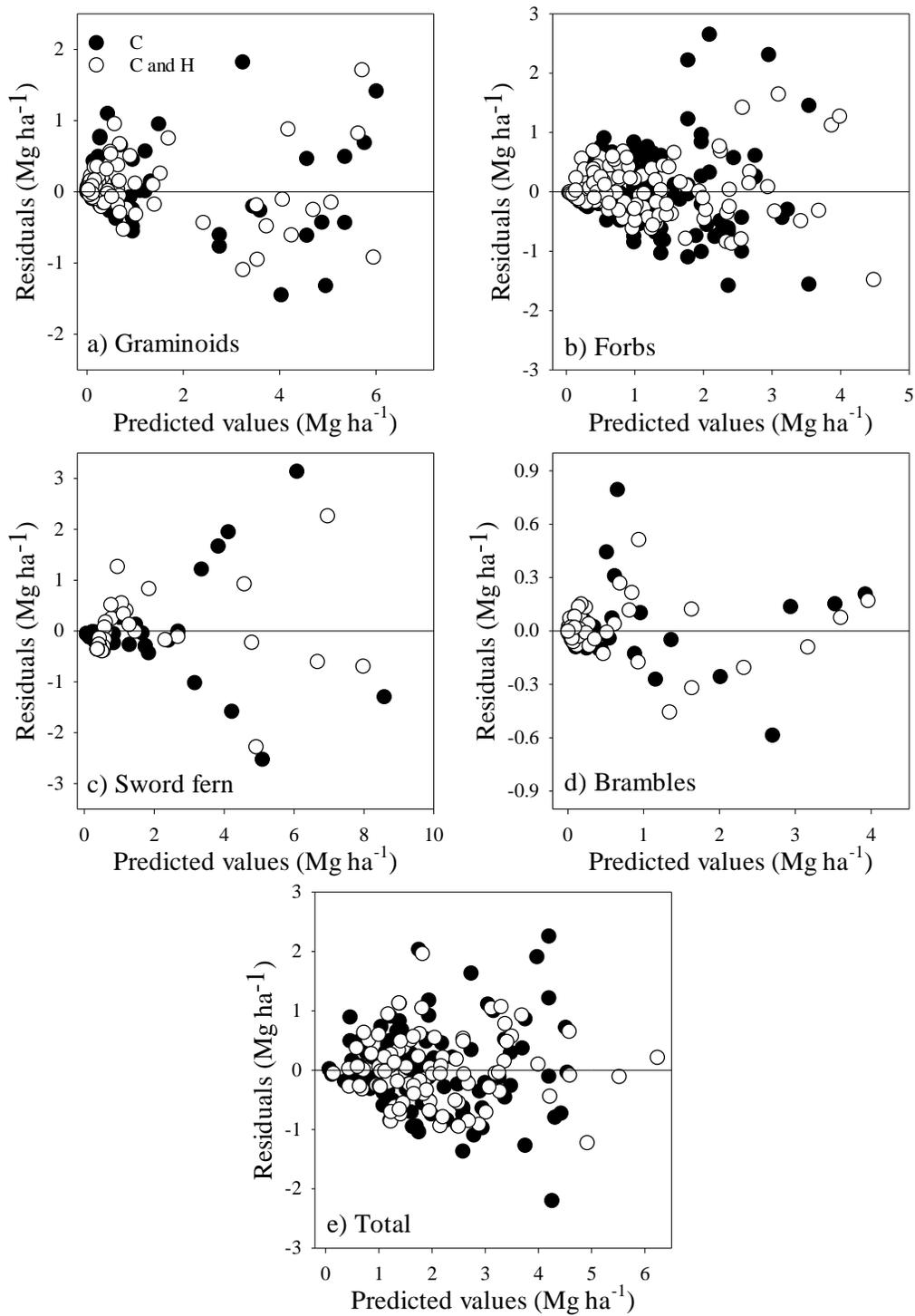


Figure 2.2 Evaluation of the biomass functions selected for a) graminoids, b) forbs, c) ferns, d) brambles, and e) the sum of all growth forms (total) when using only cover (C, filled circle) or cover and height (C and H, open circle) for the pooled data set.

A summary of the model performance test using 10-fold cross validation for the selected models is shown in Table 2.8. There was a good agreement between observed and predicted values of vegetation biomass for all growth forms across sites. Across growth forms and sites, the bias ranged between an 3.9% underestimation to a 5.4% overestimation when using cover as the only predicting variable, and from a 2.6% underestimation to a 3.7% overestimation when using cover and height (combined or as independent variables).

Table 2.8 Summary of model evaluation statistics using 10-fold cross validation for biomass estimations for each growth form of early-seral vegetation growing in Western Oregon.

Site	Growth form	Model	Explanatory Variable(s)	\bar{O}	\bar{P}	RMSE	Bias		
CW	Bf	$= a \cdot X^b$	C	0.85	0.87	0.15	(17.3)	-0.02	(-1.9)
			C and H	1.17	1.18	0.21	(18.1)	-0.01	(-0.9)
	Sf	$= a \cdot X^b$	C	1.37	1.33	0.34	(24.9)	0.05	(3.4)
			C and H	1.37	1.38	0.26	(18.9)	-0.01	(-0.6)
	F	$= a \cdot X^b$	C	1.07	1.07	0.42	(39.0)	-0.01	(-0.7)
			C and H	1.05	1.05	0.33	(31.8)	0.00	(0.0)
	G	$= a \cdot X^b$	C	0.68	0.67	0.25	(36.5)	0.01	(1.4)
			C and H	0.83	0.81	0.27	(32.1)	0.02	(2.7)
	B	$= \frac{a}{1 + b \cdot \exp^{-c \cdot X}}$	C	0.21	0.20	0.28	(133.5)	0.00	(2.1)
			C-H	0.25	0.26	0.11	(44.5)	0.00	(-1.5)
	S	$= a \cdot X^b$	C	0.11	0.11	0.03	(23.8)	0.01	(5.4)
			C and H	0.13	0.12	0.01	(7.5)	0.00	(2.9)
T	$= a \cdot X^b$	C	1.86	1.85	0.66	(35.3)	0.01	(0.5)	
		C and H	1.98	1.98	0.46	(23.3)	0.00	(0.2)	
ID	Sf	$= \frac{a}{1 + b \cdot \exp^{-c \cdot X}}$	C	1.82	1.87	1.34	(73.5)	-0.05	(-2.6)
			C and H	1.82	1.81	0.15	(8.0)	0.01	(0.7)
	F	$= a \cdot X^b$	C	1.45	1.44	0.78	(53.6)	0.00	(0.3)
			C and H	1.45	1.41	0.31	(21.4)	0.04	(2.7)
	G	$= \frac{a}{1 + b \cdot \exp^{-c \cdot X}}$	C	1.44	1.45	0.32	(22.2)	-0.02	(-1.3)
			C and H	1.44	1.40	0.21	(14.3)	0.04	(2.8)
	B	$= a \cdot X^b$	C	0.63	0.61	0.09	(14.2)	0.01	(2.4)
			C and H	0.63	0.61	0.05	(8.6)	0.01	(1.8)

	T	$= a \cdot X^b$	C	2.14	2.14	0.58	(27.2)	0.00	(0.1)
			C and H	2.14	2.15	1.37	(63.8)	-0.01	(-0.5)
Pooled	Sf	$= \frac{a \cdot X^b}{1 + b \cdot \exp^{-c \cdot X}}$	C	1.60	1.67	0.73	(45.2)	-0.06	(-3.9)
			C-H	1.60	1.65	0.54	(33.7)	-0.04	(-2.6)
	F	$= a \cdot X^b$	C	1.20	1.19	0.58	(48.5)	0.00	(0.3)
			C and H	1.22	1.20	0.45	(37.2)	0.02	(1.5)
	G	$= a \cdot X^b$	C	0.89	0.85	0.39	(43.9)	0.04	(4.1)
			C and H	1.04	1.00	0.35	(33.6)	0.04	(3.7)
	B	$= a \cdot X^b$	C	0.37	0.37	0.10	(27.0)	0.00	(-0.8)
			C and H	0.42	0.42	0.10	(23.8)	0.00	(1.0)
	T	$= a \cdot X^b$	C	1.95	1.94	0.67	(34.4)	0.01	(0.7)
			C and H	2.04	2.04	1.12	(54.9)	0.00	(0.1)

CW: Coastal - Wet site; ID: Inland - Dry site; Pooled: Pooled data set combining both sites; Bf: Bracken fern; Sf: Sword fern; F: Forbs; G: Graminoids; B: Brambles; S: Shrubs; T: Total vegetation; C: vegetation ground cover (%); H: vegetation height (cm); C-H: product of cover and height; \bar{O} : mean observed value; \bar{P} : mean predicted value; RMSE: root of mean square error (same unit as observed value); Bias: mean absolute bias (predicted-observed; same unit as observed value). Values in parenthesis are percentages relative to the observed mean.

2.4 Discussion

The vegetation community was never treated with any type of vegetation control and therefore, the sampled vegetation community is representative of the native plant community on seral sites in the PNW. The functions to estimate biomass of early-seral vegetation (classified as ferns, forbs, graminoids, brambles, and shrubs) presented in this study offer a valuable tool for the study and management of these types of vegetation, and could be applicable to any early-seral environment in the region after natural or artificial disturbances, providing a useful tool to researchers and natural resources managers. In an effort to simplify models, general functions combining different growth forms within a site, different sites within a growth form, and a broader function that can be used across sites and growth forms were presented. Depending on the focus of the study or management project, the environmental conditions, the

availability of input data, and the level of accuracy desired, users may select which model to use.

Power functions were used to estimate early-seral vegetation biomass in most cases, at both sites, and for the combined data set. Only brambles at the CW site, sword fern and graminoids at the ID site, and sword fern when both sites were combined, used a different model equation to estimate biomass (logistic in all cases). Furthermore, when power functions were preferred, most of the growth forms used cover and height separately as predicting variables. Only bracken fern and graminoids at the CW site and graminoids and brambles for the pooled data set had slightly higher precision when using cover as the only predictor. Power functions were utilized in previous studies to estimate biomass of similar types of vegetation using diameter (Paul et al., 2016, 2019), diameter and height (Blujdea et al., 2012), or cover (Gilliam & Turrill, 1993; Landuyt et al., 2019) as predicting variables.

Similar to what we found, in a study on temperate deciduous forests across Northwest Europe, Landuyt et al. (2019) used a model based on power functions with vegetation cover and shoot length as independent predictor variables to estimate biomass. On the other hand, Paul et al. (2016) found little improvement when other variables (height, wood density), or site characteristics (weather, stand age, management) were included in a study on managed and natural ecosystems across Australia.

Gilliam and Turrill (1993) analyzed the relationship between cover and biomass of herbaceous species from the Appalachian hardwood forest in West Virginia, U.S. They developed a power equation that utilized data from all species combined (not by growth form) to estimate biomass of individual species that had above 10% cover. For better biomass estimates when species had a low cover (<10%), linear regression for mean herb biomass within each 1-10% cover class was developed. Both equations only included cover as a predicting variable. Ferrari (2013) also found linear relationships between vegetation cover and biomass in a study conducted in the understory of longleaf pine stands in Georgia, U.S. This was the only study that worked at a growth form level, but the nature of their functions and the different environment make the results hard to compare. We could not find studies working on this topic at a growth form level in the PNW. Therefore, it is difficult to compare our results to other studies in this region.

One of the advantages of using cover and height as independent predictor variables is that vegetation biomass on multi-layered vegetation communities can be better estimated. Another advantage is that this allows the height to have a different weight than cover, which does not happen when using the product of cover and height ($C \cdot H$). Cover and height were used independently in 13 of the power functions that we developed. In ten of them, the $b:c$ ratio ranged from 1.78 to 5.80, indicating that cover is more closely related to biomass than height. In the three remaining functions, the $b:c$ ratio ranged between 0.94 and 1.11, indicating a more balanced distribution of cover and height on vegetation biomass prediction. The disadvantage of using two predictor

variables is that more data is needed as input for the biomass equations, thus making it difficult to apply when using cover data obtained from indirect methods such as satellite images, for instance.

When comparing the goodness of fit of the selected functions using only cover (Table 2.6) with the functions that use cover and height (Table 2.7), we found that including height (as an independent variable or multiplied with cover) improved biomass estimations in almost all the cases and reduced the bias (Table 2.8). However, in the case of bracken fern, graminoids, and brambles at the CW site, sword fern at the ID site, and sword fern, graminoids, and brambles for the pooled data set, including height slightly reduced the R^2 or increased the RMSE or the CV.

In our study, when using cover and height as predicting variables, the functions obtained using the pooled data set had an R^2 ranging between 0.91 and 0.98 for the different growth forms. Additionally, when all growth forms were combined at each study site, the developed functions had high coefficients of determination with R^2 values of 0.94, 0.96, and 0.95 for the CW, ID, and pooled data set, respectively. Paul et al. (2016) found less than 1% of prediction efficiency was lost when generalized models were used instead of species-specific models. Gilliam and Turrill (1993) did not find significant differences in the parameters of site-specific biomass equations when compared to those that tested the sites together. Goldberg (1996) wondered whether models could be general enough to be useful over a range of sites and species but specific enough to be useful for making quantitative management recommendations.

The results of this study, Paul et al. (2016), and Gilliam and Turrill (1993) demonstrate that this is possible. Selecting generalized models is a good option for predicting vegetation biomass and does not involve an important trade-off by losing too much precision.

The data utilized to develop our functions were gathered from sites with contrasting climatic conditions (Table 2.1) and during three different years (2017, 2018, and 2019). Our data includes inter-annual climatic variability and its effect on early-seral vegetation biomass allometry, making it useful for different sites and climate conditions within the region.

Indirect methods to analyze macro-scale patterns of vegetation cover can be measured using equipment such as LiDAR or remote-sensing techniques based on NDVI satellite images. Our functions have the potential of estimating early-seral vegetation biomass based on these cover measurements without the need for destructive sampling. Additionally, as vegetation cover and biomass are correlated to leaf area index, our functions could be used in ecological assessments of stand productivity, inter-specific competition dynamics, and water and nutrient use, among other potential applications.

2.5 Conclusions

Assessing vegetation cover and height in the field is an efficient and non-destructive method to estimate vegetation biomass that can be easily applied by natural resources professionals, forest managers, and scientists. Biomass estimations are essential for the

analysis of ecosystem carbon storage, water use, fire load accumulation, wildlife habitat, among other ecosystem attributes of interest. The relationship of cover and biomass varies among vegetation growth forms due to differences in morphology, biomass distribution, and carbon content, but it is comparable within species of the same growth form. Functions to estimate biomass using cover, height, or the combination of the two were developed for different vegetation growth forms (ferns, forbs, graminoids, brambles, and shrubs) and different environments (wet and dry). Generalized models combining all the growth forms and across different environments were also developed and showed acceptable predicting power. The functions presented in this study were developed for early-seral species classified in different growth forms during the first two growing seasons on two recently planted sites in the PNW. Applying our models out of this region, on non-disturbed sites, or for other age-classes should be done with caution.

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3. Early-Seral Vegetation Dynamics Modelling Utilizing Soil and Weather Variables

3.1 Introduction

Vegetation communities vary across time and space, not only in their composition and abundance but also in their growth dynamics (Franklin et al., 2020; Glenn-Lewin & van der Maarel, 1992; van der Maarel, 1988). Predicting seasonal dynamics of vegetation is complex, as they often depend on the initial composition, the influx of new species, and the interactions among them (Balandier et al., 2006), as well as on the disturbance regimes, site resource availability, neighboring communities, and environmental conditions (Franklin et al., 2020). It is important to understand the dynamics of vegetation in Mediterranean climates like the Pacific Northwest (PNW) because one of the main factors limiting reforestation success is competition for soil moisture with early-seral vegetation (Newton & Preest, 1988; Powers & Reynolds, 1999; Wightman et al., 2019), which has been found to be critical during drought periods (Dinger & Rose, 2009). Bassett (1964) concluded that the diameter growth cessation date of loblolly pine seedlings was closely related to the soil moisture and the evaporative demand of the site. With no moisture limitation, the stem diameter could continue to grow until other factors, such as photoperiod, nutrients, or temperature, would cease growth later in the season.

It is important to consider that practices such as forest vegetation management

(FVM) introduce a new disturbance in the forest that could shift the species dominance of a given vegetation community, allowing some species to acquire more resources (such as soil moisture) than before (Dinger & Rose, 2009). In a study carried out in the PNW, Dinger and Rose (2010) found that when competing vegetation was not controlled, the vegetation community was, on average, dominated by brambles (50.9%), ferns (24.6%), forbs (12.1%), and shrubs (10.7%) for the first three years after planting. However, when applying only a pre-planting fall site preparation herbicide application, the abundance of woody species was kept below 15%, allowing forbs to dominate the vegetation community by covering up to 45% of the site at age three years. Balandier et al. (2006) concluded that herbaceous species, such as forbs and graminoids, can access site resources in the upper soil layers more rapidly than woody species, changing the nature of competition and thus inducing negative consequences on soil moisture dynamics. The authors highlighted the necessity to further research the effect of competing vegetation in different environments to adjust FVM treatments and determine when these are justified, as well as the importance of studying long-term vegetation dynamics to capture the varying effect of competition throughout time and space.

In addition to its use in reforestation, modeling vegetation dynamics can be valuable for a variety of ecological applications, such as the assessment and management of carbon sequestration, fire load risk, water balance, wildlife habitat, biodiversity changes, and invasive species. In a carbon sequestration study carried out by Birdsey

(1992), it was assumed that only 1-2% of the carbon found in PNW forests corresponded to understory vegetation due to a lack of models that could accurately estimate vegetation biomass. Utilizing adequate models for early-seral vegetation biomass dynamics would have improved these estimations.

The objective of our study was to model the seasonal dynamics of early-seral vegetation emerging after a harvest operation in two different forestlands in western Oregon. The models were specific for each site, year, vegetation trait (cover, height, and biomass), and growth form (fern, forb, graminoid, bramble, and the total vegetation). In order to extend the scope of inference of the study to different years and/or sites across the region, we developed additional models that include soil and weather variables.

3.2 Materials and Methods

Two study sites located in western Oregon were selected as they exemplified contrasting and representative climatic conditions of forestlands in the PNW. A complete description of the experimental sites and experimental design was previously described in Guevara et al. (2021). Briefly, one site was located near the coast close to Pacific City, OR, (Coastal-Wet site, CW) and was planted in March 2017 with western hemlock seedlings, the second site was located near the Willamette Valley southern fringe close to Yoncalla, OR (Inland-Dry site, ID) and was planted on January 2018 with Douglas-fir seedlings.

On both sites, seedlings were planted at a 3 x 3 m spacing. Treatment plots were 36 x 36 m and measurement plots consisted of 8 rows of trees (24 x 24 m), allowing for two buffer rows on all sides (Figure 3.1). Further details about study design are reported in Chapter 2. Briefly, eight different treatments of FVM were applied at each study site, representing different combinations of pre-planting and post-planting herbicide applications. Each treatment is assigned to one treatment plot, and each treatment is replicated in four blocks at each study site. In this chapter, the analysis only utilizes data from plots that remained unsprayed with herbicides throughout the study to represent the natural conditions of early-seral vegetation communities emerging after a disturbance event. Five 3.14 m² vegetation survey plots were installed inside each measurement plot, centrally located between 4 trees (Figure 3.1). Early seral vegetation cover (%) and height (cm) by growth form (fern, forb, graminoid, and bramble) were measured following the methods of Samuelson and Stokes (2011). Measurements were carried out monthly during the growing season (April to October) for the first three years after seedling planting at the CW site (2017-2019), and the first two years at the ID site (2018-2019).

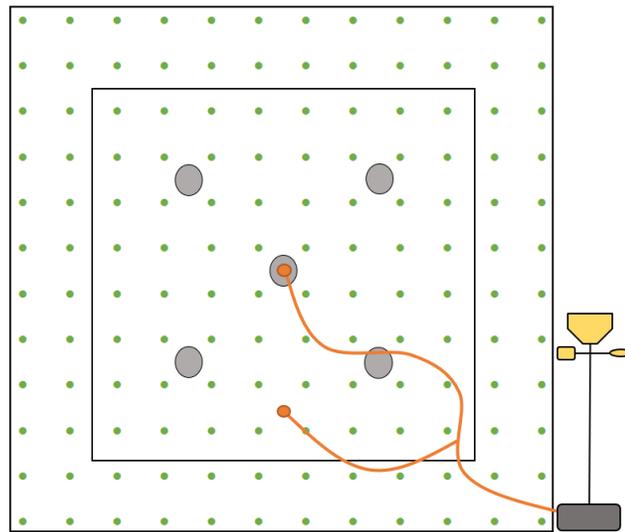


Figure 3.1 Graphical representation of a treatment plot (outside square), measurement plot (inside square), vegetation survey plots (grey circles), planted seedlings (green dots), soil moisture TDR sensors (orange circles), a data logger (grey square), and a weather station (yellow elements). Orange lines represent the communication cables between soil moisture sensors and data logger.

Data from the five vegetation survey plots were averaged to obtain the mean cover and mean height per growth form for each measurement plot. Total vegetation cover was calculated as the summed mean cover of all growth forms found inside a measurement plot and could, therefore, exceed 100% cover. Total vegetation height was calculated as the average of the mean heights of all growth forms found inside a measurement plot. Early-seral vegetation biomass was estimated using the functions developed in Chapter 2 (separate functions for each study site).

At each site, soil samples from the top 20 cm of soil were collected at the center of each measurement plot (close to the central soil moisture sensor location), using cylindrical PVC sampling cores of 425 cm³ (5.2 cm diameter, 20 cm length). All soil samples were oven-dried at 65°C until the weight remained constant (minimum of 72

hours) and fine roots were removed using a 2 mm sieve. Bulk density (BD) was calculated as the soil dry mass of the sieved soil divided by the volume of the sampling cylinder (g cm^{-3}).

To evaluate seasonal dynamics of soil volumetric water content (VWC, $\text{cm}^3 \text{cm}^{-3}$), two time domain reflectometry (TDR) soil moisture sensors (CS650, Campbell Scientific, 30 cm length) were installed in all measurement plots at both study sites. Measurements were taken every 5 minutes, then averaged and recorded every 30 minutes by a data logger (CR300, Campbell Scientific). Due to budget constraints, at the CW site, soil moisture sensors were installed in 3 blocks. At the ID site, soil moisture sensors were installed in all 4 blocks. One data logger was installed at each block. The furthest sensor from the data logger was located at the center of each measurement plot, centrally located between 4 trees (at the same place as the central vegetation survey point). The second sensor was installed at a random location within the measurement plot (Figure 3.1). In one block of each site, an automatic weather station connected to the same data logger as the soil moisture sensors was installed to measure global solar radiation (CS301, Apogee Instruments), air temperature, relative humidity, (HMP60, Vaisala), and precipitation (TE525MM, Texas Electronics). Weather measurements were taken every 30 seconds and averaged every 30 minutes on the data logger. Air temperature ($^{\circ}\text{C}$) data were used as daily maximum (T_{max}), minimum (T_{min}), and mean (T_{mean}). Air relative humidity (RH, %) data were used as a daily average. Global solar radiation (Rad, $\text{MJ m}^{-2} \text{s}^{-1}$) and precipitation (PP, mm) data were used as daily sums.

The following weather and soil indexes were derived from the data collected: potential evapotranspiration (PET); vapor pressure deficit (VPD); water deficit (WD); degree days (DD); and fractional available soil water (FASW), which were calculated using the following equations:

$$PET = k \cdot 0.1651 \cdot 216.7 \cdot N \cdot \left(\frac{e_s}{T_{mean} + 273.3} \right) \quad (\text{eqn 3.1})$$

where PET is the potential evapotranspiration (mm day^{-1}); k is a unitless calibration coefficient set to 1.2 in this study; N is the daytime length (in multiples of 12 hours); e_s is the saturation vapor pressure (mb) at a given temperature; and T_{mean} is the daily mean temperature ($^{\circ}\text{C}$), as proposed by Hamon (1963).

$$e_s = 6.1078 \cdot e^{\left(\frac{17.2693882 \cdot T_{mean}}{T_{mean} + 237.3} \right)} \quad (\text{eqn 3.2})$$

where e_s is the saturation vapor pressure (mb) and T_{mean} is the mean temperature ($^{\circ}\text{C}$), as proposed by Murray (1967).

$$VP = e_s \cdot RH \quad (\text{eqn 3.3})$$

where VP is the daily vapor pressure (mb), e_s is the daily saturation vapor pressure (mb, from equation 3.2), and RH is the daily air relative humidity (%).

$$VPD = e_s - VP \quad (\text{eqn 3.4})$$

where VPD is the daily vapor pressure deficit (mb), e_s is the estimated daily saturation vapor pressure (mb, from equation 3.2), and VP is the daily vapor pressure (mb, from equation 3.3).

$$WD = PET - PP \quad (\text{eqn 3.5})$$

where WD is the daily water deficit (mm day^{-1}) on days where the estimated potential evapotranspiration (PET , from equation 3.1) is higher than the observed precipitation (PP). When PP is larger than PET , $WD = 0$.

$$DD = \frac{T_{max} - 0}{2} - 5, \text{ when } T_{min} < 0^{\circ}\text{C} \quad (\text{eqn 3.6})$$

$$DD = \frac{30 + T_{min}}{2} - 5, \text{ when } T_{max} > 30^{\circ}\text{C} \quad (\text{eqn 3.7})$$

$$DD = \frac{T_{max} + T_{min}}{2} - 5, \text{ otherwise} \quad (\text{eqn 3.8})$$

where DD corresponds to the degree days ($^{\circ}\text{C}$), T_{min} is the daily minimum temperature ($^{\circ}\text{C}$), and T_{max} is the daily maximum temperature ($^{\circ}\text{C}$).

$$FASW = 1 - \frac{DUL - VWC}{DUL - LL} \quad (\text{eqn 3.9})$$

where $FASW$ is the fractional available soil water (unitless), DUL is the drained upper limit of extraction ($\text{cm}^3 \text{ cm}^{-3}$), VWC is the daily volumetric water content ($\text{cm}^3 \text{ cm}^{-3}$), and LL is the lower limit of extraction ($\text{cm}^3 \text{ cm}^{-3}$), as proposed by Ritchie (1981). The upper and lower limits of extraction were determined yearly for each TDR soil moisture sensor.

The Statistical Analysis Software version 9.4 (SAS Institute Inc. Cary, NC, USA) was used for all statistical analyses. To model the observed seasonal dynamics of early-vegetation cover, height, and biomass, non-linear model fitting was conducted using the procedure `proc nlin` for four different models: Gaussian; Reciprocal Quadratic; Steinhart-Hart; and Vapor-Pressure. These models aimed to re-create the observed dynamics using the Julian day of the year (DOY) as the only predicting variable. The

models were fitted for each site, plot, growth form, year, and vegetation trait separately and have the following equation structures:

$$\text{Gaussian} = a \cdot e^{-\left(\frac{(DOY-b)^2}{2 \cdot c^2}\right)} \quad (\text{eqn 3.10})$$

$$\text{Reciprocal Quadratic} = 1 / (a + b \cdot DOY + c \cdot DOY^2) \quad (\text{eqn 3.11})$$

$$\text{Steinhart - Hart} = 1 / (a + b \cdot \ln(DOY) + c \cdot (\ln(DOY))^3) \quad (\text{eqn 3.12})$$

$$\text{Vapor - Pressure} = e^{\left(a + \frac{b}{DOY} + c \cdot \ln(DOY)\right)} \quad (\text{eqn 3.13})$$

where a , b , and c are parameters of the equations and DOY is the Julian day of the year.

Quantitative criteria for model selection included the coefficient of determination (R^2), the Akaike information criterion (AIC), and the percentage of converging and significant parameters (at $\alpha = 0.10$). Qualitative criteria included a combination of good biological meaning for the parameters, simplicity of the function, and that could be used across sites and growth forms. As non-linear model fitting was carried out, an empirical R^2 (Myers, 2000) and AIC (Akaike, 1974) were determined as:

$$R^2 = 1 - \frac{SSE/df_e}{SST/df_t} \quad (\text{eqn 3.14})$$

where SSE and SST are the sum of squares of residuals and total, respectively, and df_e and df_t are the degrees of freedom of error and total, respectively.

$$AIC = -2 \cdot \ln(L) + 2 \cdot k \quad (\text{eqn 3.15})$$

where L is the value of the maximum likelihood and k is the number of independently adjusted parameters.

After selecting the model that better represented the seasonal dynamics of early-seral vegetation, multiple linear regression model fitting was conducted using the procedure `proc reg` to estimate the parameters of the equation (a , b , and c) using weather and soil data and indexes linearized with the natural logarithm as predicting variables. Only parameter estimates that were significant (at $\alpha = 0.10$) were included in this regression. A hypothetical example of the multiple linear regression models' structure to estimate the parameter a for fern cover is shown in equation 3.16.

$$\ln(a_{\text{Fern Cover}}) = a_0 + a_1 \cdot \ln(\text{Temp}) + a_2 \cdot \ln(\text{Rad}) + a_3 \cdot \ln(\text{RH}) \quad (\text{eqn 3.16})$$

where a_0 is the intercept of the equation, a_1 , a_2 , and a_3 are parameter estimates, and Temp , Rad , and RH are the only three environmental variables hypothetically selected by the model.

For both study sites, the observed daily weather and soil data, and the calculated indexes were averaged, summed, or used the maximum or minimum (as it corresponded) by month. Monthly data between April and September were selected to be used as separate input variables. Additional input variables were created by averaging (and/or adding) monthly data, to represent different periods. Such periods were: April to May; April to June; April to July; May to June; May to July; and June to July. The following 22 weather and soil variables and indexes were used: Sum of PP; Maximum T_{max} ; Average T_{max} ; Minimum T_{min} ; Average T_{min} ; Average T_{mean} ;

Maximum RH; Minimum RH; Average RH; Sum of Rad; Average Rad; Sum of PET; Average PET; Sum of WD; Average WD; Sum of DD; Average DD; Sum of VPD; Average VPD; Maximum FASW; Minimum FASW; and Average FASW, for each of the 6 months selected and the 6 periods created, as well as the BD (which does not vary monthly), for a total of 265 possible input variables. All variables were linearized using the natural logarithm and were included in the model fitting procedure for each growth form (fern, forb, graminoid, bramble, and total), vegetation trait (cover, height, and biomass), and parameter (a, b, and c) separately, for a total of 45 different models. The models were fitted independent of site and year, as the variability of these factors (spatial and temporal) are expected to be included in the weather and soil data. The multiple linear regression procedure used a stepwise selection process on which each of the 265 input variables was allowed to enter or leave the model based on their F statistic p -value and variance inflation factor (VIF). We used $P < 0.15$ and $VIF < 10$ as the selection criteria for the input variables to stay in the model (Neter et al., 1996).

The predictive ability of the selected model was evaluated by using 10-fold cross-validation (Neter et al., 1996), splitting the data set randomly into ten subsets with an approximately equal number of observations. To evaluate the goodness-of-fit between the observed and predicted values for each growth form and the root mean square difference (RMSD) were used. Normality and heteroskedasticity were checked using the Shapiro-Wilk and the White tests, respectively. All figures were produced using SigmaPlot version 14 (Systat Software, Inc. San Jose, CA, USA).

In order to evaluate the performance of the Gaussian-Environment model on seasonal growth dynamics (cover, height, and biomass) of each vegetation growth form, the final model selected was run between April 1 (DOY 91) to December 1 (DOY335) for different growing seasons and sites, using soil and weather data of the study sites. Soil data was plot-specific, while weather data was site-specific.

3.3 Results

The dynamics of cover, height, and biomass of early-seral vegetation varied across sites and years but followed a similar growth pattern throughout the growing seasons (Figure 3.2). The seasonal growth and senescence of the vegetation communities followed -in most cases- a bell shape, starting low at the start of the spring, increasing rapidly as the season progressed reaching a peak by mid-summer and decreasing again by the start of the fall due to senescence of annual species (forb and graminoid) or foliage loss by perennial species (fern and bramble).

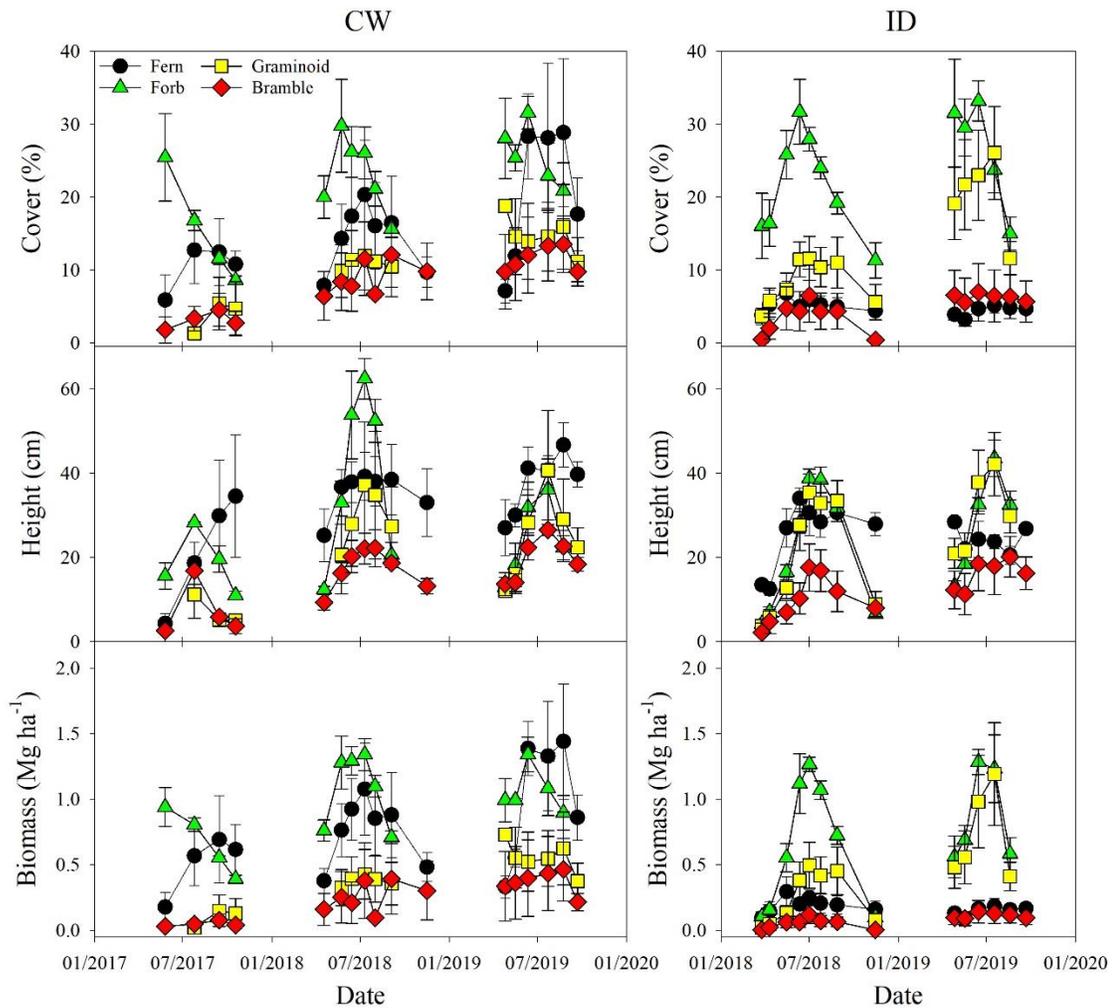


Figure 3.2 Observed dynamics by vegetation trait (cover, height, and biomass) for each growth form (fern, forb, graminoid, and bramble) of early-seral vegetation growing at the Coastal-Wet (CW) and Inland-Dry (ID) sites located in Western Oregon. The X-axis represents the date (month/year).

Vegetation cover was dominated by forb and fern at the CW site, while the ID site was characterized by a prevalence of forb and graminoid over other growth forms. This dominance persisted across successive years, reaching a maximum of 31.6% and 28.9% for forb and fern, respectively, at the CW site at year 3, and a maximum of 33.2% for

forb and 26.1% for graminoid, at the ID site during the second year after seedling establishment (Figure 3.2). Observed dynamics of vegetation height across years and sites indicate no consistent dominance of any growth form over the others, with most of them reaching a maximum around 40 cm, suggesting similar access to sunlight. Only forb at the CW site reached an average maximum height of 62 cm during the second year after seedling establishment (Figure 3.2). Seasonal dynamics of vegetation biomass were similar to those of cover, with forb and fern reaching a maximum of 1.34 and 1.44 Mg ha⁻¹, respectively, at the CW site during the third year, while at the ID site forb and graminoid reached a maximum of 1.28 and 1.19 Mg ha⁻¹, respectively, during the second year after seedling establishment (Figure 3.2).

At the CW site, total vegetation cover during July of growing season 1, 2, and 3 after seedling establishment, reached 35%, 70%, and 79%, respectively, while at the ID site it reached 44% and 61% during growing season 1 and 2, respectively (Figure 3.3). Fern and bramble cover increased consistently over time at the CW and were higher than that observed at the ID site. A similar pattern was observed for graminoid cover at the ID site, increasing over time and being higher than that of the CW site. Forb cover remained relatively constant around 20% across years and sites (Figure 3.3).

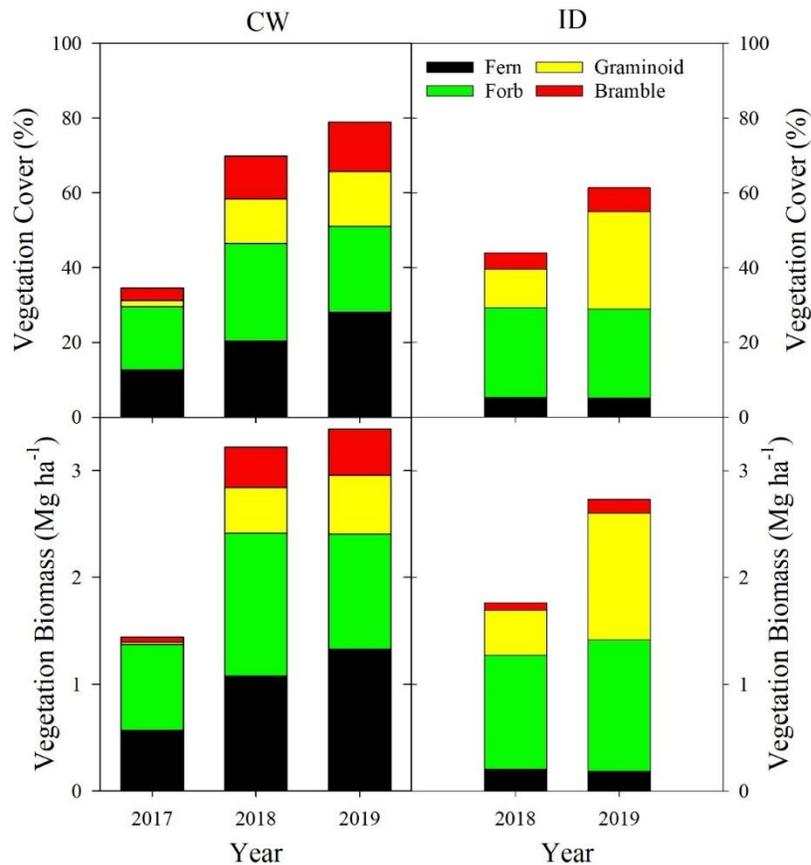


Figure 3.3 Early-seral vegetation cover (%) by growth form (fern, forb, graminoid, and bramble) during July of each year at the Coastal-Wet (CW) and Inland-Dry (ID) sites located in Western Oregon.

The goodness of fit of the four functions tested to model early-seral vegetation dynamics at the CW and ID sites are displayed in Table 3.1. All four models performed well across growth forms and sites, and differences among them were small (R^2 ranged between 0.935 and 0.993 and AIC ranged between -14.6 and 6.7). However, when considering the percentage of cases where model fit converged and the significance of the parameters estimated, the Gaussian model showed better performance across all growth forms and sites. Additionally, when considering the qualitative criteria

(biological meaning and simplicity of the function), the Gaussian model is a better candidate, as the parameter a corresponds to the peak (maximum observed), the parameter b corresponds to the DOY when the maximum (a) was observed, and the parameter c is an indicator of the slope (controls the width of the curve). When considering all these findings, we decided to select the Gaussian model for further steps in this study.

Table 3.1 Comparison of mean R^2 , AIC, and the percentage of models that converged and were significant for each growth form at both study sites located in Western Oregon.

Growth Form	Model	CW			ID		
		R^2	AIC	% conv	R^2	AIC	% conv
Fern	Gaussian	0.963	3.245	74.1%	0.947	-4.702	58.3%
	Reciprocal Quad.	0.959	3.514	48.1%	0.950	-6.125	16.7%
	Steinhart-Hart	0.967	2.552	55.6%	0.962	-7.929	25.0%
	Vapor Pressure	0.969	1.416	55.6%	0.969	-9.664	33.3%
Forb	Gaussian	0.991	-6.664	66.7%	0.982	1.155	95.8%
	Reciprocal Quad.	0.992	-6.890	59.3%	0.981	-0.030	83.3%
	Steinhart-Hart	0.993	-4.755	66.7%	0.982	-0.067	79.2%
	Vapor Pressure	0.988	-2.559	59.3%	0.969	4.772	58.3%
Graminoid	Gaussian	0.974	-5.076	37.5%	0.964	-1.667	91.7%
	Reciprocal Quad.	0.975	-5.903	25.0%	0.962	-0.999	66.7%
	Steinhart-Hart	0.975	-5.677	20.8%	0.954	-0.779	58.3%
	Vapor Pressure	0.972	-4.867	16.7%	0.944	2.337	45.8%
Bramble	Gaussian	0.980	-13.473	70.4%	0.942	-23.389	95.8%
	Reciprocal Quad.	0.983	-14.634	59.3%	0.947	-23.756	58.3%
	Steinhart-Hart	0.982	-13.113	40.7%	0.949	-24.193	54.2%
	Vapor Pressure	0.975	-10.523	18.5%	0.935	-22.558	50.0%
Total	Gaussian	0.986	4.524	77.8%	0.983	3.960	100.0%
	Reciprocal Quad.	0.983	4.360	55.6%	0.982	3.650	87.5%
	Steinhart-Hart	0.987	1.514	63.0%	0.983	2.111	75.0%
	Vapor Pressure	0.982	5.477	59.3%	0.969	6.749	50.0%

R^2 : coefficient of determination; AIC: Akaike Information Criterion; % conv: Percentage of models that converged and were significant at $\alpha = 0.10$; CW: Coastal-Wet site; ID: Inland-Dry site. Values shown represent the average across vegetation traits and years.

Across sites and years, the average parameter estimates and fit statistics from the Gaussian model are shown in Table 3.2 for the different vegetation traits and growth forms. As an example, for total vegetation, maximum cover, height, and biomass averaged 60.5%, 25.7 cm, and 2.62 Mg ha⁻¹, respectively (as indicated by the values of the parameter *a*). These maximum values were reached during DOY 187, 206, and 196, respectively (as indicated by the values of the parameter *b*). The parameter *c* for total vegetation varied between 63.2 and 76.1, indicating a relatively stable curve across vegetation traits. It is worth noticing that among growth forms, forbs reached the highest vegetation cover (31.5%), nearly twice as much as either ferns or graminoids (17.9% and 16.5%, respectively), and almost four times that of brambles (8.6%). Maximum vegetation height for forbs, ferns, and graminoids was similar, averaging 43.8, 40.4, and 38.4 cm, respectively, while brambles, due to their creeping stems, reached a maximum height of only 21.2 cm. Maximum vegetation biomass for forbs was the highest among growth forms, averaging 1.39 Mg ha⁻¹, followed by ferns with 0.97 Mg ha⁻¹, graminoids with 0.70 Mg ha⁻¹, and brambles with 0.23 Mg ha⁻¹. On average, forbs reach their peak of cover, height, and biomass earlier in the season (around DOY 180, June 29th), followed by graminoids (DOY 199, July 18th), ferns (DOY 214, August 2nd), and brambles (DOY 219, August 7th). The coefficient of determination ranged from 0.928 to 0.987 across vegetation traits and growth forms, except for graminoid cover ($R^2 = 0.859$), indicating a good agreement between the observed and predicted values. RMSE ranged between 0.82 (fern biomass) and 3.17 (fern height) across all vegetation traits and growth forms.

Table 3.2 Average parameter estimates, R^2 , and RMSE for each vegetation trait and growth form.

Veg. trait	Growth form	<i>a</i>	<i>b</i>	<i>c</i>	R^2	RMSE
Cover	Fern	17.928020	209.025058	64.108634	0.974	2.31
	Forb	31.475442	163.863199	60.123558	0.986	2.43
	Graminoid	16.507619	193.595225	77.035973	0.859	2.13
	Bramble	8.587958	220.363996	86.963191	0.968	1.10
	Total	60.585459	186.804303	76.144527	0.987	2.86
Height	Fern	40.399056	225.073030	100.505093	0.956	3.17
	Forb	43.884116	198.721458	17.441679	0.986	1.80
	Graminoid	38.399297	205.926349	31.503608	0.965	2.88
	Bramble	21.245473	213.688591	65.281435	0.975	1.15
	Total	25.700605	205.774968	65.376586	0.987	2.67
Biomass	Fern	0.972736	207.618668	74.616438	0.962	0.82
	Forb	1.385522	177.752938	62.792346	0.943	2.35
	Graminoid	0.695154	198.907088	51.946049	0.965	1.19
	Bramble	0.234845	221.849187	67.074356	0.928	0.98
	Total	2.623398	195.959730	63.237929	0.969	2.27

Cover: vegetation ground cover (%); Height: vegetation height (cm); Biomass: above ground vegetation biomass (Mg ha^{-1}); *a*, *b*, and *c*: parameter estimates from the Gaussian model; R^2 : coefficient of determination; RMSE: root of mean square error. Values shown represent the average across sites and years.

A summary of the Gaussian model performance test using 10-fold cross-validation for the different sites, vegetation traits, years, and growth forms is shown in Table 3.3. There was a good agreement between observed and predicted values, as indicated by bias, ranging from a 7.7% underestimation for forb cover to a 1% overestimation for total vegetation biomass at the CW site, and from a 1.3% underestimation for forb height to a 2.1% overestimation for fern height at the ID site.

Table 3.3 Summary of model evaluation statistics for the Gaussian model using 10-fold cross-validation for vegetation dynamics modeling for each growth form of early-seral vegetation growing in Western Oregon at different years.

Site	Veg. trait	Year	Growth Form	\bar{O}	\bar{P}	RMSD		Bias	
CW	Cover	2017	Fern	10.44	10.53	2.15	(20.6)	0.09	(0.9)
			Forb	16.25	15.01	1.34	(8.3)	-1.25	(-7.7)
			Graminoid	3.80	3.80	1.98	(52.2)	0.00	(0.0)
			Bramble	3.22	3.22	0.59	(18.2)	0.00	(0.1)
			Total	32.30	32.49	7.25	(22.5)	0.19	(0.6)
		2018	Fern	14.85	14.85	2.72	(18.3)	0.01	(0.1)
			Forb	23.14	23.12	3.19	(13.8)	-0.02	(-0.1)
			Graminoid	10.97	10.97	0.52	(4.8)	0.00	(0.0)
			Bramble	9.08	9.07	0.99	(10.9)	-0.01	(-0.1)
			Total	59.23	59.23	6.67	(11.3)	0.00	(0.0)
		2019	Fern	20.34	20.43	6.86	(33.7)	0.09	(0.4)
			Forb	25.80	25.22	2.31	(9.0)	-0.58	(-2.3)
			Graminoid	14.34	14.34	1.07	(7.5)	0.00	(0.0)
			Bramble	11.65	11.66	0.48	(4.1)	0.00	(0.0)
			Total	74.22	74.23	6.89	(9.3)	0.01	(0.0)
	Height	2017	Fern	20.69	20.59	5.61	(27.1)	-0.10	(-0.5)
			Forb	19.29	19.21	3.45	(17.9)	-0.08	(-0.4)
			Graminoid	7.13	7.11	1.14	(16.0)	-0.02	(-0.3)
			Bramble	7.65	7.43	3.62	(47.3)	-0.22	(-2.9)
			Total	11.52	11.53	0.17	(1.5)	0.01	(0.1)
2018		Fern	35.61	35.62	3.50	(9.8)	0.01	(0.0)	
		Forb	39.09	38.83	15.02	(38.4)	-0.25	(-0.7)	
		Graminoid	29.57	29.57	4.67	(15.8)	0.00	(0.0)	
		Bramble	17.18	17.17	2.28	(13.3)	-0.01	(-0.1)	
		Total	25.18	25.13	5.52	(21.9)	-0.05	(-0.2)	
2019		Fern	37.52	37.53	4.00	(10.7)	0.01	(0.0)	
		Forb	24.71	24.66	6.13	(24.8)	-0.05	(-0.2)	
		Graminoid	26.33	26.27	6.34	(24.1)	-0.06	(-0.2)	
		Bramble	19.67	19.63	3.43	(17.4)	-0.04	(-0.2)	
		Total	22.49	22.47	3.61	(16.0)	-0.02	(-0.1)	
Biomass	2017	Fern	0.50	0.50	0.08	(15.5)	0.00	(0.3)	
		Forb	0.70	0.70	0.03	(4.8)	0.00	(0.0)	
		Graminoid	0.10	0.01	0.06	(63.5)	-0.10	(-90.0)	
		Bramble	0.05	0.05	0.01	(23.7)	0.00	(-5.2)	

			Total	1.14	1.15	0.16	(14.1)	0.01	(1.0)
		2018	Fern	0.78	0.78	0.09	(11.3)	0.00	(0.1)
			Forb	1.08	1.08	0.06	(5.7)	0.00	(0.0)
			Graminoid	0.38	0.38	0.02	(6.3)	0.00	(0.0)
			Bramble	0.26	0.26	0.03	(13.2)	0.00	(-0.2)
			Total	2.52	2.52	0.17	(6.6)	0.00	(0.0)
		2019	Fern	0.98	0.99	0.20	(20.5)	0.01	(0.5)
			Forb	1.06	1.06	0.06	(5.5)	0.00	(-0.1)
			Graminoid	0.54	0.54	0.05	(10.2)	0.00	(0.1)
			Bramble	0.38	0.38	0.03	(7.7)	0.00	(0.0)
			Total	3.00	3.00	0.24	(8.0)	0.00	(0.0)
ID	Cover	2018	Fern	5.16	5.16	0.95	(18.4)	0.00	(0.0)
			Forb	21.89	21.82	4.59	(21.0)	-0.07	(-0.3)
			Graminoid	8.26	8.26	1.06	(12.8)	0.00	(0.0)
			Bramble	3.82	3.83	0.83	(21.8)	0.01	(0.2)
			Total	36.81	36.79	10.20	(27.7)	-0.03	(-0.1)
		2019	Fern	4.43	4.43	0.37	(8.2)	0.00	(0.1)
			Forb	26.61	26.62	6.82	(25.6)	0.01	(0.0)
			Graminoid	20.31	20.34	4.30	(21.2)	0.04	(0.2)
			Bramble	6.24	6.23	0.40	(6.4)	-0.01	(-0.2)
			Total	55.38	55.40	6.15	(11.1)	0.03	(0.0)
	Height	2018	Fern	25.56	25.64	4.00	(15.6)	0.08	(0.3)
			Forb	21.92	21.63	8.22	(37.5)	-0.28	(-1.3)
			Graminoid	19.80	19.78	8.38	(42.3)	-0.02	(-0.1)
			Bramble	10.29	10.28	2.67	(26.0)	-0.01	(-0.1)
			Total	13.00	12.99	2.73	(21.0)	-0.01	(0.0)
		2019	Fern	23.62	24.12	2.02	(8.5)	0.50	(2.1)
			Forb	28.04	27.85	5.91	(21.1)	-0.19	(-0.7)
			Graminoid	30.44	30.33	6.72	(22.1)	-0.11	(-0.4)
			Bramble	16.23	16.23	2.54	(15.7)	-0.01	(0.0)
			Total	17.32	17.28	2.20	(12.7)	-0.05	(-0.3)
	Biomass	2018	Fern	0.19	0.19	0.05	(24.4)	0.00	(0.2)
			Forb	0.65	0.65	0.14	(21.3)	-0.01	(-1.1)
			Graminoid	0.25	0.25	0.04	(18.0)	0.00	(0.3)
			Bramble	0.06	0.06	0.02	(34.7)	0.00	(-0.2)
			Total	1.04	1.03	0.17	(16.8)	-0.01	(-1.3)
		2019	Fern	0.15	0.15	0.02	(11.2)	0.00	(0.4)
			Forb	0.87	0.86	0.22	(25.4)	-0.01	(-0.8)
			Graminoid	0.72	0.72	0.25	(35.2)	-0.01	(-1.0)

Bramble	0.11	0.11	0.01	(9.7)	0.00	(-0.2)
Total	1.78	1.77	0.41	(23.1)	-0.01	(-0.7)

CW: Coastal - Wet site; ID: Inland - Dry site; Cover: vegetation ground cover (%); Height: vegetation height (cm); Biomass: above ground vegetation biomass (Mg ha^{-1}); \bar{O} : mean observed value; \bar{P} : mean predicted value; RMSD: root of mean square difference (same unit as observed value); Bias: mean absolute bias (predicted-observed; same unit as observed value). Values in parenthesis are percentages relative to the observed mean.

To illustrate the performance of the model, the initial and maximum observed values, along with the parameter a from the Gaussian model are presented in Table 3.4. In general, there is a good agreement between the observed maximum values and the parameter a from the Gaussian model. For instance, the maximum cover from graminoids observed during 2018 was 11.9 and 11.6% at the CW and ID sites, respectively, while the Gaussian model estimated a maximum (parameter a) of 12.0 and 11.4% for the CW and ID sites, respectively.

Table 3.4 Observed initial values, observed maximum, and the parameter a (from the Gaussian model) by vegetation trait for each growth form of early-seral vegetation growing in Western Oregon at different years.

Veg. trait	Year	Growth Form	CW site			ID site		
			Initial	Max	a	Initial	Max	a
Cover (%)	2017	Fern	5.87	12.73	21.81			
		Forb	25.47	25.47	19.60			
		Graminoid	1.30	5.40	5.72			
		Bramble	1.80	4.53	5.66			
		Total	39.27	39.27	41.30			
	2018	Fern	7.90	20.33	18.93	3.80	6.80	5.93
		Forb	20.00	29.80	28.49	16.05	31.70	29.12
		Graminoid	9.87	11.93	12.04	3.65	11.58	11.37
		Bramble	6.43	12.10	11.95	0.47	6.48	5.58
		Total	45.80	70.83	67.01	24.35	49.23	46.16
	2019	Fern	7.13	28.87	32.13	3.90	5.15	5.18

		Forb	28.07	31.60	28.74	31.55	33.20	37.44
		Graminoid	18.80	18.80	15.77	19.13	26.08	25.55
		Bramble	9.77	13.53	15.61	6.53	6.93	7.02
		Total	61.37	87.03	83.87	58.08	65.48	67.20
Height (cm)	2017	Fern	4.33	34.50	55.75			
		Forb	15.60	28.20	28.15			
		Graminoid	11.20	11.20	7.27			
		Bramble	2.60	16.80	22.32			
		Total	6.72	16.24	19.10			
	2018	Fern	25.20	39.20	40.71	13.50	34.00	33.34
		Forb	12.33	62.40	63.07	4.25	38.75	39.70
		Graminoid	20.60	37.13	36.97	3.75	35.35	36.44
		Bramble	9.33	22.20	22.88	2.20	17.60	16.38
		Total	11.93	34.85	33.20	3.73	21.63	21.64
	2019	Fern	27.00	46.67	44.57	28.40	28.40	25.71
		Forb	12.93	36.13	37.55	13.25	43.50	42.37
		Graminoid	12.00	40.60	38.49	20.95	42.10	41.35
		Bramble	13.67	26.53	26.58	12.27	20.15	20.62
		Total	15.55	29.65	29.72	11.65	23.35	22.77
Biomass (Mg ha ⁻¹)	2017	Fern	0.18	0.69	1.31			
		Forb	0.94	0.94	1.90			
		Graminoid	0.02	0.15	0.02			
		Bramble	0.03	0.08	0.03			
		Total	1.28	1.55	1.72			
	2018	Fern	0.38	1.08	1.02	0.09	0.29	0.24
		Forb	0.76	1.34	1.37	0.10	1.27	1.28
		Graminoid	0.33	0.43	0.43	0.02	0.49	0.49
		Bramble	0.16	0.39	0.39	0.00	0.12	0.09
		Total	1.67	3.22	3.01	0.20	2.00	1.90
	2019	Fern	0.33	1.44	1.55	0.13	0.18	0.24
		Forb	0.99	1.34	1.30	0.56	1.28	1.43
		Graminoid	0.73	0.73	0.61	0.48	1.19	1.16
		Bramble	0.34	0.46	0.57	0.10	0.14	0.14
		Total	2.26	3.65	3.63	1.20	2.64	2.75

CW: Coastal - Wet site; ID: Inland - Dry site; Initial: Initial observed value; Max: Maximum observed value; *a*: Parameter estimate *a* from the Gaussian function (modelled maximum); Cover: vegetation ground cover (%); Height: vegetation height (cm); Biomass: above ground vegetation biomass (Mg ha⁻¹). Missing values for cover, height, and biomass at the ID site during 2017 are because the study did not start until 2018 at that site.

The parameter estimates for the 45 multiple regression models that include weather and soil variables are shown in Table 3.5. These models offer the flexibility to utilize weather and soil data from different years and sites, aiming to extend their use to other disturbed sites across the region, and possibly to different temperate forests around the world.

Table 3.5 Multiple regression models for each combination of vegetation trait, growth form, and parameter (from the Gaussian model), displaying the intercept, the weather and soil variables selected, and the corresponding sub-parameter estimates.

Veg. trait	Growth Form	Par.	Intercept	Variable 1*	Estimate	Variable 2*	Estimate	Variable 3*	Estimate	Variable 4*	Estim.	
C	Fe	a	-109.33212	Av. Max RH ₄₋₇	24.65876							
		b	5.63500	Min FASW ₄	0.80784	Min T _{min5}	-0.04620					
		c	7.66505	Max FASW ₈	0.16399	PP ₉	-0.30045	Av. T _{min4-5}	-0.99053			
	Fo	a	2.93868	Av. FASW ₅₋₇	-0.60586							
		b	5.48827	Min FASW ₅	0.71010							
		c	4.29722	Max FASW ₄	-2.72129	Max FASW ₆	-0.62584					
	G	a	1.31901	Av. Min FASW ₅₋₆	-1.46172							
		b	-45.94295	Max RH ₄	11.18421							
		c	-0.82469	Av. T _{min5}	3.10905	Av. FASW ₈	0.33812					
	B	a	-0.30246	Min FASW ₄	-7.77808							
		b	1.64606	Max FASW ₄	1.31444	Av. Rad ₄	1.30745	Av. BD	-0.43114			
		c	1.08649	PP ₄₋₅	0.60307							
T	a	-1.70691	Min FASW ₄	-1.82970	Av. T _{min7}	2.19609						
	b	5.31447	Max FASW ₄	0.46440	Min FASW ₇	0.10032	Av. WD ₄₋₅	0.20234				
	c	-7.86498	Av. T _{min5}	5.78950	Av. FASW ₇	-0.25280						
H	Fe	a	-30.23501	Av. Max RH ₅₋₆	7.46442							
		b	5.66766	Av. FASW ₅	0.79711							
		c	-4.82389	Av. PET ₄	9.52223							
	Fo	a	8.18045	Min RH ₄	-1.09080	Min FASW ₄	1.27648					
		b	4.41369	Min RH ₄	0.11166	Min RH ₈	0.11997					
		c	3.87440	Av. Min FASW ₅₋₆	-0.17052							
	G	a	2.89882	Min FASW ₅	-1.09188							
		b	5.50606	Max FASW ₄	-0.42263	Av. Min FASW ₄₋₆	0.23897					
		c	-28.45315	Max RH ₄	7.09938							
	B	a	2.16672	Min FASW ₄	-3.07678							
		b	5.27241	Max FASW ₄	1.07892							
		c	6.99044	Min RH ₄	-0.73342							

T	a	7.02142	Av. FASW ₄	-4.68938	Max T _{max6}	-1.21960			
	b	2.99977	Max T _{max4}	-0.28758	Av. DD ₆	0.16766	DD ₉	0.50807	
	c	4.30431	Max FASW ₄	-1.67930					
Bi	Fe	a	-112.58693	Max FASW ₄	-8.98137	Av. Max RH ₅₋₇	24.91160		
		b	5.48414	Max FASW ₄	-2.11837	Av. WD ₄	-0.23777		
		c	5.69451	PP ₉	-0.25039	Av. FASW ₈	0.15903		
Fo	a	38.73403	Max RH ₄	-8.38620	Av. Max FASW ₄₋₅	1.39053			
	b	7.24622	Min FASW ₅	0.19773	Av. T _{min6-7}	-0.84102			
	c	5.05903	Max FASW ₄	-2.21399	Av. FASW ₈	0.15646	Av. WD ₄	-1.24218	
G	a	-2.44979	Av. Min FASW ₅₋₆	-1.98205					
	b	-27.44285	Max RH ₄	7.16438	Min FASW ₄	0.25748			
	c	20.71141	Av. FASW ₈	0.26105	PET ₆	-3.21386			
B	a	-5.78754	Min FASW ₄	-12.50031					
	b	2.12614	Max FASW ₄	1.24213	Av. Rad ₄	1.13583	Av. BD	-0.39768	
	c	25.11719	Max FASW ₄	-2.67547	Min FASW ₅	-0.62998	Rad ₄₋₅	-3.07805	
T	a	0.05837	Max FASW ₆	-0.61842	Av. VPD ₉	-0.61376			
	b	5.94892	Max FASW ₈	-0.05226	Av. FASW ₈	0.04354	Av. Min FASW ₄₋₇	0.23081	Rad ₉ -0.07636
	c	0.45115	Max FASW ₈	-0.11506	Av. Min T _{min5-7}	1.85650	Av. FASW ₇	-0.28200	

C: vegetation ground cover (%); H: vegetation height (cm); Bi: vegetation biomass (Mg ha⁻¹); Fe: Fern; Fo: Forb; G: Graminoid; B: Bramble; T: Total vegetation; Min: monthly minimum; Av.: monthly average; Max: monthly maximum; T_{max}: maximum temperature; T_{min}: minimum temperature; T_{mean}: mean temperature; RH: relative humidity; Rad: global solar radiation; PP: precipitation; PET: potential evapotranspiration; VPD: vapor pressure deficit; WD: water deficit; DD: degree days; FASW: fractional available soil water; BD: bulk density. Subscript numbers correspond to the specific month or period (i.e., 4= April; 4-7= from April to July). *: All the weather and soil variables were linearized with the natural logarithm. For example, Av. Max RH₄₋₇ corresponds to ln(Av. Max RH₄₋₇).

Among the 45 models developed (Table 3.5), 19 of them selected only one variable, 17 selected two variables, 8 selected three variables, and only one model selected four variables, for a total of 81 weather and soil variables selected. Out of these 81 total variables, the most widely selected was FASW (44 times; 54.3%), followed by RH (11 times; 13.6%), T_{\min} (7 times; 8.6%), and Rad (4 times; 4.9%). The least selected variables were PP and WD (three times each), T_{\max} , PET, DD, and BD (two times each), and VPD, selected only one time. Only T_{mean} was never selected by the regression models.

As an example, the basic structure of the Gaussian model (same as equation 3.10) to calculate the cover of graminoid at a given site and year would be as follows:

$$\text{Graminoid Cover (\%)} = a \cdot e^{\left(\frac{-(DOY-b)^2}{(2 \cdot c^2)}\right)}$$

however, after incorporating the specific weather and soil variables selected to calculate the parameters a , b , and c (independent of site and year), the equation expands to what we denominated the Gaussian-Environment model. This model replaces the parameters a , b , and c for their respective multiple regression models. The example for graminoid cover, derived from equation 3.16 and incorporating the environmental variables and parameter estimates from Table 3.5, would be as follows:

$$a_{\text{Gram. Cover}} = e^{(a_0 + a_1 \cdot \ln(\text{Av.Min FASW}_{5-6}))} = e^{(1.32 - 1.46 \cdot \ln(\text{Av.Min FASW}_{5-6}))}$$

$$b_{\text{Gram. Cover}} = e^{(b_0 + b_1 \cdot \ln(\text{Max RH}_4))} = e^{(-45.94 + 11.18 \cdot \ln(\text{Max RH}_4))}$$

$$c_{\text{Gram. Cover}} = e^{(c_0 + c_1 \cdot \ln(\text{Av.T}_{\min 5}) + c_2 \cdot \ln(\text{Av.FASW}_8))} = e^{(-0.82 + 3.11 \cdot \ln(\text{Av.T}_{\min 5}) + 0.34 \cdot \ln(\text{Av.FASW}_8))}$$

incorporating all together into one equation would look like the following:

$$\text{Graminoid Cover (\%)} = e^{(a_0 + a_1 \cdot \ln(\text{Av.Min FASW}_{5-6}))} \cdot e^{\left(\frac{-(DOY - e^{(b_0 + b_1 \cdot \ln(\text{Max RH}_4))})^2}{\left(2 \cdot e^{(c_0 + c_1 \cdot \ln(\text{Av.T}_{\min 5}) + c_2 \cdot \ln(\text{Av.FASW}_8))}\right)^2}\right)}$$

where a_0 , b_0 , and c_0 are the estimates of the intercepts for a , b , and c , respectively; a_1 , b_1 , c_1 , and c_2 are the estimates of the weather variables selected for a , b , and both variables selected for c , respectively; $Av. Min FASW_{5-6}$ corresponds to the average of the minimum fractional available soil water observed between May and June; $Max RH_4$ is the maximum relative humidity observed in April; $Av. T_{min5}$ is the average of the minimum temperature observed in May; $Av. FASW_8$ is the average of the fractional available soil water observed in August; DOY is the Julian day of the year.

A comparison of results obtained from the Gaussian model (taken as observed) and those from the Gaussian-Environment model (predicted) are shown in Table 3.6, along with their corresponding model evaluation statistics. There was a good agreement between the parameter estimates from the Gaussian model and those from the Gaussian-Environment model. For example, for cover, bias in the parameter a (maximum vegetation cover during the growing season) ranged between 0.28% (forb) and 1.93% (fern) underestimation, while for height, bias in the parameter a (maximum height during the growing season) ranged between 0.26 cm (total) and 2.09 cm (graminoid) underestimation. For biomass, bias in the parameter a (maximum biomass during the growing season) ranged between 0.01 Mg ha⁻¹ (forb) and 0.09 Mg ha⁻¹ (graminoid) underestimation. The parameter b (day of the year when the maximum is reached) was well predicted, with all the parameters being underestimated by only 0.05 to 0.99 days across vegetation traits and growth forms. On the other hand, the parameter c did not have a consistent trend across vegetation traits, having a bias percent ranging from a 2.2% underestimation to a 22.6% overestimation for cover, from a 1.8% underestimation to a 6.5% overestimation for height (except for an 84.8% and a 218.3% overestimation for the height of graminoid and forb, respectively), and

a good agreement between observed and predicted biomass across growth forms, with a maximum underestimation of 2.2% and negligible overestimation (Table 3.6).

Table 3.6 Summary of model evaluation statistics for the Gaussian-Environment model for each vegetation trait, growth form, and parameters.

Veg. trait	Growth Form	Param	\bar{O}	\bar{P}	RMSD		Bias	
Cover	Fe	a	17.93	16.00	9.48	(52.9)	-1.93	(-10.7)
		b	209.03	208.95	5.56	(2.7)	-0.08	(0.0)
		c	64.11	76.60	35.34	(55.1)	12.49	(19.5)
	Fo	a	31.48	31.20	4.15	(13.2)	-0.28	(-0.9)
		b	163.86	162.87	18.58	(11.3)	-0.99	(-0.6)
		c	60.12	73.71	49.01	(81.5)	13.58	(22.6)
	G	a	16.51	14.93	6.15	(37.2)	-1.58	(-9.6)
		b	193.60	193.11	14.43	(7.5)	-0.49	(-0.3)
		c	77.04	76.66	8.00	(10.4)	-0.38	(-0.5)
	B	a	8.59	6.80	7.50	(87.3)	-1.79	(-20.8)
		b	220.36	219.94	14.92	(6.8)	-0.43	(-0.2)
		c	86.96	85.04	16.76	(19.3)	-1.92	(-2.2)
	T	a	60.59	59.17	13.75	(22.7)	-1.42	(-2.3)
		b	186.80	186.61	8.99	(4.8)	-0.20	(-0.1)
		c	76.14	90.85	59.90	(78.7)	14.70	(19.3)
Height	Fe	a	40.40	40.03	5.44	(13.5)	-0.37	(-0.9)
		b	225.07	224.89	9.15	(4.1)	-0.18	(-0.1)
		c	100.51	98.66	20.64	(20.5)	-1.84	(-1.8)
	Fo	a	43.88	43.31	7.11	(16.2)	-0.57	(-1.3)
		b	198.72	198.67	4.51	(2.3)	-0.05	(0.0)
		c	17.44	55.51	60.37	(346.1)	38.07	(218.3)
	G	a	38.40	36.31	13.88	(36.1)	-2.09	(-5.4)
		b	205.93	205.81	7.07	(3.4)	-0.12	(-0.1)
		c	31.50	58.21	53.92	(171.1)	26.71	(84.8)
	B	a	21.25	20.40	5.71	(26.9)	-0.84	(-4.0)
		b	213.69	213.21	14.36	(6.7)	-0.48	(-0.2)
		c	65.28	69.50	27.47	(42.1)	4.22	(6.5)
	T	a	25.70	25.44	3.80	(14.8)	-0.26	(-1.0)
		b	205.77	205.72	4.60	(2.2)	-0.05	(0.0)
		c	65.38	64.71	9.64	(14.7)	-0.67	(-1.0)
Biomass	Fe	a	0.97	0.92	0.35	(36.1)	-0.06	(-5.7)
		b	207.62	207.33	11.27	(5.4)	-0.29	(-0.1)
		c	74.62	74.45	6.27	(8.4)	-0.17	(-0.2)
	Fo	a	1.39	1.37	0.19	(13.4)	-0.01	(-0.9)
		b	177.75	177.56	8.34	(4.7)	-0.20	(-0.1)

	c	62.79	62.32	6.08	(9.7)	-0.47	(-0.8)
G	a	0.70	0.61	0.31	(44.6)	-0.09	(-12.8)
	b	198.91	198.62	10.87	(5.5)	-0.29	(-0.1)
	c	51.95	51.75	4.46	(8.6)	-0.20	(-0.4)
B	a	0.23	0.16	0.36	(153.7)	-0.08	(-33.9)
	b	221.85	221.43	14.74	(6.6)	-0.42	(-0.2)
	c	67.07	65.62	14.72	(22.0)	-1.46	(-2.2)
T	a	2.62	2.58	0.47	(18.1)	-0.05	(-1.8)
	b	195.96	195.89	5.23	(2.7)	-0.07	(0.0)
	c	63.24	62.95	7.31	(11.6)	-0.29	(-0.5)

Cover: vegetation ground cover (%); Height: vegetation height (cm); Biomass: vegetation biomass (Mg ha^{-1}); Fe: Fern; Fo: Forb; G: Graminoid; B: Bramble; T: Total vegetation; \bar{O} : mean observed value (from Gaussian model); \bar{P} : mean predicted value (from Gaussian-Environment model); RMSD: root of mean square difference (same unit as observed value); Bias: mean absolute bias (predicted-observed; same unit as observed value). Values in parenthesis are percentages relative to the observed mean.

Figure 3.4 shows, for each vegetation trait, the relationship between the observed data and the estimations from the Gaussian (left panel) and the Gaussian-Environment (right panel) models across growth forms. The scatterplots show a good agreement between observed and predicted values. Even though the precision of the Gaussian-Environment model (right panel) is lower than the Gaussian model (left panel), the accuracy of the Gaussian-Environment model is adequate (Table 3.6; Figure 3.4), having R^2 across growth forms, of about 0.54, 0.46, and 0.71, for vegetation cover, height, and biomass, respectively.

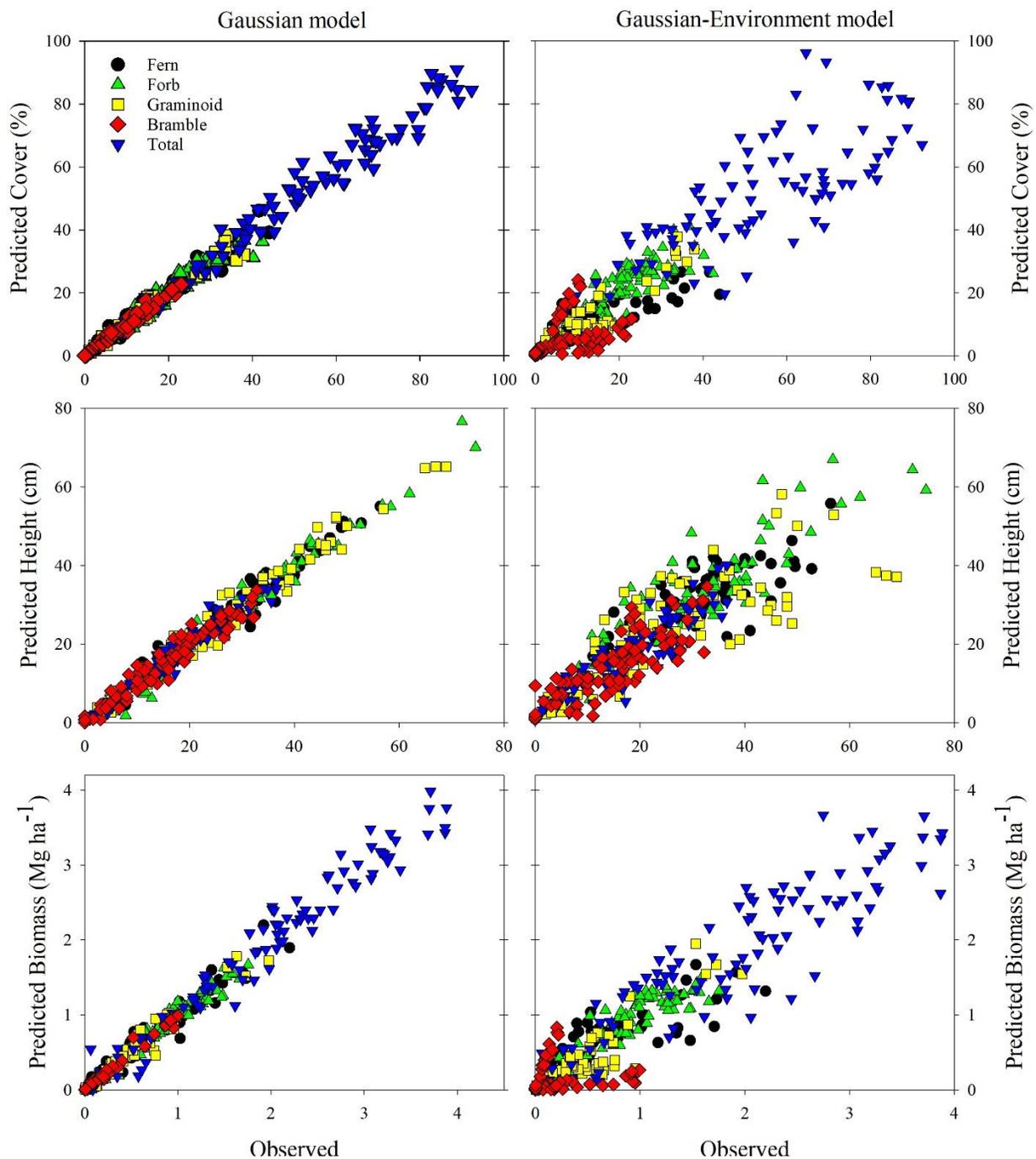


Figure 3.4 Model evaluation of vegetation cover (upper panel), height (center panel), and biomass (bottom panel) models. Observed versus predicted values using the Gaussian model (left) and the Gaussian-Environment model (right), for each growth form (fern, forb, graminoid, and bramble) and the total vegetation.

Figure 3.5 shows a comparison of the seasonal dynamics of early seral vegetation cover observed (symbols) and predicted using the Gaussian-Environment model (lines) across different sites, growing seasons, and vegetation growth forms. A similar analysis performed for vegetation height and biomass is shown in the Appendix. Overall, the Gaussian-Environment model predicts a pattern that agrees with the observed data, as it passes through the points and/or their error bars, in most cases. It is worth noticing that model predictions can capture, for each trait evaluated, different starting points, peaks of vegetation, dates when the peak occurs, and senescence patterns, among different growth forms, years, and sites, as they are influenced by weather and soil conditions that are specific for these years and sites. As an example, the maximum cover for total vegetation and the DOY when that maximum was reached varies among years within the same study site, as well as between study sites: at the CW site, total vegetation cover in 2017 was on average 41.4% (at DOY 188), in 2018 was 61.4% (at DOY 188), and in 2019 it reached 84.9% (at DOY 205), while at the ID site total vegetation cover was 45.4% in 2018 (at DOY 196) and 65.3% in 2019 (at DOY 160, Figure 3.5).

At the CW site, forb and fern dominated the vegetation community across years, as reflected by their maximum vegetation cover of 19.1 and 15.4% in 2017 (at DOY 183 and 228), 22.7 and 17.7% in 2018 (at DOY 163 and 201), and 24.7 and 29.7% in 2019 (at DOY 153 and 198), respectively. During this period, graminoid and bramble cover was much lower, with a maximum of 1.6 and 4.0% in 2017 (at DOY 135 and 245), 10.5 and 10.0% in 2018 (at DOY 190 and 256), and 15.7 and 14.2% in 2019 (at DOY 220 and 209), respectively. A different vegetation dynamic was observed at the ID site, with forb alone dominating the vegetation community during 2018 (maximum cover of 24.2% at DOY 178), but then co-dominating with graminoid during 2019 with

a maximum cover of 23.1 and 27.7% at DOY 156 and 172, for forb and graminoid, respectively. Fern and bramble maximum cover remained low across growing seasons, with 5.1 and 5.4% in 2018 (at DOY 231 and 193), and 5.4 and 6.6% during 2019 (at DOY 225 and 215), respectively.

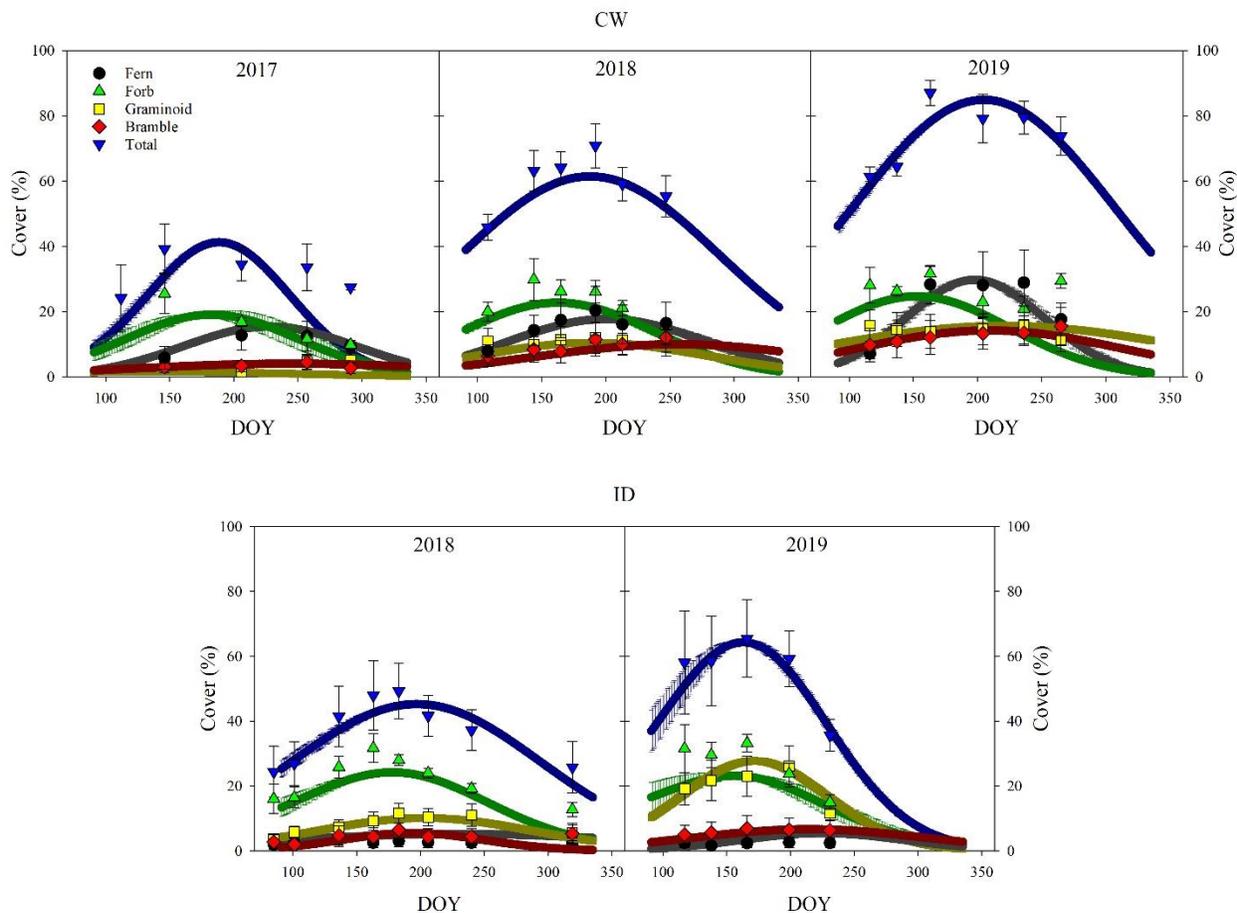


Figure 3.5 Example of model performance for the Gaussian-Environment model. Observed (symbols) and modeled (lines) dynamics of early-seral vegetation cover (%) for different growth forms (fern, forb, graminoid, bramble) and the total vegetation found at the Coastal-Wet (CW) site from 2017 to 2019 (upper panel) and the Inland-Dry (ID) site from 2018 to 2019 (lower panel). Error bars represent standard error across blocks.

3.4 Discussion

The Gaussian model offered site- and year-specific models that proved to accurately represent observed vegetation dynamics (R^2 from 0.86 to 0.99 across vegetation traits and growth forms). After developing the Gaussian-Environment model, the average R^2 across growth forms decreased to 0.54, 0.46, and 0.71, for vegetation cover, height, and biomass, respectively. These models provide adequate estimations of vegetation dynamics and allow the user to extend the scope of inference to different years and sites throughout the region.

Although for this study the Gaussian model stood out for its qualitative and quantitative characteristics, the other functions tested (Reciprocal Quadratic, Steinhart-Hart, and Vapor-Pressure), and perhaps many other functions, could also be used to model the dynamics of early-seral vegetation growth. We recommend testing a model that can generate a second peak since it has been observed that under certain climatic conditions (such as heavy rain during late summer or early fall), annual species that released their seeds during the season are capable of germinating and/or perennial species are able of generating a second growth flush. Moreover, even though most growth forms followed a bell-shaped growth curve, we found that sometimes a specific growth form (at a certain year and site) did not follow this pattern. In these cases, the Gaussian model still predicted a bell-shaped curve, creating some dissonance between the initial or maximum observed values, and those predicted by the Gaussian model. For example, vegetation cover for forb during 2017 at the CW site had an initial cover of 25.5%, which was also the maximum observed value for the season (Figure 3.2), while the Gaussian model estimated an initial value of 16.4% (for the same DOY = 146) and a maximum (parameter a) of 19.6% (at DOY = 185, Table 3.4 and Figure 3.5).

The environmental variable most widely selected by the multiple regression models was soil moisture (expressed as fractional available soil water, FASW) (54.3% of the time), suggesting that soil moisture availability is the main environmental variable driving early-seral vegetation growth in the sites included in this study. This is an important finding because it supports what has been found on different regions of the world (D’Odorico & Porporato, 2006; Roberts et al., 2005; Wang et al., 2009). As D’Odorico et al. (2007) stated: “*Soil moisture is the environmental variable synthesizing the effect of climate, soil, and vegetation on the dynamics of water-limited ecosystems*”. Consequently, we recommend assessing soil moisture throughout the growing season. The other three most selected environmental variables (RH, T_{\min} , and Rad) are directly computed by weather stations. Hence, if the objective is to reduce the amount and variety of input variables for the Gaussian-Environment model, there is no need to derive other indexes from weather data or to assess soil BD. Alternatively, if the objective is to have more input variables than those used in this study, more indexes, months, or periods could be added. We assumed that early-seral vegetation dynamics were determined by the months of active growth (April to September) and/or by periods before the growth peak (April to July), but this can be extended if the vegetation community is affected by weather conditions outside this range.

When FASW was the only variable selected into the model to estimate the parameter a for any vegetation trait and growth form, the parameter estimates were negative, indicating that high values of maximum vegetation productivity (measured as cover, height, or biomass) are related to a higher water depletion and consequently to a low soil moisture availability. When RH was the only variable selected into the model to estimate the parameter a , the parameter estimates were always positive, implying that the higher the relative humidity, the higher the maximum

productivity of vegetation. Only forb height and biomass showed a different pattern, with positive parameter estimates for FASW and negative for RH. When FASW, RH, and Rad were included in the model to estimate the parameter b for any vegetation trait and growth form, the parameter estimates were positive, indicating that a higher soil moisture availability, air relative humidity, or radiation allows vegetation to reach a maximum growth later in the season. Only fern and total vegetation biomass were the exceptions to this case, having a negative parameter estimate for FASW. When the temperature was used to estimate the parameter b , the estimates were negative, meaning that higher temperatures produce maximum productivity of vegetation earlier on the season.

Vegetation biomass dynamics predicted by the Gaussian-Environment model were in better conformity with the observed data ($R^2 = 0.71$) compared to those of cover and height ($R^2 = 0.54$ and 0.46 , respectively). Other studies use vegetation cover and height as inputs to estimate vegetation biomass (e.g. Axmanová et al., 2012; Guevara et al., 2021). This study offers a way to directly estimate vegetation biomass seasonal dynamics by utilizing the Gaussian or Gaussian-Environment models.

Our functions were developed with data collected at sites with contrasting environmental conditions during 2017, 2018, and 2019. Therefore, the observed vegetation dynamics include inter-annual variability, allowing model use on various site conditions within the region. It is advised not to extend the scope of inference from our models outside the timeframe of the study (DOY 85 to 319, namely March 26th to November 15th). Although this study was carried out at recently disturbed sites, the vegetation community was never treated with any type of vegetation control, therefore, we believe that our model could be used in other disturbed sites across the PNW,

as well as on different temperate forests with similar growth forms and environmental conditions. Applying our models out of this region, on non-disturbed sites, or for other ages or growth forms should be done with caution. If the parameter estimates derived from this study do not adjust to other conditions, we recommend replicating the methods presented in this study to create models specific to such situations.

3.5 Conclusion

The dynamics of vegetation cover, height, and biomass varied among growth forms and showed unique patterns due to differences in plant morphology and biomass distribution. These dynamics were modeled based on periodic evaluations carried out at two contrasting sites in western Oregon from 2017 to 2019. The parameters a , b , and c from the Gaussian model allowed for easy comparisons of maximum vegetation growth, the day of the year when the maximum is reached, and the slope of the curve, respectively. When soil and weather variables were included in the Gaussian-Environment model, the different vegetation traits and growth forms were allowed to select the environmental variables better associated with their growth dynamics. Both models provide adequate estimations of vegetation cover, height, and biomass dynamics and allow the user to select a model based on their research objective and data input availability. While the Gaussian model produced accurate estimations, the Gaussian-Environment model forfeited accuracy to extend its use to different sites and years across the region. Generalized models for the total vegetation (combining all the growth forms) were also developed and produced adequate estimations.

This non-destructive method can be easily applied by professionals and scientists from a variety of fields to efficiently estimate vegetation abundance at any given time during the growing

season. Understanding and quantifying vegetation growth dynamics is important and can be used on the assessment of carbon storage, fire load accumulation, water balance, wildlife habitat, biodiversity change, sustainable energy generation, invasive species management, among other ecological applications.

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4. Conclusions

Due to their intrinsic high productivity, Douglas-fir and western hemlock have been used to establish forest plantations across the U.S. Pacific Northwest (PNW). These forests are managed intensively to maximize tree growth, with practices such as Forest Vegetation Management (FVM), which has been shown to enhance forest establishment by reducing the competition between the planted seedlings and early-seral vegetation.

Some of the benefits of applying FVM methods have been widely reported in the literature and include: an increase in tree growth and survival; an increase in soil moisture availability; a decrease in seedling xylem water stress; a higher leaf area index; a higher nutrient use efficiency. However, the suppressing effect is temporary and early-seral vegetation might regenerate soon, even during the same year the treatment was applied. Additionally, the response to FVM often depends on the target tree species, vegetation composition, weather conditions, site quality, stand age, resource availability, the timing of application, and (or) silvicultural treatment. Having these multiple factors interacting, forest managers need to better understand the growth and dynamics of competing vegetation, which may allow us to anticipate their effect on site resources, as well as on seedling growth and survival during the first years after planting.

To advance in this direction, I surveyed and quantified early-seral vegetation cover, height, and biomass, and characterized the seasonal fluctuations in abundance during three years at a Coastal-Wet (CW) site, and two years at an Inland-Dry (ID) site in Western Oregon.

In Chapter 2, functions to estimate early-seral vegetation biomass using vegetation cover, height, or a combination of the two were developed for different growth forms (ferns, forbs,

graminoids, brambles, and shrubs) and environments (wet and dry). Six different linear and non-linear regression models were tested using cover or the product of cover and height as the only predicting variable, and two additional models tested the use of cover and height as independent variables. Generalized models combining all the growth forms (total) and across sites (pooled dataset) were also developed and showed adequate predicting power. It was observed that due to weather and soil differences between sites, the CW site had on average a higher vegetation cover of Sword fern than the ID site (20.4% vs 16.7%), while the latter had a higher cover of forbs, graminoids, and brambles (35.6%, 30.7%, and 18.2% vs 27.4%, 14.1%, and 7.4%, respectively). Furthermore, the estimated vegetation biomass was higher at the ID site for all the growth forms. The average vegetation biomass was estimated to range between 0.1 Mg ha⁻¹ for shrubs at the CW site and 1.8 Mg ha⁻¹ for Sword fern at the ID site (see Table 2.2).

The hypothesis that equations including both vegetation cover and height will better estimate early-seral vegetation biomass across growth forms and sites was partially accepted, as most growth forms were better estimated using cover and height. However, some growth forms (graminoids and bracken fern at the CW site, and graminoids and brambles for the pooled data set) were slightly better estimated using only cover.

The presented equations offer an efficient and non-destructive method for natural resources professionals, forest managers, and scientists to estimate vegetation biomass from simple field or aerial measurements of cover and height. Depending on the objectives and availability of input data, users may select which model to apply. Biomass estimations are essential for the analysis of ecosystem carbon storage, water use, fire load accumulation, wildlife habitat, among other ecosystem traits of interest. The functions presented in this study were developed for early-seral

species classified in different growth forms during the first two growing seasons on two recently planted sites in the PNW. Applying our models out of this region, on non-disturbed sites, or for other age-classes should be done with caution. Chapter 2 was already published in the peer-reviewed journal *Forests* (2021, 12(9), 1272; <https://doi.org/10.3390/f12091272>).

In Chapter 3, we used periodic measurements of vegetation cover and height dynamics on the same study sites used in Chapter 2. Using the equations reported in Chapter 2, I estimated biomass using direct measurements of vegetation cover and height at each study site and measurement time. The observed dynamics of vegetation cover, height, and biomass were different across growth forms (ferns, forbs, graminoids, and brambles) and for the total vegetation due to differences in plant morphology and biomass distribution. Vegetation composition varied across sites as demonstrated by vegetation cover during the summer. At the CW site, total vegetation cover during July of growing season 1, 2, and 3 after seedling establishment, reached 35%, 70%, and 79%, respectively, while at the ID site it reached 44% and 61% during growing season 1 and 2, respectively. Fern and bramble cover increased consistently over time at the CW and were higher than that observed at the ID site. A similar pattern was observed for graminoid cover at the ID site, increasing over time and being higher than that of the CW site. Forb cover remained relatively constant around 20% across years and sites (see Figure 3.3).

Four different non-linear models were tested to characterize these dynamics using the Julian day of the year as the predicting variable. The Gaussian model was found to better represent the observed data and the parameters of the equation offered a straightforward interpretation. Parameters a , b , and c represented the maximum abundance (asymptote), the day when the maximum was reached, and the slope of the increment, respectively. The analyses proceeded by

developing multiple regression models that estimated these parameters using different weather and soil variables such as; rainfall, potential evapotranspiration, water deficit, minimum, maximum, and mean air temperatures, degree days, vapor pressure deficit, solar radiation, air relative humidity, soil moisture, and soil bulk density. These environmental variables were presented by month (between April and September) or by period (6 different periods combining months) for a total of 265 possible input variables. When soil and weather variables were included in the Gaussian-Environment model, the different vegetation traits and growth forms were allowed to select the environmental variables better associated with their growth dynamics. Both the Gaussian and Gaussian-Environment models provided adequate estimations of vegetation cover, height, and biomass dynamics, allowing the user to select a model based on their research objective and data input availability. While the Gaussian model produced accurate estimations, the Gaussian-Environment model forfeited accuracy to extend its use to different sites and years across the region.

The hypothesis that early-seral vegetation cover, height, and biomass dynamics will differ across growth forms and that the models will select different weather and soil variables for their estimations was supported by our results. Different environmental variables were selected for each combination of vegetation traits (cover, height, and biomass) and growth forms. Out of the 81 environmental variables selected by the multiple regression models, the most widely selected was FASW (44 times; 54.3%), followed by RH (11 times; 13.6%), T_{\min} (7 times; 8.6%), and Rad (4 times; 4.9%). The least selected variables were PP and WD (three times each), T_{\max} , PET, DD, and BD (two times each), and VPD, selected only one time. Only T_{mean} was never selected by the regression models. Chapter 3 is in process for submission in a peer-reviewed international journal.

These non-destructive methods can be easily applied by professionals and scientists from a variety of fields to efficiently estimate vegetation abundance at any given time during the growing season. Understanding and quantifying vegetation growth dynamics is important and can be used on the assessment of carbon storage, fire load accumulation, water balance, wildlife habitat, biodiversity change, sustainable energy generation, invasive species management, among other ecological applications.

These studies were carried out as part of the Competition and Site Interactions Experiment (CoSInE) at two contrasting sites managed by the Vegetation Management Research Cooperative (VMRC) at Oregon State University. As a part of my Ph.D. work, we are advancing the CoSInE project by quantifying the water use by the different growth forms and evaluate their effect on soil moisture availability and conifer seedling physiology. I will develop a model including the vegetation biomass dynamics functions developed in this thesis as a basis to estimate soil water depletion, xylem predawn and midday water potential, stem hydraulic conductivity, and seedling mortality.

5. References

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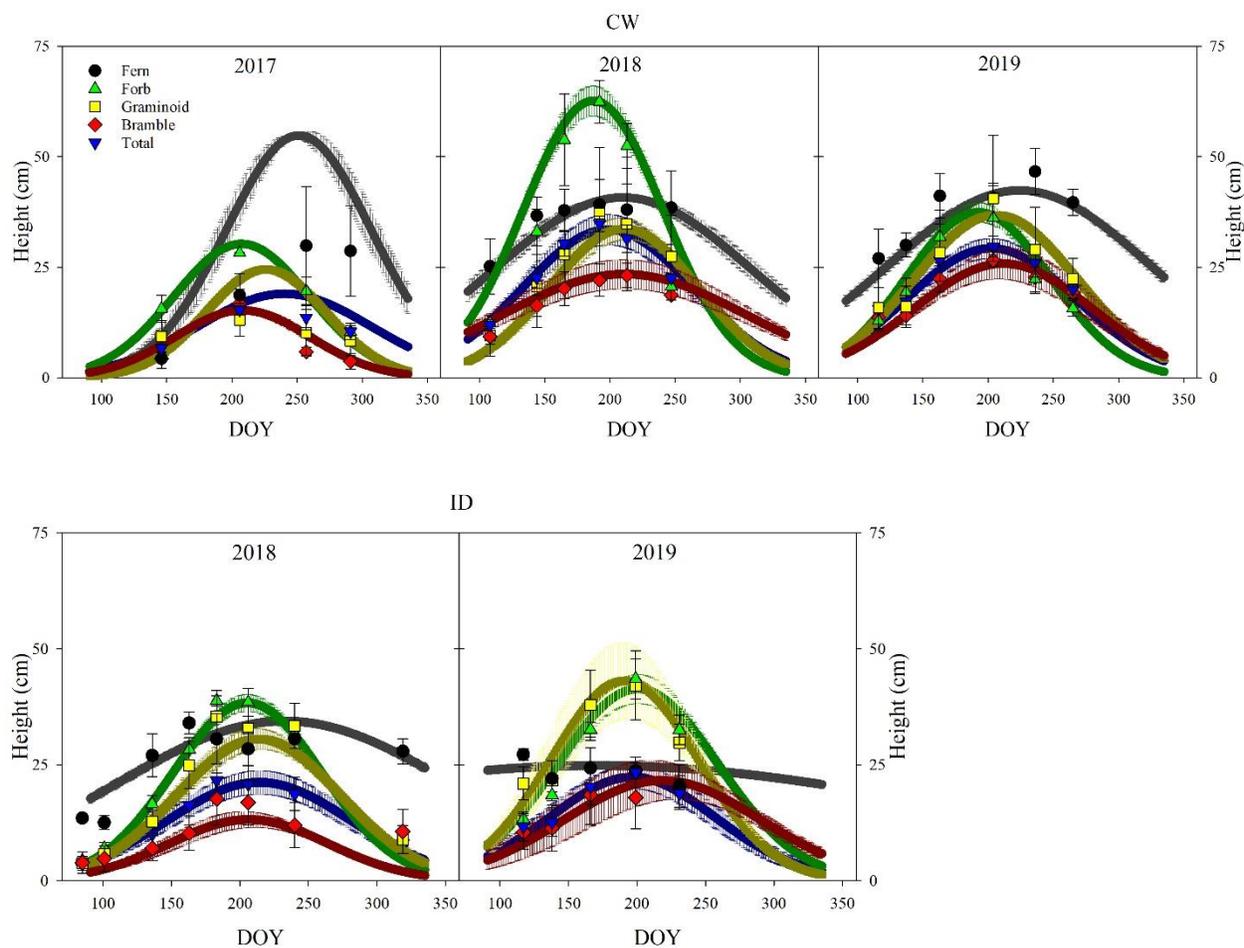
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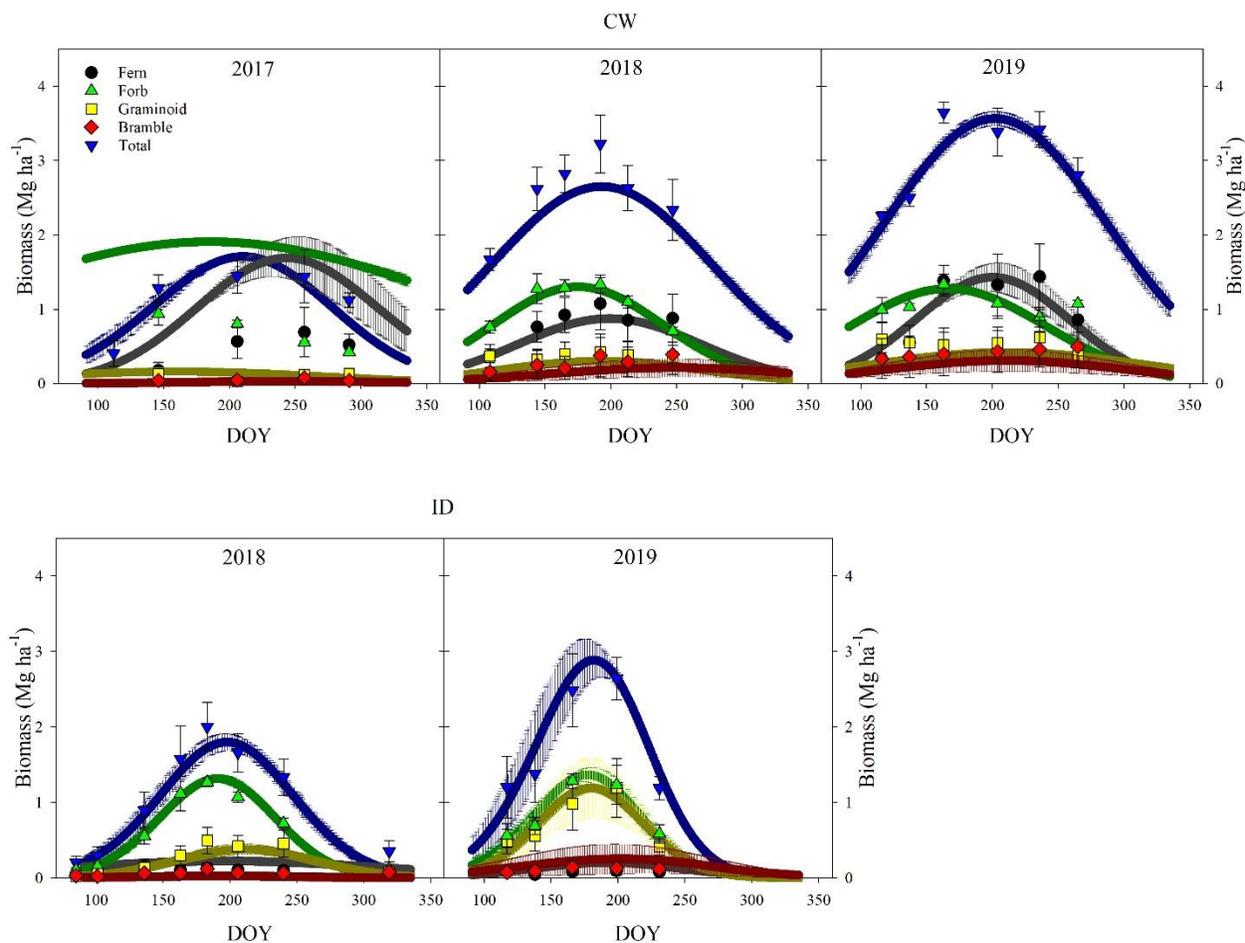
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6. Appendix



Appendix Figure 3.1. Example of model performance for the Gaussian-Environment model. Observed (symbols) and modeled (lines) dynamics of vegetation height (cm) for different growth forms (fern, forb, graminoid, bramble) and the total vegetation found at the Coastal-Wet (CW) site from 2017 to 2019 (upper panel) and the Inland-Dry (ID) site from 2018 to 2019 (lower panel). Error bars represent standard error across blocks.



Appendix Figure 3.2. Example of model performance for the Gaussian-Environment model. Observed (symbols) and modeled (lines) dynamics of vegetation biomass (Mg ha⁻¹) for different growth forms (fern, forb, graminoid, bramble) and the total vegetation found at the Coastal-Wet (CW) site from 2017 to 2019 (upper panel) and the Inland-Dry (ID) site from 2018 to 2019 (lower panel). Error bars represent standard error across blocks.