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Title: The Population Dynamics and Growth of Salmonberry (Rubus spectabilis) and Thimbleberry (Rubus parviflorus)

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Salmonberry (Rubus spectabilis) and thimbleberry (Rubus parviflorus) are clonal shrub species common to reforestation sites in the Oregon Coast Range. These species have economic importance, because they reduce conifer seedling growth and survival. A population modeling approach was used to facilitate study of the biology of these species and to assess management practices. A generic Rubus transition matrix model was developed from the literature and used to generate hypotheses and focus research on demographic processes governing population dynamics. Sensitivity analysis on the model indicated that transition from basal buds to sprouts, shoot survival, sprout transition to mature vegetative shoots, and basal bud production on mature vegetative shoots were important processes influencing population growth. High basal bud production potential and sprout survival and growth relative to seedlings indicated that populations should be

dominated by sprouts rather than seedlings. Density-biomass relationships conformed to the constant final yield theory. The influence of density on demographic processes was inconsistent over time and sites indicating that the intensity of competition is not constant. Therefore, density-dependence is a dynamic population growth regulating mechanism. The model was refined by incorporating the species specific influence of phenology, environments at different sites, and intraspecific density on demographic processes. Population simulations were compared with observations on planted and adjacent wild populations for the first three growing seasons. An average of 71% of the variation in observed planted population and 81% in wild population shoot dynamics was accounted for by the simulations. Canopy cover and height growth were simulated in the model as a function of density. Simulations of a herbicide treatment and manual cutting demonstrated the utility of the model for evaluating salmonberry and thimbleberry management tactics.

The Population Dynamics and Growth of Salmonberry (*Rubus spectabilis*) and Thimbleberry (*Rubus parviflorus*)

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THE POPULATION DYNAMICS AND GROWTH OF SALMONBERRY (*RUBUS SPECTABILIS*) AND THIMBLEBERRY (*RUBUS PARVIFLORUS*)

CHAPTER 1

INTRODUCTION

Perspective

My applied weed science experience coupled with training in basic biology and ecology has given me a broad perspective of the weed science discipline. My research goals have developed an equally broad perspective with a unifying theme that stresses the importance of creating a fundamental base of biological information on crop/weed systems. This information can be used for the identification of biological thresholds and the development of economic and environmentally sound weed control practices.

Factors that regulate the size and vigor of weed populations must be understood to evaluate weed control procedures for biological and cost effectiveness (Mortimer, 1983). This understanding can be achieved by studying the dynamics of weed populations (Mortimer, 1983; Sagar and Mortimer, 1976), which then become the basis for planning weed control strategies (Mortimer, 1983). Populations are a logical reference, because it is weed populations which ultimately dictate crop response and provide a basis for

determining weed thresholds. Weed research has traditionally concentrated on weed population response to control treatments. An alternative approach is to understand weed population dynamics before intervention. This approach should increase the effectiveness of tools used to control weeds and increases the potential for discovering new management techniques. Narrowly defining the problems of agriculture and forestry (e.g. response of weeds to treatments), inadvertently narrows their solutions (Jackson, 1984).

The research presented in this thesis is the result of a challenge to gather autecological information on salmonberry Rubus spectabilis and thimbleberry Rubus parviflorus so that the information could be used to develop control strategies. Salmonberry and thimbleberry are among the most important shrub species that interfere with conifer regeneration in the western Oregon Coast Range (Allen, 1969; Ruth, 1956). Most of the research associated with salmonberry and thimbleberry has involved control with herbicides (Krygier and Ruth, 1961; Madison and Freed, 1962; Newton and Roberts, 1977). The autecology of salmonberry in the northern Cascade Mountains was studied by Barber (1978) and Tappeiner et al. (1990) studied salmonberry clone development in the Oregon Coast Range. There are no studies that have addressed the life histories or population dynamics of salmonberry or thimbleberry.

Study approach

I employed a population modeling approach (Maxwell et al., 1988) to study the biology of salmonberry and thimbleberry. This approach allowed existing information, and new information from a set of separate experiments, to be integrated into a population model that could be used to develop control strategies. The thrust of the modeling approach is to systematically identify processes that influence weed population growth. After identifying the important processes, experiments are designed to determine the mechanisms which regulate the processes and how those mechanisms may be manipulated to reduce the adverse impacts of weeds.

Research objectives

The first objective was to develop a generic Rubus population simulation model from existing information in the literature (Chapter 2). This initial model was used to generate hypotheses and determine objectives related to the establishment and dynamics of salmonberry and thimbleberry populations.

Establishment of shrub populations following logging is determined by the success of regenerating plants from sexual (seed) and asexual (basal bud) propagules. The model was used to identify demographic processes important to establishment of populations from each mode of reproduction. The second objective was to determine the

relative importance of seed and vegetative reproduction in the establishment of salmonberry and thimbleberry populations (Chapter 3), and to utilize the information about the processes important to each mode of reproduction to refine the model.

Sensitivty analysis (Maxwell et al., 1988) on the initial model identified demographic processes associated with vegetative reproduction as most important in regulating population growth. The third objective was to determine factors that influence the important processes and to quantify the influence of each factor. Phenology stage, different environments associated with different sites, and interference were identified as factors that may act on the important demographic processes. Therefore, experiments were conducted to quantify the influence of phenology, site and intraspecific density on simulation model parameters associated with the important demographic processes (Chapter 4).

The final objective was to incorporate information from the experiments addressing the previous objectives into the simulation model, then verify and validate the model, and use it to suggest management tactics (Chapter 5).

LITERATURE REVIEW

Theory of plant population dynamics

The application of ecological theory in weed science

is to understand plant population dynamics in agricultural and forest production systems. The underlying premise is that vegetation management can be improved by understanding the population biology of a weed species. In my study, the application of biological information about the population dynamics of salmonberry and thimbleberry was developed for management of these species on forest regeneration sites. A brief review of basic population dynamics theory including discussions on population models and density-dependent and independent population regulation follows.

A plant population is a set of plants of the same species that occur within a defined geographic region. The ecology of a plant population refers to the interactions among individuals of the population and their environment (Silvertown, 1982). The study of plant population dynamics involves population changes over time.

Plant populations quantified with abundance measurements typically have an exponential growth phase after establishment which is followed by an asymptotic phase (Firbank and Watkinson, 1985; Silvertown, 1982) (Figure 1.1). The asymptote is the response of the population to the constraints of a finite resource pool (carrying capacity = K). At carrying capacity the population may be considered at equilibrium at one scale (Figure 1.1). However, there can be other sets of dynamics at a more refined scale that are created by discontinuous

flow through life history stages, and the processes of self-thinning (Aikman and Watkinson, 1980), reproductive episodes, and recruitment (Kareiva, 1989; May and Oster, 1976).

Demography is the study of population changes, and the causes of the changes throughout a life cycle (Silvertown, 1982). In plant population ecology, demography is usually the study of birth (germination and sprouting), mortality, and fecundity (seed and bud production) processes that govern population dynamics. An idealized plant life history is illustrated in Figure 1.2. Seed in the seed bank pass through an "environmental sieve" to germinate and become seedlings (Harper, 1977). The sieve is the mosaic of environmental conditions coupled with the fitness of plants which allows some to survive and grow, while others die. Different constraints influence plant development as the life cycle progresses. Thus plants must pass through an environmental sieve in the transition to each new life history stage.

Seeds which simultaneously germinate form a cohort of seedlings. Some of these seedlings then become mature reproductive plants (Figure 1.2). This process is called recruitment. A plant originating from seed is a genet, all parts have the same genotype (Harper and White, 1974; Silvertown, 1982). Alternatively, recruitment can occur through the production of vegetative daughter plants. These

potentially independent morphological units are called ramets (Sarukhan and Harper, 1973). Ramets produced from the same parent constitute a clone (Silvertown, 1982). Seed is produced on mature plants and is dispersed (seed rain) back to the seed bank (Figure 1.2).

In this study of salmonberry and thimbleberry, special definitions for ramet and genet were adapted for field data collection. A genet was defined as any independently growing individual plant, regardless of parentage, that is not connected to other individuals. Thus a genet could consist of several interconnected ramets and a ramet could become a new genet if interconnecting tissue degenerated. A ramet in this study is a single aerial shoot arising from the base of a genet below the litter. Thus, single shoots were considered functionally independent units arising from vegetative reproduction (Hutchings, 1979; Sarukhan and Harper, 1973).

Population dynamics models

Exponential and logistic models have been developed to describe population growth through time (Lotka, 1925). Improvements in these models came with the recognition that change in population size is not a function of the population size alone, but also depends on the structure of the population (Lotka, 1925). The population structure is the number of individuals that belong to different specified categories such as age groups or developmental

and functional stages (Sarukhan and Gadgil, 1974). In most plant populations, reproduction is confined to one part of the year and to plants which have reached a minimum age or size.

Projection matrix models are an alternative to the exponential and logistic models of population dynamics. These models divide a population into age or size classes which have different rates of germination, reproduction, and mortality (Abrahamson, 1980; Hubbell and Werner, 1979; Silvertown, 1982; Werner and Caswell, 1977). Age structure has been incorporated into population dynamic models as age or stage class projection matrices (Leslie, 1945; Maxwell et al., 1988; Mortimer, 1983; Sarukan and Gadgil, 1974). Age structure can have stabilizing or destabilizing effects on population dynamics. Destablization may occur, because age structure introduces time delays into the negative feedbacks that dampen population growth (Kareiva, 1989). Alternatively, age structure can stabilize a population by distributing perturbations over several different cohorts (Hastings, 1984; Levin and Goodyear, 1980). Projection matrix models provide insight into population dynamics which cannot be obtained from continuous models of population growth (Silvertown, 1982). For example, Sarukhan and Gadgil (1974) with an extension of the matrix method to include vegetative reproduction, revealed relationships between the degree of stability of the population and the

reliance of the species on seed versus vegetative reproduction. The attributes and historical application of the projection matrix approach indicated that it could be applied for the study of salmonberry and thimbleberry population dynamics.

Density-dependent population regulation

Ecological theory, supported by numerous empirical results, has established that plant density plays an important role in regulating population growth and determining equilibrium dynamics (Hassell and May, 1985). The density dependence of growth (e.g. reciprocal yield law) and mortality (e.g. -3/2 power law) have been demonstrated in numerous experiments with annual plants and trees (Shinozaki and Kira, 1956; Watkinson, 1980; White, 1980; White and Harper, 1970; Yoda et al., 1963). White and Harper (1970) and White (1980) also indicated that density biomass relationships in populations hold for components of plant yield as well as for whole plants. However, few experiments have examined population density responses in clonal species (Barkham, 1980; Hutchings, 1979), because of problems associated with the study of these species, e.g. overlapping generations (Sagar and Mortimer, 1976), difficulty of defining the individual plant (Cook, 1985), and both vegetative and seed reproduction (Thomas and Dale, 1975).

Density-dependent affects act differently on different

age or size classes (Westoby, 1984; White, 1985). A study of the density influence on specific demographic processes at different age or size classes could reveal processes that are particularly sensitive to competition. Sensitive demographic processes may then be exploited for artificial population regulation, i.e. management.

Population simulation models which incorporate the influence of density on demographic processes have been useful for studying population dynamics (Maxwell et al., 1988; Vandermeer, 1984). Density-dependence, which can be internally incorporated into models as a feedback mechanism has been most widely explored as a population growth regulation mechanism. A basic knowledge of the effect of density (intraspecific and interspecific competition) on demography of salmonberry and thimbleberry is important to develop population simulation models and subsequent management strategies.

Density-independent population regulation

Plant populations can be regulated by mechanisms which are not density-dependent. These mechanisms can be grouped into two classes of events: (1) cyclic (e.g. light and temperature changes with seasons), and (2) stochastic (e.g. predation, fire, etc.). Density-independent mechanisms are external to the population and, therefore, difficult to include in a population model without additional input information. Complexity of the model also increases.

Salmonberry and thimbleberry description

Salmonberry and thimbleberry are shrubs that grow throughout the Coast Range of western Oregon and Washington. Salmonberry was botanically described by Bailey (1945) as a perennial, branching, erect or lopping shrub with canes 2-4m tall, persisting more than two years with deciduous, trifoliolate leaves, and widely spreading by horizontal underground shoots (rhizomes). Salmonberry is regionally distributed from Alaska to western Montana, and to northern California (Anon. 1937). Thimbleberry has a wider distribution, occurring from Alaska to southern California, to New Mexico, throughout the Rocky Mountain states, and east to Michigan and western Ontario (Anon. 1937). Thimbleberry is a perennial shrub with erect stems (0.5 to 2m tall), with simple lobed leaves, no spines, and spreading from rhizomes (Bailey, 1945). Both species produce drupes with druplets containing a single hard-pitted seed. The seeds have negligible endosperm and warm and cold stratification requirements for germination (Brinkman, 1974).

Salmonberry and thimbleberry habitat

Several site characteristics have been observed which may influence the distribution of salmonberry and thimbleberry in the Coast Range. Salmonberry is typically found in association with sitka spruce (Picea sitchensis), red alder (Alnus rubra), bigleaf maple (Acer macrophyllum),

and vine maple (Acer circinatum) along streams and on low slopes in moist soils (Anon. 1937). Thimbleberry grows in moist, shaded habitats along streams, and wooded hillsides, and is more common than salmonberry on dry sites (Anon. 1937). Hemstrom and Logan (1984) indicated that salmonberry is a common component of the plant associations near the coast, while thimbleberry is more abundant in associations along the eastern half of the Coast Range.

Kelpsas (1978) found that salmonberry had a greater frequency of occurrence than thimbleberry. For example, salmonberry was the dominant shrub species in 23% of the quadrats and thimbleberry was dominant in only 1% of the quadrats at a site in the middle of the Coast Range (Kelpsas, 1978). Salmonberry and thimbleberry often dominate recently cutover or burned areas of coastal forests (Krygier and Ruth, 1961). An exponential increase in salmonberry crown cover for 8 years after partial cutting was observed by Ruth (1970). Allen (1969) found dense pure stands (30,000+ stems/ha) of salmonberry on clearcuts. Barber (1976) compared the photosynthetic behavior of salmonberry and thimbleberry over a light intensity gradient. He concluded that salmonberry was considerably more shade-adapted than thimbleberry, and had photosynthetic characteristics comparable to other shade-tolerant species.

Franklin and Pechanec (1968) measured higher frequency

and cover of salmonberry under a pure red alder canopy than under a mixed red alder-conifer canopy, or a pure conifer stand in the western Coast Range. They concluded that salmonberry may not be shade tolerant. Newton et al. (1968) reported that salmonberry is a common successor to red alder, and can become a seral dominant in the absence of an adequate conifer seed source. Henderson (1970) found salmonberry to represent about half of the accumulative crown cover and about 75% of the biomass in the understory of red alder stands. However, Newton et al. (1968) and Henderson (1970) indicated that salmonberry is not a significant portion of red alder communities that are less than 25 years old. Tappeiner et al. (1990) observed salmonberry clones in red alder stands that were larger and had greater ramet production from rhizomes than clones in conifer stands, riparian sites, or clearcuts. The association of salmonberry with red alder has led to speculation that it is a nitrophyllous species (Henderson, 1970), because of the nitrogen fixing ability of red alder. Barber (1976) also noted that early spring leaf expansion and positive net photosynthesis may be an advantage for salmonberry because of the lengthened growing season relative to alder and other deciduous species.

Salmonberry and thimbleberry reproduction and establishment

Salmonberry and thimbleberry species reproduce by vegetative means as well as by seed. Production of shoots

from rhizomes is primarily responsible for the local increase in shoot density of these plants (Barber, 1976). However, spread of the species to sites where mature plants are not present (e.g. formerly dense conifer canopies), supports establishment from seed. The relative importance of each mode of reproduction for the establishment of populations of each species has not been examined. Henderson (1970) observed that salmonberry never flowered in old conifer stands. However, viable seed can be stored on the forest floor for decades until disturbance stimulates germination (Barber, 1976).

Salmonberry and thimbleberry germination and seedling survival should have similar constraints, although little information has been reported for thimbleberry. Barber (1976) showed that germination of salmonberry seeds was regulated by a chemical inhibitor in the seed coat. Removal of the inhibitor results from exposure to cold moist conditions in the soil (stratification) and chemical or physical removal of seed coat material (scarification) (Barber, 1976). The fruits of salmonberry and thimbleberry are eaten by birds and mammals which disperse the seed and may enhance germination (Krefting and Roe, 1949; Viereck and Little, 1972). Krygier and Ruth (1961) observed increased germination with increased sunlight and soil disturbance. In a later experiment, Ruth (1970) found that the number of salmonberry seedlings decreased as the amount

of solar radiation increased, although other unidentified variables were suggested as important in determining seedling survival. Barber (1976) suggested that once salmonberry is established, subsequent low light intensities, leaf mats, and other factors associated with the cover of mature plants make seedling establishment difficult.

Vegetative reproduction is the primary mode for established salmonberry and thimbleberry stand maintenance and growth (Barber, 1976). The environmental constraints on vegetative reproduction of salmonberry and thimbleberry are currently being studied by Zasada, Tappeiner and co-workers. Tappeiner et al. (1990) determined that salmonberry rhizome length and biomass can be predicted from tree overstory basal area. They further report that salmonberry shoot densities vary among tree stand types, but stem size and age distributions remain similar. In all stand types there was frequent replacement of dying shoots by new sprouts from root crowns and rhizomes. Zasada et al. (1989) reported that shoot production from salmonberry rhizome sections was lowest when the sections were collected in June, a time corresponding to minimum carbohydrate concentration in the rhizome.

Allen (1969) noted that salmonberry increased sprouting when grown at low clump densities. Abrahamson (1975a) reported that dewberries (Rubus hispidus and R.

trivialis) in a stable, predictable habitat, favor allocation to vegetative reproduction at low stand densities, but reproduction by seed is favored when the population density is high. The total reproductive effort (seed reproduction and vegetative reproduction) of R. hispidus decreased with increased successional maturity of the site. However survival of the reproductive organs increased in more mature plant communities (Abrahamson, 1975b).

Salmonberry and thimbleberry management

Salmonberry and thimbleberry management for conifer production has focused on herbicides. Krygier and Ruth (1961) and Madison and Freed (1962) showed effective defoliation of salmonberry for one growing season when mixtures of 2,4-dichlorophenoxyacetic acid (2,4-D) and 2,4,5-trichlorophenoxyacetic acid (2,4,5-T) were applied to early spring foliage. Applications to dormant foliage were not as effective. Late summer and fall applications of glyphosate [N-(phosphonomethyl)glycine] cause mortality of salmonberry and thimbleberry, but early growing season applications only cause moderate injury (Conard and Emmingham, 1984). Manual cutting of salmonberry and thimbleberry stimulates rapid sprouting from stem bases and rhizomes and has resulted in increased total leaf area (Haeussler and Coates, 1985). Site preparation burning supresses salmonberry or thimbleberry. However, cover of

both species will increase following natural or prescribed fires unless the burn is extremely intense (Haeussler and Coates, 1985).

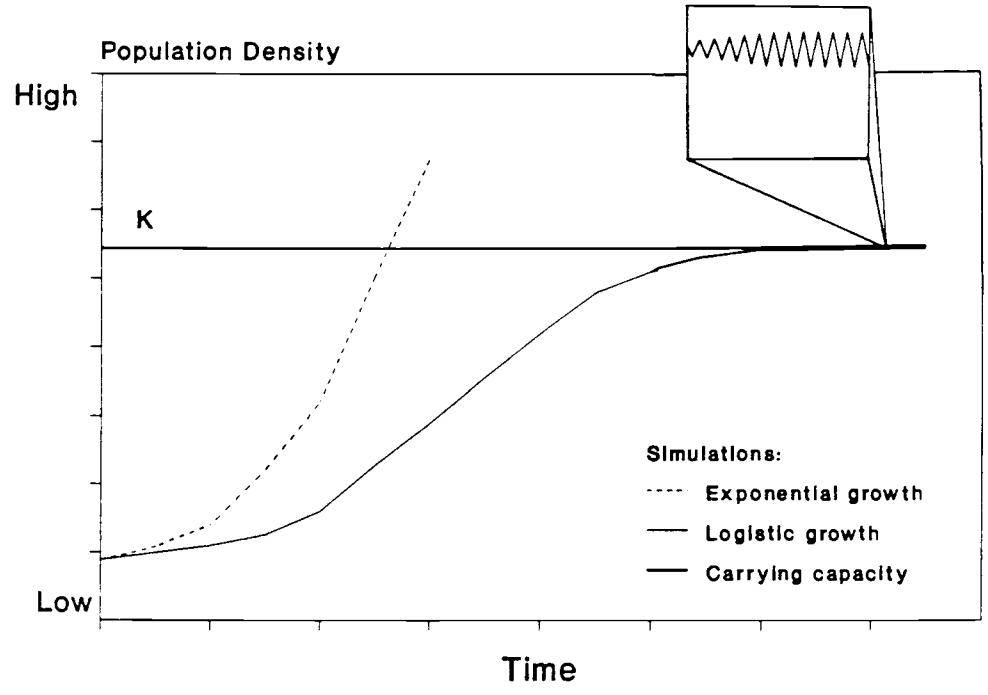


Figure 1.1. Population density conforms to an exponential growth equation when the environment does not limit growth. Population growth is sigmoidal when the environment does limit growth, and can be fit to a logistic growth curve which stabilizes as it approaches K. The stability at the asymptote (K) can be dynamic at refined scales (insert).

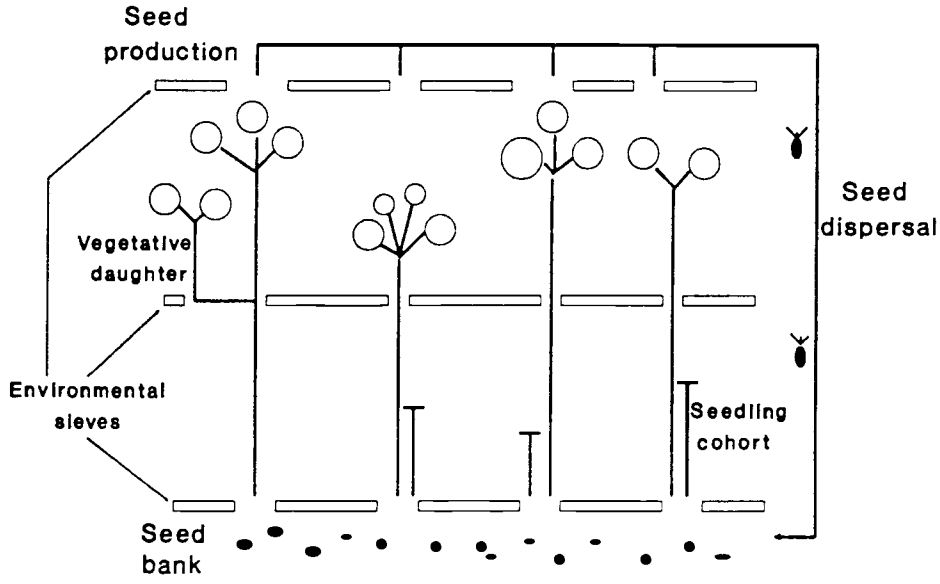


Figure 1.2. An idealized plant life history. (Adapted from Harper, 1977).

CHAPTER 2

A POPULATION MODELING APPROACH FOR STUDY AND MANAGEMENT OF SALMONBERRY AND THIMBLEBERRY

ABSTRACT

Weed population models are a framework to organize weed biology information. They also can help identify information gaps, set research priorities, facilitate hypothesis generation, and suggest weed control strategies. A generic population simulation model of salmonberry (Rubus spectabilis Pursh) and thimbleberry (Rubus parviflorus Nutt.) was developed. Sensitivity analysis on the Rubus spp. model indicated that transition from basal buds to sprouts, shoot survival, sprout transition to mature shoots, and basal bud production on mature shoots were important demographic processes regulating population growth. Hypothesized mechanisms that influence the transition from basal buds to vegetative shoots were examined. Seasonal changes and hypothetical intraspecific density effects on transitions were included in the model. An assessment of manual cutting for management of Rubus species also was simulated to demonstrate the potential use of the model.

INTRODUCTION

An important aspect of weed science is developing information about the biology of weed species. Autecological and population studies which explore the "weedy" characteristics of plants (i.e. reproductive, migration, and competitive abilities) will help develop and assess a broad set of weed control tactics. Population simulation models are useful to guide weed biology research. Simulation models have been used in research to: (1) organize existing information about a particular species, (2) conceptualize a plant population as a set of processes, (3) analyze a suite of interrelated processes, and (4) formulate testable hypotheses relevant to managing population growth (Mortimer, 1983; Maxwell, et al. 1988). The simulation model format also provides a predictive tool that is useful to assess weed management strategies and focus control practices on vulnerable stages in the life cycles of weed species (Sagar and Mortimer, 1976; Maxwell et al. 1989; Maxwell et al. 1988). Modeling populations is also appropriate to weed science, because management of vegetation is generally based on manipulating plants at that level of organization (Mortimer, 1983).

The model is a conceptualization of the population. It should be organized to reflect importance of life history stages with respect to management practices. Population dynamics should be simulated accurately with the inclusion

of population regulation mechanisms that are present in natural systems. A common regulatory mechanism used in models is density-dependence. The incorporation of population growth regulation mechanisms into a model becomes part of an iterative process of model testing and refinement which is the focus of this chapter.

Salmonberry and thimbleberry are perennial shrub species that are common components of the vegetation on clearcuts in the Coast Range of western Oregon. These species reduce growth and increase mortality of planted conifer seedlings (Newton and White, 1983; Ruth, 1956; Wagner, 1989). There was little information available on the population dynamics of salmonberry or thimbleberry. Therefore a study was initiated to gain information on the population biology of these species that would be pertinent for developing control strategies. The objective of this chapter is to describe the development of a population growth simulation model, and to demonstrate its utility for evaluating weed management decisions. Since both salmonberry and thimbleberry have similar growth habits and life history stages, a generic Rubus spp. model was developed.

MODEL DEVELOPMENT

The first generation model

Life history stages and appropriate connecting processes for Rubus species were identified from the

literature (Allen, 1969; Barber, 1976; Sagar and Mortimer, 1976) and field observations (Figure 2.1). Basal buds include all potential aerial shoot producing buds on the root crown and rhizomes. Sprouts and seedlings become mature vegetative shoots when a bud is produced at the base of the shoot (i.e. they become reproductive). Conversion of state variables (boxes) shown in the diagram to actual values, and development of equations that describe transitions (valve symbols) between life history stages follow organization of the conceptual framework. An efficient way to summarize the mathematical relationships depicted diagrammatically in Figure 2.1 is to insert the transition values into a matrix (Lefkovitch, 1967; Leslie, 1945; Sarukhan and Gadgil, 1974; Werner and Caswell, 1977). This approach has been used successfully to develop annual and perennial herbaceous weed population models (Watson, 1985; Maxwell et al. 1988; Cousens, 1986; Mortimer, 1983; Mortimer et al. 1980).

The number of individuals of the population in each stage is represented by the column vector (matrix), **N**.

$$\mathbf{N} = \begin{bmatrix} \text{Number of seeds} \\ \text{Number of basal buds} \\ \text{Number of seedlings} \\ \text{Number of sprouts} \\ \text{Number of vegetative shoots} \\ \text{Number of flowering shoots} \end{bmatrix}$$

Numbers in the column vector, **N**, change over time (i.e. model iterations) as the population size (density) changes.

As depicted in Figure 2.1, the number of individuals in each life history stage depends on the rate of transition of new individuals into that stage and the rate at which individuals die, or graduate to another stage. For example, the number of seeds in a population depends on the rate of production of seeds by flowering shoots, the ability of seeds to survive, and the rate at which seeds germinate and become seedlings (Figure 2.1). Thus, the number of individuals present in different stages is governed by the transition of individuals from one stage to another.

The rates of transition, including fecundities (production of new individuals) and survival rates (transitions into the same stage), for the entire population are summarized in a transition matrix. For the Rubus model, the transition matrix, **M**, is:

$$\mathbf{M} = \begin{bmatrix} R0 & 0 & 0 & 0 & 0 & F6 \\ 0 & R2 & 0 & 0 & V5 & V6 \\ G1 & 0 & R3 & 0 & 0 & 0 \\ 0 & G2 & 0 & R4 & 0 & 0 \\ 0 & 0 & G3 & G4 & R5 & 0 \\ 0 & 0 & 0 & 0 & G5 & R6 \end{bmatrix}$$

In this transition matrix (**M**, the values, R0 through R6 are the survival rates, F6 is the fecundity or production of seeds by flowering shoots, V5 and V6 are the production rates of basal buds on vegetative and flowering shoots, respectively. G1 through G5 are the rates at which individuals graduate from one stage to another by growth. Zero values mean there is no transition between these stages, e.g., basal buds do not produce seeds. The values taken together describe the plant population and how it changes over time. Each column, in the matrix corresponds to one of the five life history stages for the species, and shows the fates of the individuals starting within that stage. Each row, corresponds to one of the life history stages in the population at the next observation time, and shows the sources of individuals.

The transition matrix (**M**) and the population column vector (**N**) are combined through matrix algebra to create a succinct description of population changes over time:

$$\mathbf{N}(t+1) = \mathbf{MN}(t)$$

This equation states that the population size and numbers of individuals in each life history stage at the next observation [**N**(t+1), where t stands for time] is a result of the transitions (**M**) of individuals contained in life history stages at the current time [**N**(t)]. If the transition rates and population sizes can be determined accurately, this procedure predicts future population size.

Initial values for a single transition matrix were obtained from the literature (Abrahamson, 1975a and 1975b; Barber, 1976; Barkham, 1980; Brinkman, 1974; Kelpsas, 1978; Maxwell et al., 1988; Ruth, 1970; Sarukhan and Gadgil, 1974) field observations of Rubus species. This information allowed model simulations to be conducted (Figure 2.2a, dashed line). The simple transition matrix approach described here is not without weakness (Vandermeer, 1984). Transition rates between age, size, or life history stages of a population are not, in general, constant over time. If transition parameters are held constant the model predicts exponential population growth (Figure 2.2a) which does not usually occur in natural stands. Changing plant densities, weather, seasons, and management all dictate that the transition matrix should be dynamic, i.e., the transition element values should vary over time under different conditions of the biotic and abiotic environment.

Second generation model

The addition of three transition matrices, each representing a phenological stage (spring establishment, reproduction, and fall senescence) of Rubus was incorporated into the model to include the influence of seasonal variation in growth. This addition of detail reduced the model time increment from one year (used in the first generation model) to several months. Therefore, the number of parameters (transition matrix elements greater

than zero) increased from 14 to 42. Model simulations with different transition matrices for each season still predicted unlimited growth (Figure 2.2a, solid line). However, simulation of seasonal changes in the population (Figure 2.2b) demonstrates dynamics that could be valuable for detecting times for effective management (e.g. reduction of total shoot density might be most effective when the population is at a low point rather than a peak in the growing season).

Further model development was demonstrated by focusing on biotic and abiotic factors that may influence each transition parameter. Sensitivity and elasticity analysis (Maxwell et al. 1988; Moloney, 1988) was used to prioritize the transitions for further refinement and study at each step of the model development process.

Sensitivity analysis is conducted by changing the value of a parameter, or set of parameters, that describe a particular transition, while keeping the other transition parameters constant, and monitoring the population size (model output). The sensitivity value is the ratio of the proportional change in the simulation results (output) to the proportional change in the transition parameter.

$$\frac{\Delta \text{ output}}{\text{output}} \Big/ \frac{\Delta \text{ parameter}}{\text{parameter}} = \text{Sensitivity Value}$$

A large sensitivity value means that a small adjustment in

a transition parameter will cause a large change in model output. Elasticity values are calculated by setting the highest sensitivity value to unity and making all other sensitivity values a relative proportion. This procedure allows more equitable comparison among parameters than strict sensitivity analysis. Critical parameters (i.e. those associated with high sensitivity and elasticity values) were identified in the model. The sensitive parameters are associated with specific demographic processes which may represent points of vulnerability in the weed population. That is these sensitive processes are the most effective mechanism for manipulating population density. The researcher then can focus on the processes that have high sensitivity and elasticity values to learn more on the specific mechanism which regulate the sensitive processes.

Six transitions were particularly sensitive (elasticity value > 0.60) in influencing the total number of shoots in a hypothetical 5 year old open grown Rubus population established from seed and basal buds (Table 2.1). These were G2 (bud transition to sprouts at the reproductive stage), R5 (mature vegetative shoot survival at the reproductive and establishment stage), G4 (sprout transition to mature vegetative shoots at the senescence stage), and V5 (basal bud production on mature vegetative shoots at establishment). Therefore, processes associated

with vegetative reproduction were identified as important in regulating Rubus population size.

Mechanisms that influence demographic processes

The mechanisms governing basal bud production, shoot survival, and the transitions from basal buds to vegetative shoots can be divided into seasonal, interference, environmental and management factors (Figure 2.3). These factors represent different levels of biological complexity and interact in their influence on demographic processes. For example, the effect of density (an interference factor) on a population is the result of competition for resources. Environmental factors dictate the levels of resources available to plants and often the physiological status of plants. The season or a management practice may mediate any of these factors. Therefore, a hierarchy of factor types can be established which indicates a procedure for adding mechanistic detail to each generation of the model. Therefore, the model also provides a conceptual structure to link research conducted at differing scales and disciplines.

Third Generation Model

A third generation model was developed by incorporating the influence of intraspecific density into the second generation model. There are qualitative considerations that must be addressed when density-dependence is added to a stage distributed population

(Vandermeer, 1981). For example, does density-dependence act only on reproduction or survivorship or on some combination of the two? Is density dependence mediated by total population density or is the effect distributed differentially over the stage classes? Are density dependent effects felt instantaneously or is there a time lag or accumulation of influence? How do density independent factors interact with density to influence transitions?

Increased density of clonal species is negatively correlated with the number of shoots arising from vegetative reproduction (Abrahamson, 1980; Barkham, 1980; Barkham and Hance, 1982; Holler and Abrahamson, 1977; Thomas and Dale, 1975). Barkham (1980) also indicated that transitions between different life-history states of the clonal species Narcissus pseudonarcissus was influenced by density. Hutchings (1979) however, showed that ramet populations of clonal perennial herbs do not follow the -3/2 power law and self-thinning (ramet survivorship) is the result of density independent factors. Therefore, density-dependence on reproduction and transitions between life history states, but not survival parameters, were considered for inclusion into the model.

The proportion of basal buds which become sprouts (G2), the proportion of sprouts that become mature vegetative shoots (G4), and the number of basal buds

produced by mature vegetative shoots (V5) were hypothesized to decrease with increasing intraspecific density. The following hypothetical linear relationships between transition parameters and total shoot density were incorporated in the model to illustrate the potential role of density-dependence on the population size of Rubus spp. (Figure 2.4). The equations included in the model are:

$$G2 = a - b(N_{t-1})$$

$$G4 = a - b(N_{t-1})$$

$$V5 = a - b(N_{t-1})$$

where a is a constant between 0 and 1.0 which represents the maximum value for the transition after density independent factors have influenced the transition, and b is a constant which is the slope of the linear relationship between the transitions (G2, G4 and V5) and total shoot density. N_{t-1} is the sum of sprouts, mature vegetative shoots and flowering shoots from the previous phenological stage. These density-dependent relationships were not experimentally derived, however a simple negative linear relationship between transition probabilities and density was assumed to be based on density-effects observed in other clonal species (Abrahamson, 1980; Barkham, 1980; Barkham and Hance, 1982; Holler and Abrahamson, 1977; Thomas and Dale, 1975).

Simulation results from the third generation model were compared with the results from the first and second

generation model (Figure 2.5a). In the third generation model the density-dependent parameter values were arbitrarily set to demonstrate the influence of density-dependence on population simulations. The **a** parameters in the density-dependent equations for G2 and G4 were set at 0.8, and for the V5 equation at 2.0. The **b** parameters in the same equations were set at 0.0033 for G2 and G4 and 0.0015 for V5. None of the transition values were allowed to go below 0. Simulation output by month demonstrates the seasonal flux in total shoots (Figure 2.5b). When the **a** parameters in the density-dependent equations for G2 and G4 were set at their maximum potential (1.0) and simulations were extended more than 40 years (Figure 2.6), the predicted population was stable for several years followed by a period of increasing oscillations followed by consistent oscillation (bifurcation). May and Oster (1976) and DeAngelis and Waterhouse (1987) observed similar behavior from simple difference equations, and concluded that bifurcations and chaotic behavior in their models are evidence that stable population equilibriums are not necessarily fundamental properties of ecological systems.

The practical value of these simulation results lies in the demonstration of the importance of the model refinements and as an indication of how Rubus populations might behave if the hypothesized relationships were true. These results suggest the potential importance of

intraspecific density on population growth of these species, and suggest experimentally testing the hypothesized relationships.

Future generation models

A fourth generation model is posed to demonstrate the incluson of physiological mechanisms which govern transitions. Physiological effects on basal bud transition could include stored carbohydrate availability and/or hormonal regulation (Maxwell et al. 1988; McIntyre, 1979; Nissen and Folley, 1987). Salmonberry rhizome carbohydrate levels tend to follow an annual pattern which can be predicted by phenological stage (Zasada et al. 1989). Vascular induction preceding bud growth has been shown to coincide with an increase in soluble carbohydrates in other perennial species (Raju, 1975; Raju and Marchuk, 1977). Therefore, functional relationships between bud transition and carbohydrate levels could be incorporated into the model.

Environmental factors may be the preferred level of complexity to base mechanisms that drive processes in populations, because all the other factors previously discussed are generally influenced by or interact with environmental factors. Internal competition between buds for water could play a role in the mechanism controlling basal bud growth (McIntyre, 1979). A hypothetical functional relationship between available soil water and

bud transition is demonstrated in Figure 2.7.

The relationship between resources and bud transition can be hypothesized in a more complex form by linking the influence of density with environmental factors, which demonstrates the integration of levels of complexity in the model (Figure 2.7). Plant available soil water is influenced by the processes of evaporation, transpiration, and precipitation. The rate of evaporation and transpiration can be influenced by leaf area, which in turn is a function of the total number of shoots.

POSSIBLE MANAGEMENT STRATEGIES

Application of the model for assessing management strategies was demonstrated by simulating the effect of manually cutting all Rubus shoots at each phenological stage during the second year of growth with the third generation model (Figure 2.8). The simulation was performed by starting the population at Year 0 with 300 seeds and 40 buds/m^2 and letting it grow. At Year 2 manual cutting was simulated by removing all sprouts, vegetative shoots and flowering shoots at the establishment phenological stage. The population was then allowed to recover. There are two aspects of the simulation that are important for assessing the value of the control practice in relation to growing a crop: 1) the decrease in shoot density relative to a threshold weed density and 2) the length of time that the population is maintained below the threshold density. The

threshold could be defined in this case as the weed density which causes significant growth reduction in the crop. The model therefore, can be a valuable tool for evaluating management practices and suggesting efficient control strategies.

In order to accurately assess weed control tactics, interspecific competition, particularly the effect of the crop on the weed population needs to be included in the model. The weed population growth could be decreased following a treatment due to increased crop vigor in response to the treatment. That is, the slope of the recovery between years 2 and 4 (Figure 2.8) could be decreased by the influence of the crop on the weed population. This response could increase the period that the weed population remains below the threshold and improve the control treatment evaluation.

SUMMARY

By demonstrating the progression of construction of a Rubus population model I have attempted to provide an understanding of the usefulness and practicality of this approach to weed research. The modeling approach provides an avenue for application of basic biological information to develop weed control strategies. Models can be helpful in organizing existing information and providing a structure to identify where important information is needed. The process also can identify points of

vulnerability in the weed population, and allows a better understanding of how weed population growth is regulated. Assessment of existing or potential weed control tactics can ultimately be made more efficient by utilizing a weed population modeling approach.

The process of refining the second generation hypothetical Rubus model developed in this chapter will continue in the following chapters. Specific experiments will be discussed which were conducted to determine transition matrix values and the influence of factors on those values. The information from the experiments is used to refine the model.

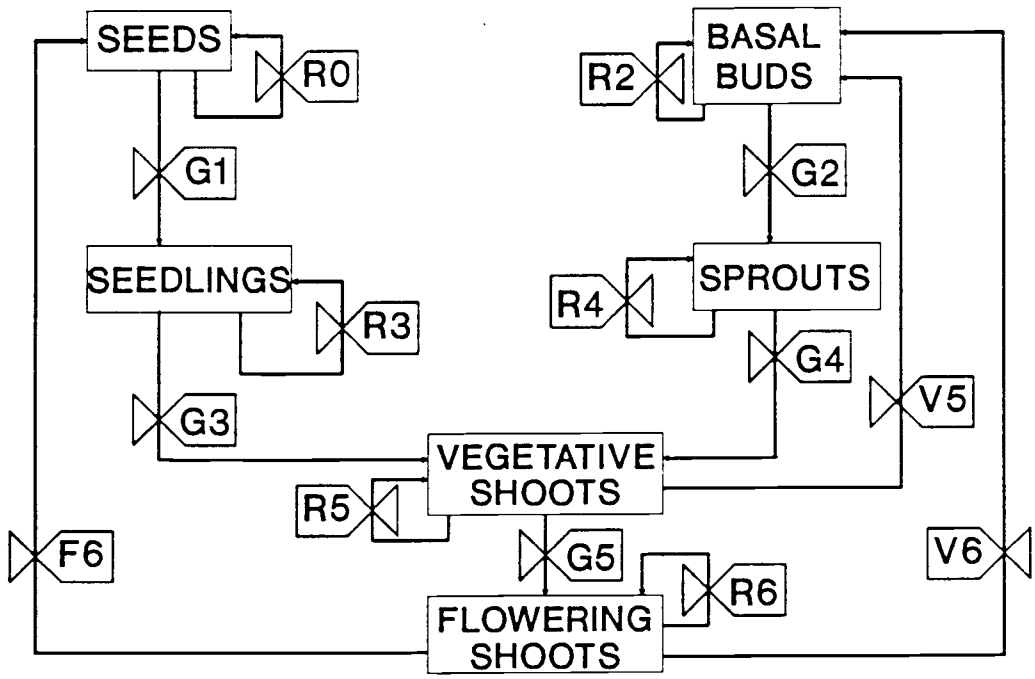
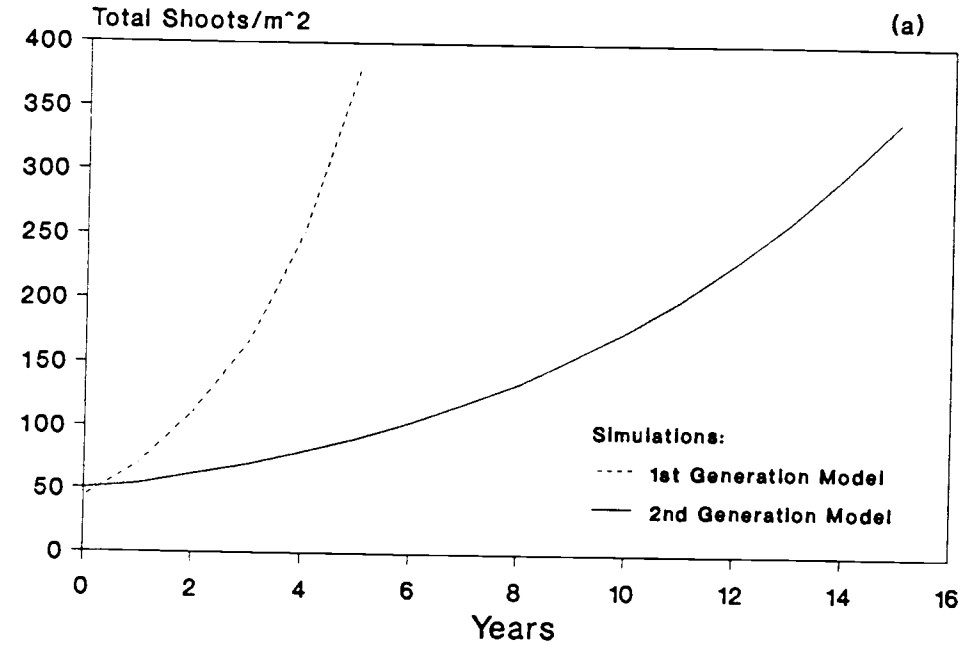


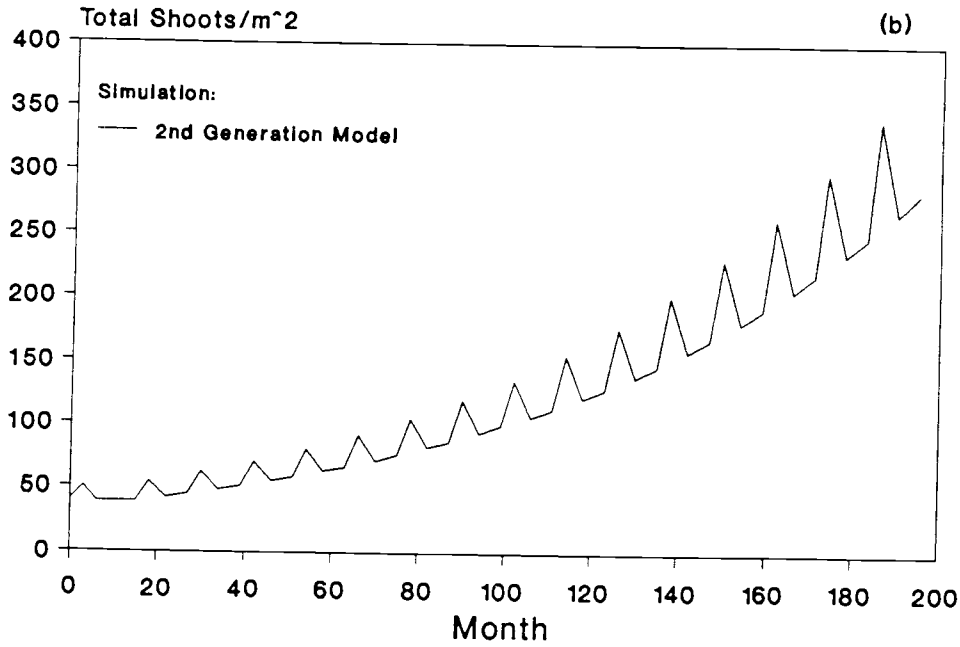
Figure 2.1. A diagrammatic representation of the Rubus population model. State variables are seeds, seedlings, basal buds, sprouts, vegetative (mature) shoots, flowering shoots. Arrows between state variables represent processes, and valves represent the rate or probability of transition from one state to the next.

G1 = germination R0 = seed survival
G2 = sprouting R2 = basal bud survival
G3 = sdl. growth R3 = seedling survival
G4 = spr. growth R4 = sprout survival
G5 = flowering R5 = veg. shoot survival
F6 = seed produced/flowering shoot
V5 = basal buds produced/veg. shoot
V6 = basal buds produced/ flw. shoot
R6 = flowering shoot survival

Figure 2.2. (a) First and second generation model simulations of total shoot density (sprouts + vegetative shoots + flowering shoots) over a 15 year time period. The second generation model output is from the reproductive stage. (b) Second generation model simulation with output at each phenological stage.

Fig. 2.2


Total Shoots/m^2
(a)
400
350
300
250
200
150
100
50
0
0
2
4
6
8
10
12
14
16
Years
Simulations:
1st Generation Model
2nd Generation Model


Total Shoots/m^2
(b)
400
350
300
250
200
150
100
50
0
0
20
40
60
80
100
120
140
160
180
200
Month
Simulation:
2nd Generation Model

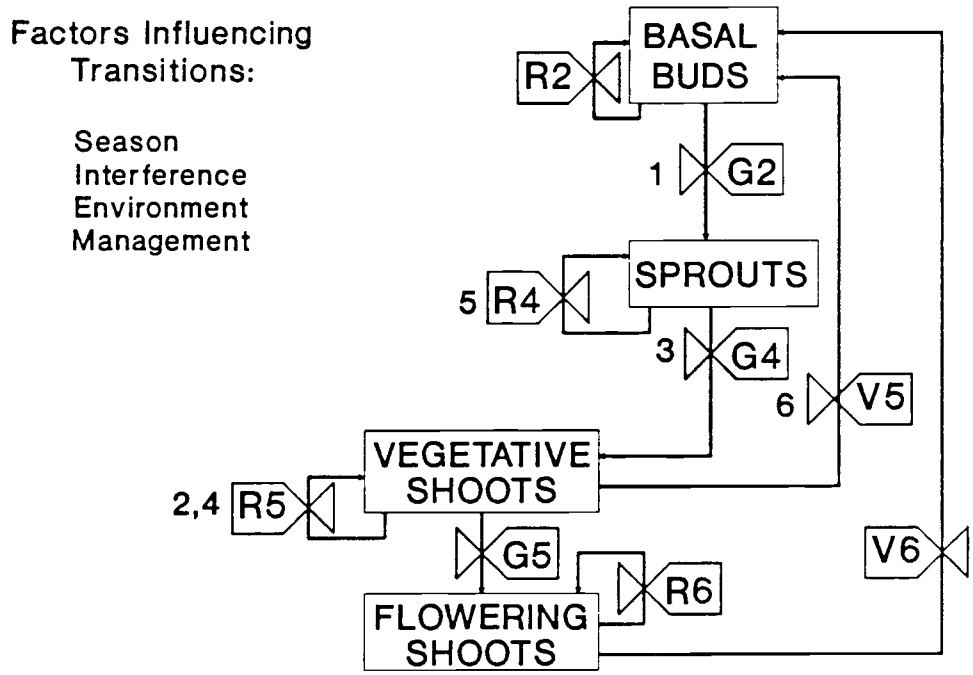


Figure 2.3. Diagrammatic sub-model representing the vegetative (asexual) reproduction side of the population model. A list of factors which may influence transition rates and importance ranking of transitions (numbers adjacent to valve symbols) also are provided.

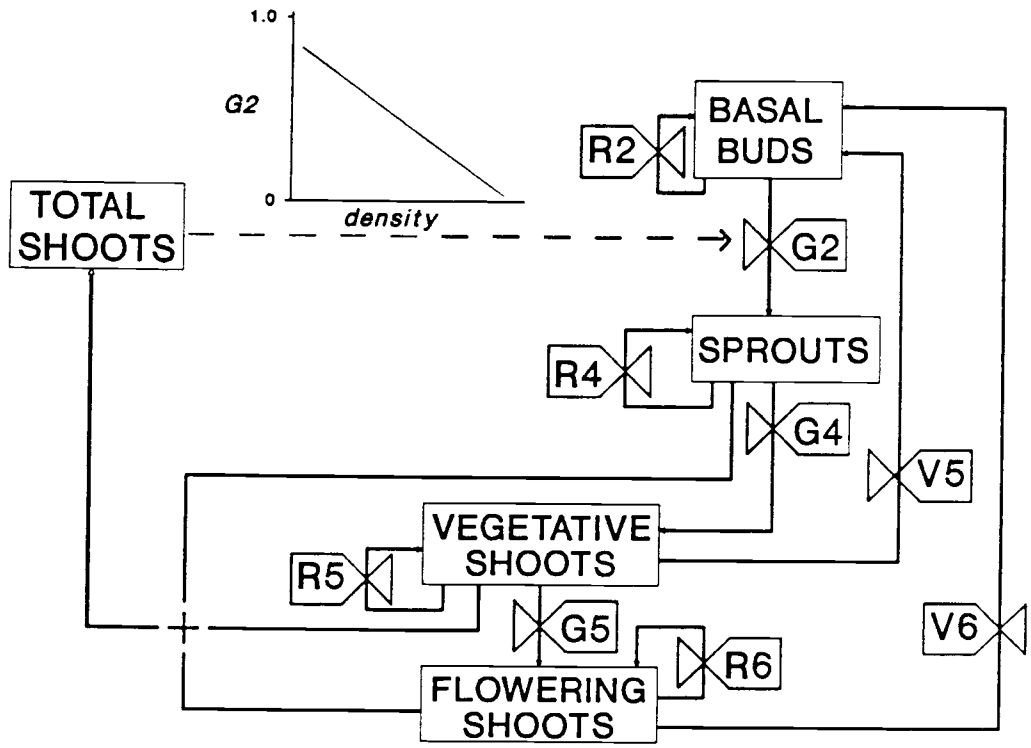
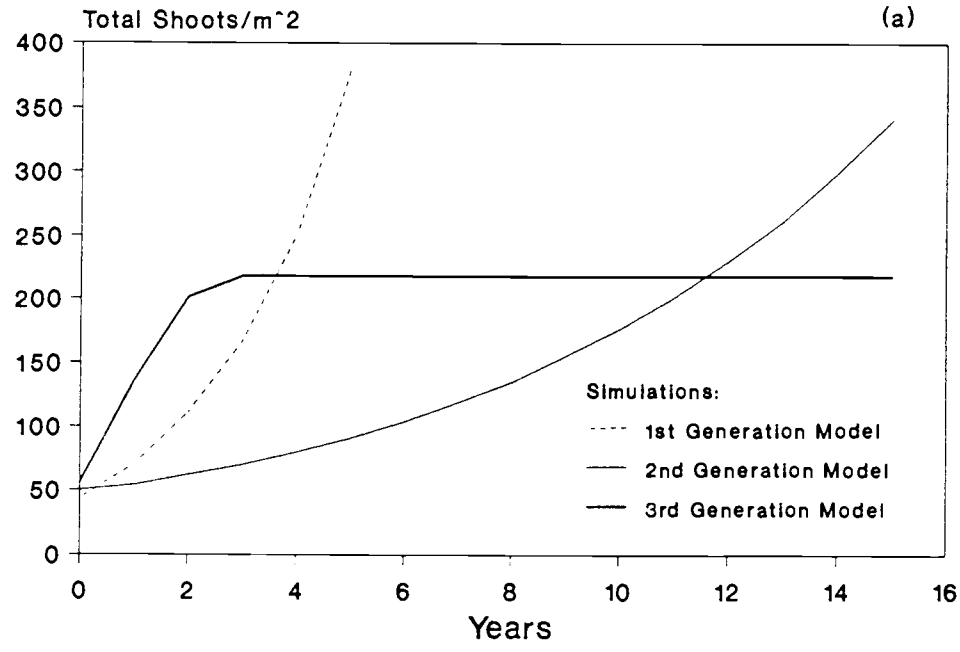
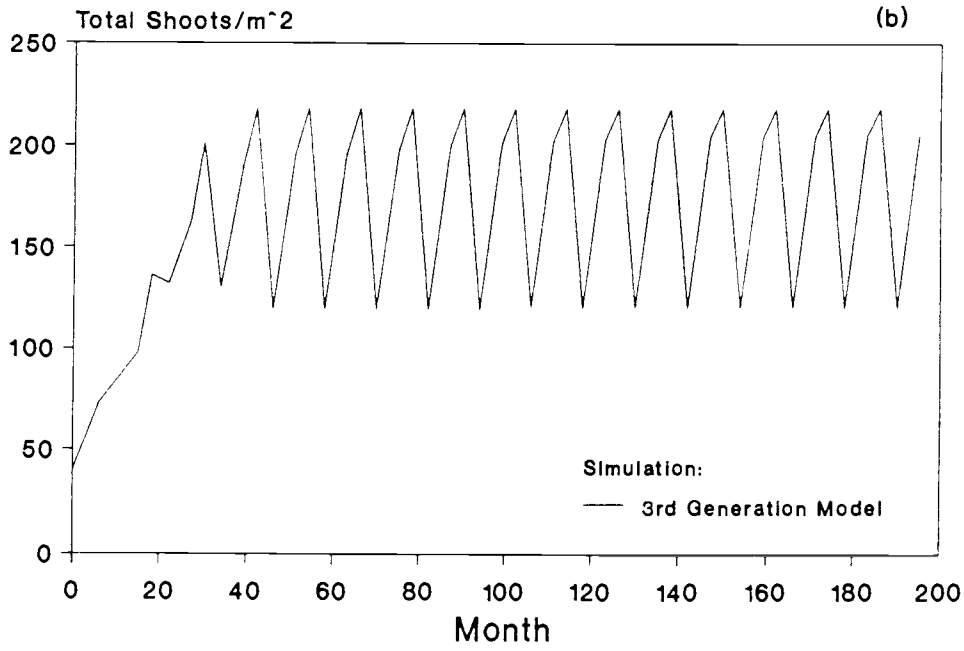


Figure 2.4. Diagrammatic sub-model representing the vegetative reproduction side of the population model with the influence of total shoot density (sum of sprouts, vegetative shoots and flowering shoots) represented as a feedback effect on the G2 transition parameter. A Hypothesized relationship for the response of G2 to total shoot density is also presented.

Figure 2.5. (a) Comparison of first second and third generation model simulations of total shoot density (sprouts + vegetative shoots + flowering shoots) over a 15 year period with output at the reproductive stage. (b) Third generation model population simulation with output at each phenological stage over a 15 year period.

Fig. 2.5


Total Shoots/m^2
(a)
400
350
300
250
200
150
100
50
0
0
2
4
6
8
10
12
14
16
Years
Simulations:
1st Generation Model
2nd Generation Model
3rd Generation Model


Total Shoots/m^2
(b)
250
200
150
100
50
0
0
20
40
60
80
100
120
140
160
180
200
Month
Simulation:
3rd Generation Model

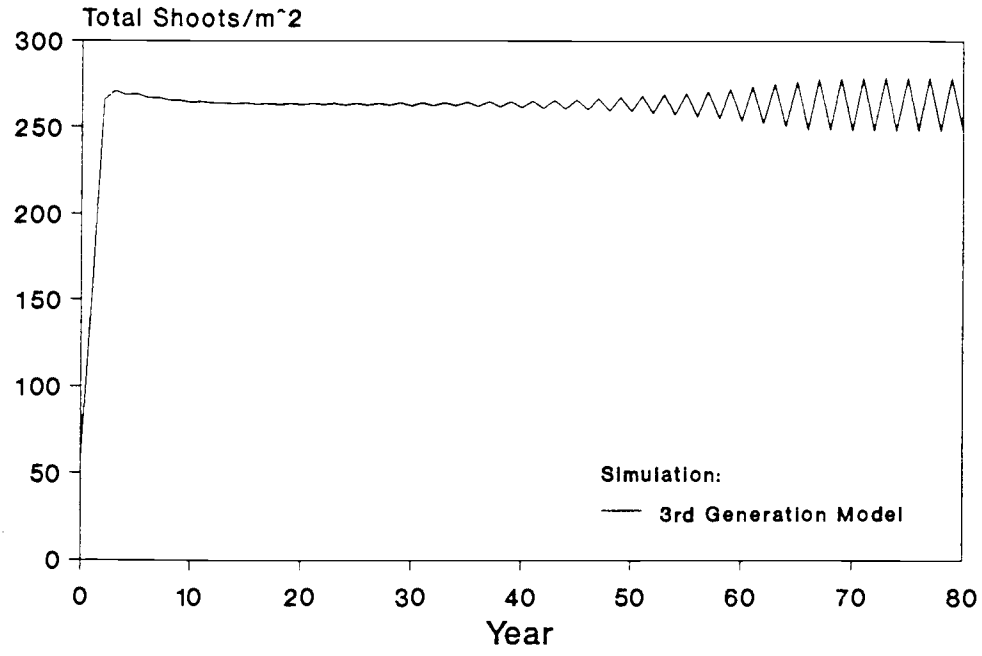


Figure 2.6. Extended population simulation with the third generation model indicating an oscillating population at equilibrium.

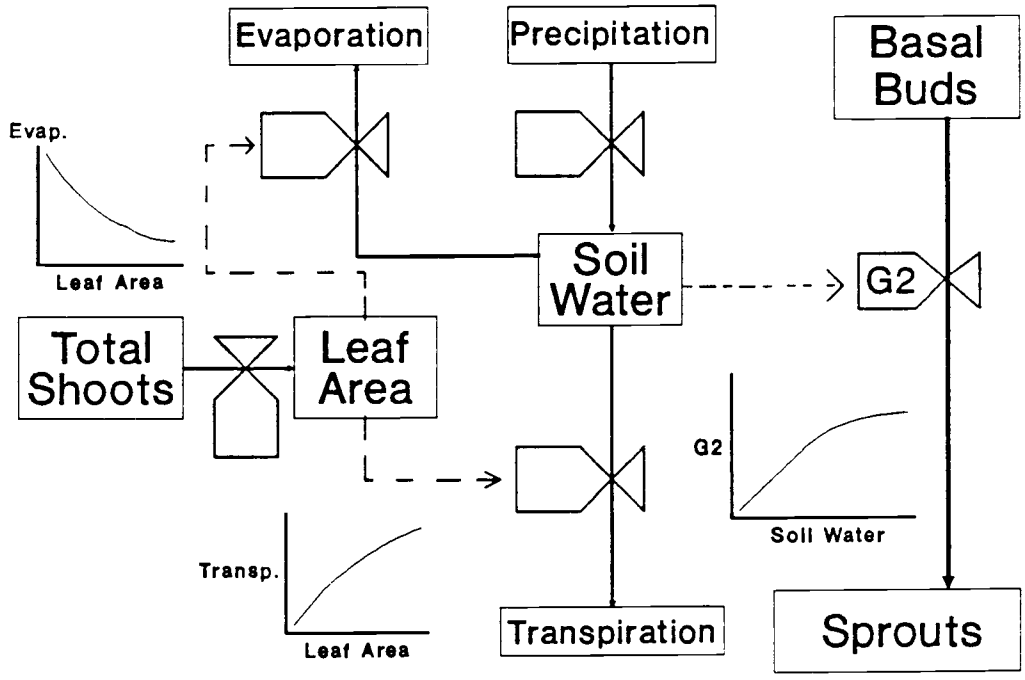


Figure 2.7. A diagrammatic sub-model representing the vegetative reproduction side of the population model with hypothetical mechanisms (factors effecting soil moisture) for the influence of density on basal bud transition to sprouts.

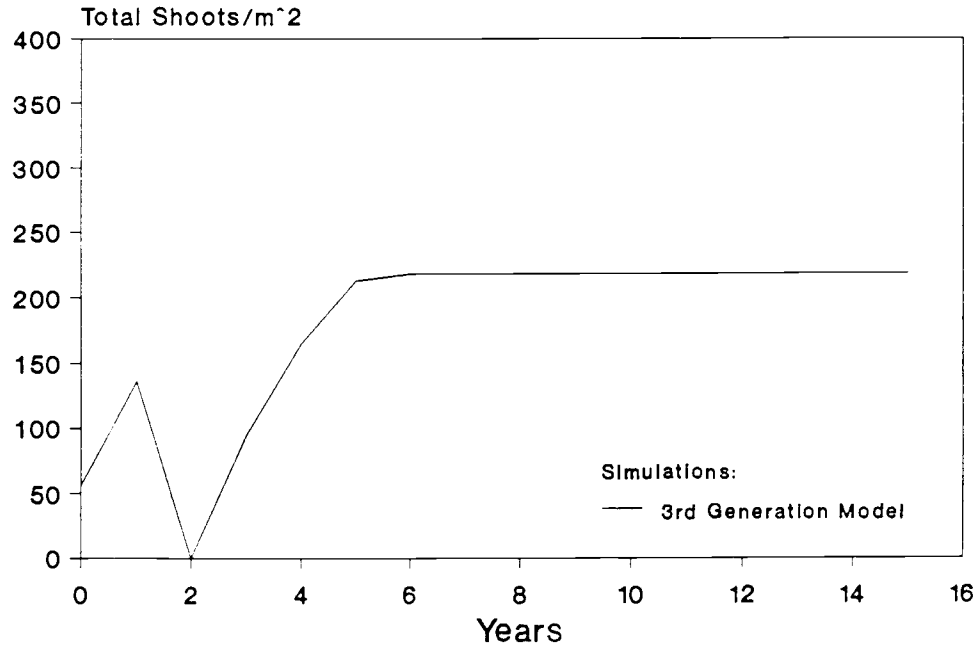


Figure 2.8. Third generation model simulation of a population response to manually cutting all sprouts, vegetative shoots and flowering shoots at all phenology stages during the second year of growth.

Table 2.1. Sensitivity and elasticity analysis of the single matrix first generation model. Sensitivity and elasticity values were calculated by decreasing each transition parameter by 10% and determining the influence on total shoot density at year 5 of the simulation. State variable inputs were set as follows: Seed = 100, Buds = 20, Seedlings = 2, Sprouts = 10, Vegetative shoots = 0, Flowering shoots = 0.

Stage	Parameter	Sensitivity value	Elasticity value	Importance rank
EST	R0	0.0001	0.0006	
EST	F6	0.0000	0.0000	
EST	R2	0.0756	0.4729	
EST	V5	0.0961	0.6011	6
EST	V6	0.0000	0.0001	
EST	G1	0.0001	0.0008	
EST	R3	0.0000	0.0000	
EST	G2	0.0647	0.4042	
EST	R4	0.0514	0.3214	
EST	G3	0.0000	0.0001	
EST	G4	0.0502	0.3136	
EST	R5	0.1411	0.8825	4
EST	G5	0.0000	0.0000	
EST	R6	0.0000	0.0001	
REP	R0	0.0002	0.0013	
REP	F6	0.0000	0.0000	
REP	R2	0.0499	0.3119	
REP	V5	0.0354	0.2212	
REP	V6	0.0000	0.0000	
REP	G1	0.0000	0.0000	
REP	R3	0.0002	0.0010	
REP	G2	0.1599	1.0000	1
REP	R4	0.1305	0.8160	5
REP	G3	0.0000	0.0000	
REP	G4	0.0238	0.1485	
REP	R5	0.1545	0.9662	2
REP	G5	0.0003	0.0021	
REP	R6	0.0000	0.0001	
SEN	R0	0.0002	0.0013	
SEN	F6	0.0000	0.0001	
SEN	R2	0.0605	0.3780	
SEN	V5	0.0625	0.3905	
SEN	V6	0.0000	0.0002	
SEN	G1	0.0000	0.0000	
SEN	R3	0.0000	0.0001	
SEN	G2	0.0314	0.1961	
SEN	R4	0.0699	0.4368	
SEN	G3	0.0002	0.0009	
SEN	G4	0.1539	0.9624	3
SEN	R5	0.0835	0.5218	
SEN	G5	0.0000	0.0000	
SEN	R6	0.0000	0.0002	

CHAPTER 3

RELATIVE IMPORTANCE OF SEXUAL AND ASEXUAL REPRODUCTION IN ESTABLISHMENT OF TWO NATIVE *Rubus* POPULATIONS

ABSTRACT

Salmonberry (*Rubus spectabilis* Pursh) and thimbleberry (*Rubus parviflorus* Nutt.) are major components of the vegetation on reforestation sites of the Oregon Coast Range. The relative importance of sexual and asexual reproductive processes in the establishment of these species following disturbance was studied. A *Rubus* population transition matrix model (2nd generation model, Chapter 2) was used to identify demographic processes important for population establishment from sexual and asexual reproduction. Germination, bud and sprout production, seedling and sprout survival and growth were processes identified. Field germination of salmonberry was 2% after 1 year. Acid scarification followed by 7 months of stratification improved salmonberry germination to 38%. Thimbleberry had 7% germination in the field the first year. In the laboratory, germination was 5% without scarification or stratification and was increased to 35% with stratification. There were 40 and 20 buds per m produced on rhizome sections collected in the field of salmonberry and thimbleberry, respectively. Thus both species had high potential bud production. Growth chamber

temperature had no influence on total number of buds or sprouts from the rhizome sections. Mean seedling survival over the first three years at 4 sites across the Coast Range was 32% and 44% for salmonberry and thimbleberry, respectively. Mean sprout survival measured at two coastal sites for salmonberry and one site for thimbleberry was 77% and 100%, respectively. Seedlings of both species were more efficient at biomass accumulation than sprouts. However, sprouts had higher initial absolute growth rates providing an early competitive edge over seedlings. Therefore, high bud production potential, sprout survival, and sprout growth, indicate that salmonberry and thimbleberry populations should be dominated by sprouts rather than plants from seedlings in clearcuts of the Coast Range.

INTRODUCTION

Salmonberry and thimbleberry are common components of the vegetation following logging in the Coast Range of western Oregon. These clonal shrub species have economic importance because they cause growth reduction and mortality of conifer seedlings (Hemstrom and Frazier, 1987; Newton and White, 1984; Ruth, 1956; Wagner, 1989). Whether salmonberry and thimbleberry populations predominantly originate on clearcuts from seed or basal buds that survive disturbance is unclear (Barber, 1976; Krygier and Ruth, 1961; Ruth, 1970). Management strategies for these species could depend on their means of establishment. For example, if populations primarily establish from seed, control of the seed source may be a primary management objective. Alternatively, if populations originate from basal buds, then efforts may be directed at reducing the abundance of structures which produce the basal buds. Thus, it is important to determine the relative importance of seed and vegetative means of population establishment.

Gathering information on population establishment processes is also important for refining the Rubus population model developed in Chapter 2. To assess the potential for population establishment from sexual (seed) and asexual (vegetative) reproduction, specific processes in the model were identified for comparison (Figure 2.1). Sensitivity and elasticity analysis (Maxwell et al., 1988;

Maloney, 1988) on the model indicated that asexual processes were more important than the sexual processes in determining the total number of shoots in Rubus spp. populations (Table 2.1). Experiments were conducted to compare and assess the role of demographic processes and factors which mediate the processes involved in population establishment from both seed and vegetative propagules. Information from these experiments was also used to refine the Rubus population simulation model (Chapter 2).

Substantial research has been conducted on salmonberry germination. Krygier and Ruth (1961) report that soil disturbance and increased light associated with logging stimulated germination of salmonberry seed. Dense stands of salmonberry seedlings were observed even when salmonberry was not present in the stand prior to logging. They also reported that vigorous sprouting occurred from shoots, roots and rhizomes when salmonberry was present in the understory of the prior stand. However, Barber (1976) found that salmonberry seedlings were rare and played no significant role in the perpetuation of established stands. He also observed that adequate light availability, regardless of the seedbed, allowed seedlings to grow. Thimbleberry seedlings were abundant within a year after disturbance (Kelpsas, 1978; Stewart, 1978), however thimbleberry is also a rapid colonizing species from rhizomes (Barber, 1976; Haeussler and Coates, 1985).

Haeussler and Coates (1985) state that germination of buried and newly deposited seed is the principal means by which thimbleberry invades new areas. It is clear that salmonberry and thimbleberry can, under appropriate conditions become established on clearcuts from seed or vegetative means. The relative role that seed and vegetative propagules play in the establishment of populations when both are present on a site remains undetermined.

Seed survival in the seed bank, germination, seedling survival, and growth from seedlings to mature shoots were processes identified for study with the Rubus population model (Chapter 2) (Figure 3.1). Salmonberry and thimbleberry seed survival was expected to be influenced most by predation, burial and time in the soil (Barber, 1976). Salmonberry and thimbleberry germination are primarily influenced by seed scarification, stratification, and light availability (Barber, 1976; Ruth 1970; Stewart, 1975). Ruth (1970) assessed the light requirements for salmonberry germination and establishment in clearcuts of the Oregon Coast Range. Stewart (1975) conducted germination experiments with salmonberry and thimbleberry following stratification. The germination experiments conducted in this study examine the interactive influence of scarification and stratification on salmonberry and thimbleberry germination. Barber (1976) conducted an

extensive set of studies on salmonberry germination and seedling establishment in western Washington. Therefore, germination experiments conducted in this study were to re-affirm the findings of Barber (1976) and Stewart (1975) and establish reliable estimates of the seed demography parameters for the model.

Barber (1976) and Ruth (1970) suggest that salmonberry and thimbleberry seedling survival are influenced by microclimatic conditions found under different forest canopy types. Therefore, seedling survival was compared among 4 different sites in the Coast Range representing 3 different microclimates as indicated by vegetation types (Franklin and Dyrness, 1973) and proximity to the Pacific Ocean.

Basal bud production, sprouting, and sprout growth were identified as important asexual reproductive processes in the Rubus model (Chapter 2). Salmonberry and thimbleberry basal bud production on rhizomes could be influenced by temperature, position on the rhizome relative to the parent plant, and parent plant neighborhood conditions. Rhizomes were collected from mature stands of each species, cut into sections and placed in growth chambers set at different temperature regimes to determine basal bud production and sprouting.

Microclimatic variation was believed to be the major factor influencing salmonberry and thimbleberry seedling

and sprout growth (Barber, 1976). Growth analysis of plants started in the field from seed and basal stem cuttings was conducted at two sites: Woods Creek at the east edge of the Coast Range which is characterized as relatively hot and dry, and Pioneer Mountain in the interior of the Coast Range which is relatively cool and moist (Table 3.1). Pioneer Mountain does not receive significantly more precipitation than Woods Creek, however morning coastal fog, which reduces the duration of vapor pressure deficits, was commonly observed during the hot days of the growing season (Hemstrom and Logan, 1984).

METHODS FOR LABORATORY EXPERIMENTS

Seed storage and scarification

Pregermination handling, storage and scarification of seed were assessed for their influence on germination. Salmonberry and thimbleberry fruits were collected in June of 1985 from the Woods Creek area (Table 3.1). The berries were divided into two lots. One lot was dried with the pulp, and the other the pulp was removed. The seed without pulp was further divided into two lots that were dried at room temperature and at 150 F. Following drying, some seed was placed in the refrigerator (dry) for 1 and 2 weeks, and 2 months prior to beginning the first germination test. The rest of the seed was stored at room temperature (approximately 27 C). Seed storage prior to refrigeration was also at room temperature. Following the storage

treatments, scarification with concentrated (10 normal) sulfuric acid, sandpaper, pinpricking, treatments with giberillic acid (10^{-3} M) were conducted. Immediately prior to the start of the germination test, additional seeds were collected from berries that dried on the shrubs in the field (Table A3.1 and A3.2). In the laboratory germination tests, growth chamber conditions were set to simulate early spring field conditions, i.e. 14 hours of light at 27 C and 10 hours dark at 8 C. In all the germination experiments there were 3 replications (germination dishes) with 20 seeds per dish placed on germination paper that was maintained moist with water. Statistical analysis was conducted on treatment means of proportions of germinated seed per dish with MSUSTAT (1986).

Germination following scarification was further tested by pregermination treatment with sodium hyperchloride and KNO_3. Seed was collected from the Woods Creek area in August of 1985, 4 months prior to the start of the experiment. The seeds were stored at room temperature. The growth chamber was set at 14 hours of light at 27 C and 10 hours of darkness at 10 C (Table A3.4).

Combined scarification and stratification

The combined influences of scarification and stratification on germination of salmonberry and thimbleberry seeds were tested in the laboratory. Seed were collected in August of 1985 and stored at room temperature.

The seeds were surface sterilized with sodium hyperchloride (chlorox) for 10 minutes, then half the seeds of each species were scarified for 15 minutes with H_2SO_4. Stratified seed was placed in moist soil at 5 C for 7 months while other seeds remained at room temperature. At the end of stratification seeds were placed on paper in germination dishes and placed in a growth chamber with 14 hours of light at 27 C and 10 hours dark at 10 C.

Natural seed scarification

Barber (1976) observed salmonberry seeds in bird droppings. The influence of natural scarification on germination by passing seed through the gut of a bird (chicken) was tested. Seeds from the current growing season which had dried on the plants in the field were collected and used directly in the experiment. Seeds (500 of each species) were forced directly into the crop of chickens and feces were collected for 48 hours following ingestion. Other storage and scarification (H_2SO_4) treatments that had proved successful in previous experiments were included as controls (Table A3.3).

Effect of substrate on germination

The effect of substrate and temperature variation on germination was tested in the laboratory by placing seeds with similar pre-treatments on soil (collected from the same location that seed was collected), and germination paper, in two growth chambers with different temperature

settings. This experiment was conducted in December of 1986 with seed that was collected in August of 1985. The seed was stored at room temperature, except for one treatment which was stored in the refrigerator at 5 C (Table A3.5). The variable environment growth chamber was set at 14 hours of light at 27 C and 10 hours dark at 10 C. The constant environment chamber was set at 27 C for 14 hours of light and 27 C for 10 hours of dark (Table A3.5 and A3.6). Statistical analysis was conducted separately for each species because they were placed in different growth chambers.

Basal bud production and sprouting

Mature stands of salmonberry were visited in December at Randal Saddle and thimbleberry at Woods Creek (Table 3.1). Rhizomes were located and followed back to the parent plants. Percent canopy cover overtopping the parent plant was estimated for conifers, broadleaf tree and shrub species. Undergrowth canopy cover was estimated for shrubs and herbs. Genet and ramet density within 1 m radius of the parent was recorded. The rhizomes were collected and taken to the laboratory where they were cut into 20 cm sections. The diameter, number of buds, and distances from the center of the section to the parent plant and end of the rhizome were recorded for each section. Rhizome pieces were placed on wet fabric and incubated in four different growth chambers each having different temperature settings (Table

3.2). The number of active buds (Table A3.8 and A3.9), and the number of sprouts (buds that broke dormancy and produced an expanding leaf) were counted for each rhizome section at 2, 3, 4, 5 and 8 weeks (Table 3.2 and 3.3). Active buds were green or white indicating recent development or expansion and subsequntly are more apt to expand into new sprouts than buds which are covered with brown scales and are dormant or dead.

METHODS FOR FIELD EXPERIMENTS

Salmonberry and thimbleberry germination and seedling survival was determined in 4 experiments at 5 sites in the Coast Range (Table 3.1). Sites were located at Woods Creek, Pioneer Mountain, Cascade Head, Waldport and Beaver Creek. All the sites were logged and burned prior to the experiments.

Salmonberry germination and seedling survival at Beaver Creek

An experiment to assess salmonberry field germination and seedling survival was conducted at Beaver Creek (Table 3.1). The site was clearcut in June 1988, intensively burned in September of the same year, and 1000 salmonberry seeds/m^2 were planted on 35 0.5 m^2 plots in December. The site was dominated by red alder (Alnus rubra) and salmonberry prior to overstory removal. Seedlings were counted in 35, 0.05 m^2 frames biweekly for the entire 1989 growing season (38 weeks).

Seed burial, germination and seedling survival

In the first experiment, salmonberry and thimbleberry seeds were collected in the summer of 1985. The seeds were placed with topsoil in 3 cm deep by 10.2 cm diameter chambers made from plastic rings covered at each end with nylon mesh (< 1 mm). Fifty seeds of a species were placed in each chamber. Topsoil was obtained from under a decaying log to minimize the naturally occurring seed in the chambered soil and to avoid using soil sterilization which could alter soil properties important for germination. The chambers were placed at the soil surface and buried 10 cm deep. The top nylon mesh cover was removed from half of the chambers to allow the activity of seed and seedling predators. Chambers were placed under the canopies of mature salmonberry and thimbleberry plants in the clearcuts at the Woods Creek and Pioneer Mountain sites. Seedlings present in chambers placed on the soil surface were counted and marked monthly. Buried chambers were recovered from the Pioneer Mountain site in the fall 1, 2 and 3 years later. The number of seeds in each chamber were counted. Empty seed coats were assumed to be from seeds that germinated and died. The difference in the number of seeds recovered from the covered and uncovered chambers less the number that germinated was used to claculate the number of seeds removed by predators. A sample of 20 seeds from each recovered chamber were placed on a germination plate to

determine immediate viability. The seeds that did not germinate were assumed to be dead or dormant. Tetrazolium tests for seed viability were attempted, but results were inconclusive.

Seedling and sprout survival at coastal sites

Two clearcuts, one near Waldport and the other at Cascade Head (Table 3.1), on the Siuslaw National Forest were selected for a second field experiment to test seedling and sprout survival. Both sites prior to harvest were mature forests with large Douglas-fir, western hemlock and sitka spruce dominating the overstory. Salmonberry was a common component in the understory before harvest. Both sites were harvested and burned in preparation for planting conifer seedlings in 1985.

Two permanent 20 m transects were established at each site in 1986. Five 1 m^2 permanent frame locations were located randomly along each transect. Seedlings and sprouts of all species dead or alive were counted in the fall of 1986, 1987, and 1988. Percent survival of salmonberry and thimbleberry seedlings and sprouts was calculated as $[1 - (d/(a + d)]*100$, where d is the number of dead individuals and a the number of live individuals at an observation time.

Seedling survival in the density experiment

The fourth study in which salmonberry and thimbleberry seedling survival was assessed (the density experiment)

will be described in detail in Chapter 4.

Growth analysis

Growth analysis was conducted on plants grown from seed and basal stem cuttings at the Woods Creek and Pioneer Mountain sites (Table 3.1). Seed was collected from wild populations near each site in the fall and stored (dry) over winter at 5 C. Basal stem cuttings were collected from wild populations at each site. The number of active (green or white) buds was counted and the fresh weight of each cutting was recorded. A subset of basal stem cuttings of each species from each site was collected, weighed, dried, and reweighed to determine a fresh weight to dry weight regression to estimate initial dry weights for each cutting planted. The cuttings and seeds were planted in pots that were buried to the soil surface. For the first 4 harvests of 1986 and 1987 plants were planted in 1 gallon pots, later harvested plants were put in 5 gallon pots, and second and third growing season plants were placed in 1 cubic meter holes lined on the sides with plastic to contain roots and rhizomes. Soil was replaced in the holes and tamped prior to planting. Planting was done in April of 1986 and 1987.

Emergence of seedlings and sprouts was recorded every 3 to 5 days. Five plants were destructively sampled every 20 to 30 days the first growing season, and once in the second and third growing seasons at estimated maximum

foliage production.

The first growing season portion of the experiment was repeated in 1987. Seeds and cuttings were planted directly in the soil, because the plants that were grown in pots the previous year were not as robust as those planted directly in the soil. Mortality also was high for the potted plants which reduced the number of observations and the accuracy of parameter estimates. Therefore, only the first season results from 1987 will be reported. The 1987 data also was used to calculate the growth parameters over three growing seasons. Comparison of growth from seed versus cuttings over the three growing seasons was restricted by salmonberry seedling mortality at both sites and thimbleberry seedling mortality at Pioneer Mountain.

Immediately prior to harvest, height and canopy diameter of each plant was measured. Following removal from the field, the number of active buds was counted, then the plants were separated into leaves, stems, root crown, roots, active buds, and rhizomes. Leaf area was measured with the Licor 3100 Area Meter. Shoots were counted and all the material was dried at 70 C for 48 hours. Dry biomass was then recorded for each structure on each plant and added to the original biomass and bud count data.

Absolute growth rate (AGR), instantaneous relative growth rate (RGR), unit leaf rate (ULR), leaf area ratio (LAR), height growth rate (HGR), leaf area growth rate

(LAGR), and root/shoot ratios are all measures of plant performance (Hunt, 1982). These parameters were used to assess the difference in growth between plants grown from seed and those grown from cuttings, and the difference in growth of each species at the two sites. The parameters were defined or calculated as follows:

AGR = The slope of the regression of total plant biomass on time in days.

RGR = The slope of the regression of the natural log (ln) of total plant biomass on time in days. Quadratic equations for the relationships between ln biomass and time improved the fits of the regressions, but the simple equations were used to compare RGR's for each species and propagule type with a single value, and to maintain the assumption of a constant RGR so ULR could be calculated.

LAR = The leaf area divided by the total plant biomass. LAR was constant over the time of the experiment (the slope of the regression of LAR on time was not significantly different from 0, $p > 0.05$).

ULR = RGR / LAR The mean LAR and ULR over the time period of the experiment were used for statistical analysis. This calculation of ULR requires that RGR and LAR are constant over the period for calculation.

HGR = The slope of the regression of height on time in days.

LAGR = The slope of the regression of leaf area on time in

days.

R:S = The root biomass (not including the root crown) divided by the shoot biomass (including stem and leaf biomass, but not the root crown).

Parameters were calculated for the first growing season in the 1986 and 1987 experiments, and for three growing seasons on a portion of the plants started in 1986. The differences between pairs of calculated values for plants grown from seed and cuttings, and plants grown at each site were determined by testing for differences in slopes and intercepts (Draper and Smith, 1981) for all parameters except LAR, ULR and R:S where PROC TTEST (SAS, 1984) was used (Tables 3.8 - 3.11).

Structural allocation differences between plants grown from seed and those grown from cuttings was qualitatively examined with areograms showing the mean biomass allocation to leaves, stems, root crown, roots, and rhizomes (Figures 3.5 to 3.8).

RESULTS OF LABORATORY EXPERIMENTS

Seed storage and scarification

Fresh salmonberry and thimbleberry seed do not readily germinate in the laboratory without scarification and stratification. These experiments substantiate the findings of Barber (1976) that a stratification period is necessary for salmonberry seed to break dormancy. These experiments also compare thimbleberry germination behavior with that of

salmonberry.

In the first experiment the only salmonberry seeds that germinated (3.3%) within 45 days were those that were stored for two weeks at 5 C (dry) and scarified for two hours in sulfuric acid (Table A3.1 and A3.2). Sulfuric acid scarification for 0.5 to 1 hours induced 44% and 42% germination of thimbleberry. The salmonberry and thimbleberry seeds used in this experiment were collected within three weeks of beginning the test, therefore little afterripening had probably occurred.

Three more experiments were conducted to determine if seed scarification and chemical treatments would induce germination without stratification (Table A3.3 to A3.6). None of the treatments induced significant germination in salmonberry, however thimbleberry germination reached 50% following 0.75 hours of H_2SO_4 scarification and 37% when germinated in a 0.1% KNO_3 solution (Table A3.4).

Combined scarification and stratification

The methodology described by Barber (1976) for inducing salmonberry germination was used. Seven months of stratification following 15 minutes of scarification with H_2SO_4 caused a significant increase in germination of both species. Additional scarification increased salmonberry, but not thimbleberry germination (Figure 3.2 and Table A3.7) which may indicate that salmonberry has a more thick seed coat.

Natural seed scarification

Out of 500 seeds of each species fed to chickens, 5.8% of the salmonberry and 1.9% of the thimbleberry seeds were recovered intact. Many remnants of seed coats were found. None of the recovered seed germinated (Table A3.3).

Effect of substrate on germination

Thimbleberry germination was 20% (Table A3.4) on paper and 22% (Table A3.6) on soil without any pretreatment. Germination on paper was significantly increased to 50% and 42% with H_2SO_4 scarification and germination in 0.1% KNO_3, respectively (Table A3.4). Thimbleberry germination on soil was not improved with H_2SO_4 scarification (Table A3.6).

Basal bud production and sprouting

When salmonberry rhizomes were removed from the soil there was a significant positive correlation ($r = 0.36$) between active bud number and distance from the parent plant. This observation indicates an increase in active buds at the distal end of rhizomes. There was not a similar correlation for thimbleberry. There also was no correlation of bud number with rhizome diameter or fresh weight for either species.

An average of 8 buds/20cm and 3 buds/15cm of salmonberry and thimbleberry rhizome, respectively, were present 4 weeks after placing in the growth chambers. It was not possible to determine if the buds were axilary or adventitious. At 8 weeks there was an average of 3

salmonberry (Table 3.2) and 2 thimbleberry (Table 3.3) sprouts per rhizome piece. There was no differences in bud production between temperature incubation treatments for either species (Table A3.8 and A3.9), except at 8 weeks when a number of buds began to die and/or sprout in some of the treatments. In the first two weeks there was a greater number of sprouts in the constant warm (60 F) growth chamber (Table 3.2 and 3.3). This difference in sprouting was not maintained, indicating that the constant warm temperature accelerated, but did not increase sprouting of either species.

There were no correlations between bud or sprout production and size of rhizomes or the number of buds at time of collection for either species. Thimbleberry bud size measured as basal diameter was positively correlated with distance from parent ($r = 0.54$), rhizome diameter ($r = 0.52$) and section fresh weight ($r = 0.51$). This correlation may indicate that distal tissues on the rhizomes are stronger sinks for assimilates, which may translate into greater reproductive potential from the rhizome as distance increases from the parent plant. However, there was a negative correlation ($r = -0.32$) between thimbleberry sprouts and distance from parent. There was a positive correlation ($r = 0.48$) between number of salmonberry sprouts after 5 weeks and distance from the parent plant. These inconsistantcies make interpretation of bud and sprout

production patterns difficult.

There was a negative correlation ($r = -0.36$) between thimbleberry clump (genet) density surrounding the parent genet and number of buds produced per rhizome section in the laboratory. The number of thimbleberry sprouts per rhizome section was negatively correlated ($r = -0.53$) with conifer cover over the parent genet, however, it was positively correlated with intraspecific genet ($r = 0.54$) and ramet density ($r = 0.54$). These correlations suggest that increased intraspecific competition (density) from genets reduces bud production potential on rhizomes, but not sprouting potential. Interspecific competition, however, may reduce sprouting potential from the thimbleberry rhizomes.

RESULTS OF FIELD EXPERIMENTS

Field germination and seedling survival

When salmonberry seeds were planted in chambers at the soil surface at Woods Creek, only 1 seed out of 500 (0.2%) germinated and that seedlings died after 2 months. Salmonberry seeds placed under the same conditions at the interior Coast Range site (Pioneer Mountain) had 3% and 5% germination the first year in both uncovered and covered chambers, respectively (Table 3.4). Germination was 7% and 3% in the buried, covered and uncovered chambers the first year, but no germination occurred after 2 and 3 years in the buried chambers. At the soil surface, germination was

1% the second year and 4% the third year in covered and uncovered chambers. The covered versus uncovered and the buried versus surface factors had no significant effect on salmonberry germination.

There was a significant number of salmonberry seeds lost from uncovered chambers the first year in the field (Table 3.3). Seed loss was attributed to seed predators which removed 27% of the seed from the surface and 12% from the buried chambers. Seed losses were greater the second and third year, but the covered versus uncovered factor was not significant the second and third year. However, more surface seeds were lost than buried seeds in the first and second year indicating that salmonberry seeds on the soil surface are more exposed to destruction and removal agents than buried seed. There was a trend of increased nondormant viabile salmonberry seed that was removed from uncovered chambers (Table 3.4). This may be the result of increased exposure at the soil surface to environmental agents that leach germination inhibitors from the seed coat (Barber, 1976). The majority of the salmonberry seed that was unaccounted and removed from the chambers were in the dead or dormant category (Table 3.4).

Thimbleberry seed, in chambers at Woods Creek had 7.4% and 4.2% germination the first and second years. Average seedling survival at the end of the first growing season was 2.2%. No seedlings survived to the end of the third

year. At Pioneer Mountain a maximum of 7% thimbleberry germination was observed the first year and no germination after 2 and 3 years (Table 3.5). However, 25% of the seedlings were still alive in October of the first year. There was no effect of chamber cover or burial on the proportion of thimbleberry seed lost after 1, 2 or 3 years in the soil. Thimbleberry seed may be less susceptible to predation because of its relatively small size. There was increased viability (readiness to germinate) of buried thimbleberry seeds as compared to seeds on the surface (Table 3.5). Buried seeds may be less exposed to destructive agents that occur at the soil surface.

No natural occurring salmonberry seedlings were observed in the density experiment during the first 3 years of study at Woods Creek. There was an average of 1 natural occurring thimbleberry seedling for every 2.3 m^2, all of which occurred in the first year at Woods Creek. No seedlings survived to the end of the third year. At Pioneer Mountain there was an average of 1 natural occurring salmonberry seedling observed in every 4.4 m^2 over the 3 year period of the density experiment. No natural occurring salmonberry seedlings survived for more than 1 year. On average, one thimbleberry seedling occurred naturally in every 6 m^2 at Pioneer Mountain. Thimbleberry germination occurred throughout the season at this site, whereas salmonberry at both sites, and thimbleberry

germination at the Woods Creek site was restricted to the spring.

An average of 21.4 salmonberry seedlings/m^2 occurred naturally the first year after disturbance at the Waldport site and 15.3 of the seedlings remained alive the second year and 8.8 were alive the third year. Salmonberry seedling survival significantly decreased the second year, but not the third year (Table 3.6). At Cascade Head there was also a decrease in salmonberry seedling survival the second year and no significant change the third year (Table 3.7). There was a consistent decrease in the number of salmonberry seedlings each year at both coastal sites (Table A3.10). Salmonberry sprout survival also decreased the second year, but increased the third year at the Waldport site (Table 3.6). Salmonberry seedling survival became significantly less than sprout survival in the third year (Table A3.11). There were few thimbleberry seedlings or sprouts at either site, therefore interpretation of trends was limited by small sample size.

Salmonberry germination reached a maximum (2.7%) in the early spring 16 weeks after fall planting in the final field germination experiment at Beaver Creek (Table A3.12). There were 1.4 natural occurring seedlings/m^2 and 4.1 seedlings/m^2 where 1000 seeds/m^2 were planted. The average germination of the planted seed was calculated to be 0.3%. Viability of the planted seed was 8.5% in a growth chamber

in the laboratory. The difference between field and laboratory germination can be partially explained by the loss and appearance of seedlings between each field census. Whereas, in the laboratory, even if a seedling dies it will still be present to count on the germination plate. Therefore, the percent germination in the field was probably underestimated in this experiment.

Growth analysis

Absolute growth rates (AGR's) were greater for sprouts than for seedlings of both species at both sites the first growing season (Table 3.9). However, there was no difference between thimbleberry sprout and seedling AGR's when calculated over three growing seasons at Woods Creek (dry) (Table 3.11). Absolute growth was greater at Pioneer Mountain (moist) the first growing season for both species, but there was no difference between the sites for seedling growth (Table 3.9). By the third growing season thimbleberry sprouts were growing faster at the dry site (Table 3.11). Thimbleberry growth was greater the first season than salmonberry when both were grown from cuttings at both sites. Growth was the same from seed for the two species. After three growing seasons salmonberry and thimbleberry were growing at the same rate at the moist site, but thimbleberry was still growing faster at the dry site.

The relative growth rate (RGR) of salmonberry and

thimbleberry seedlings was greater than sprouts (Table 3.9). There was a decrease in RGR after the first season of growth. Differences in RGR between sites were not significant until the third season (Table 3.11). Thimbleberry sprouts were more efficient (higher RGR) than salmonberry sprouts at the dry site, but there was no difference at the moist site.

Leaf area ratio (LAR) is a measure of the leafiness of plants (Radosevich and Holt, 1984) and was used with the RGR to calculate the unit leaf rate (ULR). The leaf area ratios were greater for seedlings than for sprouts the first growing season (Table 3.9), but were equivalent after three growing seasons (Table 3.11). ULR was greater for sprouts than for seedlings of both species at the moist site the first growing season (Table 3.9). The leaf area growth rate (LAGR) had the same response pattern as ULR at both sites (Table 3.10). ULR for sprouts over the first three growing seasons was greater for salmonberry at the moist site and thimblberry at the dry site. Leaf area growth rate over the three growing seasons was greater for thimbleberry seedlings than sprouts at the dry site (Table 3.11).

The ratio of root mass to shoot mass is an indicator of the general allocation pattern in plants. In the first growing season the root/shoot ratio (R:S) was greater for seedlings than sprouts for both species at both sites

(Table 3.10). Salmonberry seedlings had a greater root/shoot ratio at the dry site and thimbleberry seedlings at the moist site. Salmonberry sprouts had greater root/shoot ratios at the moist site. The seedling allocation patterns during the first growing season may indicate survival strategies based on acquiring a source of water (allocation to roots) at the dry site, and competing for light (allocation to shoots and leaves) at the moist site. Long roots 40 to 50 cm deep in the soil were observed on harvested seedlings at the dry site. Barber (1976) made similar observations of salmonberry seedlings.

Allocation patterns were also assessed with areograms (Figures 3.4 to 3.7). These areograms demonstrate that total biomass had a sharp increase for both species at both sites in the third year of growth. This increase in total biomass was accompanied by a decrease in relative allocation to the root crowns and an increase in allocation to stems and rhizomes. The plants grown from cuttings allocated biomass to the root crowns during the first season, whereas seedling allocation was to the roots.

Height growth rate was greatest for sprouts the first growing season (Table 3.12). However, thimbleberry seedling height growth rate was much greater than the sprout height growth rate when calculated over the first three seasons (Table 3.12). Height growth was generally greater at the moist site. Height growth rate the first few growing

seasons may be an important indicator for establishment potential, because it is the means for acquiring light in a system where there is competition from rapid growing annual and perennial species that frequently become established following logging.

DISCUSSION

Germination of salmonberry and thimbleberry seed is influenced by three major factors: (1) stratification, (2) scarification, and (3) light availability. The laboratory and field results supported those of Barber (1976) indicating that light was not a factor necessary for germination and without scarification or stratification, complete removal of the seed coat is necessary for salmonberry germination. Cool dry storage of seed was not a substitute for stratification. Barber (1976) concluded that a water-soluble germination inhibitor is present in the salmonberry seed coat, and that it takes at least four months of stratification for a significant improvement in germination. Stratification of salmonberry seed apparently breaks dormancy by removing inhibiting substances during the first winter following dispersal. This observation, however, does not account for the scarcity of seedlings in the field. My studies suggest that a significant amount of salmonberry seed is removed from the soil surface by seed predators.

The response of thimbleberry germination to

scarification and stratification indicated that it may be under similar germination control to salmonberry. However, stratification or scarification alone may provide a suitable environment for removal of germination inhibitors from the seed coat. Thimbleberry germination was increased with acid scarification and germination in KNO_3 solution. This may indicate that increased cation concentrations accelerate leaching of the germination inhibitor from the seed coat. Thimbleberry germination was greater than salmonberry in most of the experiments that tested different scarification treatments. Difference in seed coat thickness and/or permeability could affect leaching of germination inhibitors and therefore could explain differences in germination between salmonberry and thimbleberry.

Mechanisms which govern basal bud production and sprouting in salmonberry and thimbleberry are not well understood. Physiological and environmental mechanisms are likely to be involved and deserve more extensive study. Rinne et al. (1987) found that differences in growing environment and the condition of the root system on Betula pubescens had considerable effect on formation of adventitious buds. The observations made in this study serve as preliminary indications of some factors which may directly or indirectly influence bud production and sprouting potential from salmonberry and thimbleberry

rhizomes.

The influence of conifer cover on the parent plant may reduce thimbleberry, but not salmonberry bud production. However, intraspecific ramet and genet density were positively correlated with bud production, which suggests an internal mechanism regulating this process. Temperature had no influence other than accelerating bud and sprout production of both species. This however, does not rule out the potential influence of temperature on preconditioning rhizomes for bud production. Zasada (unpublished data) found more bud production on rhizomes collected in the winter than when collected at other times during the year.

An important finding of this study was the bud production and subsequent sprout potential of salmonberry and thimbleberry rhizomes. The mean number of active buds on rhizomes immediately following removal from the field were 2 and 29 for salmonberry and thimbleberry, respectively. The mean length of salmonberry rhizomes was 247 cm and thimbleberry was 201 cm. Therefore the bud densities were 0.8 buds/m and 14.4 buds/m for salmonberry and thimbleberry, respectively. There was an average of 99 buds produced per salmonberry rhizome (40 buds/m) and 40 buds per thimbleberry rhizome (20 buds/m). However, this was only after sectioning and incubation, which are condition that are highly unlikely in the field. Therefore, the question remains, what is the potential bud bank in the

field and how does it change with different types of disturbance? The bud bank represents a significant potential for salmonberry and thimbleberry population establishment. Tappeiner et al. (1990) reported that this potential may increase for salmonberry in new clearcuts, because of significant increases in rhizome growth in the open environment.

It appears that the dominant mechanism controlling rhizome production is internal to the plant and relies upon the connection of the rhizome with the parent plant. This hypothesis could account for the negative correlations between intraspecific genet density and reduced sprout production on rhizomes away from thimbleberry parent plants. Neighboring plants have an influence on the parent plant which subsequently affects the condition and bud production potential of the rhizome. This hypothesis coincides with the findings of Rinne et al. (1987).

Three factors were identified that have an impact on salmonberry and thimbleberry seed survival: (1) seed predation, (2) burial of seed in the soil, and (3) seed longevity. Large mammals and birds have been observed eating salmonberry and thimbleberry fruits (Barber, 1976; Viereck and Little, 1972). Krefting and Roe (1949) concluded that ingestion of fruits by robins and catbirds enhances germination of Rubus seed due to the effects of scarification in the gizzards or by digestive acids.

Chickens that were fed 500 seeds of each species, completely digested most of the seeds. Only 5.8% of the salmonberry and 1.9% of the thimbleberry seeds were found intact after passing through the chickens, and none of the recovered seeds germinated. Chickens, may not be comparable with wild birds however, because they have been bred for efficient digestive systems. Small mammal droppings were observed in most of the uncovered, surface seed chambers of the field germination and seedling survival experiment. Therefore, the increase in salmonberry seed loss from uncovered, surface chambers the first year in the field may be due to removal by small mammals (Table 3.4). Predation was apparently not the prevailing mechanism for seed loss the second and third years in the same experiment. Barber (1976) found that germination was not increased after salmonberry seeds passed through coyotes. In conclusion, animals appear to play an active role in seed bank dynamics of salmonberry and thimbleberry, however they may serve as seed dispersal agents rather than predators.

Burial slowed the rate of salmonberry seed loss (Table 3.4) and decreased seed mortality processes in thimbleberry (Table 3.5). Barber (1976) reported finding buried salmonberry seed in the litter and A horizons in a salmonberry stand and a few seeds from a 30 year old conifer stand where there was no evidence of mature salmonberry. Buried Rubus seed was the second-most abundant

of all seed recovered from forests where mature Rubus species were not present (Olmstead and Curtis, 1947). The longevity of salmonberry and thimbleberry seed in the soil has not been tested, however seeds of other Rubus species can live up to 100 years (Livingston and Allessio, 1968). Salmonberry and thimbleberry seed banks declined sharply the first year followed by a slower rate of decrease the second and third year (Figure 3.3). Salmonberry seed bank dynamics indicated more variation than thimbleberry. This may be due to the apparent preference of salmonberry seed by seed predators.

Factors which influence salmonberry and thimbleberry seedling survival were narrowed to: 1) light availability, 2) moisture availability, 3) predator removal, and 4) disease. Salmonberry and thimbleberry seedling survival increased with proximity of sites to the coast (Table 3.8). This may be due to lower moisture stress at these sites, because morning fog during the summer months reduces the duration of high vapor pressure deficits (Hemstrom and Logan, 1984). Barber (1976) concluded that seedling survival is determined by a combination of factors including: competition for soil water, light intensity, and root growth inhibition by leaf mats. He further found that seedlings survived equally well on scarified and unscarified soil as long as light was not limiting. There are no reports in the literature on the susceptibility of

Rubus seedlings to predators or disease. Seedling survival was no greater in covered than in uncovered chambers for either species in the field germination and seedling survival experiment. In the density experiment seedling survival decreased with increased ramet (shoot) density. This supports the hypothesis of Barber (1976) that competition for light and soil moisture resources influences seedling survival.

The growth of salmonberry and thimbleberry seedlings can be governed by many factors in the field. In this study, I chose to conduct a comparative growth analysis between sprouts and seedlings of salmonberry and thimbleberry grown at Woods Creek and at Pioneer Mountain.

Plant growth relative to its original size (RGR) is a measure of efficiency of biomass accumulation (Hunt, 1982), and therefore may be a preferred parameter for determining the inherent growth ability of plants. However, for determining the relative ability for plant establishment, the absolute growth may provide a more accurate estimation of a plants potential to survive and prosper in a competitive environment. The relative growth rate of salmonberry and thimbleberry seedlings was greater than sprouts. This allowed thimbleberry seedlings to gain an equivalent size with sprouts after three growing seasons when there was no competition from neighboring plants. This indicates that populations may have an equal chance of

arising from seeds or cuttings if the environment is suitable for seedling survival and competition is low during the first three growing seasons. However, if both seeds and vegetative propagules are available, rapid establishment and superior absolute growth of sprouts creates a highly competitive environment for seedlings. This scenario was demonstrated at the Waldport site where survival of salmonberry sprouts was significantly greater than seedling survival after 3 growing seasons.

Using plants grown from cuttings to compare with plants grown from seed may underestimate the potential of vegetative reproduction in population establishment under natural conditions where there are large underground structures with extensive reserves to draw upon for early growth. However, after 3 growing seasons plants grown from cuttings, appeared equal in size with wild sprouts of the same species at the margins of the study areas. Kauppi et al. (1987) suggested that sprouts originating from dormant basal buds on Betula pubescens differ morphologically from shoots of the same species grown from seed. The areograms (Figure 3.4 to 3.7) provide evidence that salmonberry and thimbleberry sprouts and seedlings have different morphologies due to differences in allocation patterns. Although in one case, thimbleberry seedlings were quite similar to sprouts at a dry site over the first 3 growing seasons (Figure 3.5).

In summary, low germination of salmonberry and thimbleberry relative to bud production and sprouting restricts the potential for populations to arise from seed. Seedling survival is lower than for sprouts when both are present which may be related to the competitive advantage assumed by sprouts as a result of higher absolute growth rates in the first season of growth. Germination and seedling survival constraints are greater for salmonberry than for thimbleberry, particularly at relatively dry sites in the Coast Range. When a combination of all aspects of population establishment are considered, salmonberry had a greater establishment potential on coastal sites, and thimbleberry was better suited to the eastern (relatively dry) portion of the Coast Range.

The results of the experiments in this chapter will be incorporated as refinements to the Rubus model developed in Chapter 2. Estimates of parmater values for germination, seed and seedling survival, and rhizome bud production for salmonberry and thimbleberry will be used in the model. This information will be used in Chapter 5 to compare model simulations with observed population dynamics and to consider management strategies.

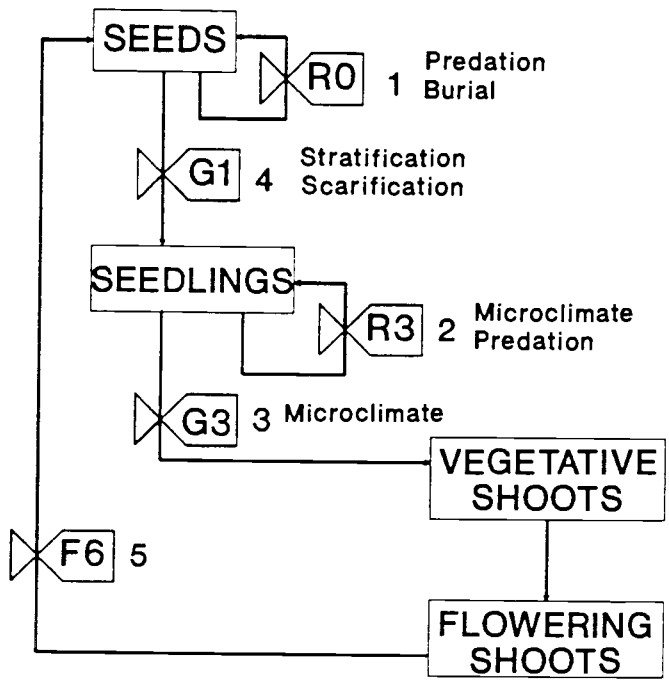


Figure 3.1. Sexual reproduction side of Rubus population model (Figure 2.1) with list of factors that may influence each demographic process. Sensitivity and elasticity importance rankings are included next to each valve symbol (1 = most, and 5 = least sensitive process).

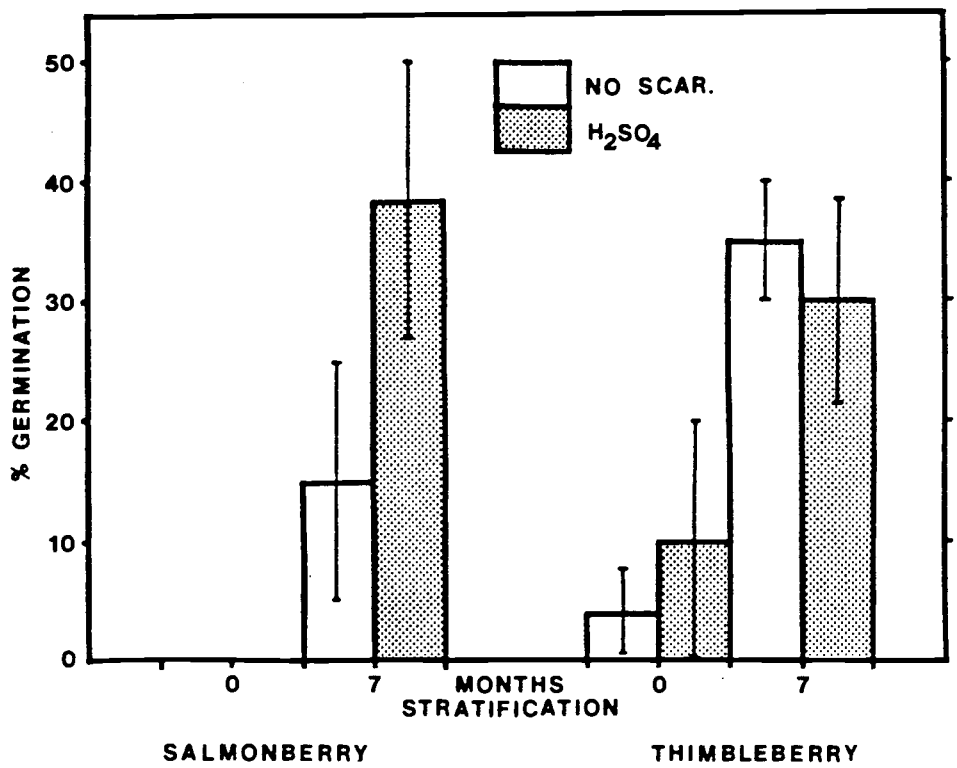
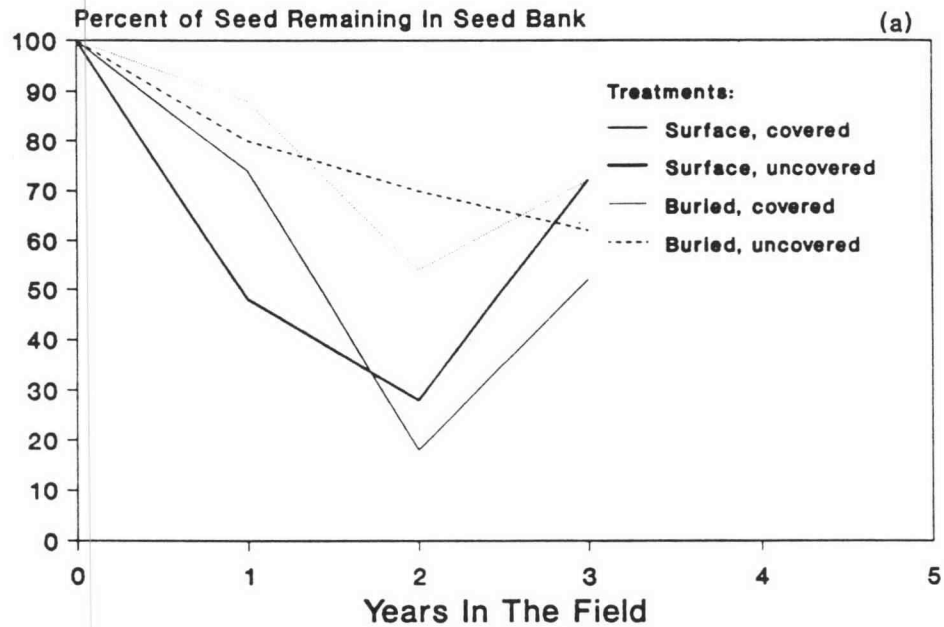


Figure 3.2. The percent germination of salmonberry and thimbleberry seed in response to no (0) or 7 months stratification and no or 15 min. of acid scarification prior to stratification.

Figure 3.3. Average percent of salmonberry (a) and thimbleberry (b) seeds remaining in the chambers 1, 2 and 3 years after placing them in the field at the soil surface and buried 10 cm at Pioneer Mountain. Half the chambers were overed with nylon mesh to exclude seed predators.


Percent of Seed Remaining In Seed Bank
(a)
100
90
80
70
60
50
40
30
20
10
0
Treatments:
Surface, covered
Surface, uncovered
Buried, covered
Buried, uncovered
0
1
2
3
4
5
Years In The Field

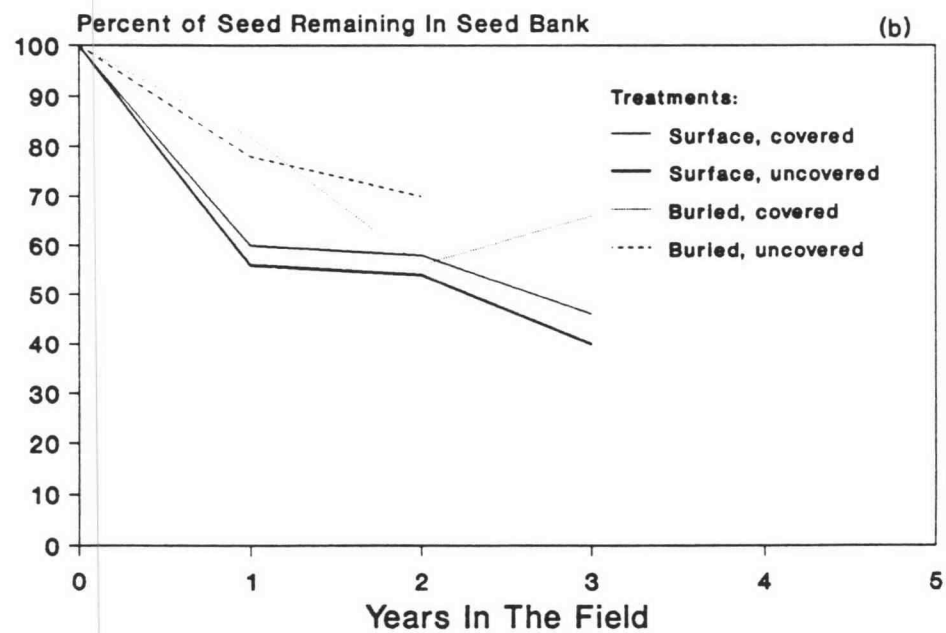
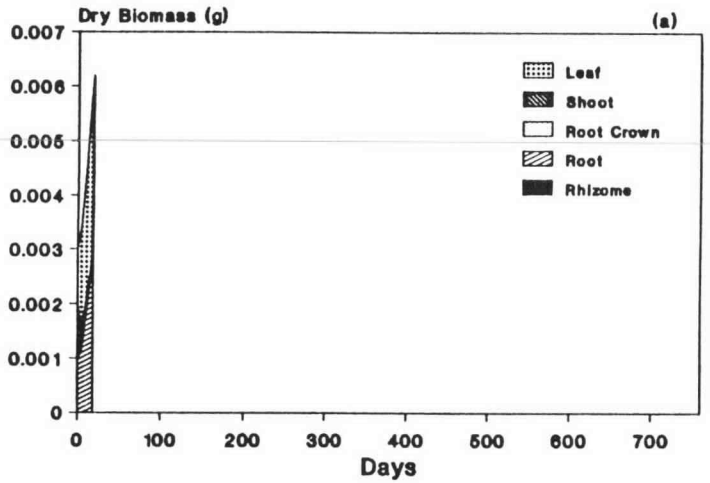
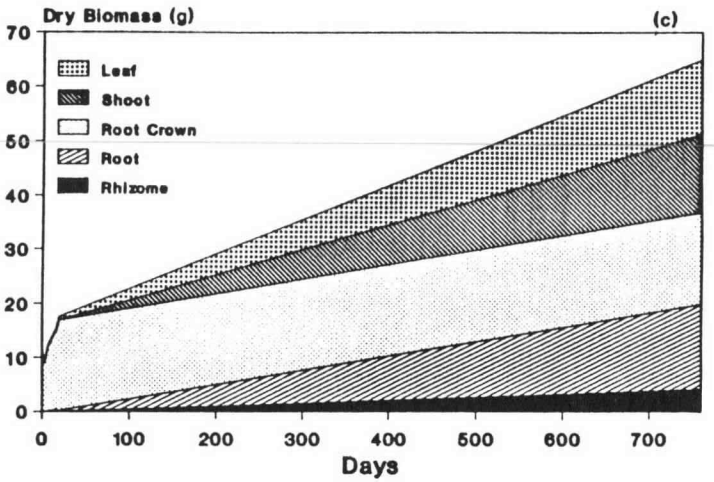
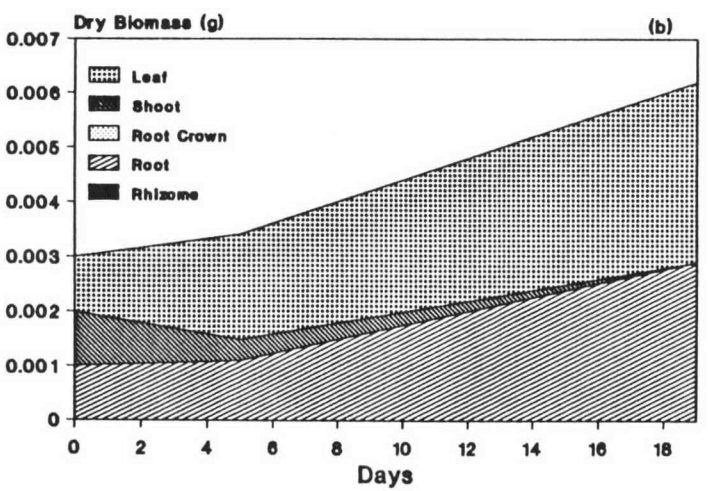

Percent of Seed Remaining In Seed Bank
(b)
100
90
80
70
60
50
40
30
20
10
0
Treatments:
Surface, covered
Surface, uncovered
Buried, covered
Buried, uncovered
0
1
2
3
4
5
Years In The Field

Fig. 3.3

Figure 3.4. Areograms of salmonberry biomass allocation to above and below ground structures at Woods Creek. (a) Seedlings over 3 growing seasons, (b) Seedlings over the first 20 days, (c) sprouts over 3 growing seasons, (d) sprouts over the first 20 days of the first growing season.


Dry Biomass (g)
(a)
0.007
0.006
0.005
0.004
0.003
0.002
0.001
0
Leaf
Shoot
Root Crown
Root
Rhizome
0
100
200
300
400
500
600
700
Days


Dry Biomass (g)
(c)
70
60
50
40
30
20
10
0
Leaf
Shoot
Root Crown
Root
Rhizome
0
100
200
300
400
500
600
700
Days


Dry Biomass (g)
(b)
0.007
0.006
0.005
0.004
0.003
0.002
0.001
0
Leaf
Shoot
Root Crown
Root
Rhizome
0
2
4
6
8
10
12
14
16
18
Days

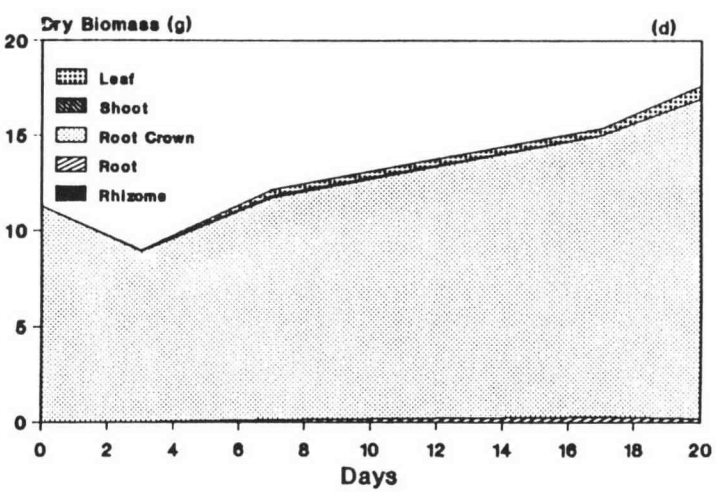

Dry Biomass (g)
(d)
20
15
10
5
0
Leaf
Shoot
Root Crown
Root
Rhizome
0
2
4
6
8
10
12
14
16
18
20
Days

Fig. 3.4.

Figure 3.5. Areograms of thimbleberry biomass allocation to above and below ground structures at Woods Creek. (a) Seedlings over 3 growing seasons, (b) Seedlings over the first growing season, (c) sprouts over 3 growing seasons, (d) sprouts over the first growing season.

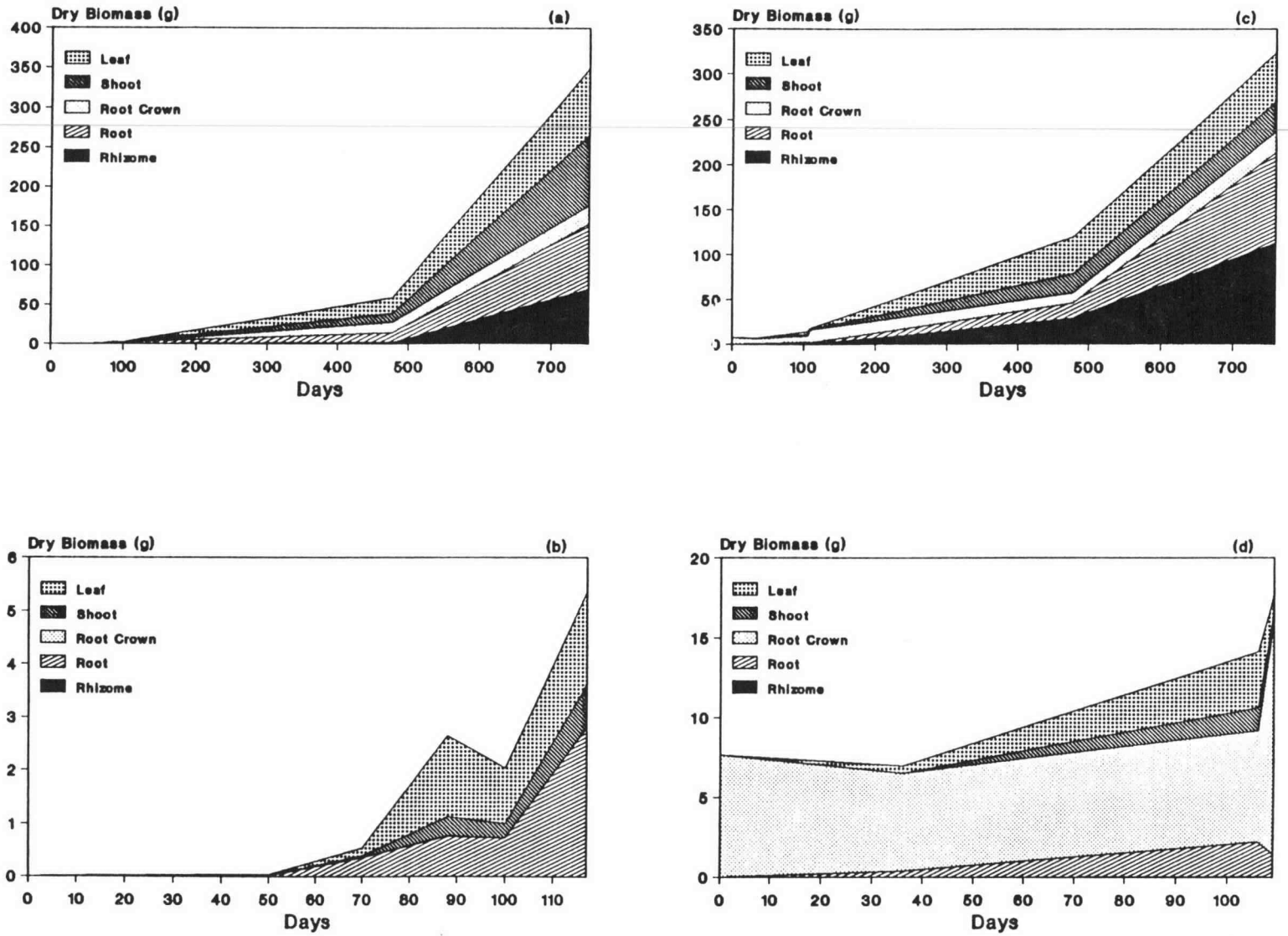
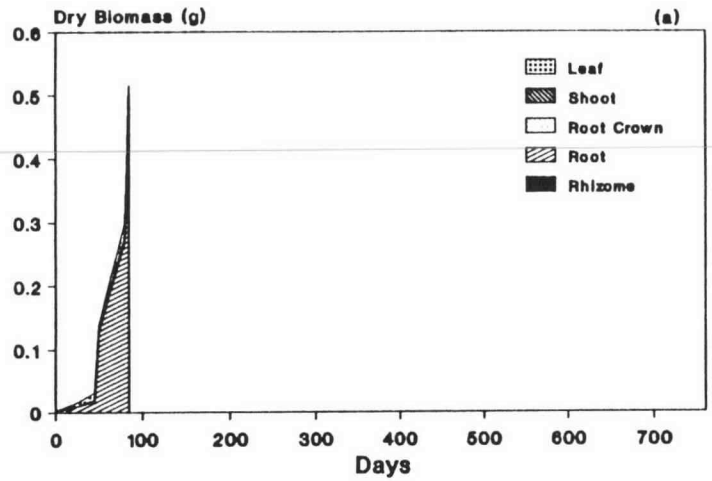
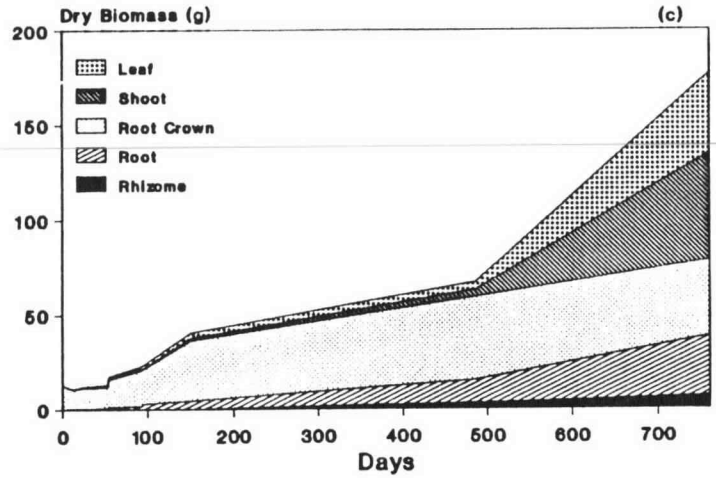
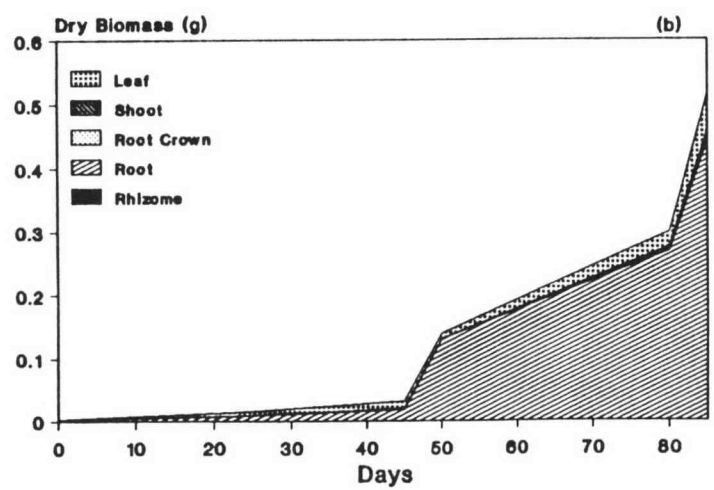

Dry Biomass (g)
(a)
Leaf
Shoot
Root Crown
Root
Rhizome
Days
Dry Biomass (g)
(c)
Leaf
Shoot
Root Crown
Root
Rhizome
Days
Dry Biomass (g)
(b)
Leaf
Shoot
Root Crown
Root
Rhizome
Days
Dry Biomass (g)
(d)
Leaf
Shoot
Root Crown
Root
Rhizome
Days

Fig. 3.5.

Figure 3.6. Areograms of salmonberry biomass allocation to above and below ground structures at Pioneer Mountain. (a) Seedlings over 3 growing seasons, (b) Seedlings over the first growing season, (c) sprouts over 3 growing seasons, (d) sprouts over the first growing season.


Dry Biomass (g)
(a)
Leaf
Shoot
Root Crown
Root
Rhizome
0.6
0.5
0.4
0.3
0.2
0.1
0
0
100
200
300
400
500
600
700
Days


Dry Biomass (g)
(c)
Leaf
Shoot
Root Crown
Root
Rhizome
200
150
100
50
0
0
100
200
300
400
500
600
700
Days


Dry Biomass (g)
(b)
Leaf
Shoot
Root Crown
Root
Rhizome
0.6
0.5
0.4
0.3
0.2
0.1
0
0
10
20
30
40
50
60
70
80
Days

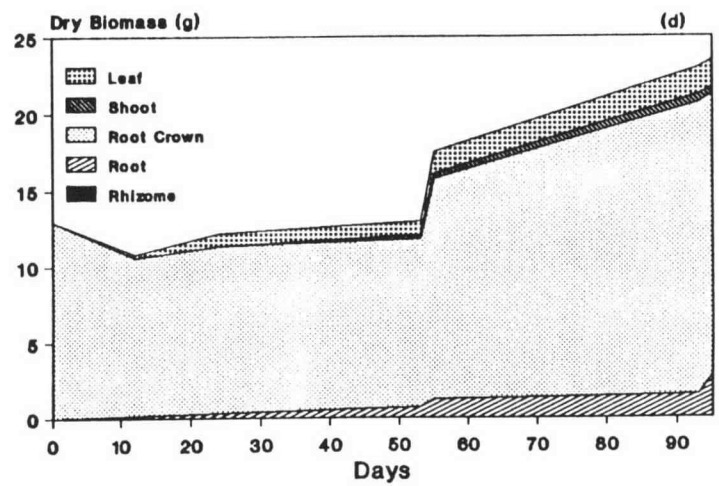
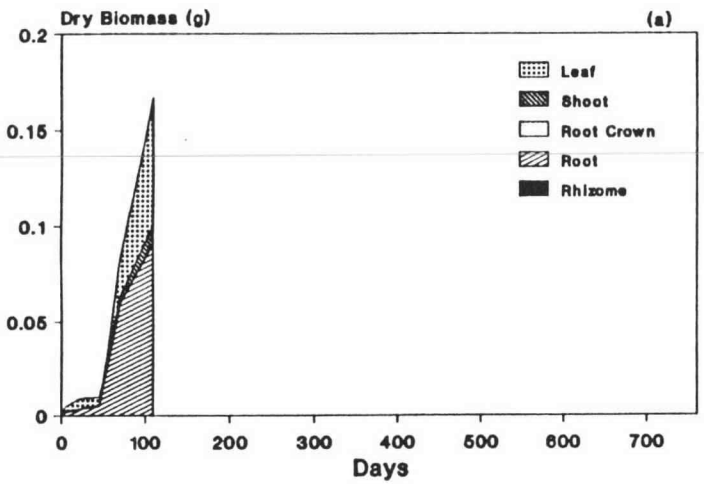
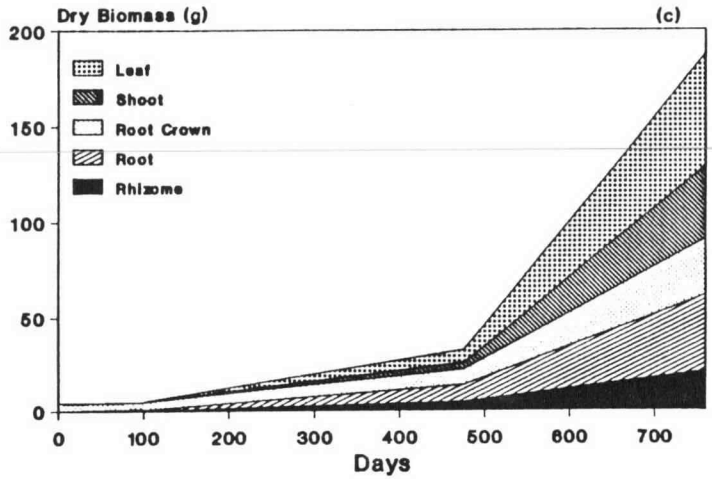
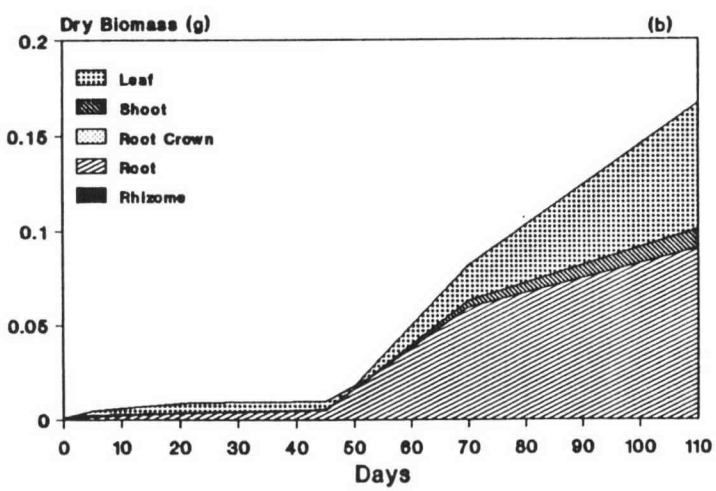

Dry Biomass (g)
(d)
Leaf
Shoot
Root Crown
Root
Rhizome
25
20
15
10
5
0
0
10
20
30
40
50
60
70
80
90
Days

Fig. 3.6.

Figure 3.7. Areograms of thimbleberry biomass allocation to above and below ground structures at Pioneer Mountain. (a) Seedlings over 3 growing seasons, (b) Seedlings over the first growing season, (c) sprouts over 3 growing seasons, (d) sprouts over the first growing season.


Dry Biomass (g)
(a)
0.2
0.15
0.1
0.05
0
Leaf
Shoot
Root Crown
Root
Rhizome
0
100
200
300
400
500
600
700
Days


Dry Biomass (g)
(c)
200
150
100
50
0
Leaf
Shoot
Root Crown
Root
Rhizome
0
100
200
300
400
500
600
700
Days


Dry Biomass (g)
(b)
0.2
0.15
0.1
0.05
0
Leaf
Shoot
Root Crown
Root
Rhizome
0
10
20
30
40
50
60
70
80
90
100
110
Days

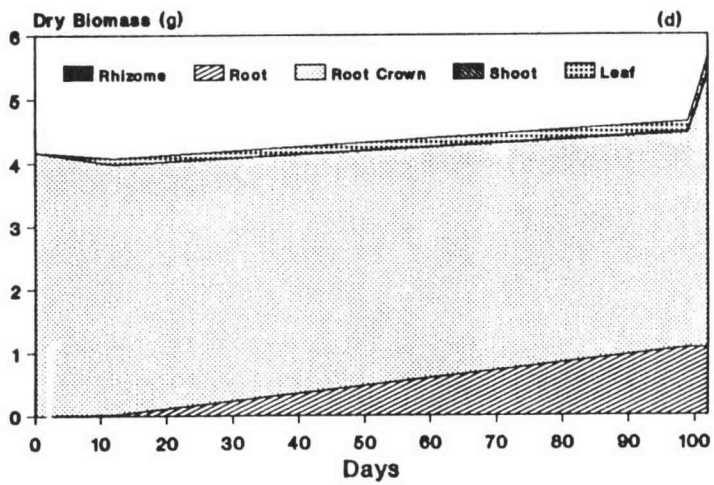

Dry Biomass (g)
(d)
6
5
4
3
2
1
0
Rhizome
Root
Root Crown
Shoot
Leaf
0
10
20
30
40
50
60
70
80
90
100
Days

Fig. 3.7

Table 3.1. Description of research sites in the western Oregon Coast Range. All but Randal Saddle were clearcuts.

Site name	Legal discription	Vegetation series[1]	Total Ann. precip. (cm)[2]	Distance to ocean (miles)[3]
Beaver Creek	S26, T12S, R11W	Sitka Spruce	229	4
Cascade Head	S22, T6S, R10W	Sitka Spruce	254	6
Pioneer Mountain (Site 2, Moist)	S23, T10S, R10W	Western Hemlock	203	8
Randal Saddle	S16, T12S, R9W	Western Hemlock	229	15
Waldport	S23, T13S, R11W	Sitka Spruce	229	3
Woods Creek (Site 1, Dry)	S2, T12S, R7W	Western Hemlock	203	30

[1] Franklin and Dyrness (1973); Hemstrom and Logan, 1984.
[2] Hemstrom and Logan, 1984.
[3] Distance in air miles

Table 3.2. Mean number of salmonberry sprouts produced on 20 cm rhizome sections collected at Randal Saddle and incubated under different temperature treatments in growth chambers.

Treatment	Weeks in the growth chambers 3	4	5	8
Constant 60 F	2.2 b	3.2 b	3.9	2.9
Constant 50 F	0.0 a	0.2 a	2.1	3.0
16 hr. 50 F 8 hr. 60 F	0.0 a	0.4 a	2.7	3.7
16 hr. 60 F 8 hr. 50 F	0.3 a	1.6 a	2.9	2.3
P-value	.0000	.0000	.0925	.3738
LSD (0.05)	0.82	1.44	-	-
n	20	20	20	20

Means followed by the same letter within a column are not significantly different (LSD 0.05).

Table 3.3. Mean number of thimbleberry sprouts produced on 15 cm rhizome sections collected at Woods Creek and incubated under different temperature treatments in growth chambers.

Treatment	Weeks in the growth chambers 3	4	5	8
Constant 60 F	0.5 b	0.8	1.5	2.3
Constant 50 F	0.0 a	0.1	0.9	2.4
16 hr. 50 F 8 hr. 60 F	0.0 a	0.1	2.0	2.5
16 hr. 60 F 8 hr. 50 F	0.0 a	0.5	1.4	2.0
P-value	.0222	.1795	.2679	.8745
LSD (0.05)	0.42	-	-	-
n	10	10	10	10

Means followed by the same letter within a column are not significantly different (LSD 0.05).

Table 3.4. The fate of salmonberry seeds 1, 2 and 3 years after planting at Pioneer Mountain in the interior Coast Range.

Treatment	Year	Field Germination			Lost			Viable in lab.			Dead or Dormant		
		1	2	3	1	2	3	1	2	3	1	2	3
		%											
Surface:													
Covered		5	1	0	22	80	49	0	1	2	73	18	49
Uncovered		3	0	4	49	73	25	2	0	6	46	27	65
Buried:													
Covered		7	0	0	6	47	29	0	2	1	86	51	67
Uncovered		3	0	0	18	30	39	4	10	5	78	60	56
Factor P-values:													
Surf. vs Buried		N.S.	N.S.	N.S.	.001	.010	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
Cov. vs Uncov.		N.S.	N.S.	N.S.	.012	N.S.	N.S.	.050	N.S.	N.S.	N.S.	N.S.	N.S.

N.S. = Not significant (P > 0.05)

Table 3.5. The fate of thimbleberry seeds 1, 2 and 3 years after planting at Pioneer Mountain in the interior Coast Range.

		Field Germination			Lost			Viable in lab.			Dead or Dormant		
Treatment	Year	1	2	3	1	2	3	1	2	3	1	2	3
		%											
Surface:													
Covered		7	0	0	33	42	54	5	13	12	55	45	34
Uncovered		4	0	0	40	46	60	9	0	2	54	54	38
Buried:													
Covered		3	0	0	16	44	35	44	26	13	38	30	52
Uncovered		2	0	-	21	30	-	36	53	-	41	17	-
Factor P-values:													
Surf. vs Buried		N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	.000	.015	N.S.	N.S.	N.S.	N.S.
Cov. vs Uncov.		N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.

N.S. = Not significant (P > 0.05)

Table 3.6. Mean salmonberry and thimbleberry seedling and sprout survival on a clearcut near Waldport in the Coast Range that was burned in preparation for planting of conifer seedlings.

Years after burning	Salmonberry		Thimbleberry	
	Seedling	Sprout	Seedling	Sprout
	%			
1	86 b	99 b	100	100
2	62 a	81 a	92	100
3	59 a	100 b	83	100
P-value	.0462	.0090	.3795	-
n	30	29	16	4

Means followed by the same letter within a column are not significantly different (LSD 0.05).

Table 3.7. Mean salmonberry and thimbleberry seedling and sprout survival on a clearcut at Cascade Head in the Coast Range that was burned in preparation for planting of conifer seedlings.

Years after burning	Salmonberry		Thimbleberry	
	Seedling	Sprout	Seedling	Sprout
	%			
1	100 b	100	100	-
2	63 a	50	67	-
3	87 ab	100	83	-
P-value	.0501	.4659	.5090	-
n	23	6	8	0

Means followed by the same letter within a column are not significantly different (LSD 0.05).

Table 3.8. Mean percent seedlings surviving from the previous year at 4 sites across the Coast Range.

Year	Woods Creek	Pioneer Mountain	Wald-Port	Cascade Head
	%			
Salmonbewrry:				
1	0	1	86	100
2	0	0	62	63
3	0	0	59	87
Thimbleberry:				
1	2	25	100	100
2	3	10	92	67
3	0	0	83	83

Table 3.9. The first season absolute growth rate (AGR), instantaneous relative growth rate (RGR), unit leaf rate (ULR), and leaf area ratio (LAR) of salmonberry and thimbleberry grown from seed and basal stem cuttings at Woods Creek (dry site) and Pioneer Mountain (moist site) in 1987.

	AGR		RGR		ULR		LAR	
	dry	moist	dry	moist	dry	moist	dry	moist
	g/day		g/g/day		$g/cm^2/day$		cm^2/g	
Salmonberry:								
Seed	0.003	0.001	0.042	0.020	0.002	0.001	49	53
		**	*	*		*	*	*
Cutting	0.042 *	0.143	0.013	0.016	0.003	0.002	13	14
Thimbleberry:								
Seed	0.0002	0.002	0.016	0.014	0.001	0.0002	54	93
	**	**	*	*		*	*	*
Cutting	0.137 *	0.496	0.020	0.025	0.003	0.001	24	31

* Adjacent means within a column or row are significantly different ($p < 0.05$).

** Adjacent means within a column or row are significantly different ($p < 0.01$).

Table 3.10. The first season height growth rate (HGR), leaf area growth rate (LAGR), and root/shoot ratio (R:S) for salmonberry and thimbleberry grown from seed and basal stem cuttings at Woods Creek (dry site) and Pioneer Mountain (moist site) in 1987.

	HGR		LAGR		R:S	
	dry	moist	dry	moist	dry	moist
	cm/day		cm^2/day			
Salmonberry:						
Seed	0.046 **	0.016 **	0.143 *	0.025 **	1.591 **	1.250 **
Cutting	0.067 *	0.096	1.495	3.626	0.373 **	0.511
Thimbleberry:						
Seed	0.004 **	0.025 **	0.012	0.107 **	0.623 **	3.284 **
Cutting	0.143 **	0.331	7.565 **	21.66	0.385	0.466

* Adjacent means within a column or row are significantly different ($p < 0.05$).

** Adjacent means within a column or row are significantly different ($p < 0.01$).

Table 3.11. The absolute growth rate (AGR), instantaneous relative growth rate (RGR), unit leaf rate (ULR), and leaf area ratio (LAR) of salmonberry and thimbleberry grown from seed and basal stem cuttings at Woods Creek (dry site) and Pioneer Mountain (moist site) for 3 growing seasons.

	AGR		RGR		ULR		LAR	
	dry	moist	dry	moist	dry	moist	dry	moist
	g/day		g/g/day		$g/cm^2/day$		cm^2/g	
Salmonberry:								
Seed	--	--	--	--	--	--	--	--
Cutting	0.071 **	0.205	0.002 **	0.004	0.0004	0.0005	16	16
Thimbleberry:								
Seed	0.413	--	0.014 **	--	0.0009	--	55	--
Cutting	0.396 **	0.218	0.005 *	0.004	0.0007 **	0.0001	26	31

* Adjacent means within a column or row are significantly different ($p < 0.05$).
** Adjacent means within a column or row are significantly different ($p < 0.05$).

Table 3.12. The height growth rate (HGR), leaf area growth rate (LAGR), and root/shoot ratio (R:S) of salmonberry and thimbleberry grown from seed and basal stem cuttings at Woods Creek (dry site) and Pioneer Mountain (moist site) for 3 growing seasons.

	HGR		LAGR		R:S	
	dry	moist	dry	moist	dry	moist
	cm/day		cm^2/day			
Salmonberry:						
Seed	--	--	--	--	--	--
Cutting	0.043 **	0.078	2.939 **	6.316	0.397	0.836
Thimbleberry:						
Seed	0.116 **	--	26.598 **	--	0.638 **	--
Cutting	0.080	0.080	13.903 *	8.480	1.025	0.895

* Adjacent means within a column or row are significantly different ($p < 0.05$).

** Adjacent means within a column or row are significantly different ($p < 0.01$).

CHAPTER 4

THE ROLE OF DENSITY IN REGULATION OF SALMONBERRY AND THIMBLEBERRY POPULATION GROWTH

ABSTRACT

Salmonberry (Rubus spectabilis) and thimbleberry (R. parviflorus) are major components of the shrub vegetation found in association with conifer seedlings on clearcuts in the Coast Range of western Oregon. This study was initiated to assess processes which naturally regulate salmonberry and thimbleberry population dynamics as part of the refinement of a Rubus population simulation model. The influence of intra- and inter-specific density on biomass production and demographic processes (survival and reproduction at, and transition between life history classes) was investigated at different phenological stages, and in two microclimate environments. Monoculture populations of each species were established at several densities from basal stem cuttings at two sites. Three formulations of intraspecific density were used in the analyses: genets, ramets, and ramets per genet. Genet density was stable after initial mortality resulting from planting. Ramet density increased rapidly from low planting (genet) densities, but asymptotically from high genet densities indicating that high density populations were approaching a carrying capacity. Total plot biomass

increased and leveled at an asymptote with increasing ramet density, which conforms to the law of constant final yield. Some populations showed a decrease in total plot biomass at the highest densities. Individual ramet mass formed a negative hyperbolic relationship with ramet density, but only after weighting the individual ramet mass with genet density to account for the added influence of genet density. The influence of inter-specific density on mean ramet mass was investigated in an addition series with salmonberry and thimbleberry planted in mixture. Thimbleberry had a greater influence on salmonberry than salmonberry had on thimbleberry. Population trajectory plots of ln ramet mass/genet against ln ramet density over time indicated that self-thinning did not occur in most of the ramet populations even though the slopes of linear regressions included and exceeded -3/2. Phenology stage and site, alone, were significant factors influencing demographic processes. Regressions of demographic parameter values against intraspecific density indicated that density rarely accounted for more than 10% of the variation in the values calculated from the planted populations. Site and species were added as independent variables in the regressions which in most cases improved the models. Even with these additions the full regressions generally accounted for less than 40% of the variation in demographic parameters. However, a few important demographic processes

(bud transition to sprouts, sprout transition to mature shoots, and mature shoot survival) showed a significant response to density, site and species, which may result in effective population regulation.

INTRODUCTION

The vegetation on clearcuts in the Coast Range of western Oregon is typically dominated by shrub species. Salmonberry and thimbleberry populations are common components of this vegetation and have a significant impact on conifer seedling survival and growth (Ruth, 1956; Newton and White, 1983; Wagner, 1989). Salmonberry and thimbleberry have a clonal growth habit with extensive rhizome systems which allow populations to rapidly invade large areas and prevent establishment of other species (Marchant and Sherlock, 1984; Hausler and Coates, 1986). Information on the mechanisms which naturally regulate salmonberry and thimbleberry population growth following disturbance can be useful in developing management strategies (Mortimer, 1983).

A population modeling approach was used to study the biology of salmonberry and thimbleberry populations (Chapter 2). A generic (Rubus spp.) stage class projection matrix model (Figure 2.1) was developed from existing information in the literature (Chapter 2). Sensitivity and elasticity analysis (Maxwell et al., 1988; Moloney, 1988) on the initial model indicated that vegetative reproduction and associated transition and survival parameters were important in governing the number of total shoots produced (Chapter 3). Therefore, research was focused on studying the demographic processes involved with vegetative

reproduction (basal bud production), establishment (transition from buds to sprouts), and perpetuation (survival at each life history class) of salmonberry and thimbleberry populations.

Four suites of factors were hypothesized which may influence the demographic processes: phenological stage, interference, environment (microclimate and resource availability), and management. This study focused on the influence of interference at different phenological stages and at two different sites representing different growing season climates. Two approaches were used to study the effect of interference on salmonberry and thimbleberry. First, the influence of inter- and intra-specific density on biomass production was considered by assessing conformity of these species with theoretical density-biomass relationships developed with primarily annual species (Bleasdale and Nelder, 1960; Harper, 1977; Radosevich, 1987; Shinozaki and Kira, 1956; Yoda et al., 1963; White, 1980). The second approach was to assess the direct influence of intraspecific density on demographic processes identified to be important in regulating population growth. Since salmonberry and thimbleberry tend to grow in monoculture stands, intraspecific competition was hypothesized to be a central interference factor influencing transitions and subsequent population growth (Figure 4.1). Barkham (1980) concluded that control of the

size of the adult population of Narcissus pseudonarcissus (a clonal herb) was through the plastic response of clonal growth to density.

There are no known studies which have experimentally assessed the influence of intraspecific density on clonal-shrub species growth or demographics. By understanding which demographic parameters (processes) are most influenced by intraspecific density, processes most vulnerable and subsequently most appropriate for population control practices may be identified. For example, control tools could be chosen or designed to specifically influence demographic processes that have been identified as vulnerable. Interspecific competition could be added to the system in the form of cover crops or living mulch to enhance the influence of intraspecific competition at a vulnerable phenological stage or life history class. The information on mechanisms which govern population dynamics can be incorporated into a population model. Development of a model which elucidates the demographic behavior of these species would allow hypotheses to be formulated on management alternatives.

The effect of intraspecific competition on clonal-herbaceous plant species was studied by Hutchings (1979) and Barkham (1980). A common issue raised in these studies was the definition of the functional individual in order to determine population density. Hutchings (1979) used the

term ramet to denote vegetatively-produced progeny. Sarukhan and Harper (1973) define the ramet as the functional unit in a vegetatively-reproducing species. The functional independence of a ramet may not, however, be realized until it achieves physical independence from the parent plant. The term genet has been used consistently among studies to indicate the genetic individual or product of a seed, which may be a large clone (set of ramets). In mature salmonberry and thimbleberry populations, it is usually impossible to determine a genet or a functionally independent ramet, therefore individual aerial shoots that arise from basal buds (below the litter layer) were considered ramets as defined by Hutchings (1979). Three measures of salmonberry and thimbleberry population density were selected for analysis: ramets, genets, and ramets/genet (Figure 4.2).

The influence of interspecific density (competition) on biomass production was assessed in an addition series experiment (Radosevich, 1987; Roush et al., 1989) where salmonberry and thimbleberry were planted together at different densities and proportions.

The first objective of this study was to determine if the experimental (planted) salmonberry and thimbleberry populations growing in Coast Range clearcuts were approaching a density carrying capacity which could indicate possible density-dependent effects on demographic

processes. Second, to determine if density-biomass relationships exist for these species that are consistent with the law of constant final yield (Harper, 1977), the reciprocal yield rule (Bleasdale and Nelder, 1960; Radosevich, 1987; Shinozaki and Kira, 1956), and the self-thinning rule (Yoda et al., 1963; White, 1980). These models have evolved from research on annuals, and perennial species with single above ground shoots. Clonal growth form species have rarely been assessed for compliance with these established density-biomass relationships (Hutchings, 1979). The third objective was to determine if density had an influence on demographic processes, and how that influence might change with different phenological stages and at different sites. An underlying objective was to incorporate density-dependence as a population growth regulating mechanism into the Rubus model as part of the refinement process described in Chapter 2.

METHODS

Populations of salmonberry and thimbleberry were established from basal stem cuttings (root crowns) at two sites in the Coast Range of western Oregon. The Woods Creek site (Site 1) was approximately 30 miles inland from the Pacific Ocean at the eastern edge of the Coast Range. The Pioneer Mountain site (Site 2) was approximately 8 miles inland in the interior Coast Range. Both sites were in the Douglas-fir/Hemlock type (Franklin and Dyrness, 1962),

although the Pioneer Mountain site was near the eastern edge of the Sitka Spruce type and received morning fog which decreased the duration of vapor pressure deficits throughout the dry summer periods. Therefore, the Woods Creek site is sometimes referred to in this report as the dry site and Pioneer Mountain as the moist site (Table 3.1). Both sites were clearcut followed by intensive burns during the spring of 1985. The following summer, study sites were selected within the clearcuts where previous populations of salmonberry and thimbleberry were growing. The ground was cleared of all debris except rooted tree stumps. Exposed salmonberry and thimbleberry root crowns and rhizomes were also removed. All sprouts that appeared during the first growing season were treated with glyphosate (N-phosphonomethylglycine isopropylamine) at 0.75 kg ai/ha). In January of 1986, basal stem cuttings (root crowns) were collected from mature wild populations of salmonberry and thimbleberry located adjacent to each experimental site. In February and March the cuttings were planted into 4 m^2 plots at 1, 9, 25, and 81 cuttings per m^2 in monocultures. The plots were organized into blocks (4/species at site 1 and 3/species at site 2) and 3 strips per block representing harvest years (1986, 1987, 1988) (Figure 4.3).

Three separate blocks at each site were planted with mixtures of salmonberry and thimbleberry root crowns in an

addition series. Densities were 8, 13, and 36 cuttings per m^2 and mixture proportions were 0.375 for one species and 0.625 for the other, and the reciprocal. All the plots were weeded constantly.

Demographic data was collected for the first three growing seasons at the establishment (early spring bud brake), reproductive (early summer fruit set), and senescence (fall) phenological stages from a 1 m^2 sample in the center of each plot. All flowering shoots, vegetative mature shoots (with basal buds), sprouts (new shoots with no basal buds), seedlings, rhizomes and basal buds within 3 cm of the soil surface were mapped at each phenological stage (e.g. Figure 4.4). Basal buds include all potential ramet producing buds on the root crown and on rhizomes. Maps were then compared by counting numbers of individuals in each life history class at each each phenological stage over 3 growing seasons. Transition, survival, mortality and reproductive (number of basal buds produced and seed fecundity) values were then calculated .

Above ground biomass samples were collected from the central 1 m^2, at the reproductive stage of 1, 2, and 3 year old planted monoculture populations of each species. Similar biomass samples were collected from the addition series, but only in the third year. Plant material was dried for 48 hours at 70 C and weighed. The number of ramets and genets was recorded for each population at

harvest. Mean ramet biomass was calculated as the total biomass divided by the ramet density.

Population growth rate and density biomass relationships were assessed using linear (PROC REG) and nonlinear (PROC NLIN) regression in SAS (1986). Constant final yield was determined by comparing the fit of linear and nonlinear asymptotic models (Table 4.1). Mean ramet mass in populations was predicted by fitting the Watkinson (1980, 1984) equation to the data:

$$w = w_m(1 + a * N)^b$$

where w is the mean ramet mass per genet, N is the ramet density, w_m is the dry matter production of an isolated ramet, a is the area required to achieve w_m, and b can be interpreted as a resource use efficiency index for the population (Watkinson, 1980, 1984; Firbank and Watkinson, 1985). When the exponent b = -1 the relationship conforms to the reciprocal yield rule (Watkinson, 1980). Since w_m and a are time dependent parameters, the b parameter was used for comparing density-biomass relationships between phenological stages and sites.

An expanded version of the Watkinson (1980, 1984) model was used to predict the mean ramet mass of one species (A) growing in mixture with another species (B):

$$w_A = w_{mA}(1 + a_A(N_A + z_{BA}N_B))^b$$

where w, N, w_m, a, and b are as previously defined and z_{BA} is the competition coefficient (the relative competitive

ability of species B on species A) (Firbank and Watkinson, 1985).

There was no previous theory on the form of the density-demographic parameter relationships. Therefore, the best model form for each parameter and each species at each site at each phenological stage was selected by comparing mean square errors from a set of linear and nonlinear model forms (Table 4.2) fit through the untransformed data. In every case where density was the primary independent variable, ramet density, genet density and density in terms of mean ramets per genet were independently tested.

RESULTS

Observations on population growth

The influence of intraspecific density on planted populations of salmonberry and thimbleberry was determined by plotting genet and ramet density over time. Genet density remained constant over time after initial mortality caused by planting shock (Figure 4.5 and 4.6). The early mortality was constant (34%) across all the planting densities. Therefore, each population stabilized near a single genet density. There were no new natural established genets over the period of the experiment. All seedlings observed in the populations died (Chapter 3).

Larger ramet populations were observed for salmonberry at the Pioneer Mountain site than at Woods Creek. The opposite was true for thimbleberry. Ramet density

consistently increased over the three growing seasons of the experiment (Figures 4.7 and 4.8). Ramet population growth was exponential for most of the populations at low planting (genet) density and more linear (with decreasing slope) as genet densities increased. Ramet population growth rate (ramets/m^2/month) increased with increasing genet density up to approximately 25 genets/m^2. Then, with further increases in genet density, the ramet population growth rate remained constant or decreased slightly (Figure 4.9). These trends indicate that the high genet density populations (25 and 81 genets/m^2) were approaching a ramet carrying capacity and the low genet densities (1 and 9 genets/m^2) were still in the exponential population growth phase where resources were not limiting (Whittaker, 1975). Increased ramet mortality was observed between the 3 and 6 and 14 and 19 month periods which correspond to the senescence stages of the first and second growing seasons (Figure 4.7 and 4.8). Seasonal flux in ramet population density increased with increased genet density.

The number of ramets produced per genet consistently increased over the period of the experiment with low genet density populations increasing faster than high density genet populations (Figure 4.10 and 4.11). The population growth rate, defined as mean number of ramets/genet/m^2/month, sharply decreased from low (1 genet/m^2) to medium (25 genets/m^2) densities, and decreased

only slightly with further increased genet densities. This trend indicates that individual genets have a ramet carrying capacity that is influenced by the genet density, and that ramets/genet may be a sensitive indicator of early resource limitations to genets of salmonberry and thimbleberry.

Density-biomass relationships

The influence of intraspecific density on salmonberry and thimbleberry populations was analyzed further by assessing density-biomass relationships. In all cases (except where noted) ramet density was the independent (density) variable that produced the lowest mean square errors in the regressions. Total above-ground dry biomass was plotted over ramet density for each species at each site and each harvest year. Linear, quadratic and non-linear asymptotic models were fit to each data set and compared for goodness of fit. The best models were selected based on the lowest mean square errors (Table 4.3).

The first year, salmonberry at Pioneer Mountain and thimbleberry at Woods Creek had best fits with asymptotic models (constant final yield was reached), whereas the other populations were best described with linear equations indicating that individual ramets within the populations were not yet competing for resources and limiting growth (Figure 4.12). During the second and third years, a constant biomass was reached each growing season suggesting

compliance with the law of constant final yield (Harper, 1977). The increase in the constant final yield asymptote each year was the result of accumulation of perennial tissues (e.g. wood in stems). The decline after reaching an asymptote (carrying capacity) in the second and third years for thimbleberry at Pioneer Mountain was indicative of populations where mature individuals are self-thinning (Hutchings, 1979). The planted thimbleberry cuttings were quick to establish and grew rapidly at Pioneer Mountain, therefore those populations may have been more mature (reaching carrying capacity sooner) relative to other populations growing at Woods Creek or salmonberry populations at either site.

After plant populations reach the biomass carrying capacity, average individual plant biomass decreases as density increases (the reciprocal yield rule) (Shinozaki and Kira, 1956; Bleasdale and Nelder, 1960). This relationship has been shown to produce a negative hyperbolic curve when individual plant mass is plotted over density (Radosevich, 1987). When salmonberry and thimbleberry mean ramet mass was plotted against ramet density, all ramets fit the typical density response curve except those planted at the lowest density, which fell well below where they were expected (Figure 4.13a). Smaller ramets at the low ramet density, which was also the low genet density, may be the result of increased intra-genet

competition, because there are more ramets per genet at the low genet densities. Therefore, the reciprocal yield rule did not fit these clonal plants unless genet density as well as ramet density was accounted for by dividing the mean ramet mass by the genet density to produce a mean ramet mass per genet. This weighting of the data provided the expected negative hyperbolic relationship between mean ramet mass and ramet density (Figure 4.13b). These plots were fit to the Watkinson (1980, 1984) equation, and the resource use efficiency index (b) was estimated for each species and each year at each site (Table 4.4; Figure 4.14).

Thimbleberry mean ramet mass generally conformed more to the reciprocal yield rule (b = -1) than salmonberry, but both species had b values between -3.0 and -0.6 (Table 4.4). The resource use efficiency was lower (more negative) for salmonberry at Woods Creek (Site 1) than at Pioneer Mountain (Site 2). Salmonberry and thimbleberry showed similar patterns at Site 2 with an increase in resource use efficiency the second growing season (Year 2) (Figure 4.14). There was a consistent increase in the mean square error from the first to the third growing season (Table 4.4). This trend could be interpreted as a decrease in the importance of competition over time in regulating growth in the populations (Weldon and Slauson, 1986).

The influence of interspecific density on mean ramet

mass per genet was analyzed using data from populations of salmonberry and thimbleberry growing in mixture in an addition series. The data was fit with the Firbank and Watkinson (1985) equations to determine relative competitive values (z) and resource use efficiency values (b). Interpretations drawn from these parameters are restricted by the lack of full (density of species A by density of species B) data matrices (Figure A4.1). The predicted 3-dimensional surfaces (Figure 4.15) indicates that thimbleberry responds similarly to intra- and inter-specific density, whereas salmonberry at Pioneer Mountain is more influenced by the presence of thimbleberry than other salmonberry ramets. The influence of thimbleberry density on salmonberry mean ramet mass per genet was greater ($z = 4.13$) than the influence of salmonberry density on thimbleberry mean ramet mass per genet ($z = 0.519$) at Pioneer Mountain (Figure 4.16a and Table 4.5). There was not enough data to predict the influence of thimbleberry density on salmonberry at Woods Creek. There were no differences in the resource use efficiency index between the species or sites or between the mixture and monoculture populations (Figure 4.16b).

The salmonberry and thimbleberry planted monoculture populations were next analyzed to determine if they were self-thinning. If the slope of a linear regression of the natural log (ln) of mean individual plant mass against ln

of density is near -3/2 the population is generally self-thinning (White, 1980). Regressions were performed on data for each species, year and site using ln mean ramet mass and ln mean ramet mass per genet as dependent variables against ln ramet density. The slopes, using ln mean ramet mass as the dependent variable, were all less than -1, however when ln ramet mass per genet was used as the dependent variable, the slopes ranged from -1.01 to -2.44. The weighting of mean ramet mass with genet density, again improved regressions by increasing F and r^2 values. However, it could not be concluded that the ramet populations were necessarily self-thinning, because plots of ln mean ramet mass per genet against ln ramet density for each population showed that 87% of the populations were following a trajectory of increasing ramet density after three growing seasons indicating that any ramets that died were replaced by more than one new ramet (Figure 4.17).

Hutchings (1979) analyzed several data sets from clonal perennial herbs and found that most populations exhibit a cyclic trajectory over time, returning to approximately the same position on the ln ramet mass by ln ramet density graph every 12 months. He concluded that the -3/2 power rule was not applicable to ramet populations of clonal herbs, because ramet density is restricted by environmental controls and controls internal to the plant rather than strictly ramet growth. It was not possible to

determine if the salmonberry and thimbleberry populations would follow trajectories similar to those Hutchings (1979) found, because the populations were apparently just beginning to reach a ramet density equilibrium where density-dependent mortality may occur, at the end of the study (Figure 4.7 and 4.8).

The ln of mean genet mass was plotted against ln genet density for each population to see if genet population trajectories were conforming to the thinning rule. Some genet populations (43%) had decreased in genet density along a thinning line (slope = -3/2) the third growing season, conforming to the self-thinning rule (Figure 4.18). This response was most evident in the thimbleberry populations, and may indicate that genets of these clonal shrub species conform to the -3/2 thinning rule (Figure A4.2). Genet populations with efficient utilization of resources, self-thin along a line with a gradient of -3/2 (White, 1985; White, 1980). At maturity, most clonal herbs approach this thinning line, but do not transgress it (Hutchings, 1979).

Density-demographic parameter relationships

The density-biomass relationships consistently indicated that ramet density was influencing the biomass production of salmonberry and thimbleberry populations. Therefore, it was assumed that ramet density would influence demographic processes involved with biomass

allocation or growth, like basal bud production (V5), bud transition to sprouts (G2), and sprout transition to mature vegetative shoots (G4). It was not clear, however, if ramet density would have an influence on survival or mortality of basal buds, sprouts or vegetative shoots, since there was no evidence for self-thinning in ramet populations. Three-dimensional scattergrams with a demographic parameter as the dependent (vertical axis) variable, and ramet density and time as independent variables, provided an initial screening of the demographic data for response patterns (Figure A4.3 to A4.5). The scattergrams made it clear that ramet density may influence some parameters, but not others, and it may not act uniformly for salmonberry and thimbleberry at different sites or at different phenological stages. Therefore, mean values for each demographic parameter and species at each site and phenological stage were compared to determine the significance of these factors in determining demographic parameter values.

Analysis of variance for all the demographic parameters (G2, R2, G4, R4, R5 and V5) compared indicated that site and phenological stage were significant factors ($p < 0.05$). Species was also a significant factor for R4, R5 and V5. Environmental differences between sites and climatic differences and physiological status of the plants associated with different phenological stages had an

influence on demographic parameters. Therefore, equations to predict each demographic parameter as a function of density were determined separately for each phenological stage with indicator variables in the equations for each species and each site.

Table 4.6 lists the equations which provided the best fit for the response of each demographic parameter to density at each phenological stage. Figure 4.19 demonstrates the scatter of the data that was typical for most of the demographic parameters plotted against density. Density typically was a significant parameter in the regressions, but it accounted for less than 10% of the variation in the data when it was the only independent variable in the models. However, r^2 values increased to an average of 0.256 when site and species were included as independent variables. This still represents a small proportion of the total variation that was accounted for by the models. These results indicate that most of the demographic processes as defined by the conceptual model (Figure 4.1) are primarily constrained by factors other than intraspecific ramet density. The results also indicate that differences in the environment at the two sites as well as species differences explains little about the behavior of demographic processes associated with clonal population development. However, viewing the general trend in the response of demographic processes to density, site and species factors might be

misleading. Three out of the 4 most sensitive (Table 2.1) demographic parameters (R5 at reproduction, G4 at senescence, and R5 at establishment), had r^2 values of 0.40, 0.37 and 0.33, respectively (Table 4.6). This indicates that intraspecific density, site and species were playing a stronger role in regulating these particular processes which may be the primary population growth regulating mechanisms. So even though these factors were not strongly influencing all the demographic processes, the influence on a single process at a cetain time may be enough to have a profound effect on population growth.

DISCUSSION

Plant population dynamics theory has been centered on density-dependent interactions in plants, and yet the theoretical models have omitted the influence of density on clonal growth habit plants (Pacala, 1989). The reason for this omission is primarily due to the difficulties in defining the functional individual in clonal species populations (Cook, 1985).

In the search for the best formulation of density to account for variation in mean ramet mass, a pattern in response to different density formulations was found that provides insights into the functional individual in salmonberry and thimbleberry populations recovering from disturbance. The first growing season mean ramet mass was best accounted for by density in terms of ramets/genet. In

the first growing season, the ramets were primarily utilizing reserves in the planted cutting for growth, therefore competition was occurring within the genet. A similar situation may occur when sprouting (ramet establishment) occurs from disturbed genets. The second growing season root systems began to grow and competition for resources in the soil probably increased, consequently genet density provided the best formulation of density for predicting mean ramet mass. Between the second and third growing seasons, extensive rhizome growth occurred and ramet establishment away from the parent plants was occurring. At the same time the canopies of all but the lowest density populations were closing, possibly causing increased competition among ramets for light. At this point ramet density became the best formulation for predicting mean ramet mass. However, weighting mean ramet mass with genet density gave further improvement in the predictions indicating that the density formulation should include the effects of ramet and genet density in the third growing season.

The results of the experiments in this study indicate that biomass accumulation was strongly and negatively correlated with density, but survival, reproduction and transitions between life history states (demographic parameters) were not necessarily correlated with density. However, density-dependence of several demographic

paramters was found in some growing seasons (Chapter 5). Thus, density may be regulating population growth, but only at certain times and for certain paramters.

The lack of a general strong density influence on demographics suggests that mechanisms internal to the plant like hormonal regulation are also acting on these processes. It is difficult to identify density-independent mechanisms since many internal physiological processes are directly or indirectly influenced by the biotic and abiotic environment (Gross, 1989).

Detection of density-dependence of demographic processes may be restricted by the use of inappropriate measures of density. Some ramets arise from the root crown and consequently have many close neighbors, whereas other ramets sprout away from the parent plant on rhizomes. Therefore, there is always high variation in the paramters due to the variation in the density within the population. A measure of ramet density that would account for the proportion of ramets that occur on rhizomes versus crowns may allow detection of density effects. Further factors which complicate the interpretation of the lack in strong density-dependence of demographics involve the degree of integation between ramets, the ability for rhizomes to place ramets in low density neighborhoods, and the degree that genetic programming plays in the regulation of demographic processes (Harper, 1985; Maillette, 1985).

There was evidence that density-dpendence was acting on specific demographic parameters defined in the Rubus model. Therefore, the next step was to refine the model by incorporating density-dependent feedback functions into the model in place of the transition matrix parameters (Chapter 5).

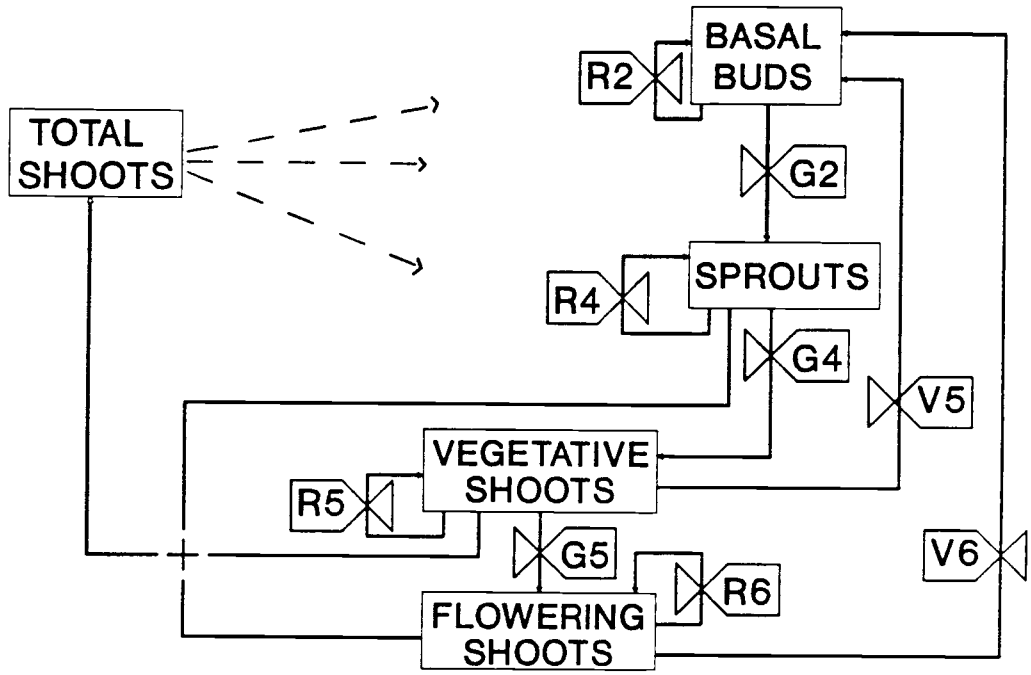


Figure 4.1. Diagram of the vegetative reproduction side of the Rubus population model indicating the feedback influence (dashed arrows) of total shoots (sprouts + vegetative shoots + flowering shoots) on demographic parameters (R2, G2, R4, G4, V5, and R5).

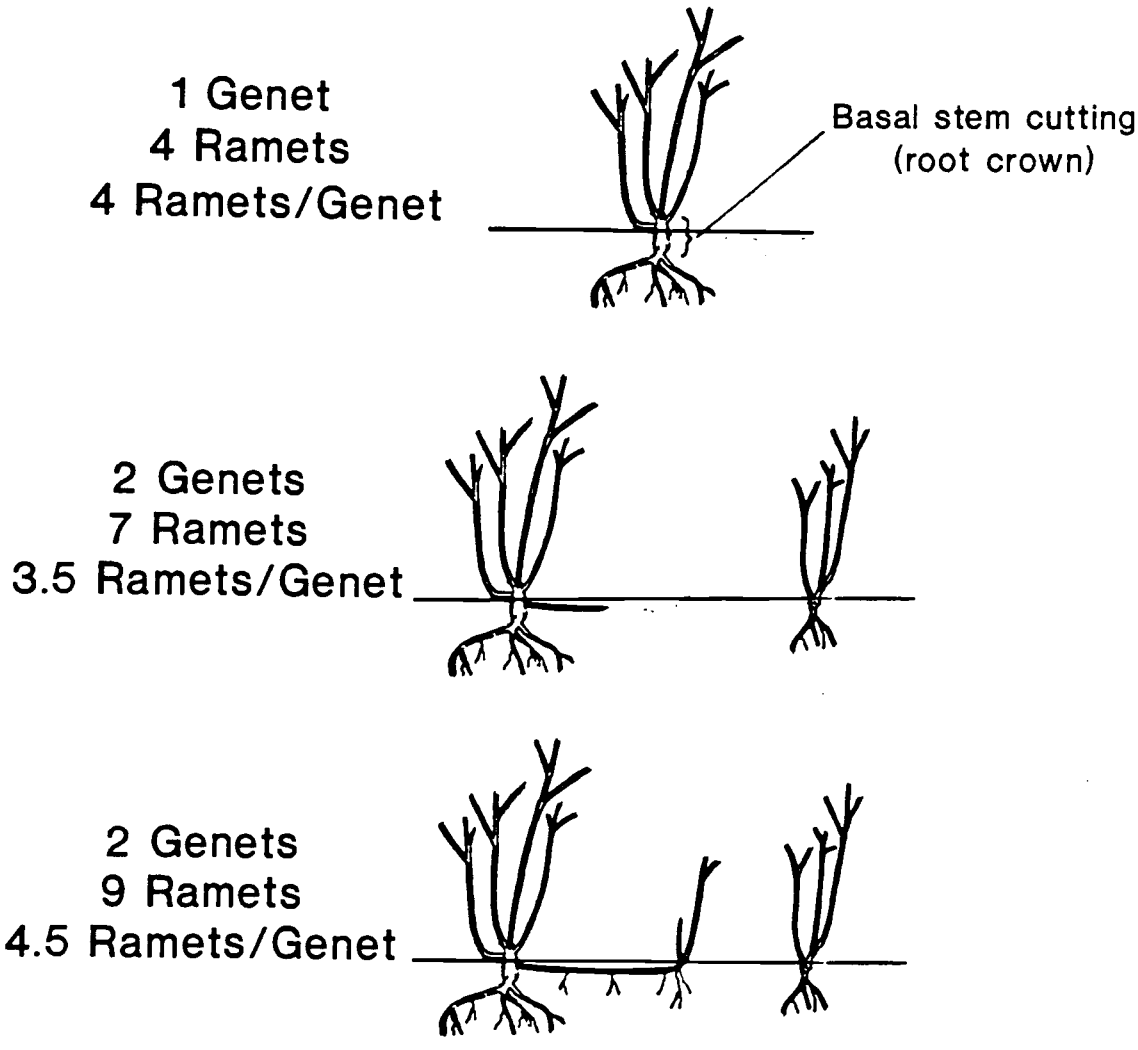


Figure 4.2. Diagram which demonstrates the three formulations of intraspecific density. Each basal stem cutting (root crown) that was planted was considered a genet and each aerial stem was a ramet.

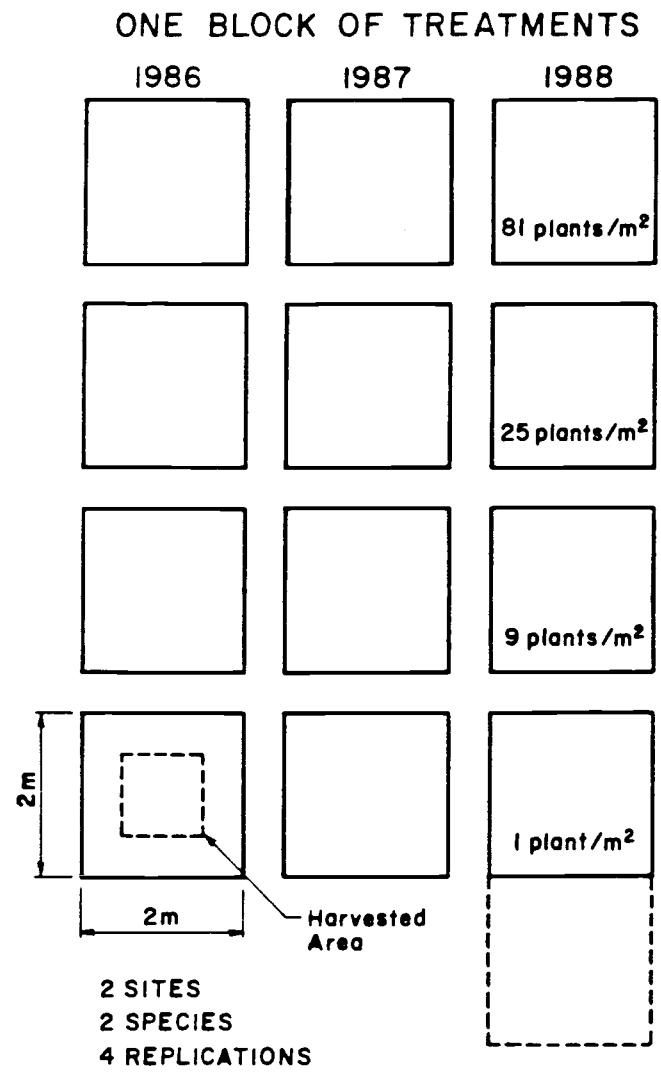


Figure 4.3. Map of the plot layout in one block of treatments indicating the years (strips) for each harvest. Demogrphic data was collected in 1988 plots. Densities were randomized within a strip.

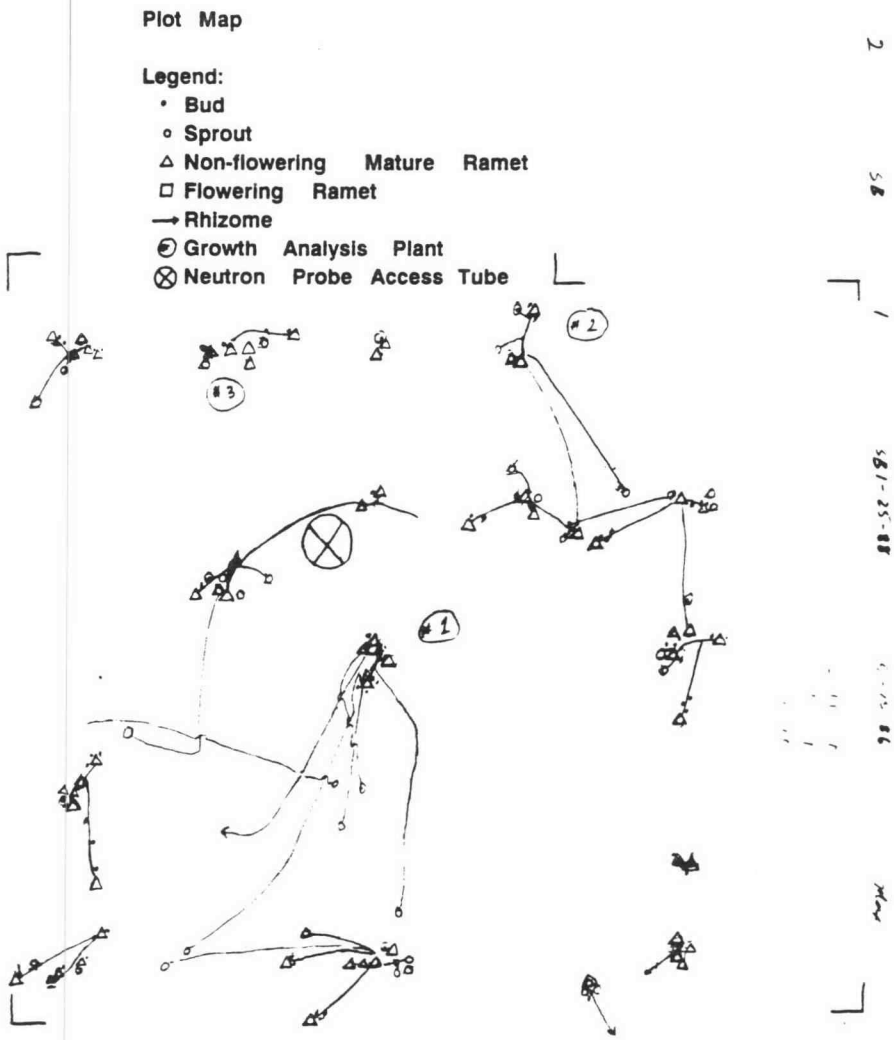


Figure 4.4. An example of the field plot maps used for locating individuals in salmonberry and thimbleberry populations. With each visit to a plot, individuals in each stage class were censused and located on the map. The maps were used to derive the demographic parameter values.

Figure 4.5. Salmonberry genet density plots over time for each population where demographics were studied at Woods Creek (Site 1) and Pioneer Mountain (Site 2). The genet density at month 0 was the number of cuttings (planting density) planted.

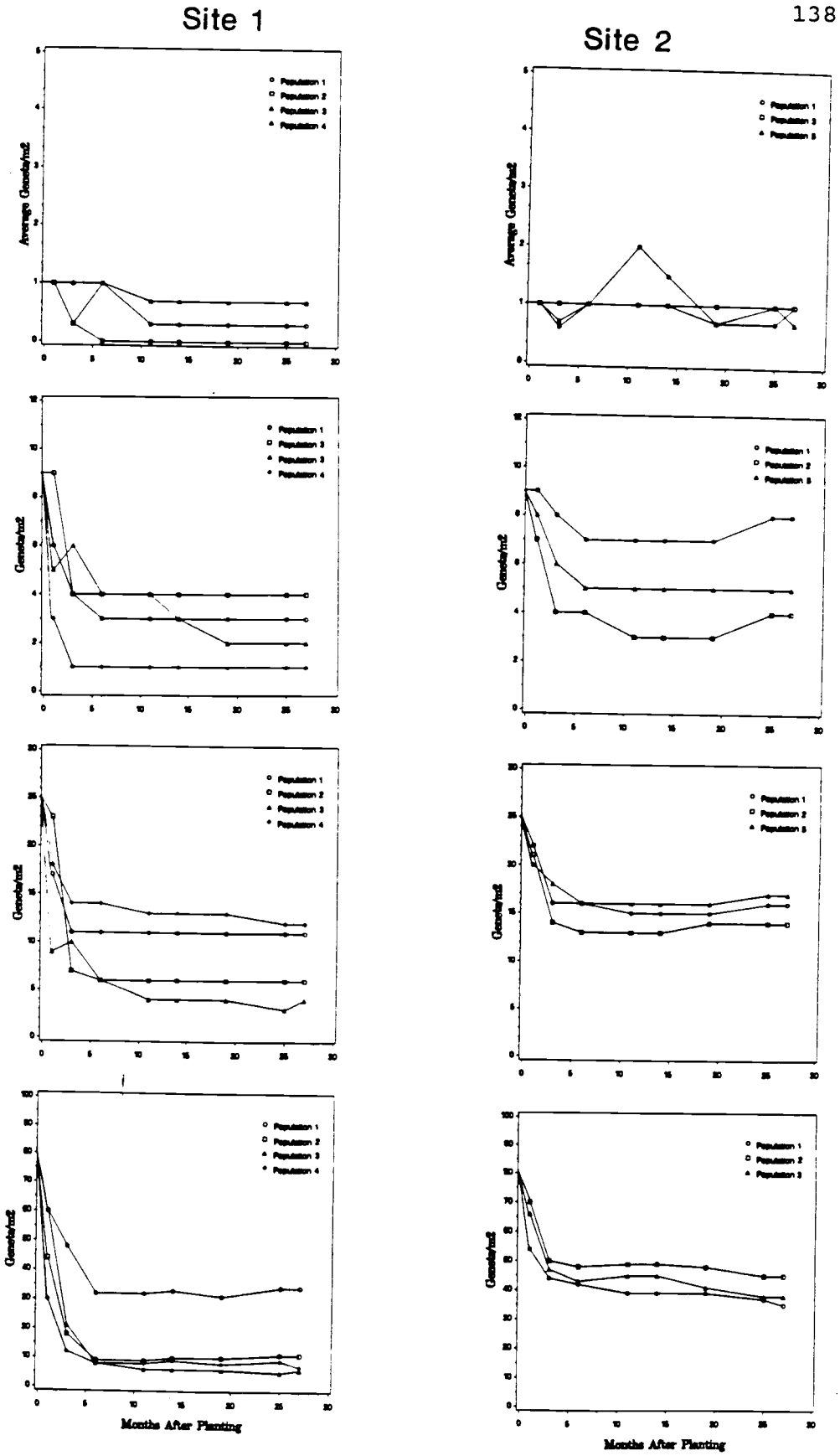


Fig.4.5.

Figure 4.6. Thimbleberry genet density plots over time for each population where demographics were studied at Woods Creek (Site 1) and Pioneer Mountain (Site 2). The genet density at month 0 was the number of cuttings (planting density) planted.

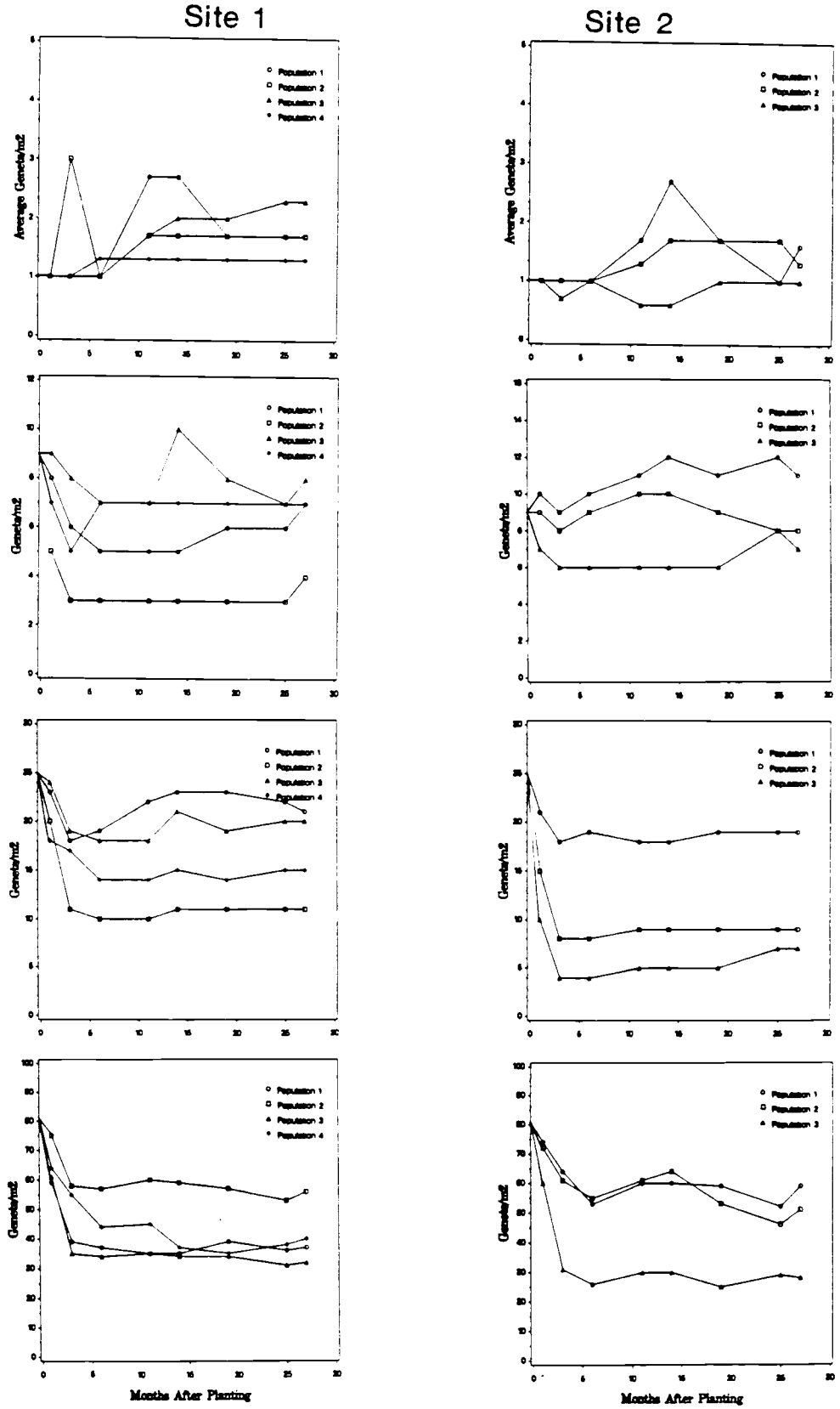

Site 1
Site 2
Population 1
Population 2
Population 3
Population 4
Average Gametes/m2
Gametes/m2
Months After Planting

Fig. 4.6

Figure 4.7. Salmonberry ramet density plots over time for each population where demographics were studied at Woods Creek (Site 1) and Pioneer Mountain (Site 2). The ramet density at month 0 was 0 (not plotted).

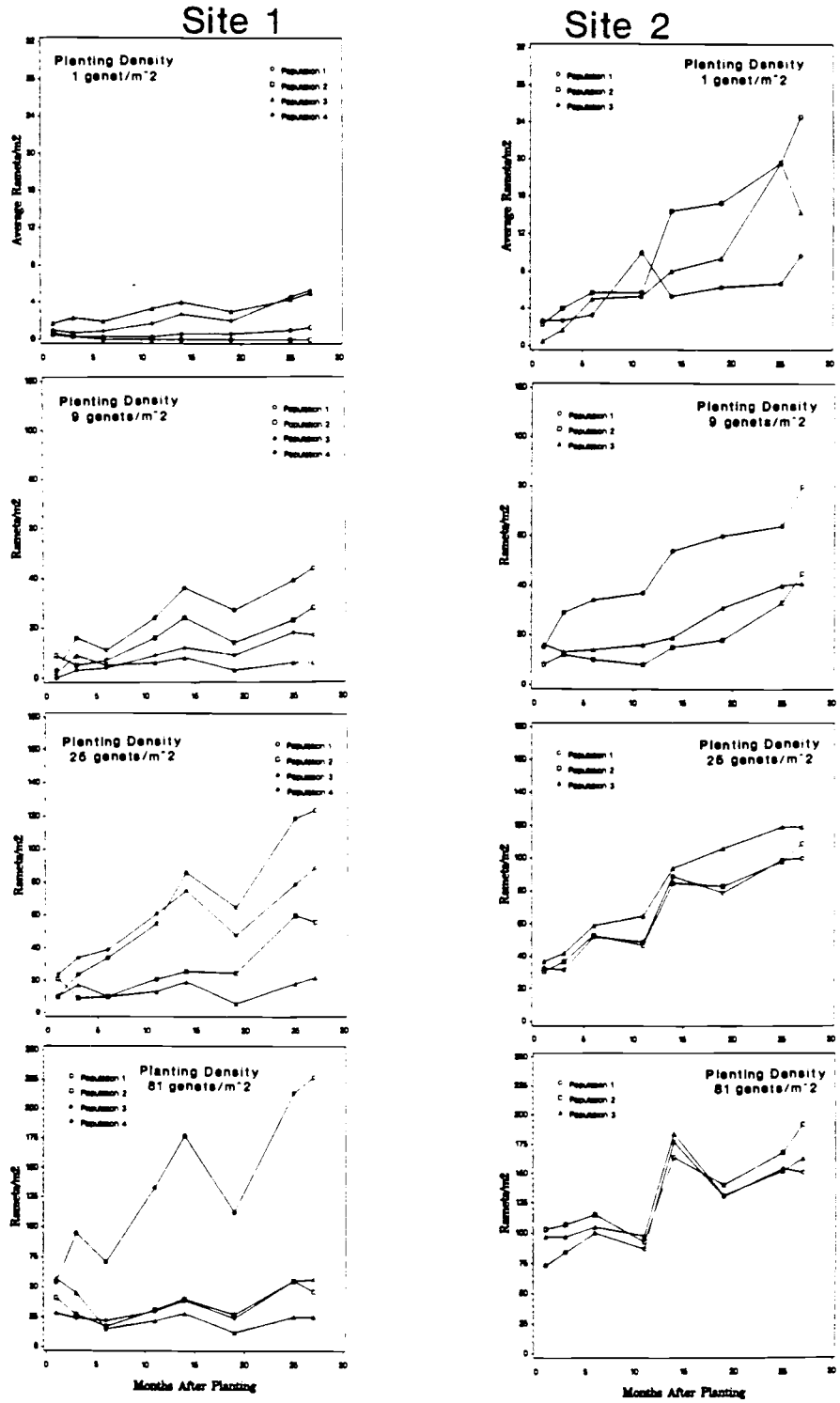

Site 1
Site 2
Planting Density
1 genet/m^2
Planting Density
9 genets/m^2
Planting Density
25 genets/m^2
Planting Density
81 genets/m^2
Average Ramets/m2
Ramets/m2
Months After Planting

Fig. 4.7.

Figure 4.8. Thimbleberry ramet density plots over time for each population where demographics were studied at Woods Creek (Site 1) and Pioneer Mountain (Site 2). The ramet density at month 0 was 0 (not plotted).

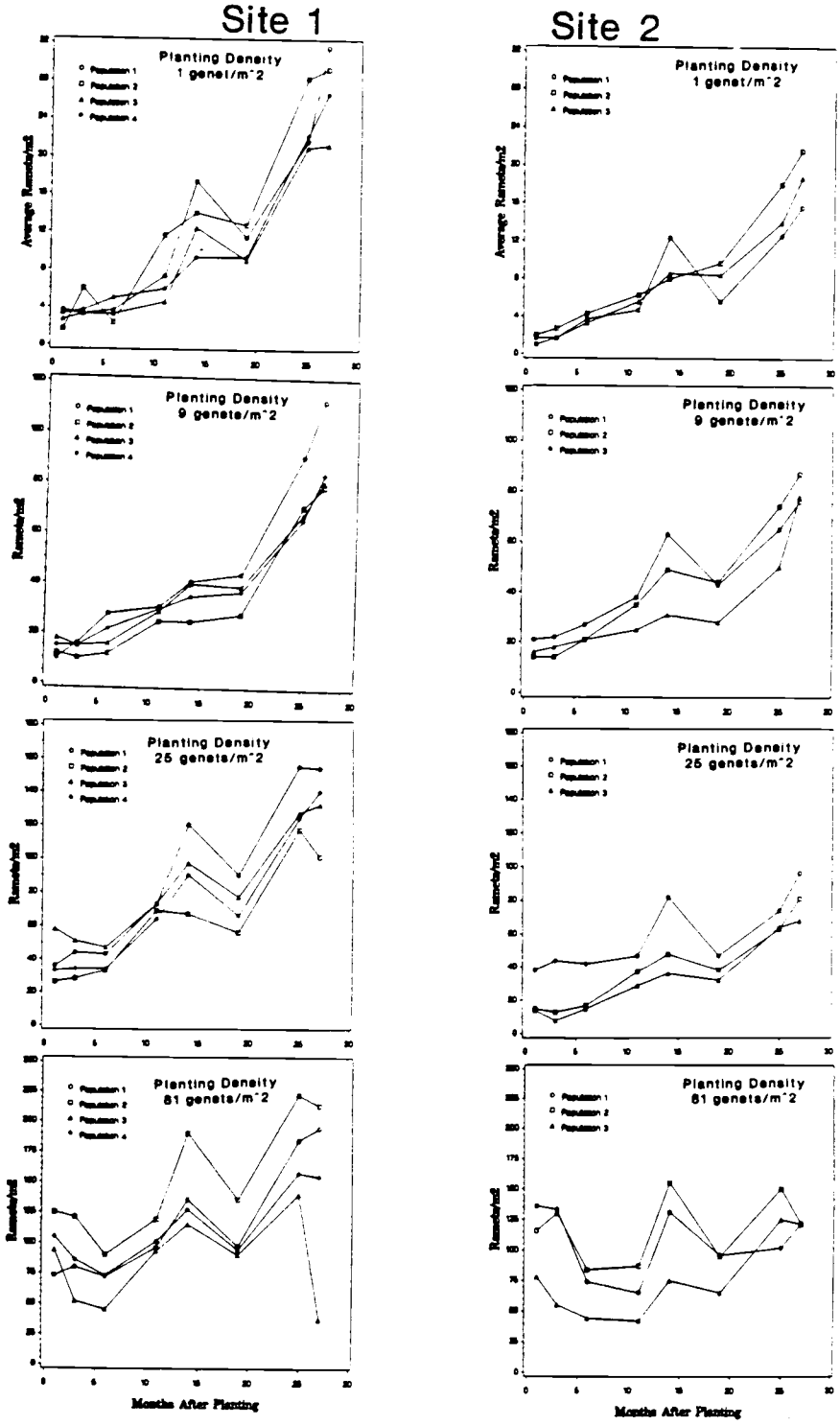

Site 1
Site 2
Planting Density
1 genet/m^2
Planting Density
9 genets/m^2
Planting Density
25 genets/m^2
Planting Density
81 genets/m^2
Months After Planting

Fig. 4.8.

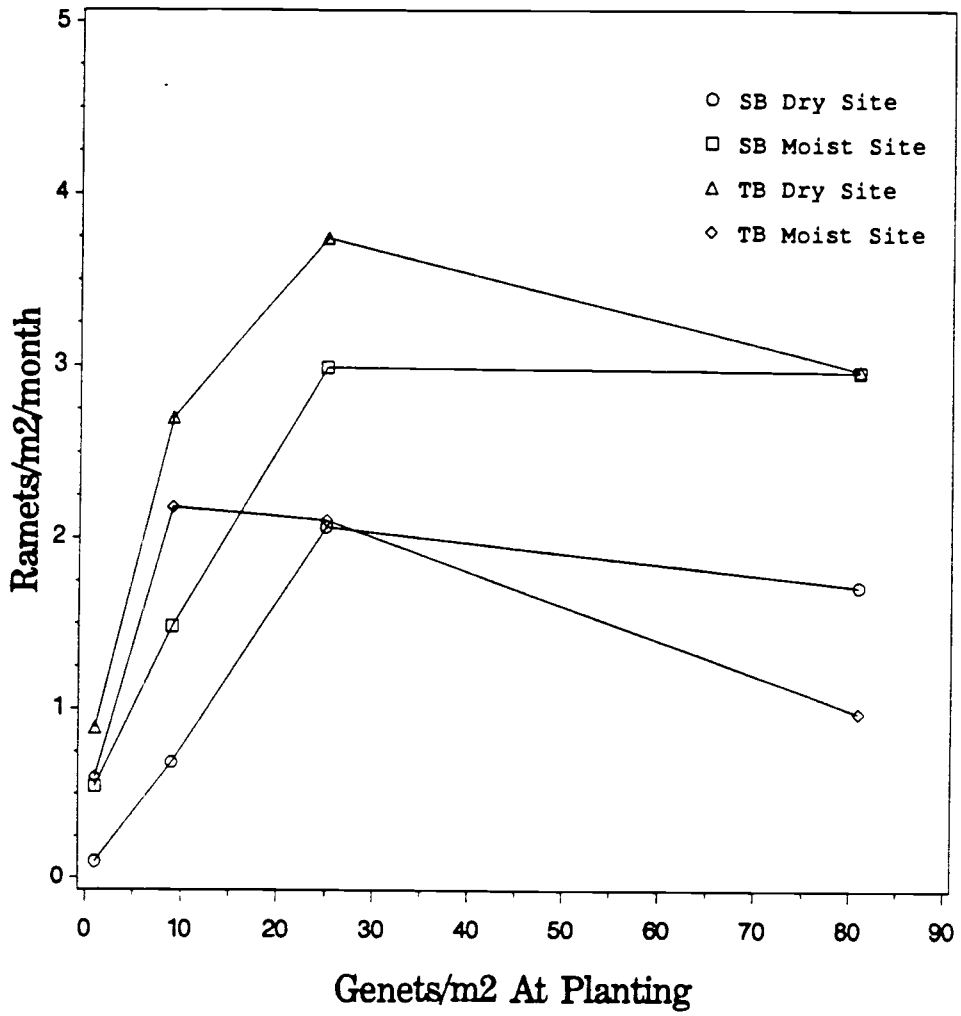


Figure 4.9. Salmonberry (SB) and thimbleberry (TB) ramet population growth rate over planting density at the Woods Creek (dry) and Pioneer Mountain (moist) sites.

Figure 4.10. Salmonberry mean ramets/genet plots over time for each population where demographics were studied at Woods Creek (Site 1) and Pioneer Mountain (Site 2). The ramet/genet at month 0 was 0 (not plotted).

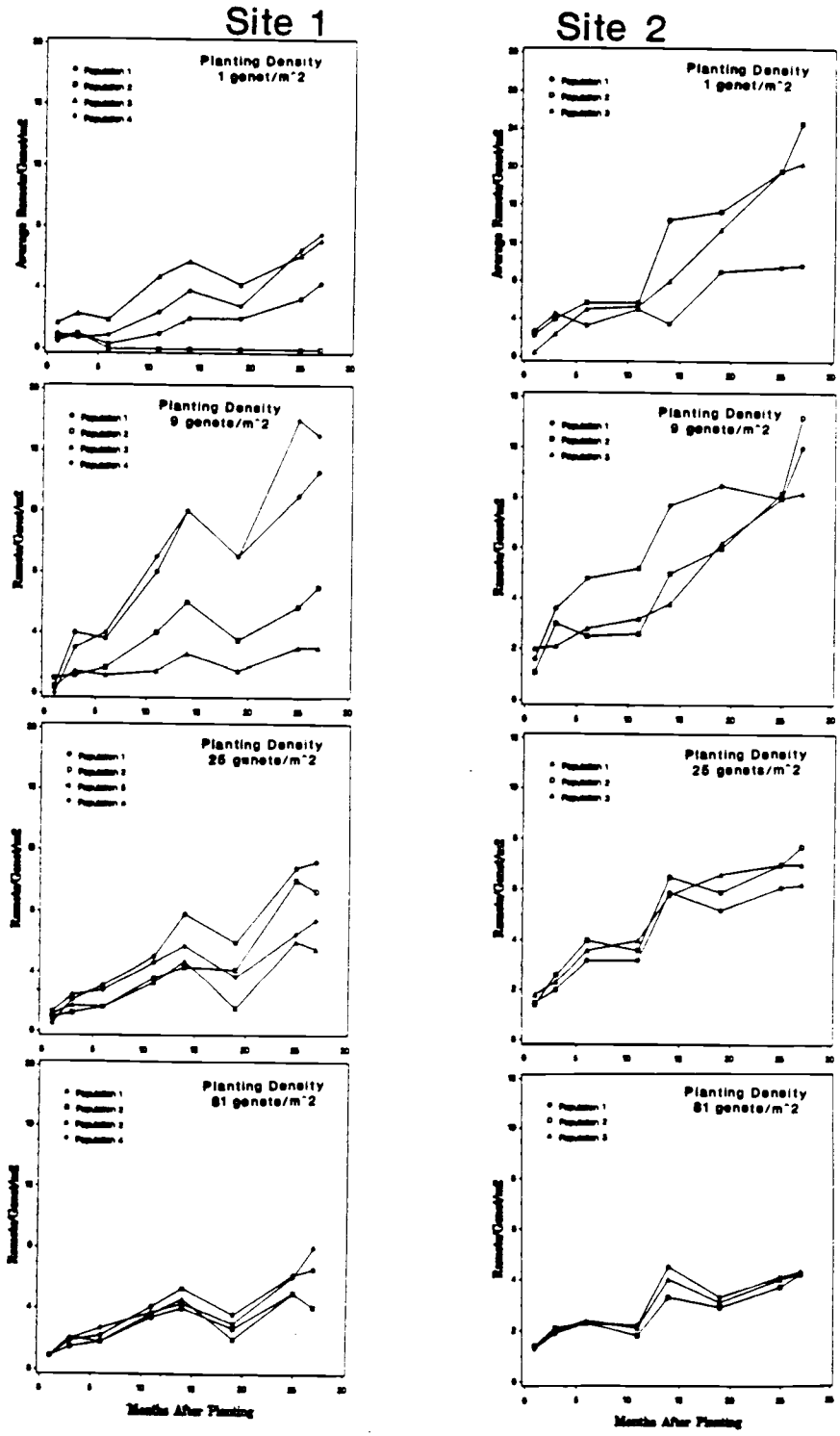

Site 1
Site 2
Planting Density
1 genet/m^2
Planting Density
9 genets/m^2
Planting Density
25 genets/m^2
Planting Density
81 genets/m^2
Months After Planting

Fig. 4.10.

Figure 4.11. Thimbleberry mean ramets/genet plots over time for each population where demographics were studied at Woods Creek (Site 1) and Pioneer Mountain (Site 2). The ramet/genet at month 0 was 0 (not plotted).

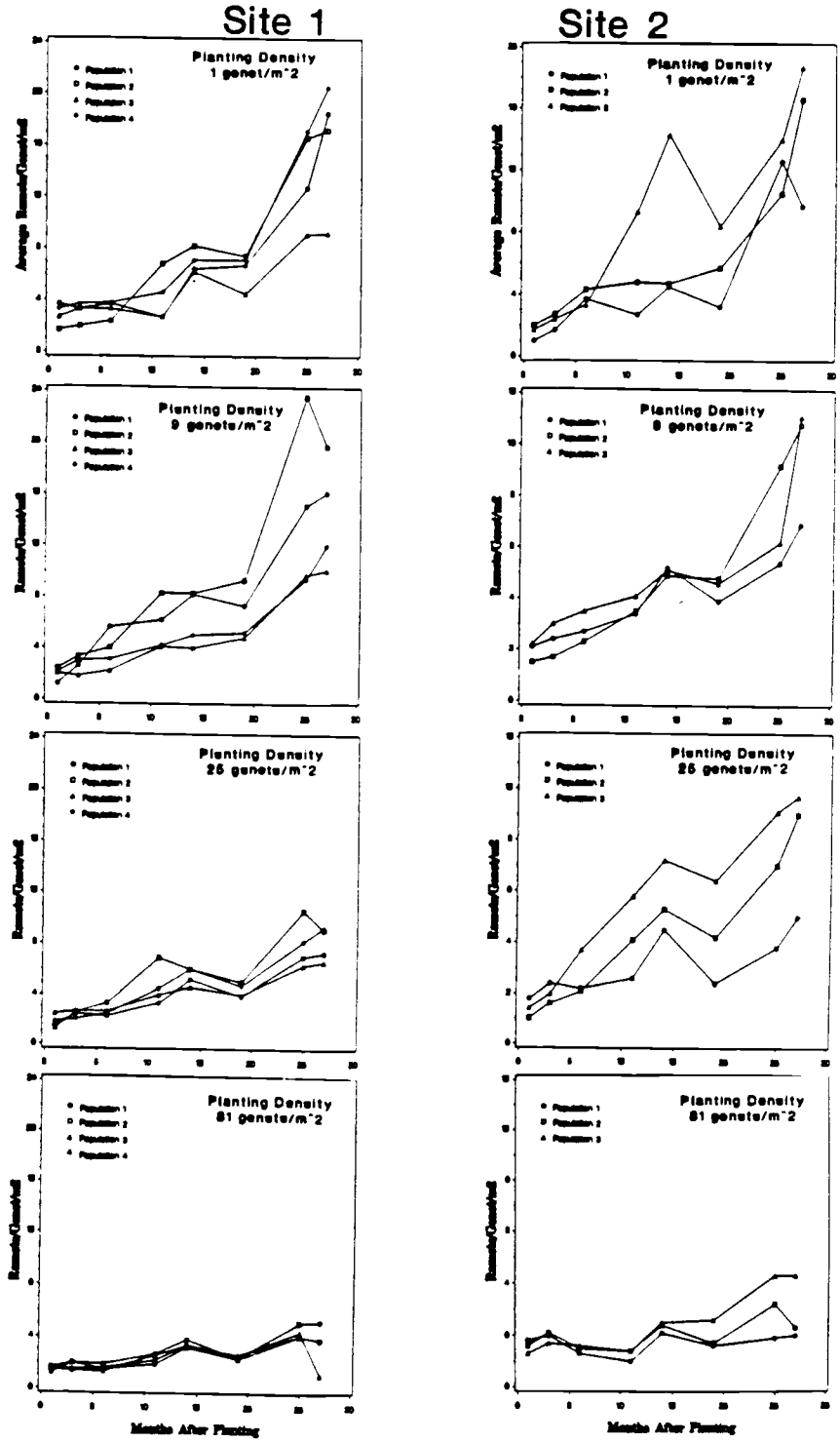

Site 1
Site 2
Planting Density
1 genet/m^2
Planting Density
9 genets/m^2
Planting Density
25 genets/m^2
Planting Density
81 genets/m^2
Months After Planting

Fig. 4.11.

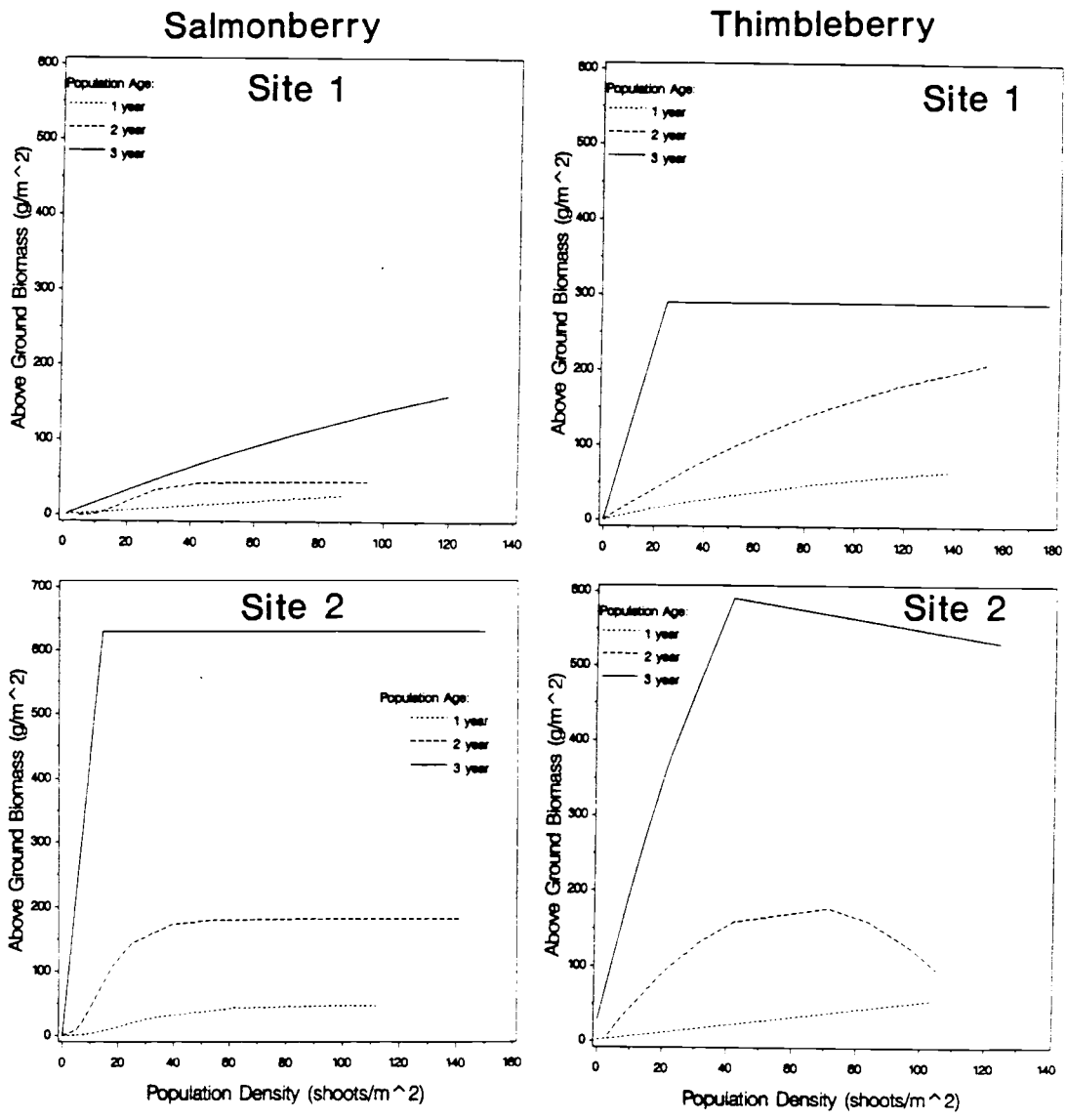


Figure 4.12. Salmonberry and thimbleberry constant final yield plots for the first three growing seasons at Woods Creek (site 1) and Pioneer Mountain (site 2). Shoots/m^2 is equivalent to ramet density. Equations and statistics for the regression lines are in Table A4.3.

Figure 4.13. Salmonberry mean ramet mass (a) and mean ramet mass/genet (b) plotted against ramet density (1987 data). Circles represent plots planted at 1 cutting/m^2, squares were 9 cuttings/m^2, triangles were 25 cuttings/m^2, and diamonds were 81 cuttings/m^2 planting (genet) density.

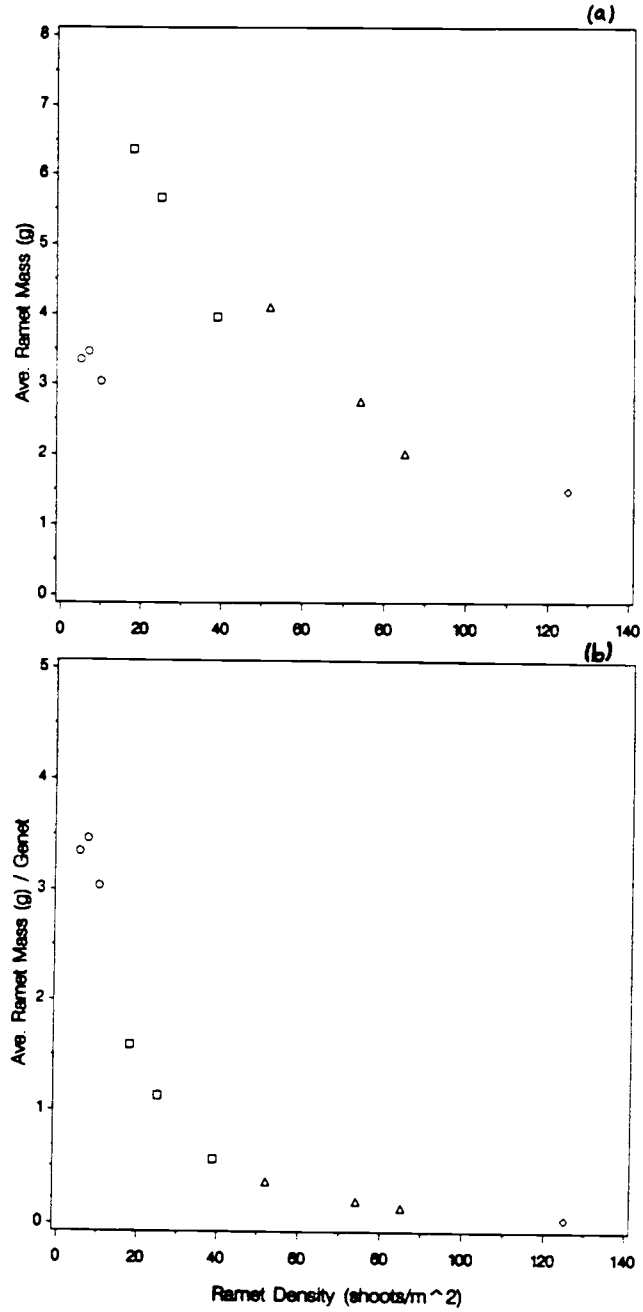
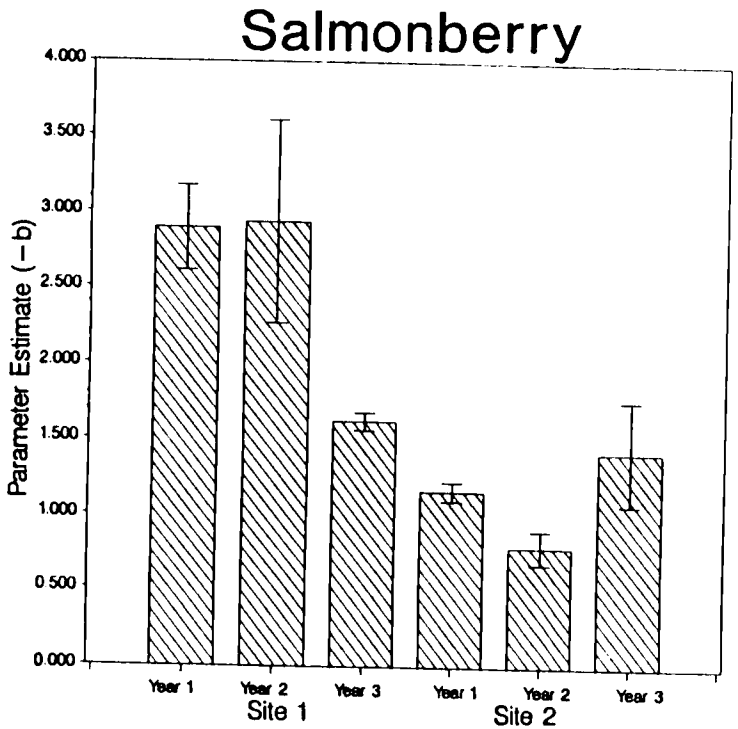

(a)
Ave. Ramet Mass (g)
0
1
2
3
4
5
6
7
8
0
20
40
60
80
100
120
140
(b)
Ave. Ramet Mass (g) / Genet
0
1
2
3
4
5
0
20
40
60
80
100
120
140
Ramet Density (shoots/m^2)

Fig. 4.13.

Figure 4.14. Salmonberry and thimbleberry resource use efficiency parameter (b) (see Table 4.4). The Y-axis values are negative values of b, therefore they decrease from bottom to top.


Salmonberry
Parameter Estimate (-b)
4.000
3.500
3.000
2.500
2.000
1.500
1.000
0.500
0.000
Year 1
Year 2
Year 3
Year 1
Year 2
Year 3
Site 1
Site 2

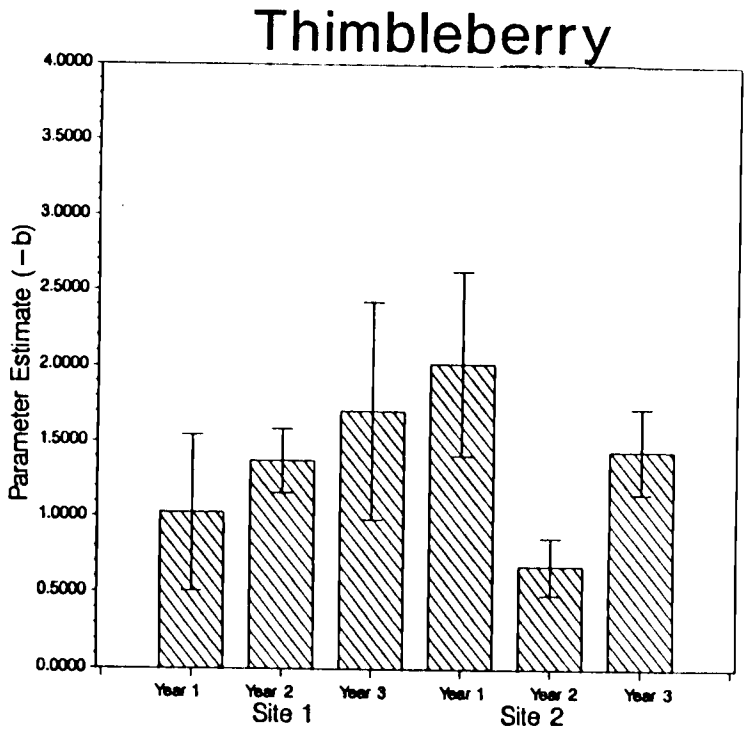

Thimbleberry
Parameter Estimate (-b)
4.0000
3.5000
3.0000
2.5000
2.0000
1.5000
1.0000
0.5000
0.0000
Year 1
Year 2
Year 3
Year 1
Year 2
Year 3
Site 1
Site 2

Fig. 4.14.

Figure 4.15. Thimbleberry at Woods Creek (site 1) and Pioneer Mountain (site 2), and salmonberry at Pioneer Mountain addition series surface plots of mean ramet mass/genet (verticle axis, SB_RWPG and TB_RWPG) versus ramet density (SB_RAMD and TB_RAMD) of both species grown in mixture for 3 growing seasons.

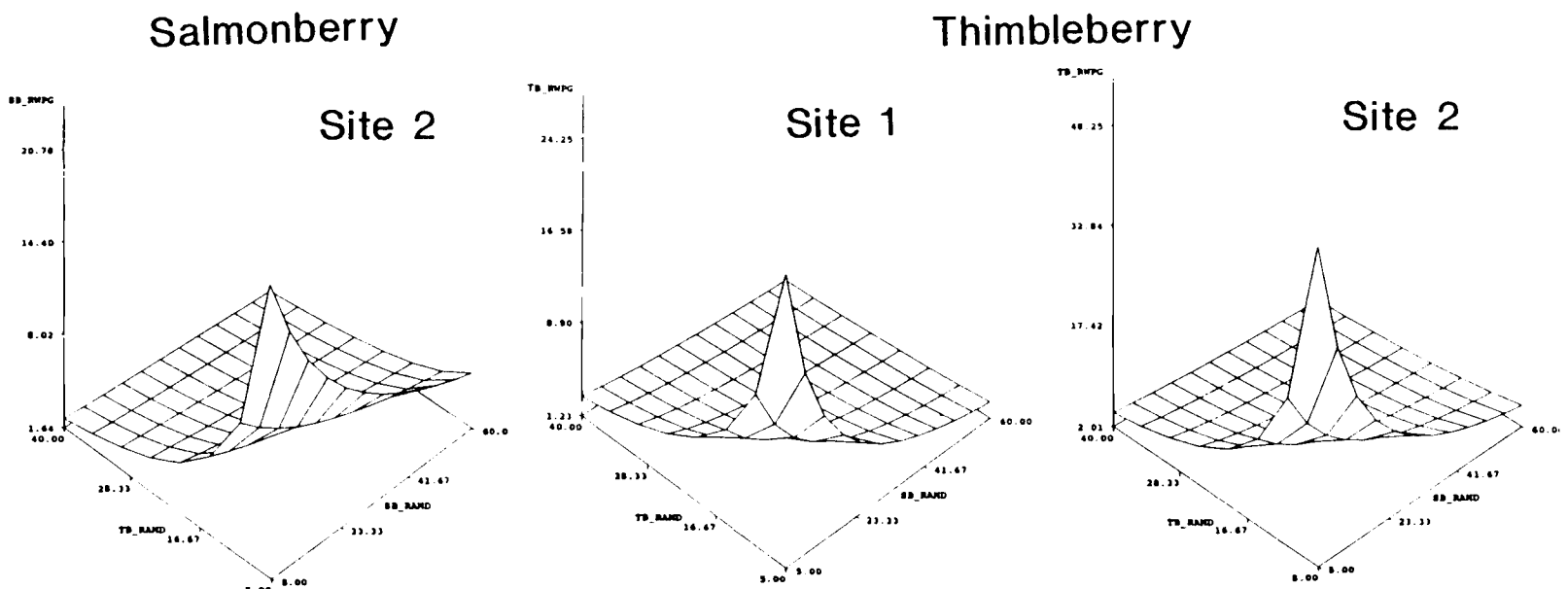


Fig. 4.15.

Figure 4.16. Relative competive ability (z)(graph a) and resource use efficiency index (b) (graph b) for salmonberry (RUSP) and thimbleberry (RUPA) population mixtures at Woods Creek (site 1) and Pioneer Mountain (site 2), calculated from Firbank and Watkinson (1985) equations (Table A4.5).

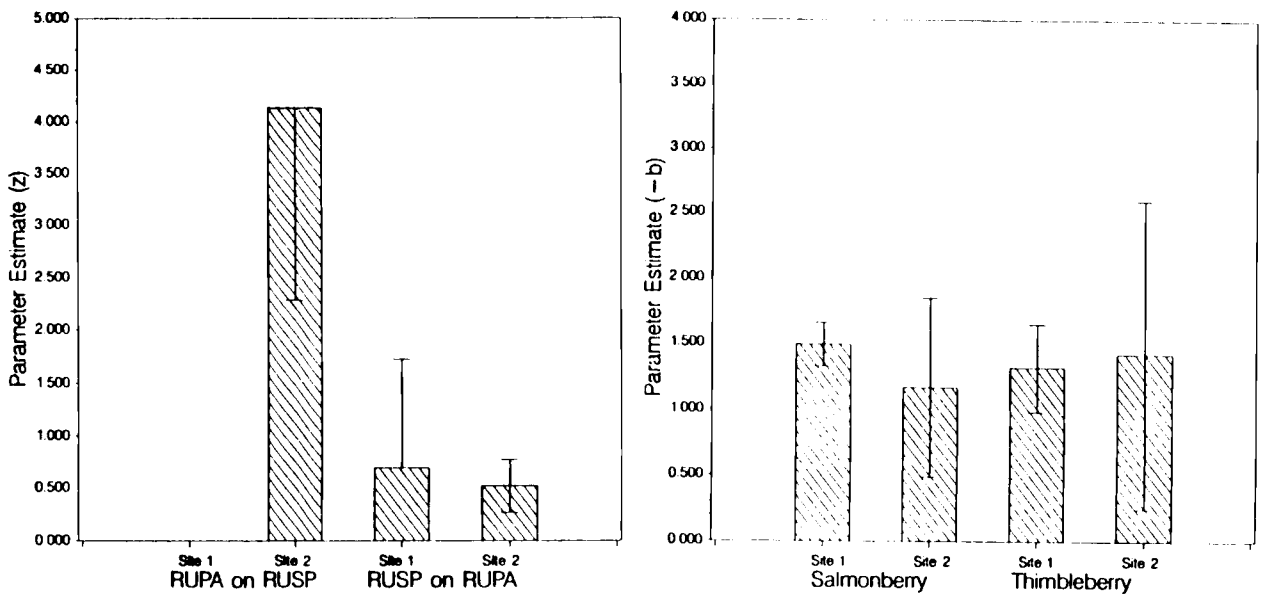

Parameter Estimate (z)
5.000
4.500
4.000
3.500
3.000
2.500
2.000
1.500
1.000
0.500
0.000
Site 1
Site 2
Site 1
Site 2
RUPA on RUSP
RUSP on RUPA
Parameter Estimate (-b)
4.000
3.500
3.000
2.500
2.000
1.500
1.000
0.500
0.000
Site 1
Site 2
Site 1
Site 2
Salmonberry
Thimbleberry

Fig. 4.16.

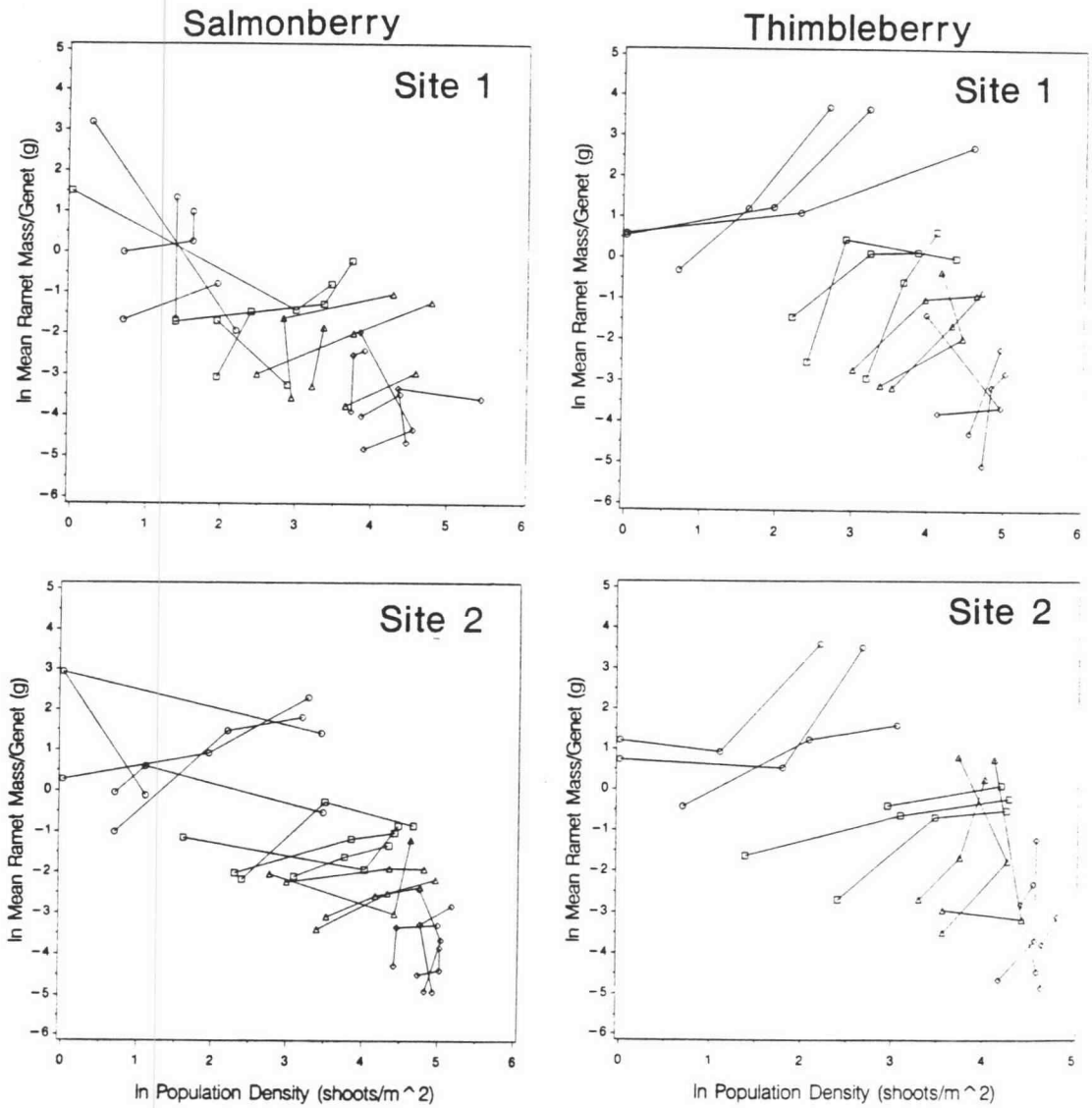


Figure 4.17. Ln mean ramet mass plotted on ln ramet density (shoots/m^2 to demonstrate populations on self-thinning graph. Three populations for each species were matched (connected with a line) based on starting density (circles = 1, squares = 9, triangles = 25, and diamonds = 81 genets (cuttings)/m^2 at planting), block, and harvest time. Connecting the points of similar populations for each harvest over the three growing seasons, simulates remeasured populations.

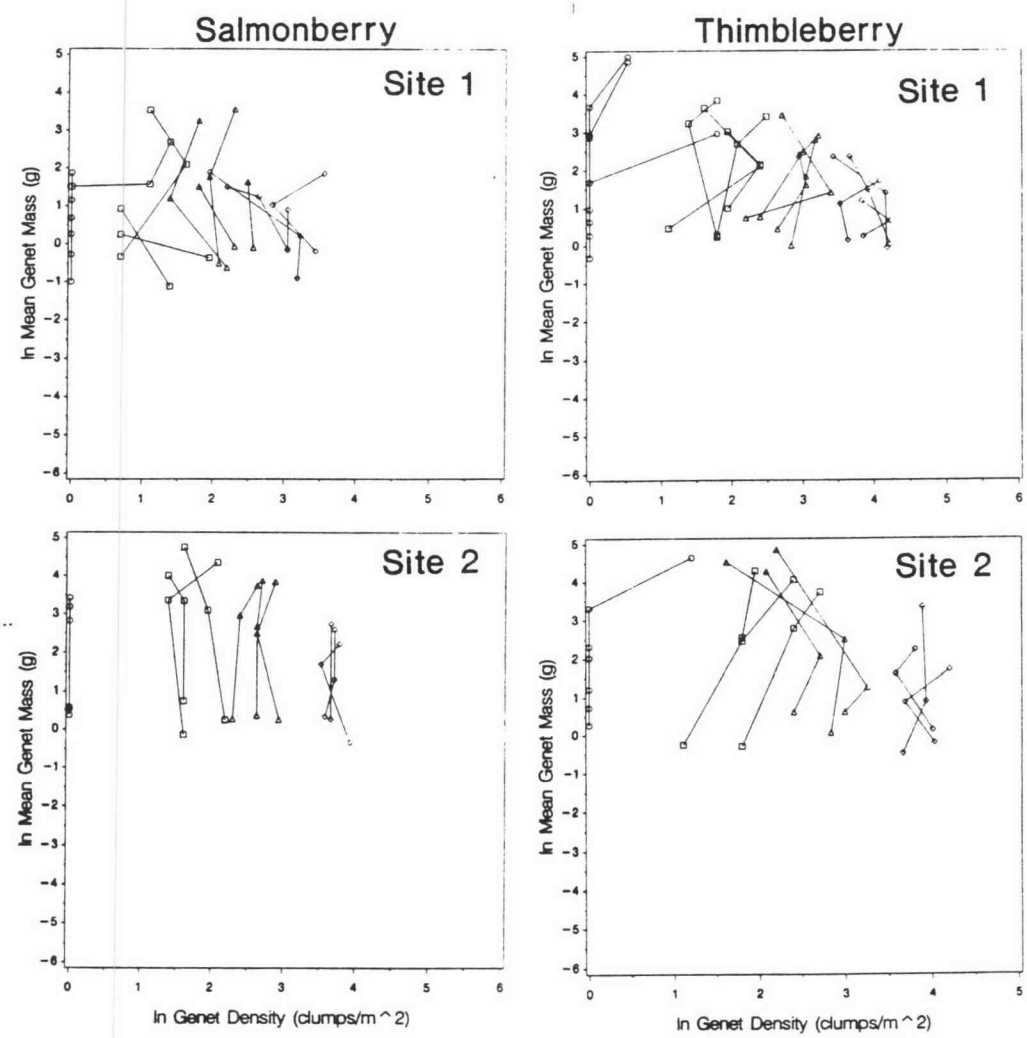


Figure 4.18. Ln mean genet mass plotted on ln genet density (clumps/m^2) to demonstrate populations on self-thinning graph. Three populations for each species were matched (connected with a line) based on starting density (circles = 1, squares = 9, triangles = 25, and diamonds = 81 genets (cuttings)/m^2 at planting), block, and harvest time. Connecting the points of similar populations for each harvest over the three growing seasons, simulates remeasured populations.

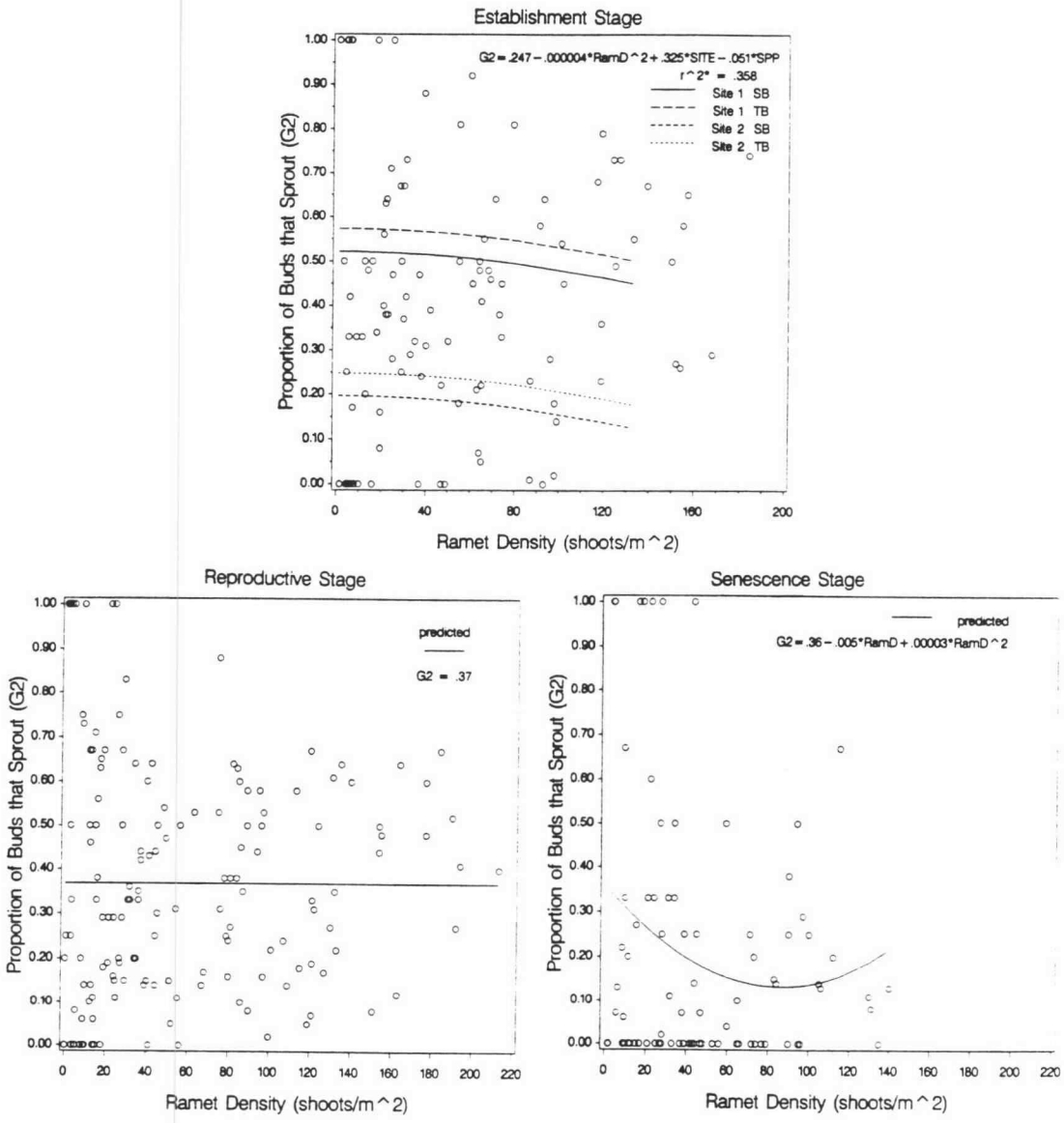


Figure 4.19. Proportion of buds that sprout (G2) at the establishment (top), reproductive (bottom left), and senescence (bottom right) stage plotted against ramet density. Both species and both sites data are included in each graph. Lines for fitted equations are shown (see Table 4.6 for statistics on regressions).

Table 4.1. Linear and nonlinear equations used to determine density-biomass relationships. Total (plot) above ground biomass (y) regressed against ramet density (N) to test for constant final yield.

Name	Model equation
Mean	$y = a$
Linear	$y = a + b * N$
Exponential	$y = b * \exp(n * N)$
Power function	$y = b * N^n$
Hyperbola	$y = (b * N)/(a + N)$
Richards function	$y = b * (1 - \exp(a * N))^n$
Maxima function	$y = b * N * \exp(n * N)$
Quadratic	$y = a + b * N + b_2 * N^2$

exp = base of the natural logrithm
a, b and n are fit regression coefficients

Table 4.2. Linear and nonlinear equations used to determine density-demographic parameter relationships. Demographic parameter (y) regressed against ramet and genet density (N).

Name	Model equation
Mean	$y = a$
Linear	$y = a + b * N$
Exponential	$y = b * \exp(n * N)$
Power function	$y = b * N^n$
Hyperbola	$y = (b * N)/(a + N)$
Weibull function	$y = \exp(-1 * ((N - a)/b)^n)$
Exponential saturation	$y = b * (1 - \exp(n * N))$
Modified inverse	$y = b/(a + N)$
Sigmoid	$y = b/(1 + a * N^n)$
Richards function	$y = b * (1 - \exp(a * N))^n$
Maxima function	$y = b * N * \exp(n * N)$
Quadratic	$y = a + b * N + b_2 * N^2$

exp = base of the natural logrithm
a, b and n are fit regression coefficients

Table 4.3. Equations with best fit to total plot biomass data over a range of ramet densities for salmonberry (RUSP) and thimbleberry (RUPA) at Woods Creek (Site 1) and Pioneer Mountain (Site 2) over three growing seasons (86, 87 and 88) in planted monocultures.

Spp.	Site	Year	Equation	n	MSE	F	r^2
RUSP	1	86	$y = 0.632 + 0.295(RamD)$	18	5.76	151.60	.9045
		87	$y = 44.92(1 - \exp(-0.12RamD))^{9.628}$	17	32.83	177.38	.9268
		88	$y = 1.747RamD * \exp(-0.002RamD)$	14	4024.28	22.11	.6480
RUSP	2	86	$y = 47.198(1 - \exp(-0.06RamD)^{3.429}$	15	31.45	134.43	.9181
		87	$y = 181.44(1 - \exp(-0.11RamD)^{3.528}$	14	294.76	298.80	.9645
		88	$y = 629.07(1 - \exp(-2.0RamD)^{2.993}$	15	50703.5	18.73	.6100
RUPA	1	86	$y = 146.49RamD/(170.36 + RamD)$	20	9.90	965.59	.9817
		87	$y = 2.23RamD * \exp(0.003RamD)$	20	1397.86	70.12	.7957
		88	$y = 288.8(1 - \exp(-2.0RamD))^{2.999}$	20	11050.3	24.15	.5869
RUPA	2	86	$y = 1.804 + 0.515(RamD)$	14	55.94	83.67	.8746
		87	$y = -10.43 + 6.05RamD - 0.048RamD^2$	15	1213.83	56.36	.8245
		88	$y = 28.62 + 18.5RamD - 0.116RamD^2$	15	75800.7	16.07	.5725

r^2 values for nonlinear equations are approximated.

Table 4.4. The Watkinson (1980, 1984) equation fit to mean ramet mass/genet (y) data over a range of ramet densities (RamD) for salmonberry (RUSP) and thimbleberry (RUPA) at Woods Creek (Site 1) and Pioneer Mountain (Site 2) over three growing seasons (86, 87 and 88) in planted monocultures.

Spp.	Site	Year	Equation	b	n	MSE	F	r^2
RUSP	1	86	$y = 1070694(1 + 71.12(RamD))^{-2.893}$		15	.0275	384.1	.9810
		87	$y = 3784239(1 + 32.59(RamD))^{-2.932}$		14	.0246	39.0	.7816
		88	$y = 1889014(1 + 808.2(RamD))^{-1.619}$		13	.1054	2896.7	.9978
RUSP	2	86	$y = 2896.9(1 + 591.7(RamD))^{-1.161}$		12	.0019	1820.9	.9962
		87	$y = 10100(1 + 4078.8(RamD))^{-0.790}$		11	.1705	103.2	.9197
		88	$y = 601000(1 + 55.3(RamD))^{-1.421}$		12	60.393	23.1	.7506
RUPA	1	86	$y = 3.405(1 + 1.585(RamD))^{-1.027}$		16	.0246	46.5	.8690
		87	$y = 577978(1 + 1878.7(RamD)^{-1.372}$		16	1.364	133.9	.9422
		88	$y = 1394319(1 + 66.24(RamD)^{-1.703}$		16	2.499	22.6	.6596
RUPA	2	86	$y = 51055(1 + 129.34(RamD))^{-2.020}$		11	.0937	81.5	.9313
		87	$y = 12576(1 + 74482(RamD))^{-0.676}$		12	.4299	20.7	.6917
		88	$y = 3043030(1 + 267.7(RamD))^{-1.443}$		12	23.738	46.7	.8738

r^2 values for nonlinear equations are approximated.

Table 4.5. The Firbank and Watkinson (1985) equations fit to mean ramet mass/genet (y) data over a range of ramet densities for salmonberry (N_s) and thimbleberry (N_t) at Woods Creek (Site 1) and Pioneer Mountain (Site 2) over three growing seasons (86, 87 and 88) planted in mixtures in an addition series.

Spp.	Site	Year	Equation	z	b	n	MSE	F	r^2
RUSP	1	88	$y = 1183700(1 + 1056(N_s + .019N_t))^{-1.495}$			21	1.404	147.0	.9517
RUSP	2	88	$y = 158599(1 + 81.27(N_s + 4.13N_t))^{-1.170}$			32	34.992	28.7	.6461
RUPA	1	88	$y = 102829(1 + 66.81(N_t + .689N_s))^{-1.318}$			27	2.600	15.2	.5455
RUPA	2	88	$y = 194316(1 + 45.14(N_t + .519N_s))^{-1.421}$			34	39.482	18.6	.5706

r^2 values for nonlinear equations are approximated.

Table 4.6. Equations for predicting selected demographic parameter values at establishment (Est.), reproduction (Rep.), and senescence (Sen.) phenological stages, calculated from monoculture populations of salmonberry and thimbleberry. RamD = ramet density.

Stage	Parameter[1]	Equation	F	r^2
Est.	R2	$= .586-.000006*RamD^2-.278*Site$	44.89	.2956
Rep.	R2	$= .419-.0026*GenD-.158*Site$	16.28	.0973
Sen.	R2	$= .382-.162*Site$	6.75	.0752
Est.	G2	$= .247+.000004*RamD^2+.325*Site-.051*Spp$	58.58	.3581
Rep.	G2	$= .369$	-	-
Sen.	G2	$= .358-.0052*RamD+.00003*RamD^2$	4.46	.0516
Est.	R4	$= .285-.201*Site+.140*Spp$	35.25	.2461
Rep.	R4	$= .773/(1-.032*GenD^{-4})$	15.23	.0864[1]
Sen.	R4	$= .155+.0004*RamD+.090*Site+.183*Spp$	38.74	.2658
Est.	G4	$= .314-.0033*GenD-.105*Site+.167*Spp$	28.55	.2091
Rep.	G4	$= .104-.0010*GenD-.035*Site+.024*Spp$	9.86	.0581
Sen.	G4	$= .722-.004*GenD-.156*Site-.213*Spp$	64.68	.3724
Est.	R5	$= .594-.000005*RamD^2-.107*Site+.300*Spp$	52.21	.3321
Rep.	R5	$= .799-.003*GenD-.268*Site+.275*Spp$	79.48	.3964
Sen.	R5	$= .406+.096*Site-.127*Spp$	4.64	.0419
Est.	V5	$= .225-.021*GenD+.0005*GenD^2+.157*Site$	28.84	.2139
Rep.	V5	$= -.018+.123*Spp$	9.08	.0525
Sen.	V5	$= .737-.00002*RamD^2+.348*Spp$	30.12	.2180

[1] Parameters are defined in Fifure 2.1.
[2] Approximate r^2 calculated for non-linear equations.

CHAPTER 5

SIMULATION OF SALMONBERRY AND THIMBLEBERRY POPULATION ESTABLISHMENT, GROWTH AND MANAGEMENT

ABSTRACT

A salmonberry (Rubus spectabilis) and thimbleberry (Rubus parviflorus) population model was developed and simulations were compared to field observations of these species. The species specific influence of phenology, environment at different sites, and intraspecific density on demographic processes was incorporated into the model. The resultant model predicts the numbers of individuals in life history classes (seeds in the seed bank, basal buds on crowns and rhizomes, seedlings, sprouts, mature vegetative shoots, flowering shoots and rhizomes) at 3 phenological stages (establishment, reproduction and senescence) during a growing season. Ramet density was used to predict canopy cover and population above ground biomass. Biomass was then used to predict mean ramet height. Simulations were most accurate when compared to planted middle density (9 cuttings (genets)/m^2) populations. Salmonberry populations were most accurately simulated. Thimbleberry simulation accuracy was reduced by poor prediction of sprout densities. Salmonberry and thimbleberry population response to an application of glyphosate was simulated. The simulation was compared to observed canopy cover reduction

and recovery for a period following herbicide application. The response was accurately simulated the first year, but did not account for continued reduction in canopy cover in the observed populations. Salmonberry canopy cover and mean ramet height in response to manual cutting at three phenological stages was also simulated. The model simulations indicated that the most effective salmonberry control with mannual cutting is when ramets are cut at the reproductive (early summer) phenological stage.

INTRODUCTION

Establishment and early growth of salmonberry and thimbleberry populations are an important consideration for vegetation management. Within three growing seasons following clearcutting, salmonberry and thimbleberry populations can dominate Coast Range sites (Ruth, 1956). A generic Rubus population model was developed from information in the literature (Chapter 2) to simulate population development of these two species and to generate hypotheses on the mechanisms which regulate population growth. Hypothetical mechanisms which influence salmonberry and thimbleberry population establishment and early growth were posed (Chapter 2). Factors which influence population establishment from sexual and asexual reproduction were compared (Chapter 3). The influence of competition on demographic processes, as defined in the model was assessed in field experiments (Chapter 4). In this chapter, information from these previous experiments was included in the model to improve its accuracy. Simulations from this refined model were compared to field populations and used to evaluate management tactics.

The model is conceptually based on a transition matrix technique (Leslie, 1945). However, the Rubus populations were divided into life history classes based on development and reproductive potential, rather than age (Hubbell and Werner, 1979; Law, 1983; Lefkovitch, 1965; Vandermeer,

1975). An assumption of the transition matrix technique is that the transition probabilities between life history classes, and fecundities specific to each stage, are constant over time and space. The Rubus model was refined, based on the hypothesis that mortality, reproduction and transition are not solely a function of life history class. For example, internal plant conditions associated with phenolgy, different physical environments represented by geographic location, and intraspecific density also are mechanisms which effect population dynamics. Therefore, the demographic behavior of salmonberry and thimbleberry was assessed at three phenological stages, establishment (spring leaf-bud break), reproduction (fruit set), and senescence (leaf fall), at two field sites, and across a series of densities. The behavior of the species in response to these variables was incorporated into the simulation model.

Modeling the population dynamics of salmonberry and thimbleberry was complicated by their clonal growth habit. Above ground shoots arising from the root crown and rhizomes beneath the litter layer were assumed to be functional individuals (ramets) in an inter-conected clone (genet) (Harper, 1985). The shoots were divided into three categories: (1) non-reproductive shoots without basal buds (sprouts), (2) mature shoots with basal buds (vegetative shoots), and (3) flowering shoots. The model also included,

basal buds, rhizomes, seed in the seed bank, and seedlings as other life history classes in the model (Figure 5.1). The model predicts the number of individuals in the different classes over time.

In this chapter, the refined simulation model is described, the assumptions in the model are discussed, and the predictive ability is assessed. Some salmonberry and thimbleberry management options also are considered.

MODEL DESCRIPTION

Model output

The refined Rubus model was written into a Quikbasic (Microsoft, 1987) computer program (RUBSM) to facilitate simulations. All further reference to the model refers to the computer program. The model output is a population census table for a specified number of years at a specified phenological stage (establishment, reproduction, senescence), or at all the phenological stages (Table 5.1). Density (numbers/m^2) of individuals in each lihe history class (seeds, basal buds, seedlings, sprouts, vegetative mature shoots, flowering shoots and rhizomes) are output. The population growth rate (lamda) is updated at each phenological stage. All of these outputs are graphically presented along with percent canopy cover and average height of ramets.

Model input

Model inputs that are supplied by the user include:

initial density of individuals in each stage class, the specified phenological stage at time 0, the phenological stage to recieve output on an annual basis, the number of years to run the simulation, and the number of months (prior to time 0) since disturbance. The user is given the option of choosing whether to invoke density-dependent population regulation, which set of transition matrices (Table A5.1) to use, to change matrix element values (demographic parameter values), and to select the species salmonberry or thimbleberry and the site location. Site 1 corresponds to the Woods Creek field site and Site 2 to Pioneer Mountain (Table 3.1). Species and site location only have significance in the height and density dependence equations.

Model calculations

The density of individuals in each life history class at a phenological stage is calculated by multiplying the transition matrix for the i'th phenological stage ($\mathbf{M}_i$) by the vector of the density of individuals in each class at the previous phenological stage ($\mathbf{P}_{t-1}$).

$$\mathbf{P}_t = \mathbf{M}_i * \mathbf{P}_{t-1}$$

When density dependence is included into the model, an equation predicting each transition variable (demographic paramter) as a function of the ramet density (sprouts + vegetative shoots + flowering shoots) or genet density is substituted into the transition matrix before the

calculation (Vandermeer, 1985). Genet density is calculated in the model as a function of ramet density (Figure 5.2).

Certain assumptions were required in order for density, site and species dependent equations to be included in the model. The quadratic equations selected in Chapter 4 to predict demographic parameters were not appropriate outside of the data range used to fit them. At both high and low densities, the quadratic equations (Chapter 4, Table 4.3) would in some cases predict proportions greater than 1.00 or less than 0. Therefore, a model form restricted by an upper asymptote less than or equal to 1.00 and a lower asymptote greater than or equal to 0 was fit to predict demographic parameter proportions in response to intraspecific density. The sigmoid equation was used:

$$Y = b/(1 + aN^C)$$

where Y is the demographic parameter value (proportion), N is the intraspecific ramet density, b is the upper asymptote, a is the lower asymptote, and c is an exponent. The c parameter can be interpreted as the intensity of the density effect because of its influence on the relationship (slope) between the upper and lower asymptotes (Figure 5.3). The parameter c changes with different species and sites, therefore indicator variables for site and species were added to the c parameter. Thus the equation takes the form:

$$Y = b/(1 + aN^{(c1*X11 + c2*X12 + c3*X21 + c4*X22)})$$

where a was set to 0.001 and b, c1, c2, c3 and c4 were estimated by nonlinear regression, when:

X11 = 1 if site = 1 and spp = RUSP, otherwise X11 = 0,

X12 = 1 if site = 1 and spp = RUPA, otherwise X12 = 0,

X21 = 1 if site = 2 and spp = RUSP, otherwise X21 = 0,

X22 = 1 if site = 2 and spp = RUPA, otherwise X22 = 0.

When regression coefficients associated with a particular species and site were not significantly different from 0 ($p < 0.05$), they were dropped from the sigmoid equation and the mean value for the parameter was used (Table A5.2).

The c parameter in the sigmoid equation varied between years within a phenological stage for most of the parameters (Table A5.2). This result placed a major constraint on the ability of the population simulation model to predict beyond the third growing season if the density response changed over time. However, the density biomass relationships and the population growth rate (Chapter 4) indicated that the populations rapidly approach carrying capacity. Therefore, the density-dependent functions for predictng demographic parameter values in the third growing seasons were used to predict beyond the third year. That is, the populations were assumed to be at equilibrium by the third growing season with respect to density-dependence.

Mortality was calculated for each observation time,

each species, and each stage class by adding survival and transition parameter values for a stage and subtracting the sum from 1, (e.g. sprout mortality, M4 = 1 - (R4 + G4). Mortality was then fit as a function of density with the sigmoid equation.

The sum of survival, mortality and transition for each stage was assumed to be unity. However, when the transition, survival and mortality values are predicted as separate functions of density, as in the simulation model, the sum is often not 1. Therefore, the values are rescaled by dividing each parameter value by the sum of the survival, transition and mortality values after they are calculated in the density dependence equations. Borders (1989) suggests that this approach of accounting for simultaneous equation bias provided similar solutions to other more complicated approaches.

Population canopy cover and height are common measurements of forest shrubs used to assess vegetation management practices. Therefore, percent canopy cover and average ramet height were included as output parameters in the model. Percent canopy cover was predicted as a function of intraspecific ramet density utilizing the Richards function (Figure 5.4). No direct relationships were found between salmonberry and thimbleberry height and density. However, a significant relationship was found between average height and total above ground biomass (Figure 5.5).

This relationship, coupled with the density-biomass equations (Chapter 4), allowed for the indirect prediction of average ramet height from ramet density.

Model verification and validation

Model simulations were compared qualitatively to the mean and one standard deviation from the mean of populations of total shoots, buds, sprouts and vegetative shoots. The planted monoculture populations used to derive the density-dependence relationships were first compared to the simulations to verify general conformity to the observed populations. Initial conditions were set in the model to coincide with the planted populations. This procedure assumed that each planted cutting (genet) represents a root crown with four basal buds and no above ground shoots.

Wild populations adjacent to the planted populations at each site were cut to ground level at the time the other population were planted. Observations of the clipped wild populations were compared to simulations for model validation.

Quantitative comparisons were made between the simulations and the verification data set (from planted populations) and the validation data set (from wild populations). Bud, sprout, vegetative shoot, and total shoot (ramet) densities were compared with observed data from the first 3 growing seasons (27 months). Plots of the

predicted and observed (Figures 5.9 and 5.10) populations were used to qualitatively assess the general behavior of the model (i.e. simulated increases and decreases in density were compared with observed increases and decreases). The accuracy of the model was tested by comparing predicted population values with the observed mean and one standard deviation from the mean. The average of observed minus predicted residuals (Table 5.2 and 5.4) and the r^2 values (Table 5.3 and 5.5) from regressions of the observed on the predicted also were used to quantify model performance against the verification and validation data sets (Barber, 1984).

RESULTS

Influence of phenology and environment (site) on demography

In the field studies (Chapters 3 and 4) salmonberry demographic paramters showed a consistent pattern over phenological stages, although mortality and survival at each stage class was more consistent than transitions between classes (Figure 5.6 and 5.7). Phenology was therefore, a significant factor influencing salmonberry demography. There was little difference in mean demographic parameter values between sites for salmonberry. Thimbleberry demographics generally showed a less consistent pattern across the phenological stages and between sites than salmonberry. The inconsistencies between thimbleberry and salmonberry mean demographic parameter values may be

caused by slight differences in phenologies between the two species which resulted from determining data collection times based on salmonberry phenology rather than thimbleberry.

Transition matrices for each phenological stage were constructed with mean and maximum values for each demographic parameter at each site and for each species (Figure A5.1). Population simulations using the maximum values for transitions and without density-dependence produced exponential growth (Figure 5.8). Simulations using mean values in the transition matrices without density-dependence suggested that populations, after an initial increase in ramet density, would slowly decline to extinction (Figure 5.8). Neither simulations is an accurate portrayal of observed Rubus spp. population behavior. Density-dependent functions and means (Table A5.2) were substituted for the parameters in the transition matrices and simulations were performed (Figure 5.8). This produced a population growth trajectory more typical of natural populations including oscillations coinciding with phenological stages.

Model verification

Population simulations were compared with the planted monoculture populations for each species at each site and each planting density. The simulated behavior of the populations was improved over using mean or maximum

transition values. Simulations were within 1 standard deviation of the mean of observed populations at the 9 and 25 planting densities. Salmonberry simulations were more accurate than thimbleberry (Figures 5.9 and 5.10 and A5.2 to A5.9). In almost all cases, the model underestimated the density in planted populations. General salmonberry population behavior was simulated accurately at a planting density of 9 at site 2 (Figure 5.9). Only predicted basal bud density showed general deviations from the observed population behavior. This deviation may be the result of relying on density as the primary mechanism to regulate basal bud dynamics when other factors are having a stronger influence. Thimbleberry population behavior at both sites was less accurately simulated (Figures 5.10 and A5.5 to A5.9). Increases in observed sprout density at the establishment and reproductive stages of the second and third growing season were not predicted with the model. Thus total thimbleberry shoots as well as sprouts were under predicted. Comparison of the mean residuals (Table 5.2) and r^2 values (Table 5.3) further indicate that predicted thimbleberry sprout density at site 1 was inaccurate.

Sensitivity and elasticity analysis (Maxwell et al., 1988; Maloney, 1989) indicated that the intercept on the equation that predicts basal bud production (V5) at the senescence stage (Time = 19 in Table A5.2) had the greatest

influence on thimbleberry sprout density (Figure 5.11). The intercept is the basal bud production per vegetative shoot at 0 density. Arbitrarily raising the value of the intercept from 1.14 to 3.0 increased the r^2 value for the regression of observed on predicted sprouts from 0.345 to 0.516. An under estimate of this parameter may be the result of measurement error, because the basal buds can be hidden in the soil and not counted. The number of basal buds at low densities is also more variable than at high densities. Therefore, data to accurately estimate the intercept are difficult to obtain.

Model validation

Population simulations were compared to wild salmonberry and thimbleberry populations that were clipped at the same time the cuttings were planted (Chapter 4). The observations from the clipped wild populations were used to validate the model over the first three growing seasons. The wild populations developed densities similar in magnitude and pattern to the planted populations (Figure 5.12). The model generally under predicted shoot densities in the first two growing seasons, then over predicted them in the third (Figures 5.12 and 5.13). The number of basal buds counted immediately prior to clipping and an estimated number of rhizomes equal to the number of shoots were used as starting values to simulate wild population dynamics after clipping. The starting values used to initiate the

simulation can have an influence on predictions. When starting values for basal buds and rhizomes were doubled, the explanatory value of the model relative to the observed data increased by 28% for thimbleberry at Site 1 (Figure 5.14). Site 2 salmonberry simulations following similar input changes also were improved for years 1 and 2 (Figure 5.14). Most of the prediction improvement was the result of first and second growing season increases in sprouts. The simulation improvement in response to increased bud and rhizome input values, indicates that clipping shoots in natural populations may increase the basal bud bank or the sprouting rate to produce more shoots in the months following clipping. Under-predictions of wild population density may also be due to decreased accuracy in estimating the number of basal buds, because of the extent of the underground root crowns and rhizomes and the subsequent difficulty of finding buds.

Management simulations

Management of salmonberry and thimbleberry for associated conifer seedling survival and growth involves reducing population densities, cover and/or height. The simulation model was used to address two management related objectives. The first objective was to determine the "Achille's heel" of salmonberry and thimbleberry and thereby suggest management practices which would have the greatest effect on the identified points of vulnerability.

The second objective was to assess some current management practices to determine if the model can simulate the response of the populations to a particular practice.

Sensitivity and elasticity analysis (Maloney, 1989; Maxwell et al., 1988) was used to identify parameters and subsequent demographic processes which have the greatest influence on predicted ramet density and therefore represent points of vulnerability. Basal bud production (Figure 5.1) on rhizomes (V7) and rhizome survival (R7) were indicated as most important for thimbleberry population growth at both sites. Vegetative shoot survival (R5) followed by rhizome survival were most important for salmonberry.

Observed canopy cover of salmonberry and thimbleberry populations treated with 0.75 kg a.i./ha of glyphosate (Harrington and Wagner, 1986) were compared to simulated treatments (Figure 5.15). Observations of the treated populations were made prior to, and for three years following herbicide application. Input values for the population model were adjusted so that percent canopy cover was within 5% of the observed cover prior to treatment. The glyphosate application was simulated by removal of 96% (i.e. 96% control) of the shoots for both species (Newton and White, 1984) and reduced the basal bud population on crowns and rhizomes by 10% the season of application (senescence stage). These assumptions produced an accurate

simulation of the observed populations response to the herbicide the first year following application. The second and third year after application the simulated populations recovered (increased canopy cover) more rapidly than the observed ones. Over-prediction following treatment may be due to omission of inter-specific effects on demographics, particularly the influence of the crop tree. Reduction in the cover of shrub species is typically followed by an increase in crop tree growth which may result in a reduction in the shrub population growth for a period following treatment. The deviation of observed from simulated populations may also be explained by either retention and continued effects of the glyphosate beyond the first year, or greater intial effects on the rhizome and basal bud production systems. The observed cover in response to glyphosate treatment was more accurately simulated when rhizome mortality was arbitrarily increased in the model.

Management of salmonberry populations with manual cutting was assessed with the model. Population growth was initiated from 9 rhizomes and 36 buds per m^2. Pioneer Mountain (Site 2) parameters were used in the density-dependent equations. Simulation of manual cutting assumed that all shoots were cut near the ground in the second year of growth, but the root crown was not disturbed. A further assumption was a 20% increase in basal bud production

following cutting due to loss of apical dominance. The simulated response of canopy cover and height to manual cutting was compared at each phenological stage (establishment, reproduction and senescence). The longest reduction of cover followed cutting at the reproductive stage (Figure 5.16). This simulation coincides with the most prolonged reductions in salmonberry cover following manual cutting that were observed by Zasada (personal communication). Simulated salmonberry height assumed its original (prior to cutting) growth trajectory within three months regardless of the season of cutting.

DISCUSSION

The simulation model provides reasonably accurate predictions of salmonberry and thimbleberry population behavior over the first three growing seasons at two sites in the Coast Range. Prediction of basal bud production for both species was a general weaknesses in the model. This weakness was attributed to inaccuracy in basal bud counts. Basal buds of Rubus were often hidden in the soil. The inaccuracy also can be attributed to the use of density as the primary mechanism governing basal bud dynamics. Other internal plant factors may have a greater influence on basal bud demography. Further refinement and improvement of the model will result when information from other studies (Tappeneir et al, 1990) is included and parameter optimization (Kuester and Mize, 1973; Wagner et al., 1989)

is conducted with the verification and validation data.

Sensitivity analysis indicated that reduction of thimbleberry density would be most efficiently accomplished with management practices that inhibit basal bud production and survival of rhizomes. Management options that will accomplish this are limited to herbicides until more is learned about the mechanisms which regulate basal bud and rhizome demographics. The model suggests that salmonberry populations may be effectively supressed (density reduced) by focussing on management options that reduce the number of vegetative shoots and rhizomes. The relative importance of basal buds and rhizomes to the maintenance of salmonberry and thimbleberry populations is a factor which reduces the potential for developing an accurate population model. However, the difficulty in obtaining basal bud and rhizome demographic data increases the need for models which can be used to generate hypotheses on the mechanisms governing underground population dynamics.

An important aspect of shrub management for conifer production is determining the period of time that shrub populations must be reduced for conifer seedlings to avoid competition from the shrubs (Wagner et al., 1989). Wagner (1989) found that if over topping shrubs are removed Douglas-fir seedling height growth can be increased and seedlings can assume dominance within three years of planting. Therefore, the time span that the simulation

model has been tested is appropriate for management considerations. The salmonberry simulations of the response of canopy cover and height to manual cutting (Figure 5.16) shows the potential use of the model for assessing management practices for their ability to produce a height and cover "window" in the shrub population. With the addition to the model of the influence of the crop tree on the shrub population, coupled with the crop tree response to shrub population abundance (Wagner, 1989), management tactics that fit the critcal period threshold could be suggested with the model.

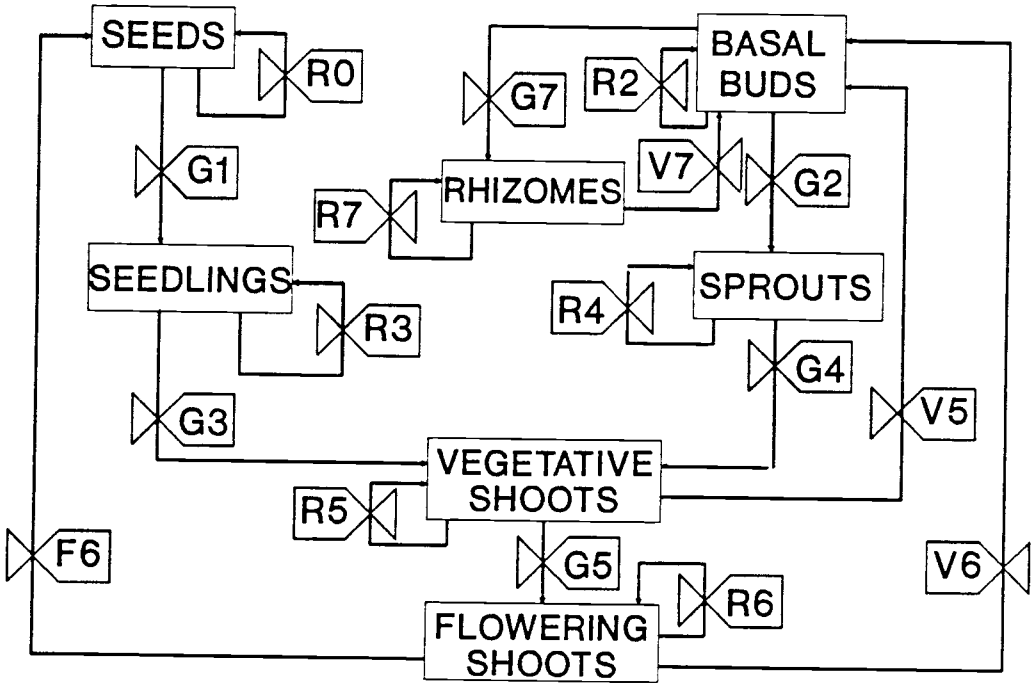
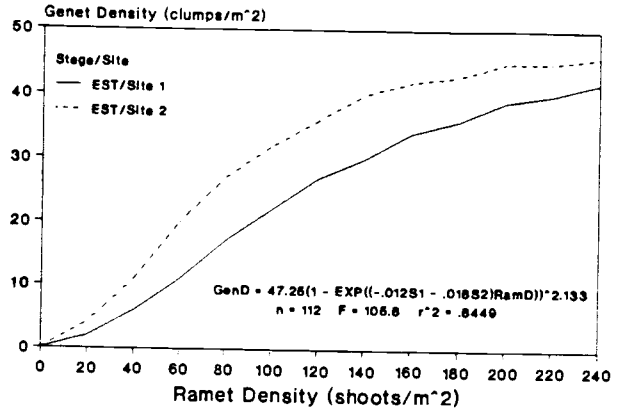
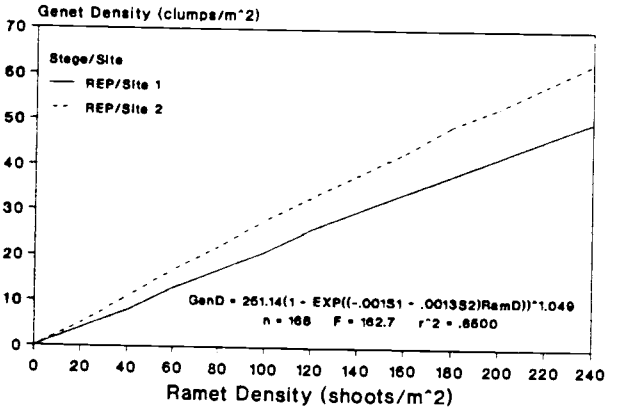


Figure 5.1. A diagrammatic representation of the refined Rubus population model. State variables are seeds, seedlings, basal buds, rhizomes, sprouts, vegetative (mature) shoots, flowering shoots. Arrows between state variables represent demographic processes, and valves represent the rate or probability of transition from one state to the next.

G1 = germination R0 = seed survival
G2 = sprouting R2 = basal bud survival
G3 = sdl. growth R3 = seedling survival
G4 = spr. growth R4 = sprout survival
G5 = flowering R5 = veg. shoot survival
G7 = buds become rhizomes
F6 = seed produced/flowering shoot
V5 = basal buds produced/veg. shoot
V6 = basal buds produced/ flw. shoot
V7 = buds produced/rhizome
R6 = flowering shoot survival
R7 = rhizome survival

Figure 5.2. The functional relationships used to predict Salmonberry (RUSP) and thimbleberry (RUPA) genet density from ramet density at Woods Creek (Site 1) and Pioneer Mountain (Site 2) at the establishment (EST), reproduction (REP) and senescence (SEN) phenological stages.


Genet Density (clumps/m^2)
Stage/Site
EST/Site 1
EST/Site 2
GenD = 47.26(1 - EXP((-.0125 1 - .0168 2)RamD))^2.133
n = 112 F = 106.8 r^2 = .8449
Ramet Density (shoots/m^2)


Genet Density (clumps/m^2)
Stage/Site
REP/Site 1
REP/Site 2
GenD = 261.14(1 - EXP((-.0015 1 - .0013 2)RamD))^1.049
n = 168 F = 162.7 r^2 = .8600
Ramet Density (shoots/m^2)

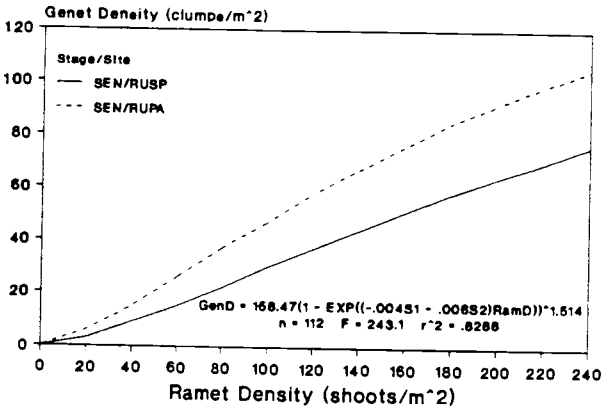

Genet Density (clumps/m^2)
Stage/Site
SEN/RUSP
SEN/RUPA
GenD = 158.47(1 - EXP((-.0045 1 - .0068 2)RamD))^1.514
n = 112 F = 243.1 r^2 = .8288
Ramet Density (shoots/m^2)

Fig. 5.2.

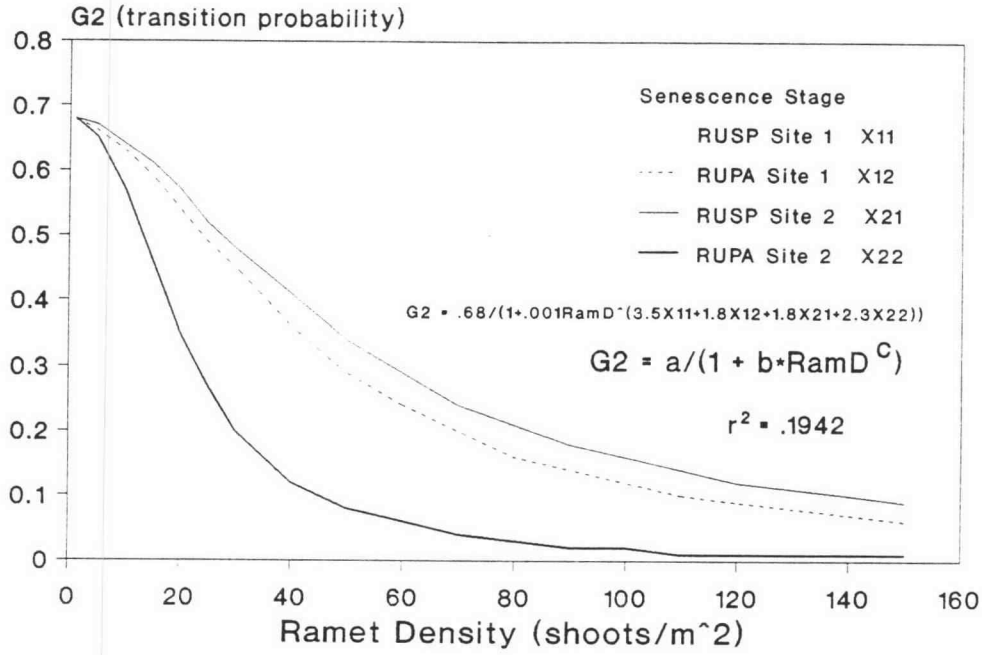


Figure 5.3. The sigmoid relationship between sprouting of basal buds (G2) and ramet density at the senescence stage for salmonberry (RUSP) and thimbleberry (RUPA) at Woods Creek (Site 1) and Pioneer Mountain (Site 2). See text for variable definitions.

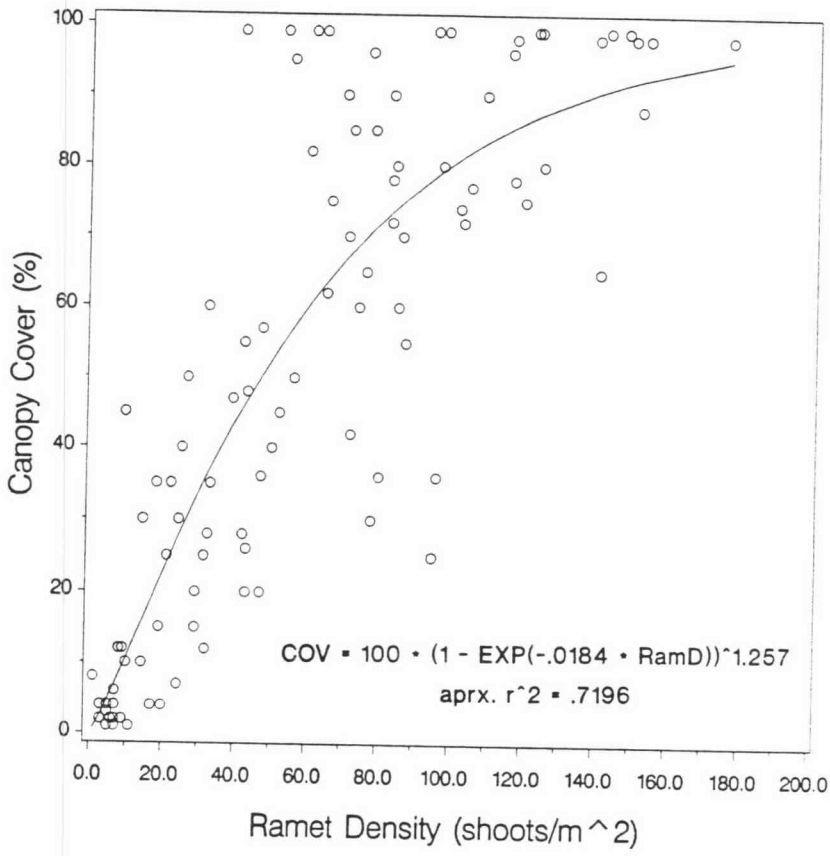
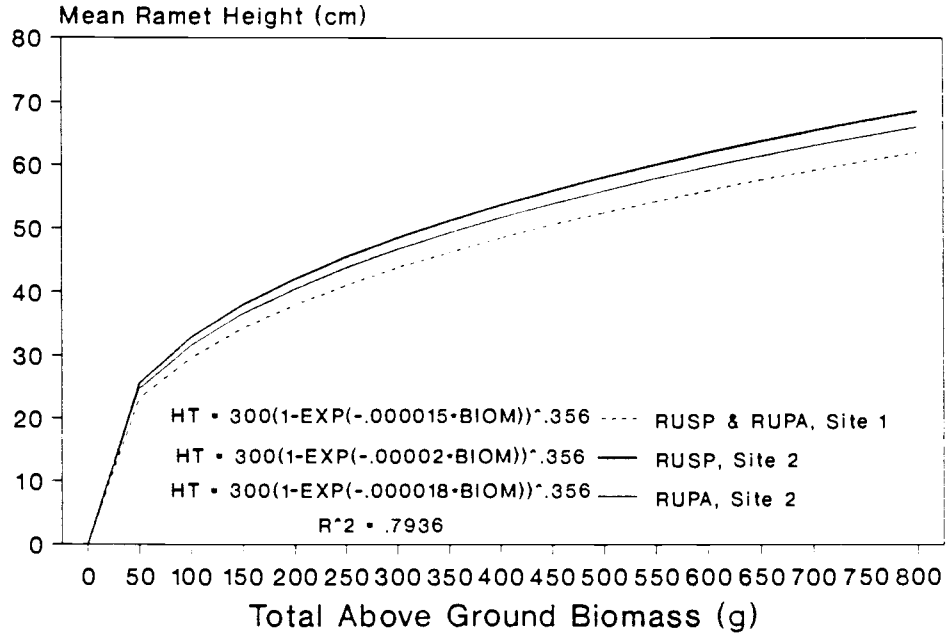


Figure 5.4. The functional relationships used to predict percent canopy cover of both species from ramet density at both sites and all phenological stages.

Figure 5.5. The functional relationships used to predict Salmonberry (RUSP) and thimbleberry (RUPA) mean ramet height from population above-ground dry biomass at Woods Creek (Site 1) and Pioneer Mountain (Site 2) (top), and relationships for Site 2 salmonberry for different asymptote (a) values for first growing season (a = 300), second growing season (a = 600) and third growing season (a = 800) (bottom).


Mean Ramet Height (cm)
80
70
60
50
40
30
20
10
0
HT = 300(1-EXP(-.000015*BIOM))^.356
HT = 300(1-EXP(-.00002*BIOM))^.356
HT = 300(1-EXP(-.000018*BIOM))^.356
R^2 = .7936
RUSP & RUPA, Site 1
RUSP, Site 2
RUPA, Site 2
0 50 100 150 200 250 300 350 400 450 500 550 600 650 700 750 800
Total Above Ground Biomass (g)

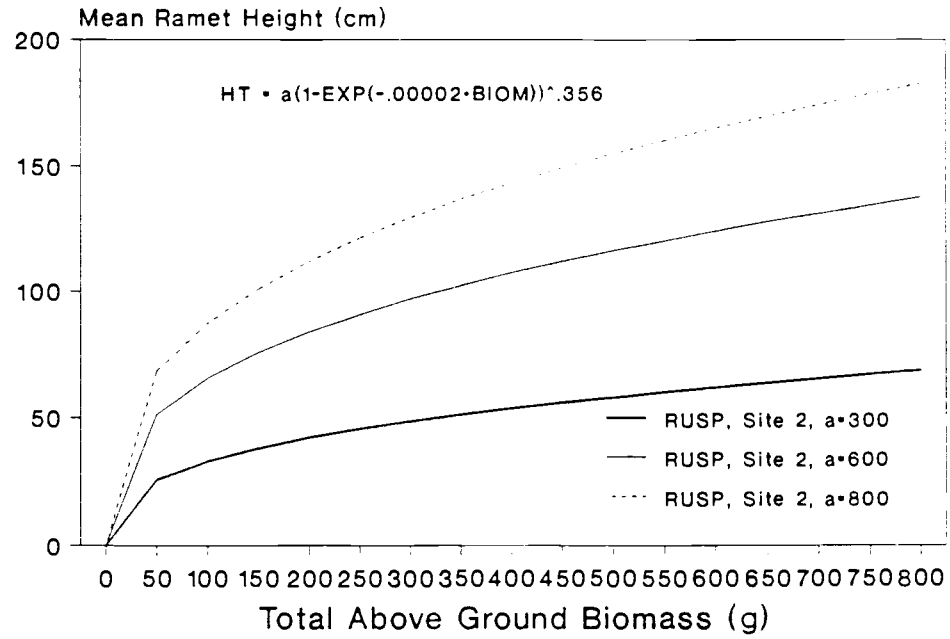
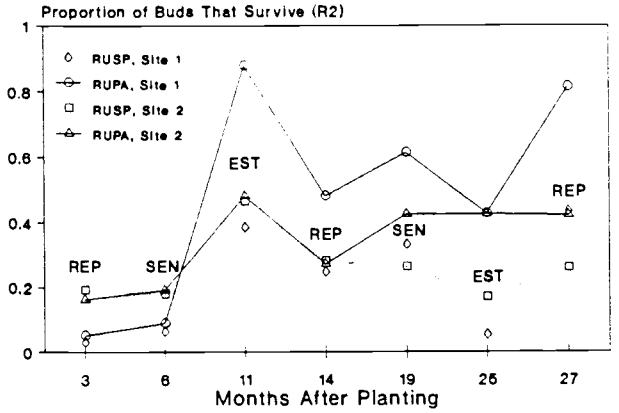
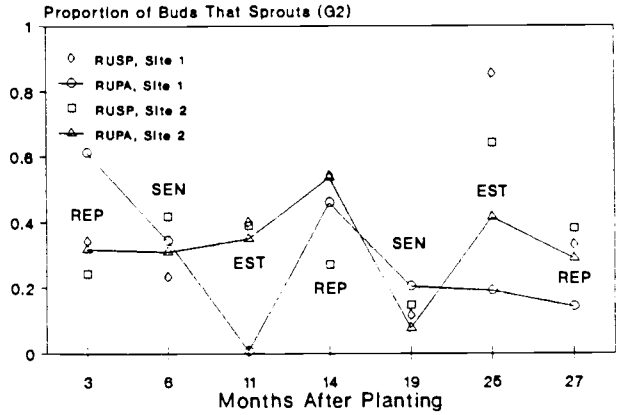

Mean Ramet Height (cm)
200
150
100
50
0
HT = a(1-EXP(-.00002*BIOM))^.356
RUSP, Site 2, a=300
RUSP, Site 2, a=600
RUSP, Site 2, a=800
0 50 100 150 200 250 300 350 400 450 500 550 600 650 700 750 800
Total Above Ground Biomass (g)

Fig. 5.5.

Figure 5.6. The mean proportion of buds that survive (top), sprout (middle), and die (bottom) over the first three growing seasons in planted populations of Salmoberry (RUSP) and thimblberry (RUPA) at Woods Creek (Site 1) and Pioneer Mountain (Site 2) at the establishment (EST), reproductive (REP) and senescence (SEN) phenological stages.


Proportion of Buds That Survive (R2)
RUSP, Site 1
RUPA, Site 1
RUSP, Site 2
RUPA, Site 2
REP
SEN
EST
REP
SEN
REP
EST
REP
0
0.2
0.4
0.6
0.8
1
3
6
11
14
19
25
27
Months After Planting


Proportion of Buds That Sprouts (G2)
RUSP, Site 1
RUPA, Site 1
RUSP, Site 2
RUPA, Site 2
REP
SEN
EST
REP
SEN
EST
REP
0
0.2
0.4
0.6
0.8
1
3
6
11
14
19
25
27
Months After Planting

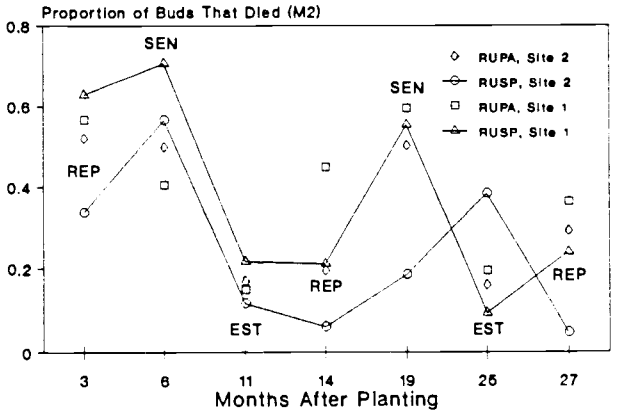
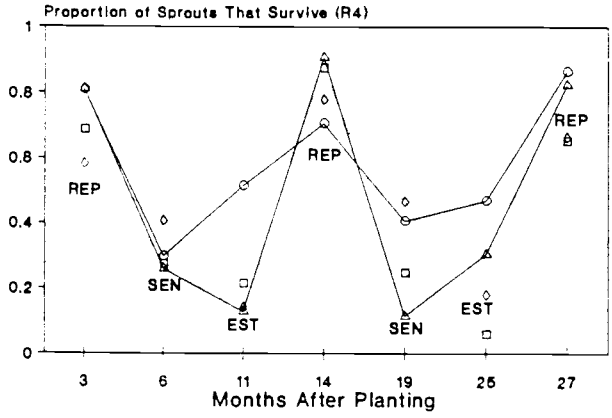
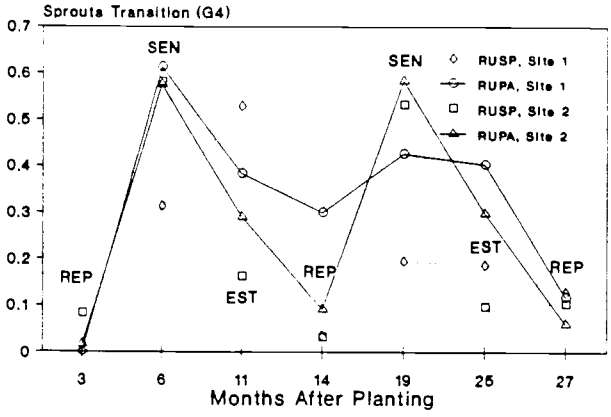

Proportion of Buds That Died (M2)
RUPA, Site 2
RUSP, Site 2
RUPA, Site 1
RUSP, Site 1
REP
SEN
EST
REP
SEN
EST
REP
0
0.2
0.4
0.6
0.8
3
6
11
14
19
25
27
Months After Planting

Fig. 5.6.

Figure 5.7. The mean proportion of sprouts that survive (top), graduate to mature vegetative shoots (middle), and die (bottom) over the first three growing seasons in planted populations of Salmoberry (RUSP) and thimblberry (RUPA) at Woods Creek (Site 1) and Pioneer Mountain (Site 2) at the establishment (EST), reproductive (REP) and senescence (SEN) phenological stages.


Proportion of Sprouts That Survive (R4)
1
0.8
0.8
0.4
0.2
0
REP
SEN
EST
REP
SEN
EST
REP
3
6
11
14
19
25
27
Months After Planting


Sprouts Transition (G4)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
SEN
SEN
RUSP, Site 1
RUPA, Site 1
RUSP, Site 2
RUPA, Site 2
REP
EST
REP
EST
REP
3
6
11
14
19
25
27
Months After Planting

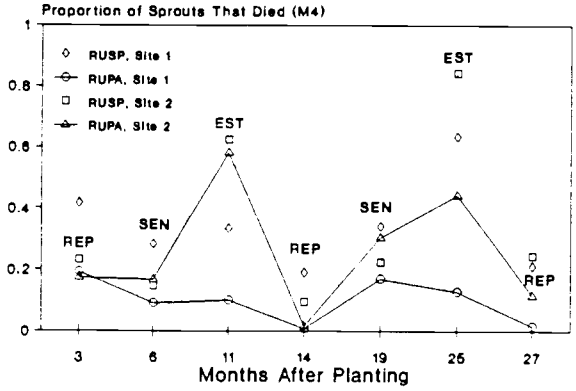

Proportion of Sprouts That Died (M4)
1
0.8
0.6
0.4
0.2
0
RUSP, Site 1
RUPA, Site 1
RUSP, Site 2
RUPA, Site 2
EST
EST
SEN
SEN
REP
REP
REP
3
6
11
14
19
25
27
Months After Planting

Fig. 5.7.

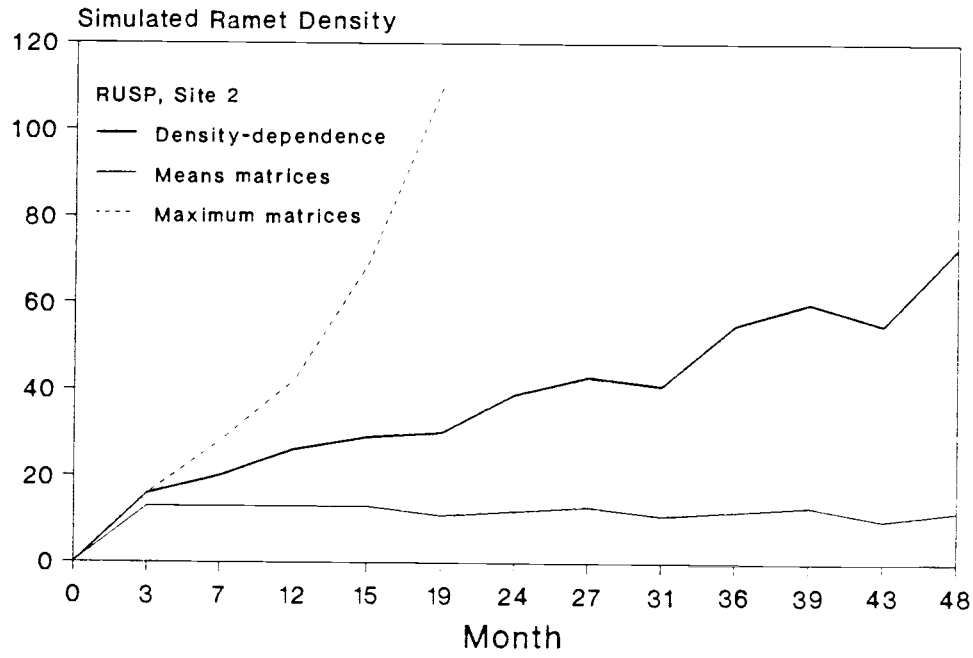
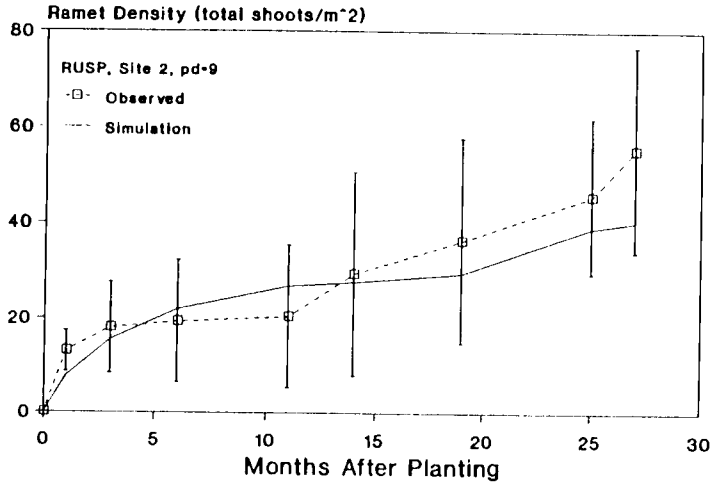
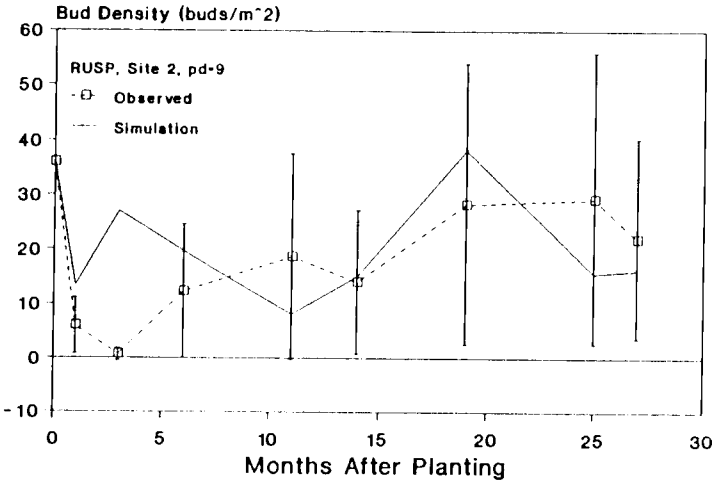


Figure 5.8. Model simulations of salmonberry (RUSP) population (ramet density) development over time using mean or maximum values for demographic parameters in the transition matrices or substituting density-dependent functions for parameters in the matrices.

Figure 5.9. Simulated salmonberry ramet density (sprouts + veg. shoots + flowering shoots) (top left), basal bud density (top right), sprout density (bottom left) and vegetative shoot density (bottom right) over the first three growing seasons plotted with mean and 1 standard deviation of observed populations planted with 9 cuttings/m^2 at Pioneer Mountain (Site 2).


Ramet Density (total shoots/m^2)
RUSP, Site 2, pd-9
Observed
Simulation
80
60
40
20
0
0
5
10
15
20
25
30
Months After Planting


Bud Density (buds/m^2)
RUSP, Site 2, pd-9
Observed
Simulation
60
50
40
30
20
10
0
-10
0
5
10
15
20
25
30
Months After Planting

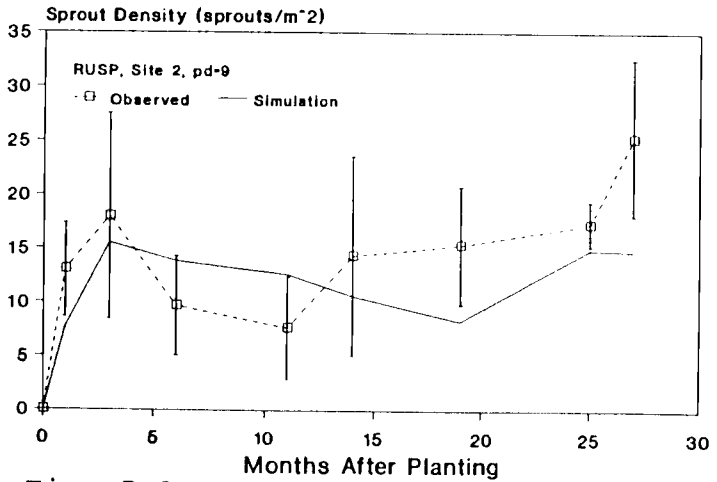

Sprout Density (sprouts/m^2)
RUSP, Site 2, pd-9
Observed
Simulation
35
30
25
20
15
10
5
0
0
5
10
15
20
25
30
Months After Planting

Fig. 5.9.

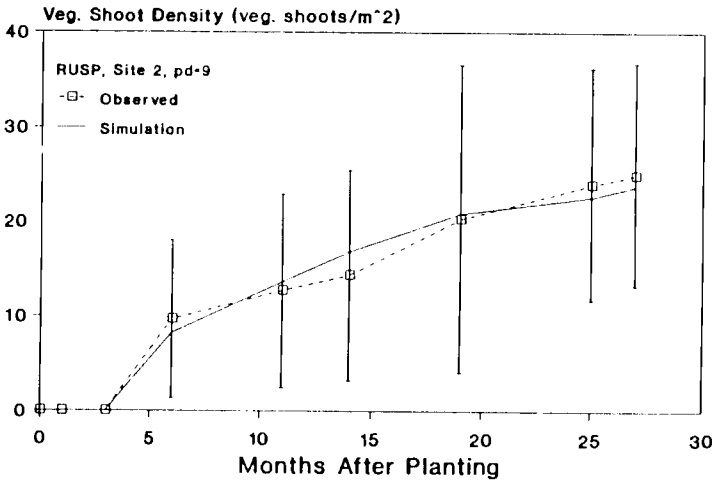
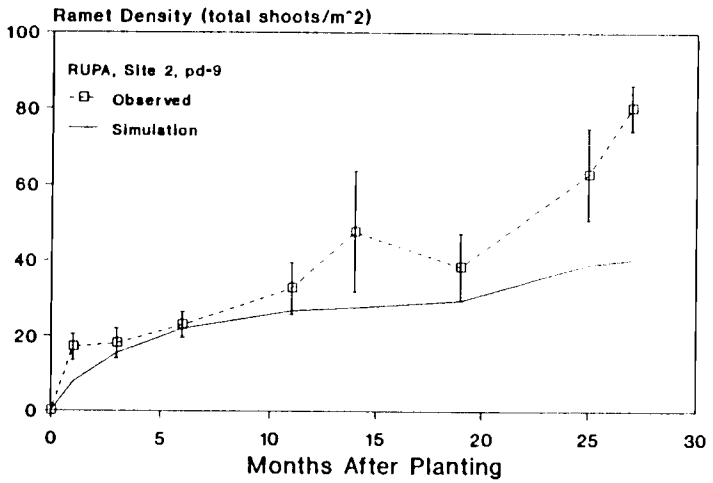
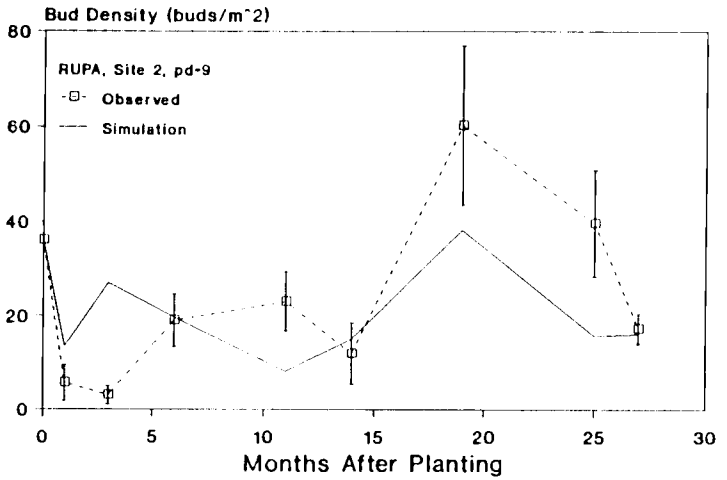
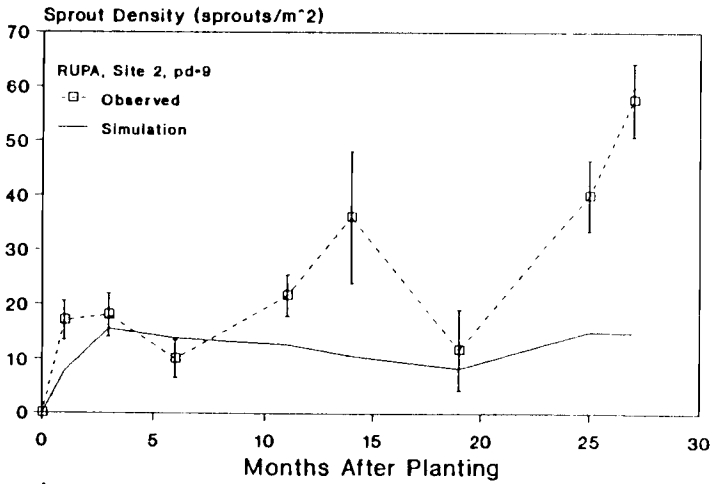

Veg. Shoot Density (veg. shoots/m^2)
RUSP, Site 2, pd-9
Observed
Simulation
40
30
20
10
0
0
5
10
15
20
25
30
Months After Planting

Figure 5.10. Simulated thimbleberry ramet density (top left), basal bud density (top right), sprout density (bottom left) and vegetative shoot density (bottom right) over the first three growing seasons plotted with mean and 1 standard deviation of observed populations planted with 9 cuttings/m^2 at Pioneer Mountain (Site 2).


Ramet Density (total shoots/m^2)
RUPA, Site 2, pd-9
Observed
Simulation
100
80
60
40
20
0
0
5
10
15
20
25
30
Months After Planting


Bud Density (buds/m^2)
RUPA, Site 2, pd-9
Observed
Simulation
80
60
40
20
0
0
5
10
15
20
25
30
Months After Planting


Sprout Density (sprouts/m^2)
RUPA, Site 2, pd-9
Observed
Simulation
70
60
50
40
30
20
10
0
0
5
10
15
20
25
30
Months After Planting

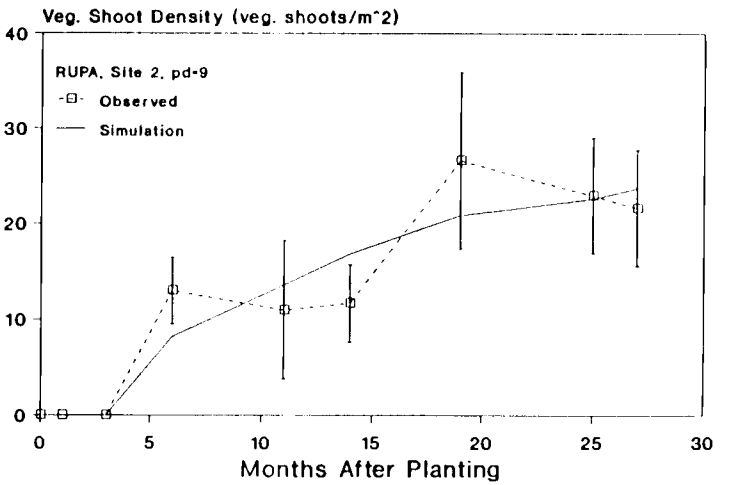

Veg. Shoot Density (veg. shoots/m^2)
RUPA, Site 2, pd-9
Observed
Simulation
40
30
20
10
0
0
5
10
15
20
25
30
Months After Planting

Fig. 5.10.

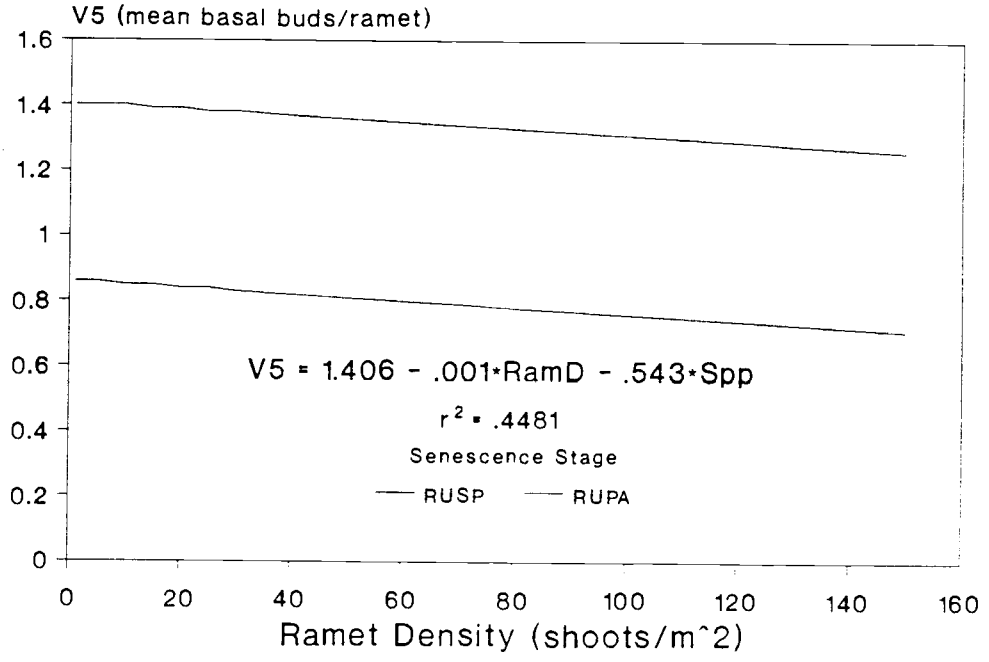
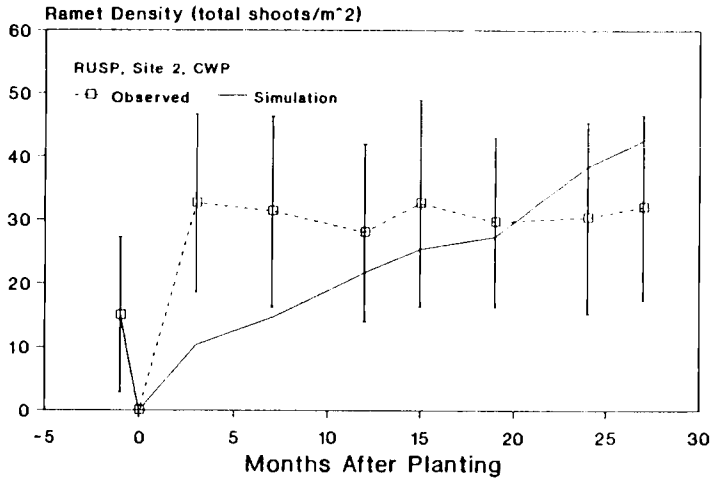
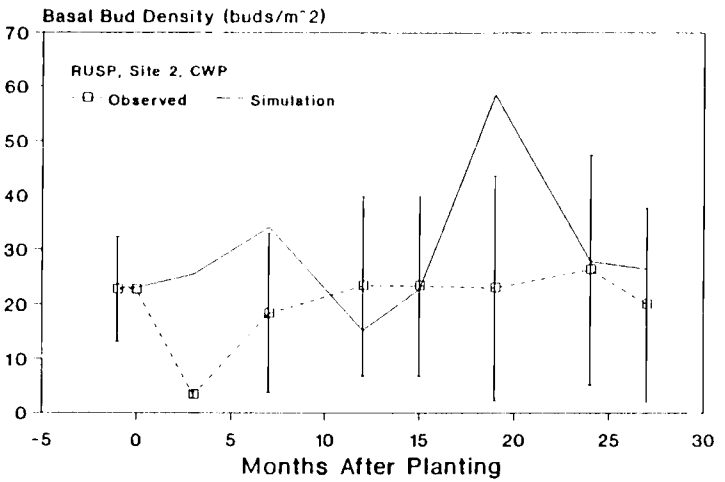
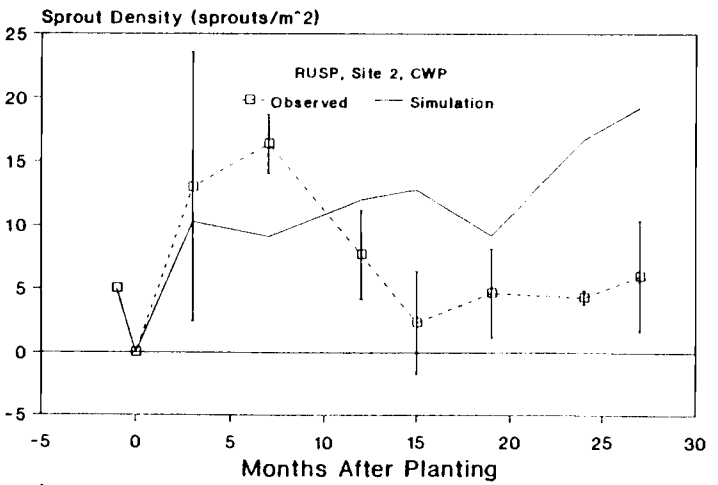


Figure 5.11. The function used to predict salmonberry (RUSP) and thimbleberry (RUPA) basal bud production from ramet density.

Figure 5.12. Simulated salmonberry ramet density (top left), basal bud density (top right), sprout density (bottom left) and vegetative shoot density (bottom right) over the first three growing seasons (month 0 = time of clipping) plotted with mean and 1 standard deviation of observed clipped wild populations at Pioneer Mountain (Site 2).


Ramet Density (total shoots/m^2)
RUSP, Site 2, CWP
Observed
Simulation
60
50
40
30
20
10
0
-5
0
5
10
15
20
25
30
Months After Planting


Basal Bud Density (buds/m^2)
RUSP, Site 2, CWP
Observed
Simulation
70
60
50
40
30
20
10
0
-5
0
5
10
15
20
25
30
Months After Planting


Sprout Density (sprouts/m^2)
RUSP, Site 2, CWP
Observed
Simulation
25
20
15
10
5
0
-5
-5
0
5
10
15
20
25
30
Months After Planting

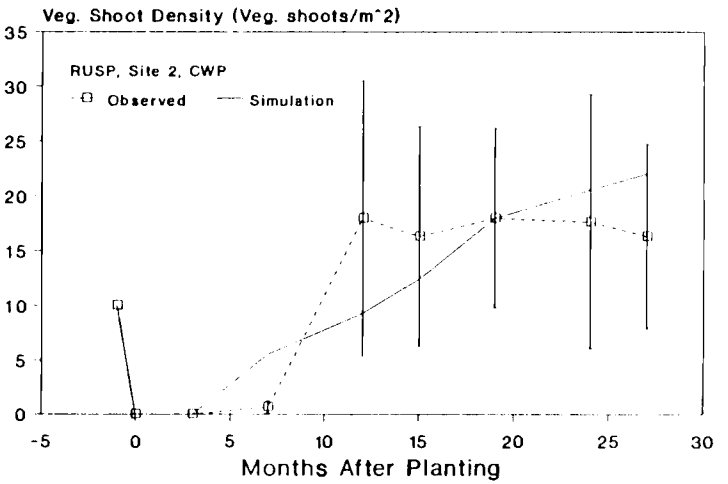
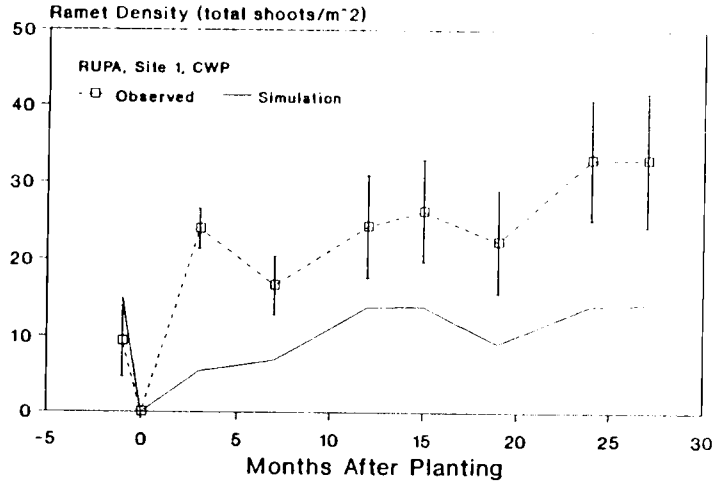
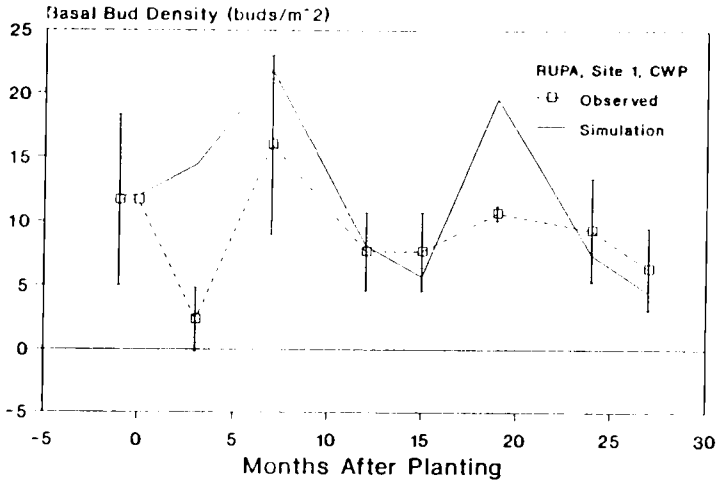
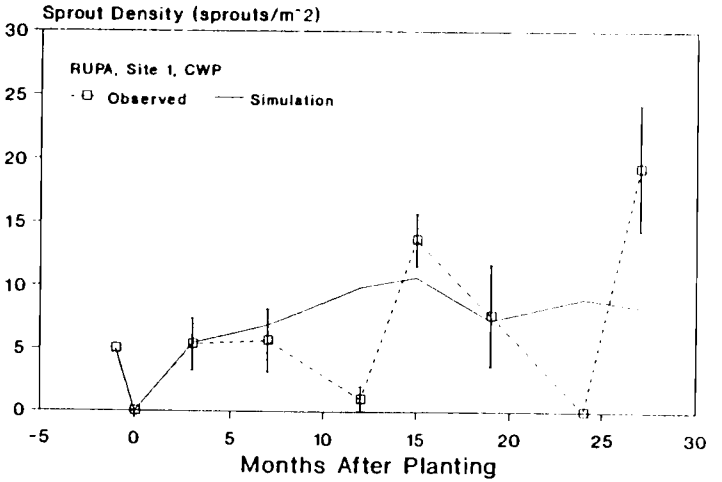

Veg. Shoot Density (Veg. shoots/m^2)
RUSP, Site 2, CWP
Observed
Simulation
35
30
25
20
15
10
5
0
-5
0
5
10
15
20
25
30
Months After Planting

Fig. 5.12.

Figure 5.13. Simulated thimbleberry ramet density (top left), basal bud density (top right), sprout density (bottom left) and vegetative shoot density (bottom right) over the first three growing seasons (month 0 = time of clipping) plotted with mean and 1 standard deviation of observed clipped wild populations at Pioneer Mountain (Site 2).


Ramet Density (total shoots/m^2)
RUPA, Site 1, CWP
Observed
Simulation
Months After Planting


Basal Bud Density (buds/m^2)
RUPA, Site 1, CWP
Observed
Simulation
Months After Planting


Sprout Density (sprouts/m^2)
RUPA, Site 1, CWP
Observed
Simulation
Months After Planting

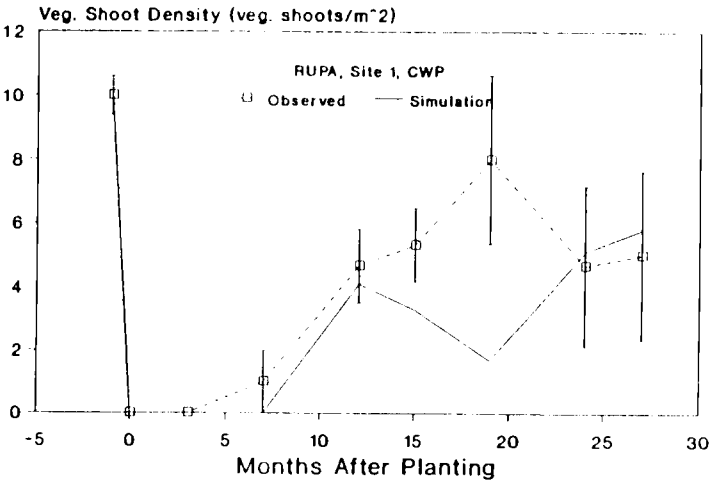

Veg. Shoot Density (veg. shoots/m^2)
RUPA, Site 1, CWP
Observed
Simulation
Months After Planting

Fig. 5.13.

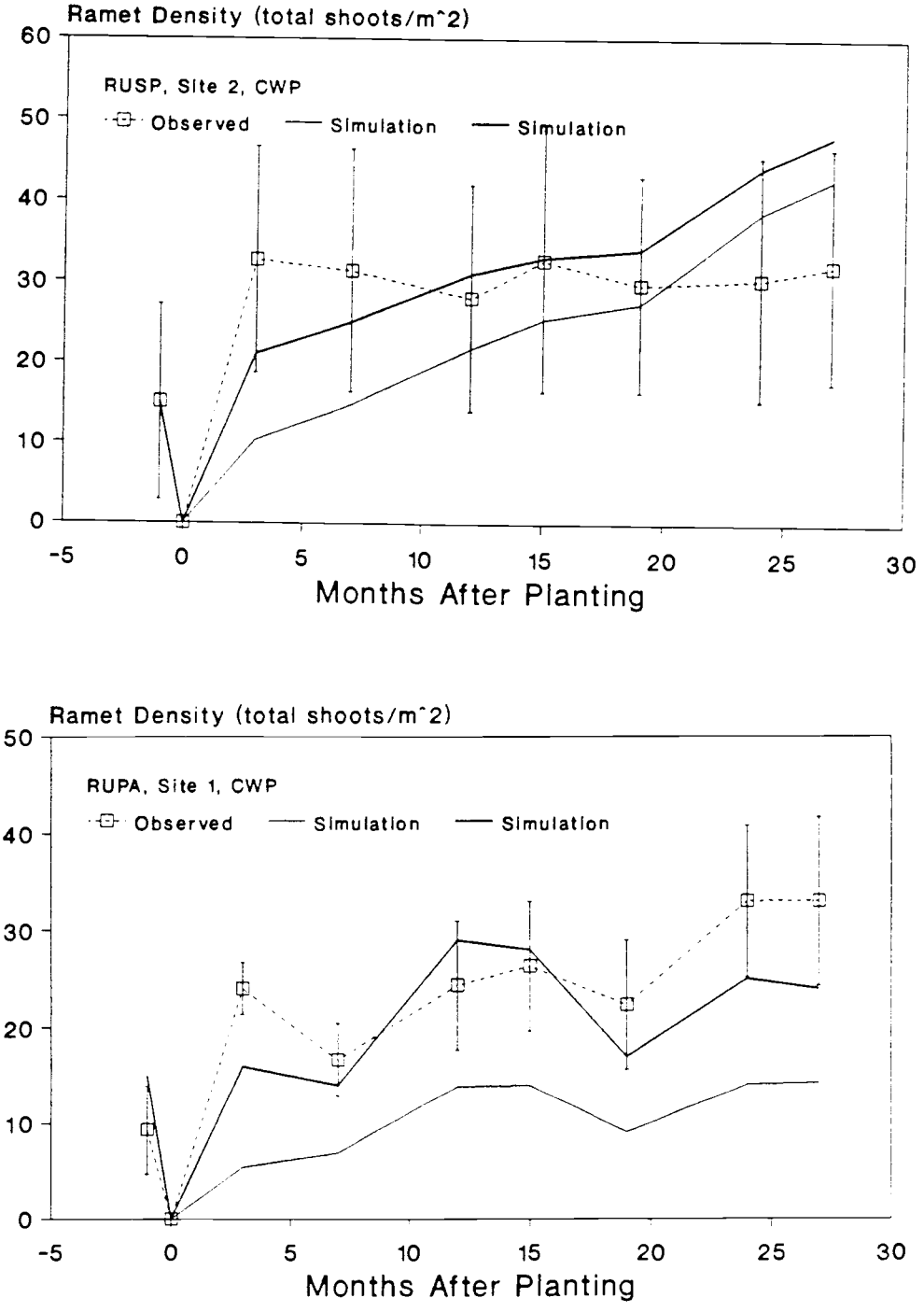


Figure 5.14. Simulated salmonberry (top) and thimbleberry (bottom) ramet density over the first three growing seasons (month 0 = time of clipping) plotted with mean and 1 standard deviation of observed clipped wild populations at Pioneer Mountain (Site 2). The bold line represents a simulation with starting values that were doubled from the values used for the first simulation.

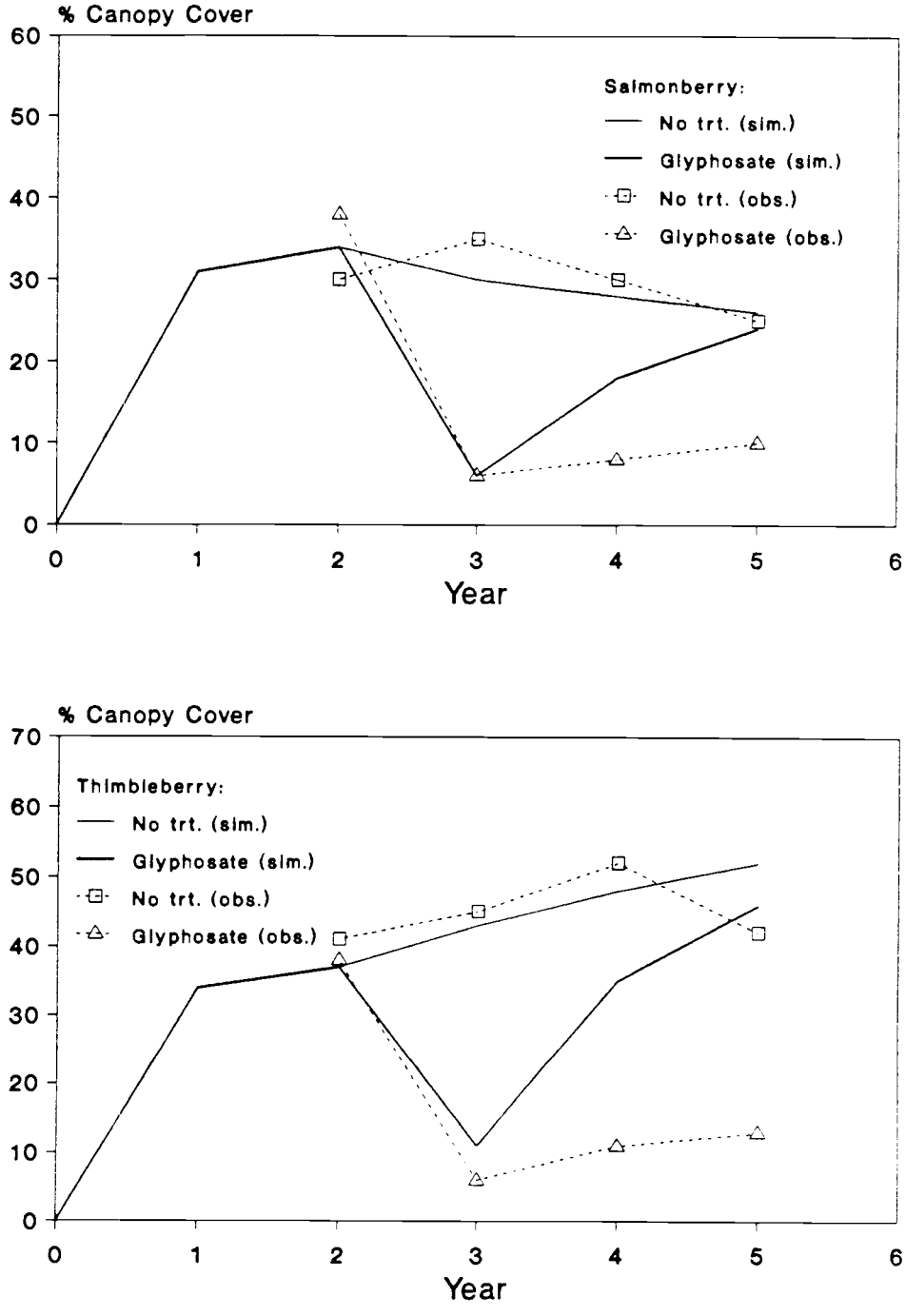
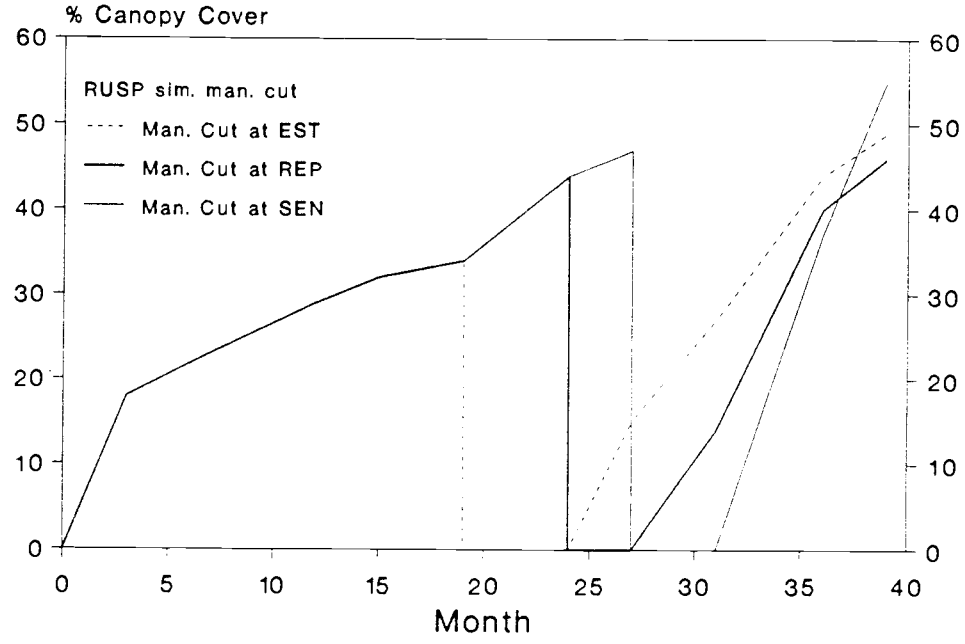


Figure 5.15. Salmonberry (top) and thimbleberry (bottom) percent canopy cover in response to a 3 kg. a.i./ha glyphosate application at the senescence stage of year 2 compared with observed data from treatments and controls.

Figure 5.16. Simulated response of salmonberry (RUSP) canopy cover to manual cutting treatments in the second growing season at establishment (EST), reproduction (REP) and senescence (SEN) (top). Simulation of salmonberry cover and height in response to manual cutting at reproduction (Bottom).

Fig. 5.16.


% Canopy Cover
RUSP sim. man. cut
Man. Cut at EST
Man. Cut at REP
Man. Cut at SEN
0
10
20
30
40
50
60
0
5
10
15
20
25
30
35
40
Month

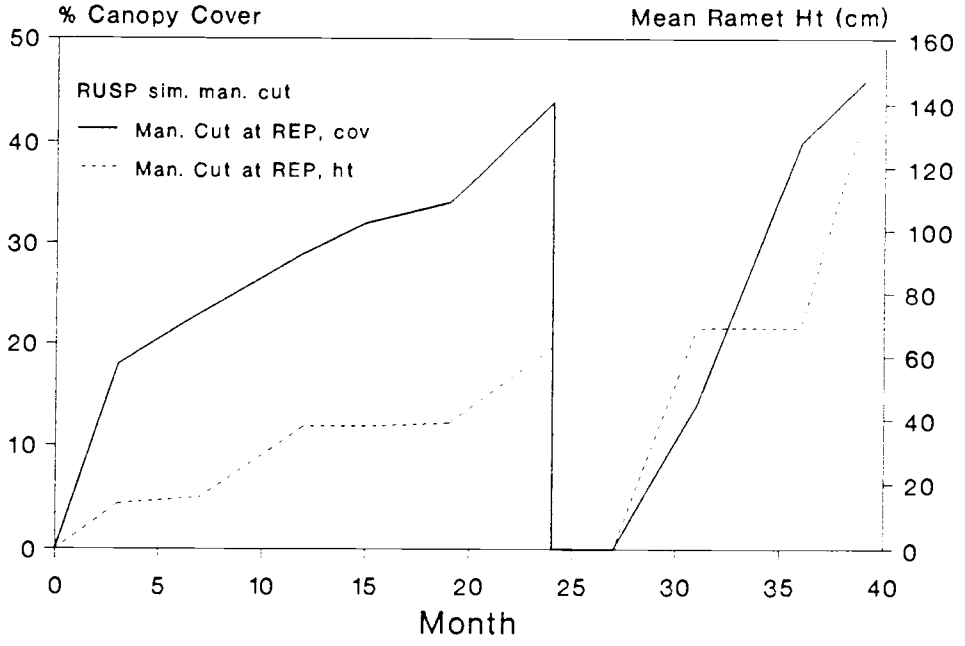

% Canopy Cover
Mean Ramet Ht (cm)
RUSP sim. man. cut
Man. Cut at REP, cov
Man. Cut at REP, ht
0
10
20
30
40
50
0
20
40
60
80
100
120
140
160
0
5
10
15
20
25
30
35
40
Month

Table 5.1. Rubus population model output for a simulation of a salmonberry population at Pioneer Mountain (Site 2) started at the establishment stage in year 0 and output at the reproductive stage year 0 through 5. Lamda is a seasonal population growth rate.

Year	Seed	Buds	Seed-lings	Sprouts	Veg. shoots	Flowering shoots	Rhizomes	lamda
0	100	36	0	0	0	0	9	0.000
0	95	25	5	16	0	0	12	1.062
1	57	20	2	12	16	0	28	1.072
2	42	23	0	17	24	2	43	1.009
3	87	36	0	25	32	2	59	0.989
4	144	48	0	34	41	3	78	0.974
5	206	59	0	42	50	4	97	0.963

Table 5.2. Average of observed minus predicted residuals from simulations of salmonberry (RUSP) and thimbleberry (RUPA) compared to the planted populations at Woods Creek (Site 1) and Pioneer Mountain (Site 2).

			Average Residual					
Site	Spp	Planting Density	Buds	Sprouts	Vegetative shoots	Total shoots	% Canopy cover	Height (cm)
1	RUSP	1	1.4	0.6	0.7	1.3	4.2	15.1
		9	6.7	4.6	0.8	4.8	6.1	7.0
		25	14.8	16.0	3.6	18.4	13.9	5.0
		81	35.1	41.3	6.6	44.4	20.4	6.1
2	RUSP	1	2.4	1.7	2.6	4.3	5.6	22.2
		9	10.5	3.3	0.8	4.2	8.4	11.5
		25	31.0	10.2	5.2	14.3	15.5	7.4
		81	82.1	24.7	11.6	18.4	17.8	13.8
1	RUPA	1	1.6	6.7	1.7	8.2	13.9	14.1
		9	7.9	20.1	5.6	23.4	17.6	10.8
		25	16.0	33.0	10.9	39.7	19.1	5.3
		81	54.4	47.8	12.9	48.9	14.8	5.4
2	RUPA	1	1.3	2.3	1.6	3.9	8.2	16.8
		9	9.2	10.4	8.4	18.6	23.3	9.4
		25	26.0	8.2	6.6	11.8	20.3	6.4
		81	74.0	14.9	14.4	26.7	22.7	10.8

Values are observation means from 4 populations per species at site 1 and 3 populations at site 2.

Table 5.3. R^2 values from regressions of observed on predicted values from simulations of salmonberry (RUSP) and thimbleberry (RUPA) compared to the planted populations at Woods Creek (Site 1) and Pioneer Mountain (Site 2).

			r^2					
Site	Spp	Planting Density	Buds	Sprouts	Vegetative shoots	Total shoots	% Canopy cover	Height (cm)
1	RUSP	1	.000	.737	.165	.375	.410	.239
		9	.335	.757	.948	.867	.395	.825
		25	.485	.601	.878	.728	.488	.928
		81	.419	.179	.734	.476	.535	.833
2	RUSP	1	.786	.751	.660	.720	.567	.783
		9	.616	.923	.997	.968	.922	.900
		25	.367	.887	.962	.950	.847	.939
		81	.256	.825	.926	.945	.830	.653
1	RUPA	1	.819	.296	.491	.394	.267	.691
		9	.746	.345	.366	.463	.594	.834
		25	.654	.504	.430	.590	.816	.960
		81	.382	.601	.290	.733	.856	.937
2	RUPA	1	.900	.728	.661	.742	.510	.775
		9	.860	.715	.556	.708	.686	.912
		25	.432	.864	.733	.888	.777	.966
		81	.365	.930	.660	.887	.795	.840

If r^2 = .000 then the regression was not significant ($p < 0.05$).

Table 5.4. Average of observed minus predicted residuals from simulations of salmonberry (RUSP) and thimbleberry (RUPA) compared to clipped wild populations at Woods Creek (Site 1) and Pioneer Mountain (Site 2).

		Average Residual				
Site	Spp	Buds	Sprouts	Vegetative shoots	Total shoots	% Canopy cover
1	RUSP	10.7	6.3	1.1	2.9	31.6
2	RUSP	11.3	6.8	3.3	9.2	15.6
1	RUPA	4.2	4.2	1.4	12.7	13.2
2	RUPA	8.9	9.2	3.9	10.0	24.6

Values are observation means from 3 populations per species at each site.

Table 5.5. R^2 values from regressions of observed on predicted values from simulations of salmonberry (RUSP) and thimbleberry (RUPA) compared to clipped wild populations at Woods Creek (Site 1) and Pioneer Mountain (Site 2).

		r^2				
Site	Spp	Buds	Sprouts	Vegetative shoots	Total shoots	% Canopy cover
1	RUSP	.000	.000	.943	.941	.519
2	RUSP	.410	.077	.896	.843	.736
1	RUPA	.645	.578	.726	.672	.597
2	RUPA	.753	.000	.728	.769	.451

If r^2 = .000 then the regression was not significant ($p < 0.05$).

SYNOPSIS

This thesis had two main goals: 1) to develop information on the population biology of salmonberry and thimbleberry pertinent to management of these species, and 2) to test an approach for conducting weed biology research. The suggested approach uses a population simulation model to organize existing information, generate hypotheses on population growth regulation, and identify the "achille's heel" of the weed. The model also can be used to evaluate weed control strategies.

Salmonberry and thimbleberry population establishment

Salmonberry and thimbleberry populations are common components of the vegetation on Coast Range clearcuts. A general conclusion of this thesis is that populations of these species growing in the Coast Range primarily originate from vegetative propagules. I concluded from my observations that seedlings are rarely present without vegetative sprouts. Therefore, the low survival and absolute growth rate of seedlings relative to sprouts provides an advantage for sprouts to dominate populations in clearcuts.

The Rubus model was used to compare populations started from 100 seeds with populations started from 100 buds. The number of years (averaged for both species and sites) for a population to reach 20% canopy cover was 14 for seed and 1 for buds. These simulations further indicate

that population establishment is more likely from vegetative propagules than from seed.

Population growth regulation

A major focus of this thesis was to investigate the mechanisms which naturally regulate clonal plant population growth. Intraspecific density (competition) was identified as a potentially important population growth regulating mechanism. The hypothesis that population and individual plant biomass is influenced by intraspecific density was accepted as a result of my study. However, when the influence of density on specific demographic processes was tested the results were less clear than the density-biomass relationships. The influence of density on demographic processes was not constant over time. At some phenological stages and in some growing seasons, density was accounting for over half the variation in some demographic parameters. However, the same demographic parameter, at a different time may not be significantly influenced by density.

The variable response of demography to density compared to the consistant response of biomass to density indicates the difference of demographic parameters and biomass as dependent variables representing plant stress. The biomass dependent variable was a measure of accumulated response to density over all previous growing seasons, whereas the demographic parameters were measured at each phenological stage and the

density affects were not accumulated as in biomass. Therefore, it may be easier to detect competition with density-biomass relationships, whereas demographic parameters are a more discrete dependent variable, which may be more sensitive to intra-season variability in response to density.

Intensity versus importance of competition

Weldon and Slawson (1986) introduced the concept that the intensity of plant competition could be separated from the importance of competition. They concluded that the slope of the density-biomass relationship represents intensity, and the amount of variability accounted for in the relationship represents the importance of competition in governing population dynamics. The importance of competition may be more directly and appropriately assessed by accounting for the amount of variability in density demographic parameter relationships. Density-biomass relationships are not as directly associated with population dynamics as demographic parameters. Therefore, density-biomass relationships are not as appropriate as density-demographic relationships for determining the importance of competition in governing population dynamics.

In this study, the amount of population biomass variation accounted for by density decreased as the populations aged. This indicates a decrease in the importance of competition as the populations aged.

The opposite trend was observed for variation when demographic parameters were used as the dependent variable, indicating that the importance of competition in regulating population dynamics was increasing. These observations raise the question of which dependent variable is most appropriate for determining the importance of competition relative to other factors influencing population dynamics.

Population biology and management

After the first growing season salmonberry and thimbleberry planted populations consisted of nearly equal numbers of sprouts and non-flowering mature vegetative shoots. In the third growing season thimbleberry sprouts were more abundant than mature vegetative shoots in populations, particularly at the dry site. Sprout density was seasonally dynamic with more occuring in the spring than later in the growing season. Seasonal flux in sprout density increased at high (25 and 81 genets/m^2) genet densities. Basal bud density also varied over the growing season with most buds produced at senescence for both species.

An equilibrium density was not reached in planted populations during the first three years of growth. However, populations planted at high densities were rapidly approaching an asymptote (carrying capacity). Initial ramet production was from the parent plant root crown (planted basal stem cutting). In the second and third growing

seasons, extensive rhizome growth and subsequent sprouts away from the parent plant, filled most of the open spaces between plants in the low density plots. Canopy closure occurred by the third growing season in all but the lowest density plots. The same patterns of population development were observed in the wild populations that were clipped and allowed to recover. However, population growth was retarted in wild populations that were invaded by herbs following clipping.

Observations and conclusions from the experiments suggest that effective management of salmonberry and thimbleberry can be accomplished with reduction of vegetative propagules to inhibit population establishment. Efforts to accomplish this have been centered on prescribed burns following logging. This practice appears to reduce the regrowth potential of these species, but the degree of reduction depends on the intensity of the fire. Conifer stand management prior to logging may offer options to reduce propagules. Maintaining closed conifer canopies on sites known to have salmonberry or thimbleberry populations also may reduce the extent of rhizome systems and root crowns.

Modeling approach

The modeling approach was useful for organizing existing information and focusing on demographic processes that influence salmonberry and thimbleberry population

growth. The conceptualization of the populations into life history classes and related demographic processes in the model were adequate for simulating observed natural population behavior.

An "Achille's heel" for salmonberry and thimbleberry could not effectively be identified with the model. Bud production and basal bud dynamics were identifed as important processes which influence population growth. However, seed and seedling survival, which were relatively insensitive parameters in determining total population numbers, could also be viewed as an "Achille's heel". That is, salmonberry and thimbleberry population establishment from seed is restricted and therefore could act as a major point of vulnerability.

Future model refinement

Future model refinement should include mathematical optimization (Opalach, 1989) of the density-dependent parameters when the model output is compared against the observations in the planted populations. Information from Tappeneir et al. (1990) should be incorporated into the model to further refine rhizome and basal bud bank dynamics. Other data sets which have salmonberry and thimbleberry cover estimates and height measurements could be used to improve the height and cover growth predictions.

The influence of interspecific competition on demographic processes should be included in the model. This

could be accomplished simplisticly by incorporating the competition modifiers on cover and height growth developed for the ICIPS model (Wagner et al., 1989). If the main objective is to predict salmonberry and thimbleberry canopy cover and height then it may be best to incorporate the Rubus model as a subroutine into the ICIPS (Wagner et al., 1989) or the DF et al. model (Opalach, 1989).

The influence of conifer seedlings on salmonberry height and cover could be determined from data gathered by Wagner (1989). The Rubus model developed in this study could be linked with the regression models developed by Wagner (1989) to predict the early influence of salmonberry and thimbleberry populations on Douglas-fir growth. This linkage of models would increase the utility of the Rubus model for evaluating young Douglas-fir plantation management tactics.

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APPENDICES

Table A3.1. Mean number of salmonberry and thimbleberry seed that germinated out of 20 seeds placed in each dish after pregermination, storage, and scarification treatments.

Pregermination treatment	Storage treatment	Scarification treatment	Mean number of seed germinated: Days after test began 5	10	15	20	45
SALMONBERRY							
Uncleaned	Rm Temp.	None	0	0	0	0	0
Cleaned							
(Dried, 150F)	Rm Temp.	None	0	0	0	0	0
"	Rm Temp.	.5h H2SO4	0	0	0	0	0
"	Rm Temp.	1h H2SO4	0	0	0	0	0
"	5 C 1wk	None	0	0	0	0	0
"	5 C 2wk	None	0	0	0	0	0
"	5 C 2wk	.5h H2SO4	0	0	0	0	0
"	5 C 2wk	1h H2SO4	0	0	0	0	0
"	5 C 2wk	2h H2SO4	0	0	.7	1	1
"	5 C 2wk	Pin prick	0	0	0	0	0
"	5 C 2wk	Sandpaper	0	0	0	0	0
"	5 C 2wk	None	0	0	0	0	0
"	5 C 2mo	.5h H2SO4	0	0	0	0	0
Dried On							
Bush	5 C 2mo	.5h H2SO4	0	0	0	0	0
"	Rm Temp.	2h H2SO4	0	0	0	0	0
"	Rm Temp.	2.5h H2SO4	0	0	0	0	0
"	5 C 2wk	None	0	0	0	0	0
Dried	Rm Temp.	.5h H2SO4	0	0	0	0	0
Dried	Rm Temp.	1h H2SO4	0	0	0	0	0
Dried	Rm Temp.	GA 10-3 M	0	0	0	0	0
THIMBLEBERRY							
Dried							
(Rm Temp)	Rm Temp.	None	0	0	0	0	0
"	Rm Temp.	.5h H2SO4	2	5	7	8	8
"	Rm Temp.	1h H2SO4	3	7	8	8	8
"	Rm Temp.	GA 10-3 M	0	0	0	.3	.3
"	Rm Temp.	Pin prick	0	0	0	0	0
"	Rm Temp.	Sandpaper	0	0	0	0	0
"	Rm Temp.	Dark	0	0	0	0	0
"	5 C 1wk	None	0	0	0	0	0
"	5 C 1wk	.5h H2SO4	0	0	0	0	0
"	5 C 1wk	.75h H2SO4	1	6	9	9	9
"	5 C 1wk	Sandpaper	0	0	0	0	0
"	5 C 1wk	Dark	0	0	0	0	0
Dried							
(Oven 150F)	5 C 1wk	2h H2SO4	0	0	0	0	0
"	5 C 1wk	2.5h H2SO4	0	0	0	0	0

Rm Temp. = 27 C

Table A3.2. Mean percent germination of salmonberry and thimbleberry in respnse to seed storage and scarification treatments.

	Days after beginning the test								
	4	7	10	13	16	19	23	45	75
THIMBLEBERRY									
Dried and stored at 27 C									
.5h H_2SO_4	10.60	12.33	26.67	30.23	37.57	41.10	41.10	41.10	41.67
1h H_2SO_4	13.57	19.50	35.87	37.97	44.20	44.20	44.20	44.20	44.20
GA 10^{-3}M	.0000	.0000	.0000	.0000	.0000	1.667	1.667	1.667	1.667
Dried and stored at 5 C									
.5h H_2SO_4	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
.75h H_2SO_4	7.033	21.17	32.43	39.53	44.43	44.43	44.43	44.43	44.43
SALMONBERRY									
Dried and stored at 5 C									
2h H_2SO_4	.0000	.0000	.0000	.0000	3.333	3.333	3.333	3.333	3.333
SUMMARY STATISTICS:									
TRTS MS	110.2	307.3	927.8	1190.	1611.	1563.	1563.	1563.	1563.
ERROR MS	34.75	39.60	23.32	20.00	54.30	56.77	56.77	56.77	56.77
ERROR DF	12.00	12.00	12.00	12.00	12.00	12.00	12.00	12.00	12.00
F-RATIO TRTS	3.171	7.762	39.79	59.52	29.66	27.54	27.54	27.54	27.54
P-VALUE TRTS	.0470	.0022	.0000	.0000	.0000	.0000	.0000	.0000	.0000
STD DEV (S)	5.895	6.293	4.829	4.472	7.369	7.535	7.535	7.535	7.535
SE TRT MEANS	3.403	3.633	2.788	2.582	4.255	4.350	4.350	4.350	4.350
CV (S/MEAN)	113.4	71.24	30.51	24.91	35.04	33.55	33.55	33.55	33.55
CV (SE/MEAN)	65.45	41.13	17.61	14.38	20.23	19.37	19.37	19.37	19.37
LSD (0.05)	10.49	11.19	8.591	7.956	13.11	13.40	13.40	13.40	13.40

Table A3.3. Mean percent germination of salmonberry and thimbleberry seed in response to scarification treatments.

	Days after beginning test					
	9	16	21	31	49	60
SALMONBERRY						
Chicken Gut*	.0000	.0000	.0000	.0000	.0000	.0000
None*	.0000	.0000	.0000	.0000	.0000	.0000
1h H2SO4	.0000	.0000	1.667	1.667	1.667	1.667
1h H2SO4+2wk Refer	.0000	.0000	.0000	.0000	1.667	1.667
1h H2SO4+2wk Refer*	.0000	.0000	.0000	.0000	.0000	.0000
THIMBLEBERRY						
Chicken Gut*	.0000	.0000	.0000	.0000	.0000	.0000
1h H2SO4	.0000	5.000	8.333	10.00	10.00	10.00
1h H2SO4*	3.333	3.333	5.000	5.000	8.333	8.333
1h H2SO4+2wk Refer	.0000	.0000	.0000	5.000	11.67	13.33
1h H2SO4 in soil	.0000	.0000	.0000	.0000	.0000	.0000

* Fungicide was applied to seeds prior to germination test.

SUMMARY STATISTICS:						
TRTS MS	3.333	9.722	24.91	35.28	66.67	76.76
ERROR MS	3.333	5.833	4.167	8.333	15.83	18.33
ERROR DF	20.00	20.00	20.00	20.00	20.00	20.00
F-RATIO TRTS	1.000	1.667	5.978	4.233	4.211	4.187
P-VALUE TRTS	.4716	.1633	.0065	.0037	.0039	.0004
STD DEV (S)	1.826	2.415	2.041	2.887	3.979	4.282
SE TRT MEANS	1.054	1.394	1.179	1.667	2.297	2.472
CV (S/MEAN)	547.7	289.8	136.1	133.2	119.4	122.3
CV (SE/MEAN)	316.2	167.3	78.57	76.92	68.92	70.63
LSD (0.05)	3.110	4.114	3.477	4.917	6.777	7.293

Table A3.4. Mean salmonberry and thimbleberry germination in response to scarification treatments.

	Days after beginning test						
Treatment	7	14	21	28	35	45	60
SALMONBERRY							
0.1% KNO3	.0000	.0000	.0000	.0000	.0000	.0000	1.667
1.0% KNO3	.0000	.0000	.0000	.0000	.0000	.0000	.0000
*Chlorox .5 hr	.0000	.0000	.0000	.0000	.0000	.0000	.0000
*Chlorox 1 hr	.0000	.0000	.0000	.0000	.0000	.0000	.0000
*Chlorox 2 hr	.0000	.0000	.0000	.0000	.0000	.0000	.0000
*H2SO4 2 hr	.0000	.0000	.0000	.0000	.0000	1.667	1.667
Control	.0000	.0000	.0000	.0000	.0000	.0000	.0000
THIMBLEBERRY							
0.1% KNO3	.0000	.0000	13.33	16.67	35.00	36.67	41.67
1.0% KNO3	.0000	.0000	.0000	5.000	10.00	13.33	16.67
*Chlorox 1 hr	.0000	3.333	6.667	10.00	13.33	18.33	18.33
*H2SO4 .75 hr	16.67	36.67	40.00	45.00	50.00	50.00	50.00
Control	.0000	.0000	5.000	5.000	16.67	18.33	20.00
* Scarification treatments							
SUMMARY STATISTICS:							
TRTS MS	69.44	333.3	407.8	517.4	812.3	846.1	922.0
ERROR MS	.6944	3.472	20.14	31.94	47.22	57.64	74.31
ERROR DF	24.00	24.00	24.00	24.00	24.00	24.00	24.00
F-RATIO TRTS	100.0	96.00	20.25	16.20	17.20	14.68	12.41
P-VALUE TRTS	.0000	.0000	.0000	.0000	.0000	.0000	.0000
STD DEV (S)	.8333	1.863	4.488	5.652	6.872	7.592	8.620
SE TRT MEANS	.4811	1.076	2.591	3.263	3.967	4.383	4.977
CV (S/MEAN)	60.00	55.90	82.85	83.05	65.97	65.86	68.96
CV (SE/MEAN)	34.64	32.27	47.83	47.95	38.09	38.02	39.81
LSD (0.05)	1.404	3.140	7.562	9.525	11.58	12.79	14.53

Table A3.5. Mean percent germination of salmonberry in response to soil and paper substrates in variable and constant temperature environments with apprporiate storage and scarification treatments.

Treatment	Days after beginning test						
	7	14	21	28	35	45	60
SALMONBERRY							
Soil,H2SO4 2hr	.0000	.0000	.0000	.0000	.0000	1.667	1.667
*Soil,H2SO4 2hr	.0000	.0000	.0000	.0000	.0000	.0000	.0000
Dish,H2SO4 2hr	.0000	1.667	1.667	1.667	3.333	3.333	3.333
**Soil,H2SO4 2hr	.0000	.0000	.0000	.0000	.0000	1.667	3.333
Soil,H2O	.0000	.0000	.0000	.0000	.0000	.0000	.0000

* Treatment in germination chamber.

** Seeds stored in refrigerator prior to experiment.

SUMMARY STATISTICS:							
TRTS MS	.0000	1.667	1.667	1.667	6.667	5.833	8.333
ERROR MS	.0000	1.667	1.667	1.667	6.667	10.00	15.00
ERROR DF	10.00	10.00	10.00	10.00	10.00	10.00	10.00
F-RATIO TRTS	.0000	1.000	1.000	1.000	1.000	.5833	.5556
P-VALUE TRTS	.0000	.4527	.4527	.4527	.4527	.6840	.7020
STD DEV (S)	.0000	1.291	1.291	1.291	2.582	3.162	3.873
SE TRT MEANS	.0000	.7454	.7454	.7454	1.491	1.826	2.236
CV (S/MEAN)	.0000	387.3	387.3	387.3	387.3	237.2	232.4
CV (SE/MEAN)	.0000	223.6	223.6	223.6	223.6	136.9	134.2
LSD (0.05)	.0000	2.349	2.349	2.349	4.697	5.753	7.046

Table A3.6. Mean percent germination of thimbleberry in response to soil and paper substrates in variable and constant temperature environments with apprporiate storage and scarification treatments.

	Days after beginning test						
Treatment	7	14	21	28	35	45	60
THIMBLEBERRY							
Soil,H2SO4 1hr	.0000	1.667	3.333	3.333	3.333	3.333	3.333
*Soil,H2SO4 1hr	.0000	.0000	.0000	.0000	.0000	1.667	1.667
**Soil,H2SO4 2hr	.0000	.0000	.0000	.0000	.0000	.0000	.0000
Soil,H2O	.0000	.0000	.0000	.0000	.0000	20.00	21.67
Dish,H2SO4 2hr	1.667	10.00	11.67	13.33	13.33	13.33	13.33

* Treatment in germination chamber.

** Seeds stored in refrigerator prior to experiment.

SUMMARY STATISTICS:							
TRTS MS	1.667	56.67	76.67	100.0	100.0	223.3	255.8
ERROR MS	1.667	6.667	3.333	8.333	8.333	25.00	16.67
ERROR DF	10.00	10.00	10.00	10.00	10.00	10.00	10.00
F-RATIO TRTS	1.000	8.500	23.00	12.00	12.00	8.933	15.35
P-VALUE TRTS	.4527	.0034	.0000	.0011	.0011	.0003	.0052
STD DEV (S)	1.291	2.582	1.826	2.887	2.887	5.000	4.082
SE TRT MEANS	.7454	1.491	1.054	1.667	1.667	2.887	2.357
CV (S/MEAN)	387.3	110.7	60.86	86.60	86.60	65.22	51.03
CV (SE/MEAN)	223.6	63.89	35.14	50.00	50.00	37.65	29.46
LSD (0.05)	2.349	4.697	3.322	5.252	5.252	9.096	7.427

Table A3.7. Mean salmonberry and thimbleberry germination in response to scarification followed by stratification.

Species	Scarification	Stratification (mo.)	# seeds germinated	% germination	% germination during strat.
SALMONBERRY					
	NONE	0	.0000	.0000	
	.5 hr H2SO4	0	.0000	.0000	
	NONE	7	3.000	15.00	0
	.5 hr H2SO4	7	7.667	38.33	5.4
THIMBLEBERRY					
	NONE	0	.6667	3.333	
	.5 hr H2SO4	0	2.000	10.00	
	NONE	7	7.000	35.00	2.0
	.5 hr H2SO4	7	6.000	30.00	13.2
SUMMARY STATISTICS:					
TRTS MS			30.23	755.8	
ERROR MS			2.208	55.21	
ERROR DF			16.00	16.00	
F-RATIO TRTS			13.69	13.69	
P-VALUE TRTS			.0000	.0000	
STD DEV (S)			1.486	7.430	
SE TRT MEANS			.8580	4.290	
CV (S/MEAN)			45.15	45.15	
CV (SE/MEAN)			26.06	26.06	
LSD (0.05)			2.572	12.86	

Table A3.8. Mean number of salmonberry buds produced on 20 cm rhizome sections that were incubated under different temperature treatments in growth chambers.

Treatment	Weeks in the growth chambers 2	3	4	5	8	
Constant 60 F	7.0	6.8	6.3	5.2	2.7	a
Constant 50 F	4.9	6.9	8.1	6.8	5.0	b
16 hr. 50 F 8 hr. 60 F	6.5	7.7	8.4	6.7	4.8	b
16 hr. 60 F 8 hr. 50 F	6.7	8.9	8.6	7.3	4.1	ab
P-value	.4684	.3857	.2024	.1344	.0196	
LSD (0.05)	-	-	-	-	1.45	

Means followed by the same letter within a column are not significantly different (LSD 0.05).

Table A3.9. Mean number of thimbleberry buds produced on 15 cm rhizome sections that were incubated under different temperature treatments in growth chambers.

Treatment	Weeks in the growth chambers 2	3	4	5	8	
Constant 60 F	2.5	2.4	2.7	2.2	0.3	a
Constant 50 F	2.3	3.0	3.4	3.4	1.3	ab
16 hr. 50 F 8 hr. 60 F	3.2	3.6	3.7	2.2	1.6	b
16 hr. 60 F 8 hr. 50 F	2.5	2.9	3.3	2.9	1.8	b
P-value	.1836	.1628	.4780	.2504	.0209	
LSD (0.05)	-	-	-	-	1.21	

Means followed by the same letter within a column are not significantly different (LSD 0.05).

Table A3.10. Mean number and frequency of salmonberry and thimbleberry seedlings and sprouts on two clearcuts in the Spruce/Hemlock zone of the western Coast Range.

Years after site prep. burning	Salmonberry Seedlings/m^2		Salmonberry Sprouts/m^2		Thimbleberry Seedlings/m^2	
	Waldport	Cascade Head	Waldport	Cascade Head	Waldport	Cascade Head
1	21.4	3.7	5.5	0.2	0.9	0.3
2	15.3	2.8	3.6	0.2	1.3	0.3
3	9.7	2.6	8.0	0.6	0.6	0.4
Frequency	97%	70%	97%	17%	53%	23%

Frequency, was the average frequency of seedling or sprout occurance in 1 m_2 frames that were observed over the 3 years.

Table A3.11. Mean salmonberry and thimbleberry seedling and sprout survival on two clearcuts in the Spruce/Hemlock zone of the western Coast Range.

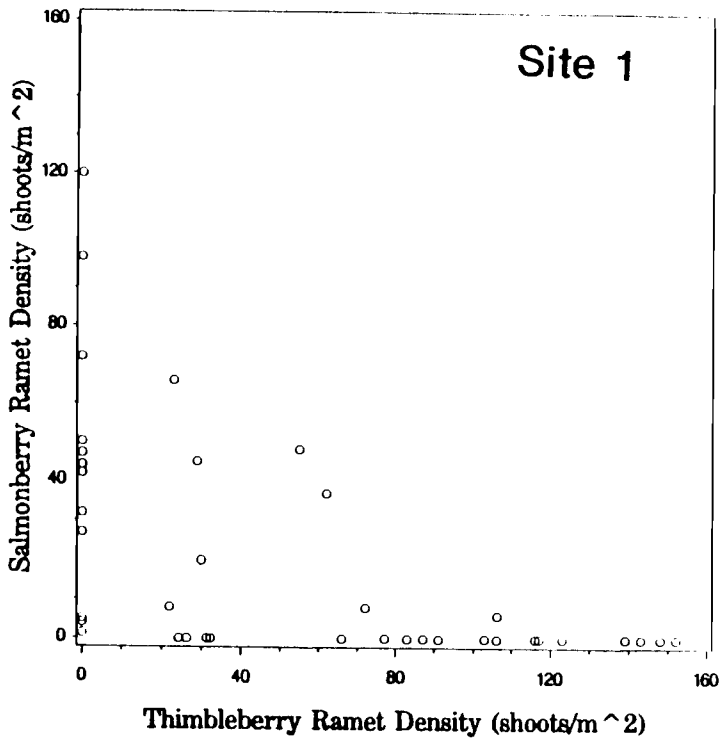
	1986		1987		1988	
	Waldport	Cascade Head	Waldport	Cascade Head	Waldport	Cascade Head
Salmonberry:	%					
Seedlings	86	100	63	63	59	87
Sprouts	99	100	81	50	100	100
P-value	.091	-	.441	-	.000	-
Thimbleberry:						
Seedlings	100	100	92	67	83	100
Sprouts	100	-	-	-	-	-

P-values less than 0.050 indicate a significant difference between mean salmonberry seedling and sprout survival.

Table A3.12. Mean number of salmonberry seedlings/m^2 at Beaver Creek the first year after logging and site-prep. burning.

	Weeks after planting					
	14	16	17	19	21	38
Field:						
No seeds planted	0.2	1.4	0.7	0.8	0.6	0.5
1000 seeds/m^2 planted	2.2	4.1	1.9	1.8	1.3	1.3
Seedlings of planted seed	2.0	2.7	1.2	1.0	0.7	0.8
% germination of planted seed	0.2	0.3	0.1	0.1	0.1	0.1
Lab (Control):						
On plate, % germination	1.0	1.0	1.0	1.0	1.0	8.5

Figure A4.1. Raw data scatters for Woods Creek (site 1) and Pioneer Mountain (site 2) addition series experiments showing the extent of the data matrix.


Site 1
Salmonberry Ramet Density (shoots/m ^ 2)
Thimbleberry Ramet Density (shoots/m ^ 2)
0
40
80
120
160

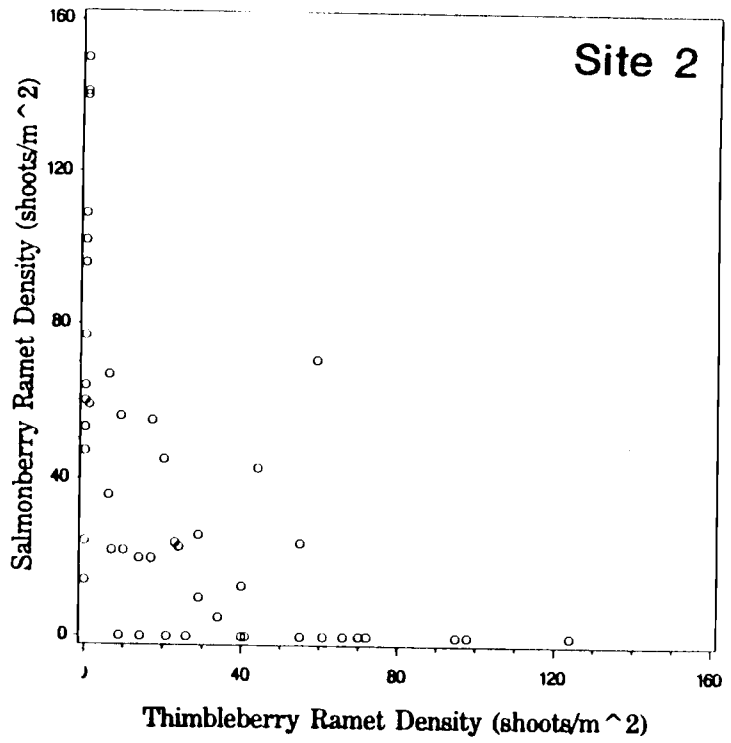

Site 2
Salmonberry Ramet Density (shoots/m ^ 2)
Thimbleberry Ramet Density (shoots/m ^ 2)
0
40
80
120
160

Fig. A4.1.

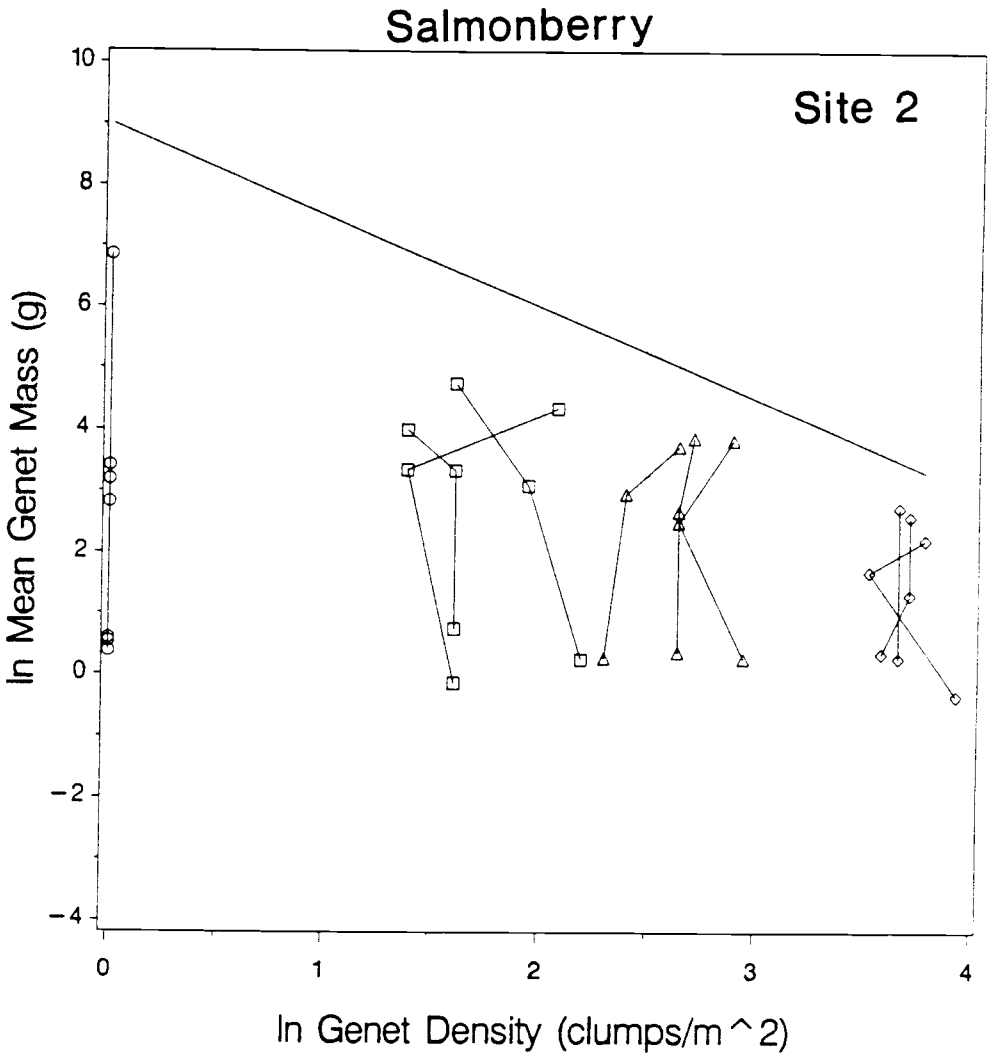


Figure A4.2. Ln mean genet mass plotted on ln genet density plus a self-thinning line (slope=-3/2) with an arbitrarily set intercept to demonstrate approach of populations to self thinning.

Figure A4.3. Basal bud transition to sprouts (G2) and survival (R2) over time (phenology stage) and ramet density (TOTST) for salmonberry at Pioneer Mountain.

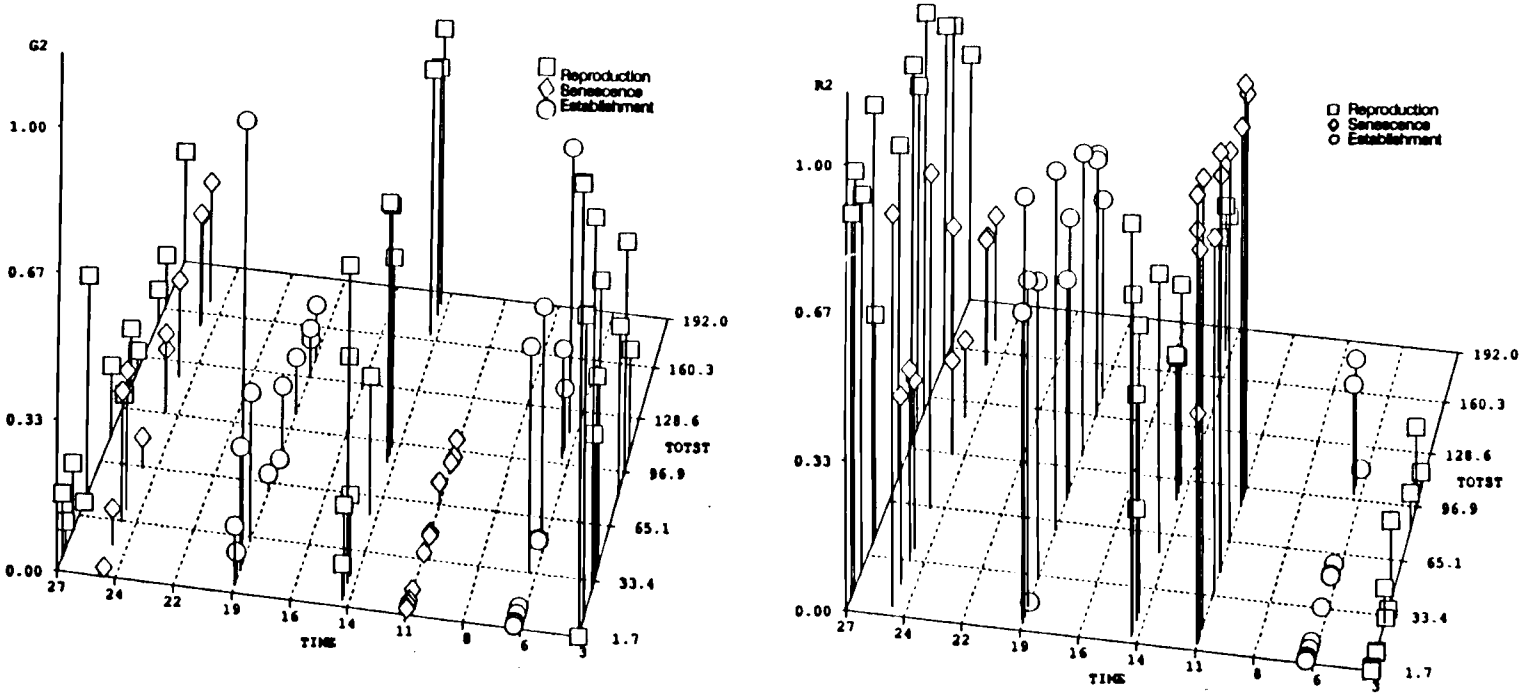

G2
1.00
0.67
0.33
0.00
Reproduction
Senescence
Establishment
192.0
160.3
128.6
TOTST
96.9
65.1
33.4
1.7
27
24
22
19
16
14
11
8
6
3
TIME
R2
1.00
0.67
0.33
0.00
Reproduction
Senescence
Establishment
192.0
160.3
128.6
TOTST
96.9
65.1
33.4
1.7
27
24
22
19
16
14
11
8
6
3
TIME

Fig. A4.3.

Figure A4.4. Sprout transition (G4) and survival (R4) over time (phenology stage) and ramet density (TOTST) for salmonberry at Pioneer Mountain.

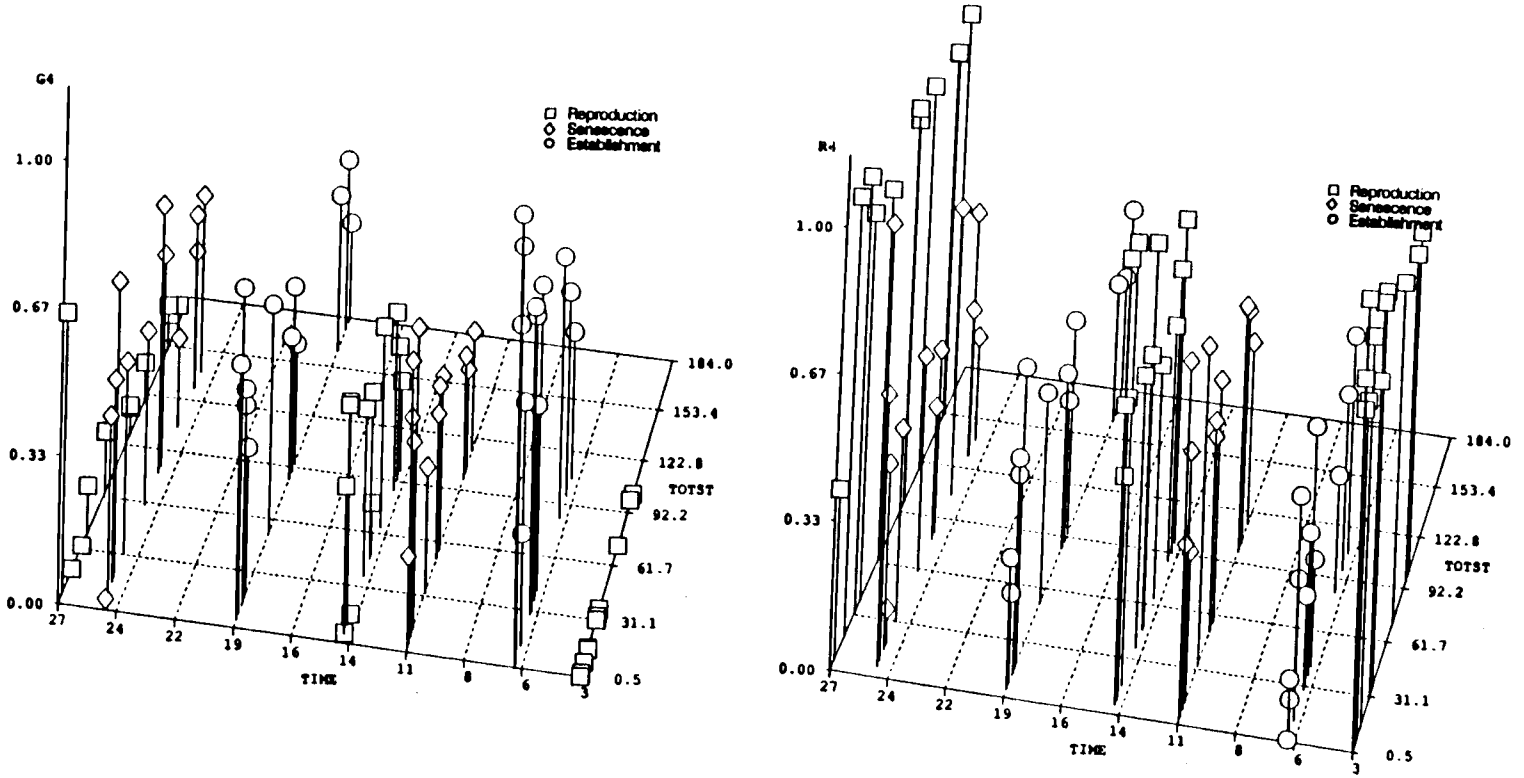

G4
1.00
0.67
0.33
0.00
27
24
22
19
16
14
11
8
6
3
TIME
Reproduction
Senescence
Establishment
184.0
153.4
122.8
TOTST
92.2
61.7
31.1
0.5
R4
1.00
0.67
0.33
0.00
27
24
22
19
16
14
11
8
6
3
TIME
Reproduction
Senescence
Establishment
184.0
153.4
122.8
TOTST
92.2
61.7
31.1
0.5

Fig. A4.4.

Figure A4.5. Basal bud production (V5) and survival (R5) over time (phenology stage) and ramet density (TOTST) for salmonberry at Pioneer Mountain.

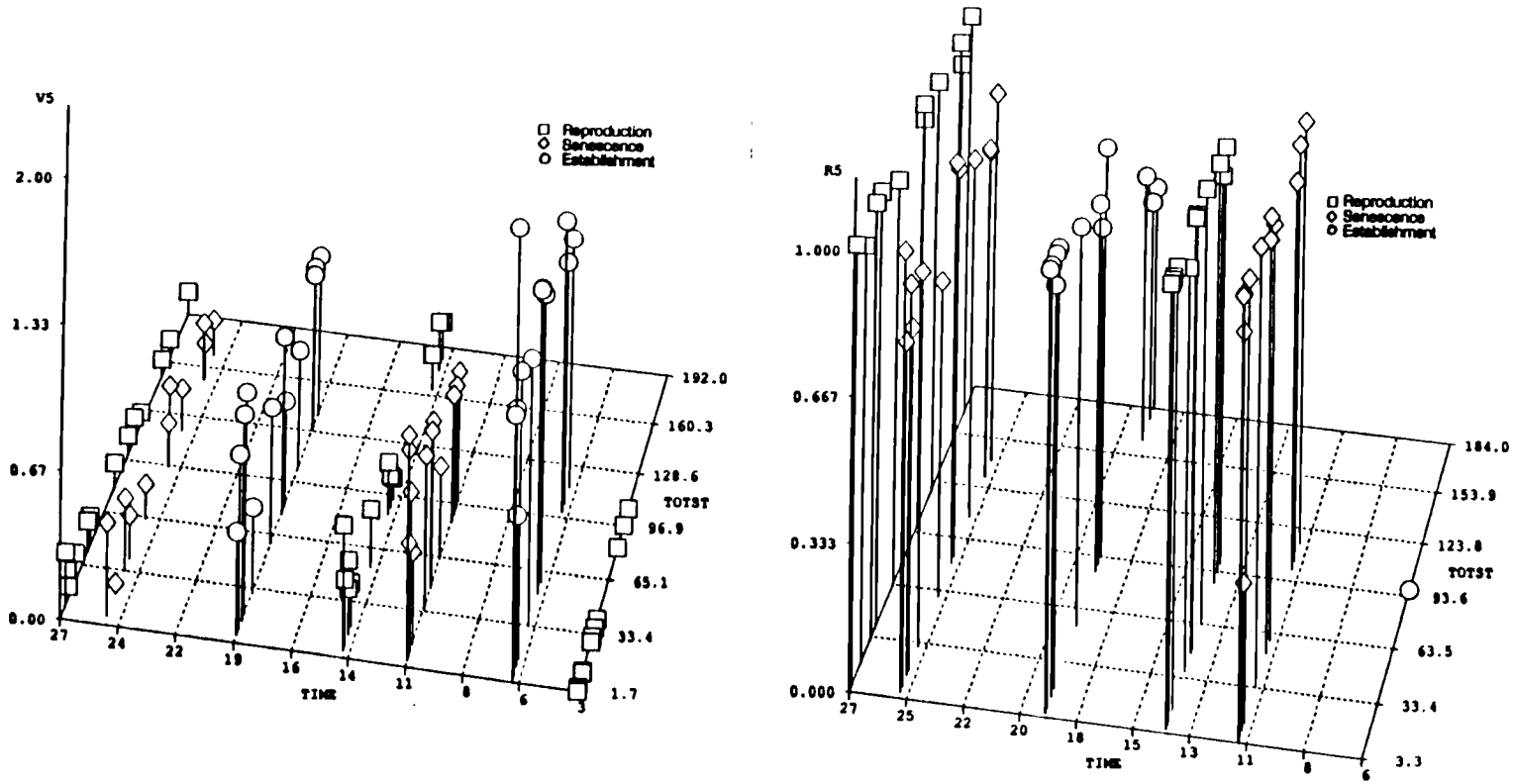
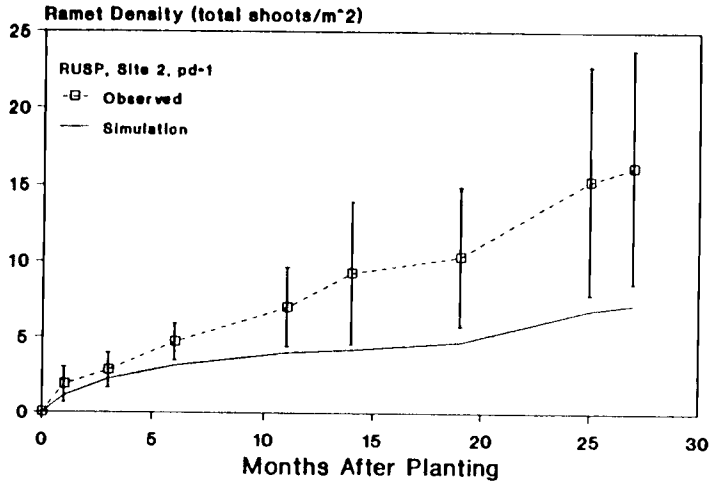
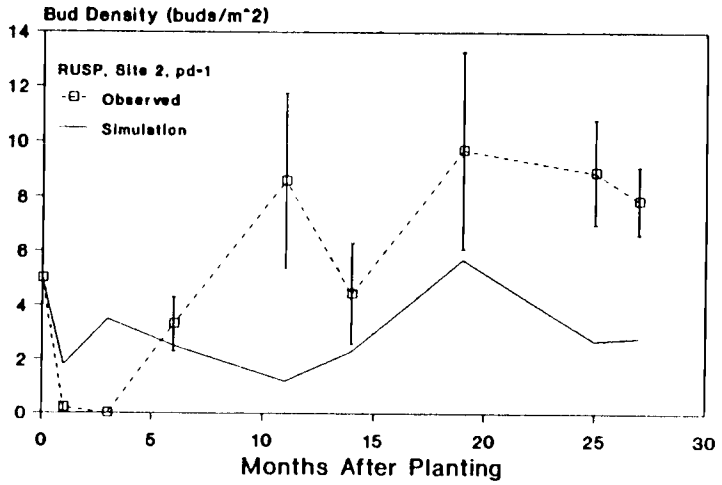
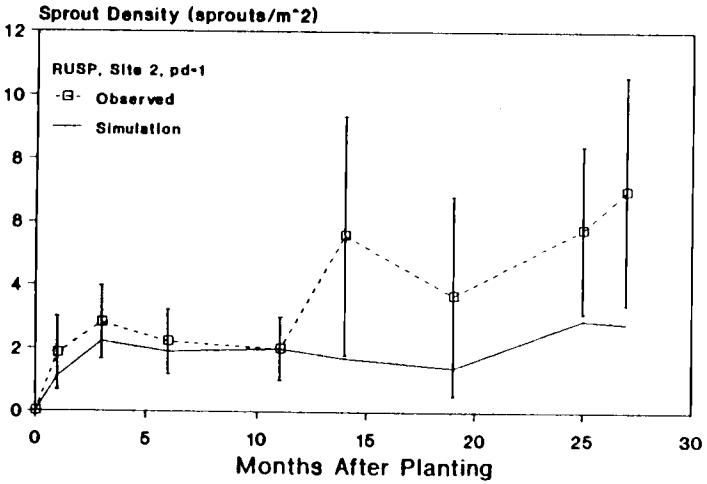

V5
2.00
1.33
0.67
0.00
27
24
22
19
16
14
11
8
6
3
TIME
192.0
160.3
128.6
TOTST
96.9
65.1
33.4
1.7
Reproduction
Senescence
Establishment
R5
1.000
0.667
0.333
0.000
27
25
22
20
18
15
13
11
8
6
TIME
184.0
153.9
123.8
TOTST
93.6
63.5
33.4
3.3
Reproduction
Senescence
Establishment

Fig. A4.5.

Figure A5.1. Simulated salmonberry ramet density (top left), basal bud density (top right), sprout density (bottom left) and vegetative shoot density (bottom right) over the first three growing seasons plotted with mean and 1 standard deviation of observed populations planted with 1 cutting/m^2 at Pioneer Mountain (Site 2).


Ramet Density (total shoots/m^2)
RUSP, Site 2, pd-1
Observed
Simulation
Months After Planting


Bud Density (buds/m^2)
RUSP, Site 2, pd-1
Observed
Simulation
Months After Planting


Sprout Density (sprouts/m^2)
RUSP, Site 2, pd-1
Observed
Simulation
Months After Planting

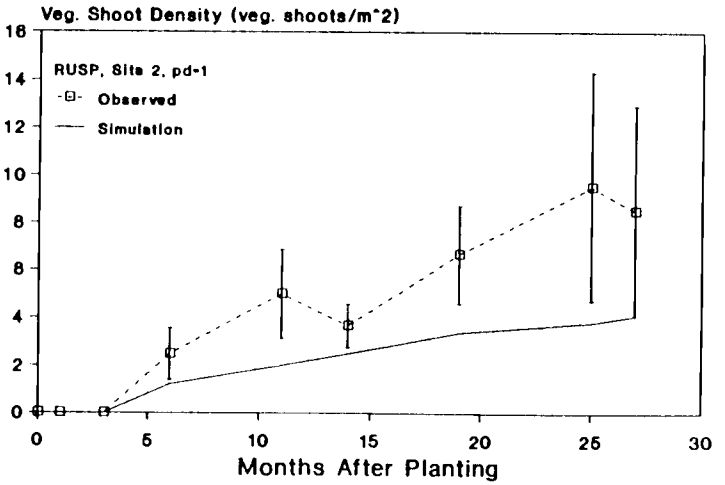
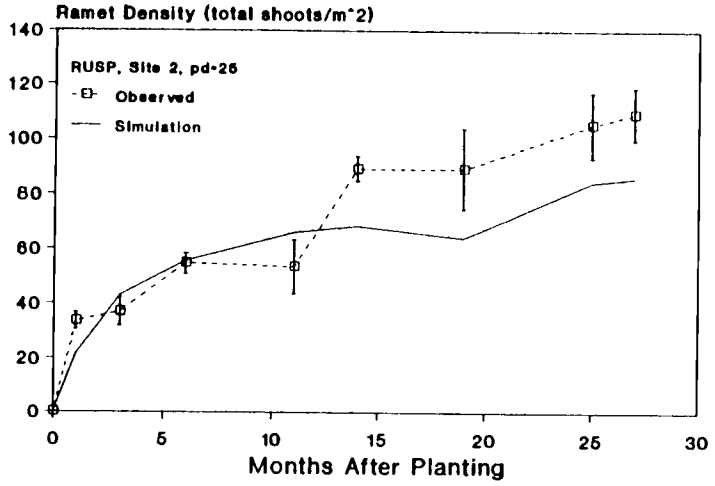
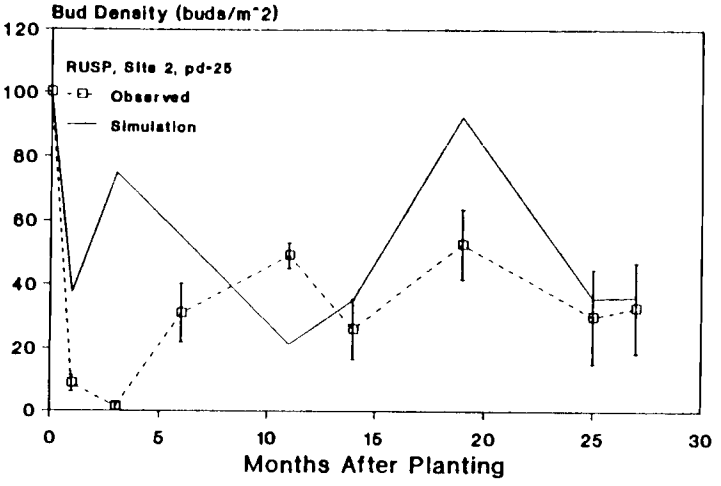
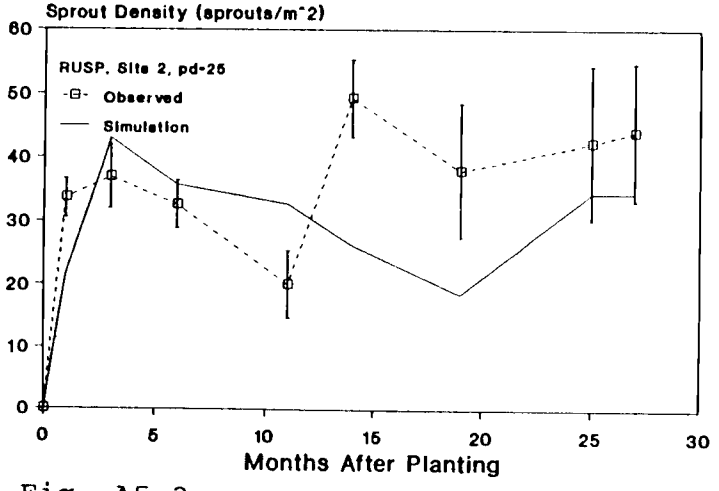

Veg. Shoot Density (veg. shoots/m^2)
RUSP, Site 2, pd-1
Observed
Simulation
Months After Planting

Fig. A5.1.

Figure A5.2. Simulated salmonberry ramet density (top left), basal bud density (top right), sprout density (bottom left) and vegetative shoot density (bottom right) over the first three growing seasons plotted with mean and 1 standard deviation of observed populations planted with 25 cuttings/m^2 at Pioneer Mountain (Site 2).


Ramet Density (total shoots/m^2)
RUSP, Site 2, pd-25
Observed
Simulation
140
120
100
80
60
40
20
0
0
5
10
15
20
25
30
Months After Planting


Bud Density (buds/m^2)
RUSP, Site 2, pd-25
Observed
Simulation
120
100
80
60
40
20
0
0
5
10
15
20
25
30
Months After Planting


Sprout Density (sprouts/m^2)
RUSP, Site 2, pd-25
Observed
Simulation
60
50
40
30
20
10
0
0
5
10
15
20
25
30
Months After Planting

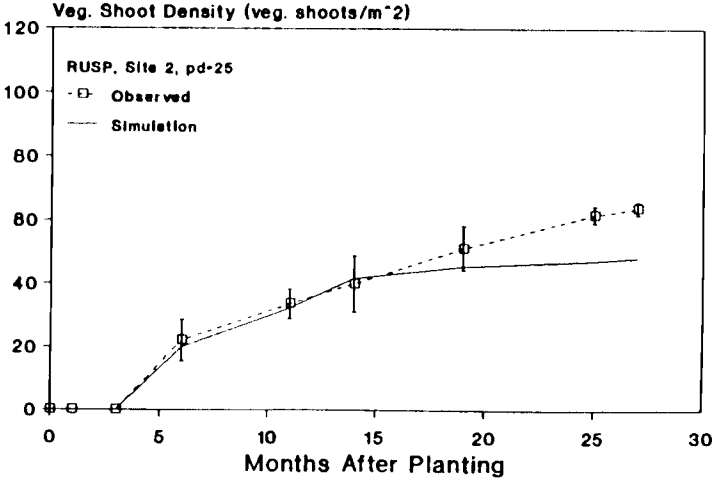
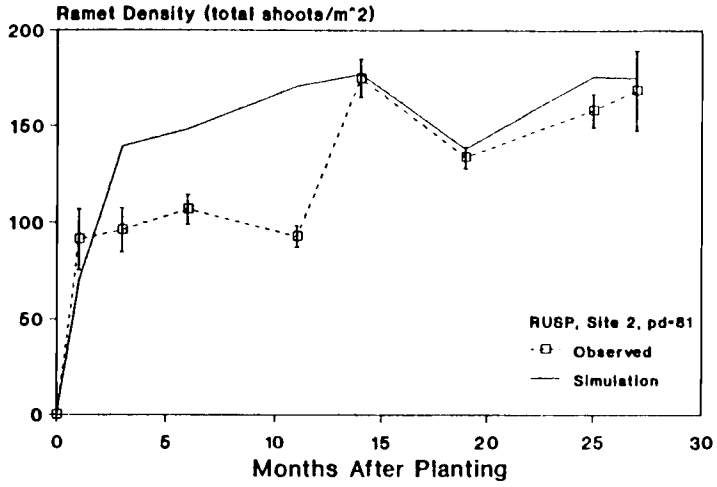
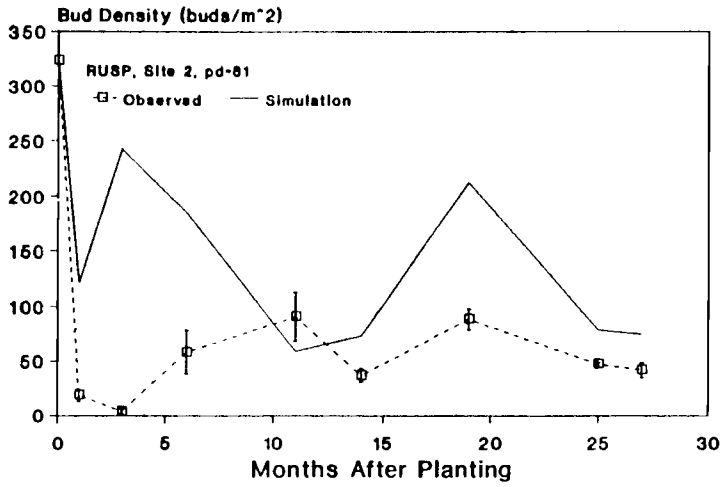
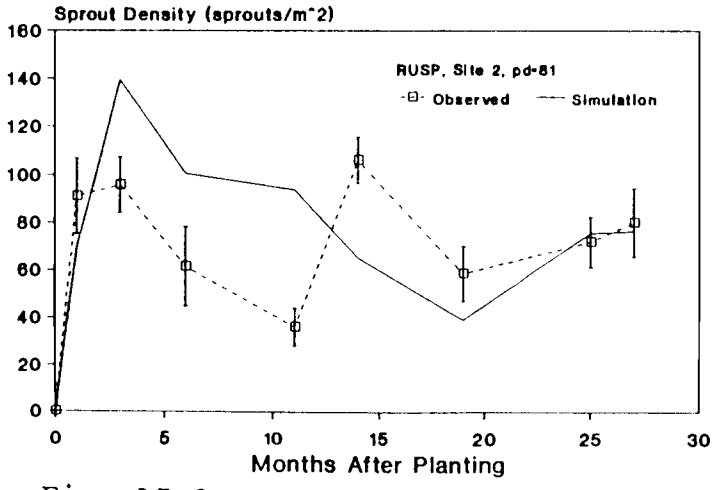

Veg. Shoot Density (veg. shoots/m^2)
RUSP, Site 2, pd-25
Observed
Simulation
120
100
80
60
40
20
0
0
5
10
15
20
25
30
Months After Planting

Fig. A5.2.

Figure A5.3. Simulated salmonberry ramet density (top left), basal bud density (top right), sprout density (bottom left) and vegetative shoot density (bottom right) over the first three growing seasons plotted with mean and 1 standard deviation of observed populations planted with 81 cuttings/m^2 at Pioneer Mountain (Site 2).


Ramet Density (total shoots/m^2)
200
150
100
50
0
0
5
10
15
20
25
30
Months After Planting
RUSP, Site 2, pd-81
Observed
Simulation


Bud Density (buds/m^2)
350
300
250
200
150
100
50
0
0
5
10
15
20
25
30
Months After Planting
RUSP, Site 2, pd-81
Observed
Simulation


Sprout Density (sprouts/m^2)
160
140
120
100
80
60
40
20
0
0
5
10
15
20
25
30
Months After Planting
RUSP, Site 2, pd-81
Observed
Simulation

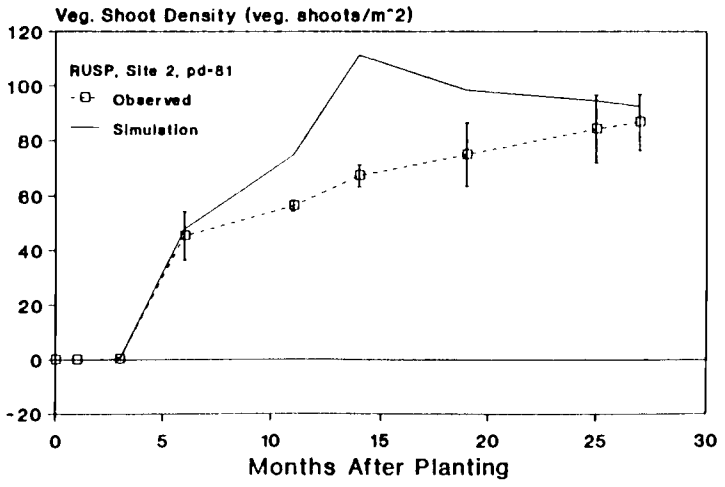
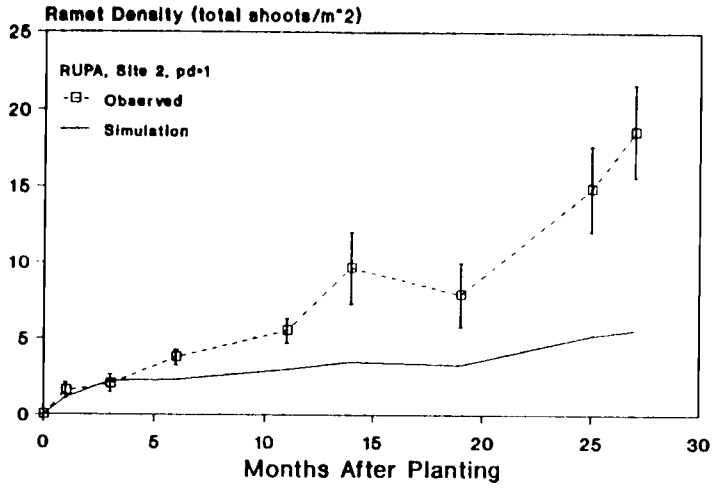
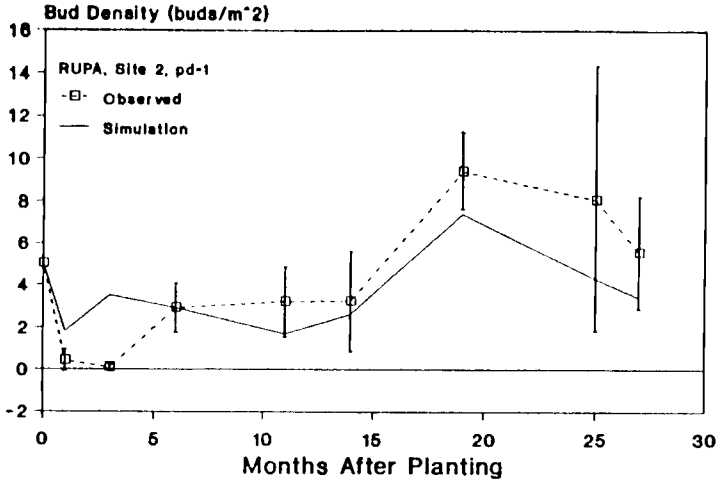
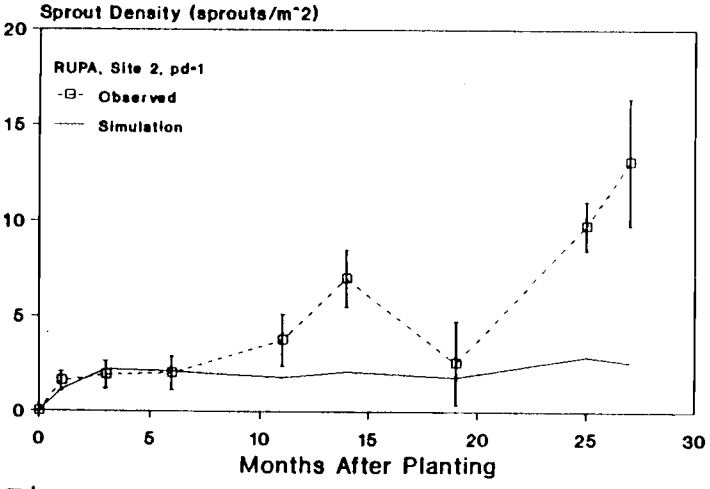

Veg. Shoot Density (veg. shoots/m^2)
120
100
80
60
40
20
0
-20
0
5
10
15
20
25
30
Months After Planting
RUSP, Site 2, pd-81
Observed
Simulation

Fig. A5.3.

Figure A5.4. Simulated thimbleberry ramet density (top left), basal bud density (top right), sprout density (bottom left) and vegetative shoot density (bottom right) over the first three growing seasons plotted with mean and 1 standard deviation of observed populations planted with 1 cutting/m^2 at Pioneer Mountain (Site 2).


Ramet Density (total shoots/m^2)
RUPA, Site 2, pd-1
Observed
Simulation
Months After Planting


Bud Density (buds/m^2)
RUPA, Site 2, pd-1
Observed
Simulation
Months After Planting


Sprout Density (sprouts/m^2)
RUPA, Site 2, pd-1
Observed
Simulation
Months After Planting

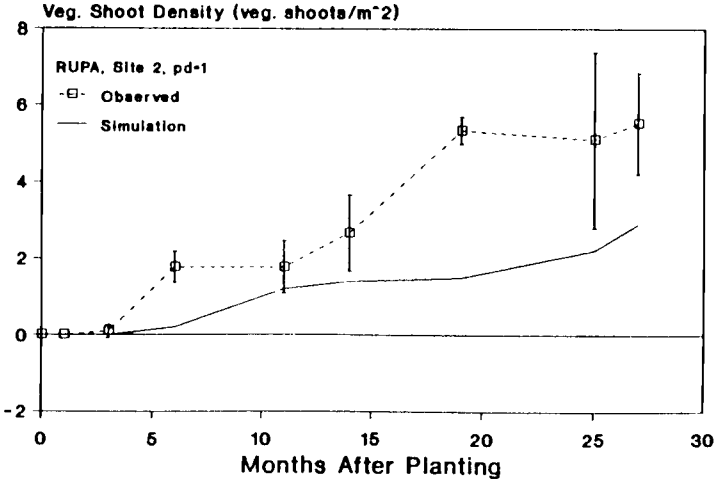
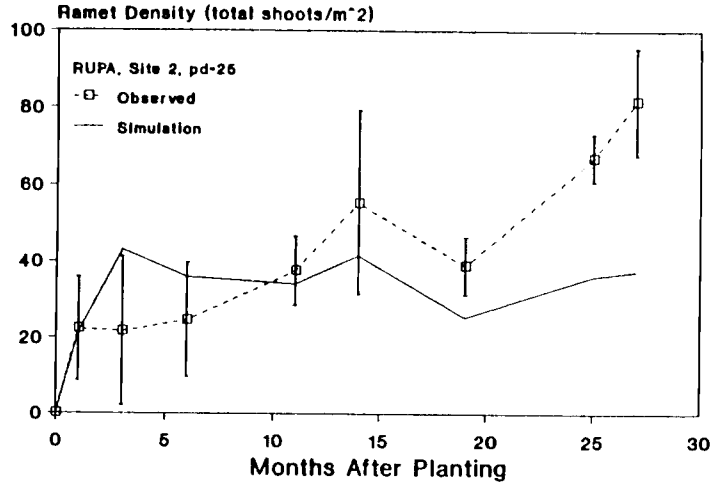
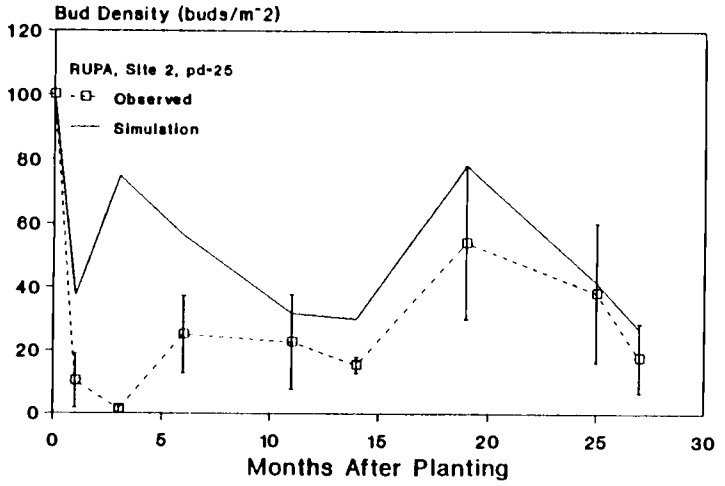
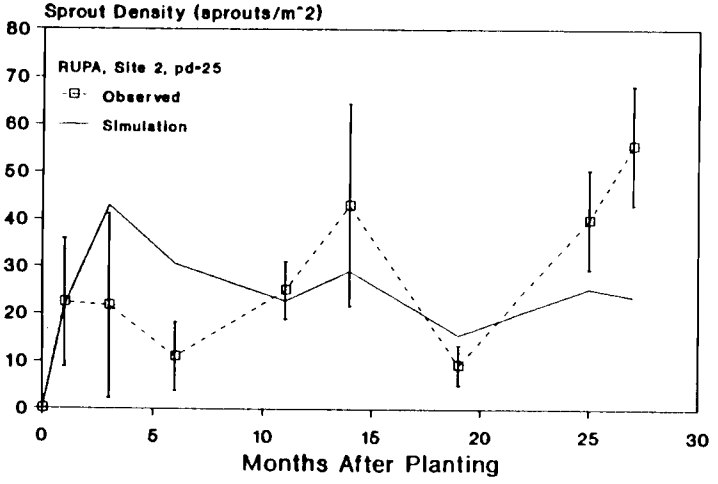

Veg. Shoot Density (veg. shoots/m^2)
RUPA, Site 2, pd-1
Observed
Simulation
Months After Planting

Fig. A5.4.

Figure A5.5. Simulated thimbleberry ramet density (top left), basal bud density (top right), sprout density (bottom left) and vegetative shoot density (bottom right) over the first three growing seasons plotted with mean and 1 standard deviation of observed populations planted with 25 cuttings/m^2 at Pioneer Mountain (Site 2).


Ramet Density (total shoots/m^2)
RUPA, Site 2, pd-25
Observed
Simulation
100
80
60
40
20
0
0
5
10
15
20
25
30
Months After Planting


Bud Density (buds/m^2)
RUPA, Site 2, pd-25
Observed
Simulation
120
100
80
60
40
20
0
0
5
10
15
20
25
30
Months After Planting


Sprout Density (sprouts/m^2)
RUPA, Site 2, pd-25
Observed
Simulation
80
70
60
50
40
30
20
10
0
0
5
10
15
20
25
30
Months After Planting

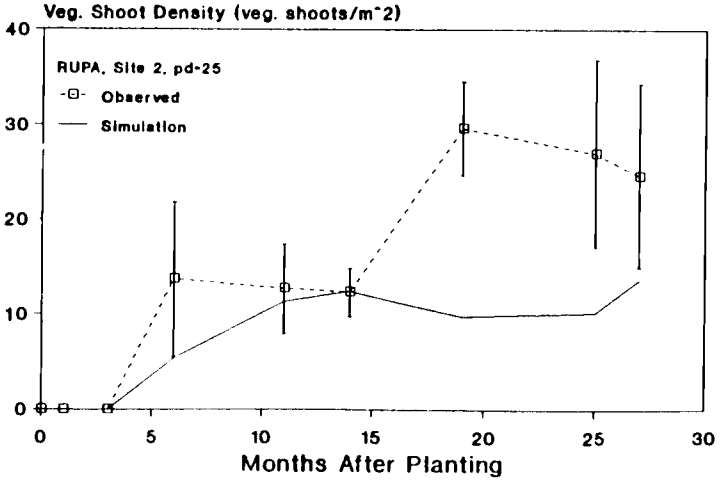
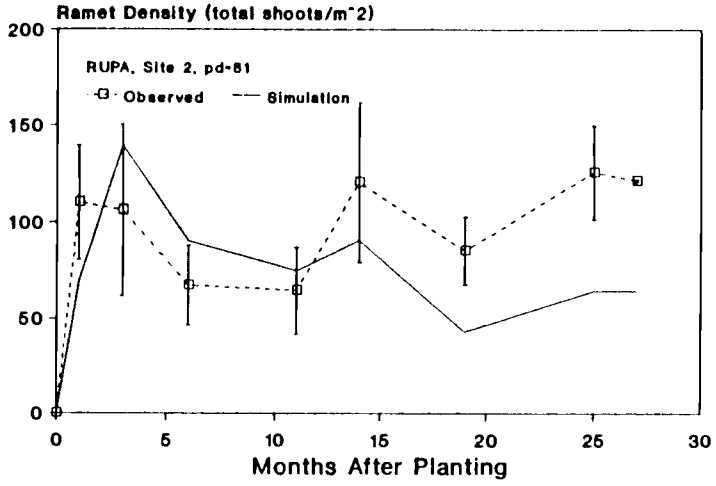
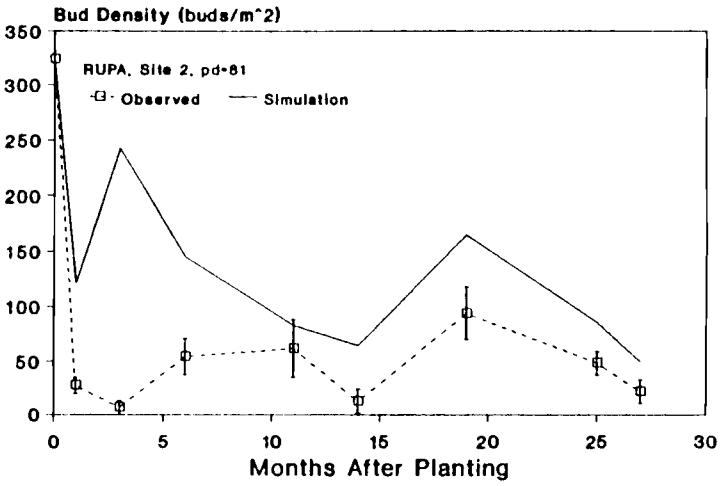
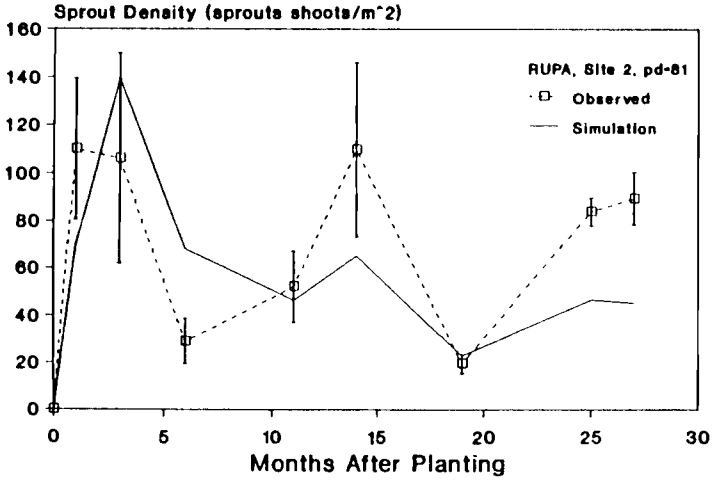

Veg. Shoot Density (veg. shoots/m^2)
RUPA, Site 2, pd-25
Observed
Simulation
40
30
20
10
0
0
5
10
15
20
25
30
Months After Planting

Fig. A5.5.

Figure A5.6. Simulated thimbleberry ramet density (top left), basal bud density (top right), sprout density (bottom left) and vegetative shoot density (bottom right) over the first three growing seasons plotted with mean and 1 standard deviation of observed populations planted with 81 cuttings/m^2 at Pioneer Mountain (Site 2).


Ramet Density (total shoots/m^2)
RUPA, Site 2, pd-81
Observed
Simulation
200
150
100
50
0
0
5
10
15
20
25
30
Months After Planting


Bud Density (buds/m^2)
RUPA, Site 2, pd-81
Observed
Simulation
350
300
250
200
150
100
50
0
0
5
10
15
20
25
30
Months After Planting


Sprout Density (sprouts shoots/m^2)
RUPA, Site 2, pd-81
Observed
Simulation
160
140
120
100
80
60
40
20
0
0
5
10
15
20
25
30
Months After Planting

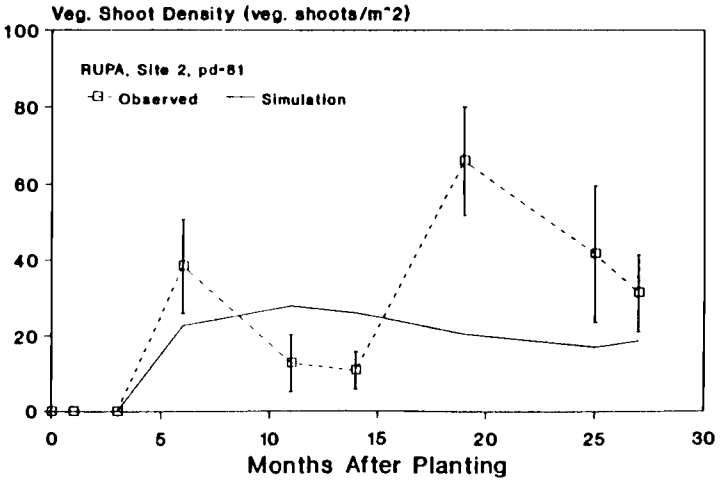
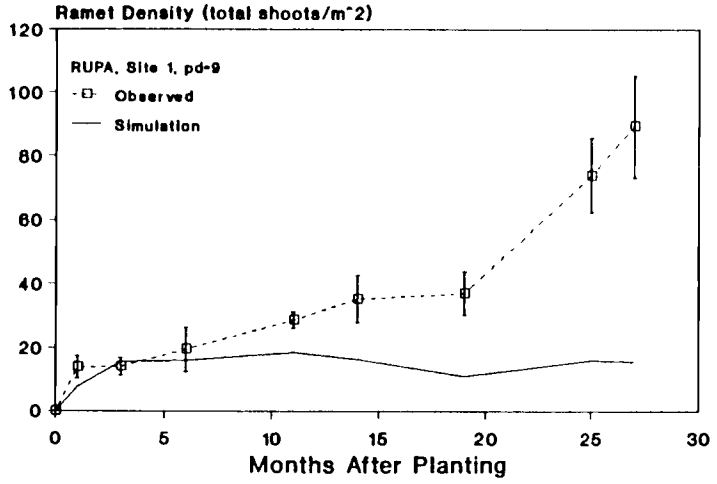
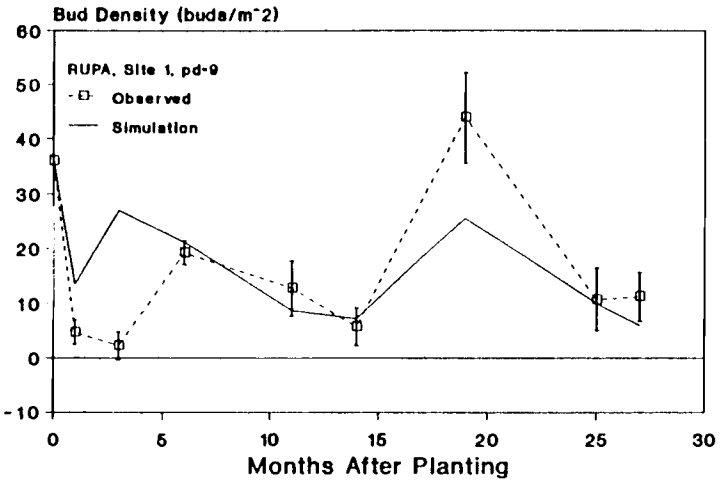
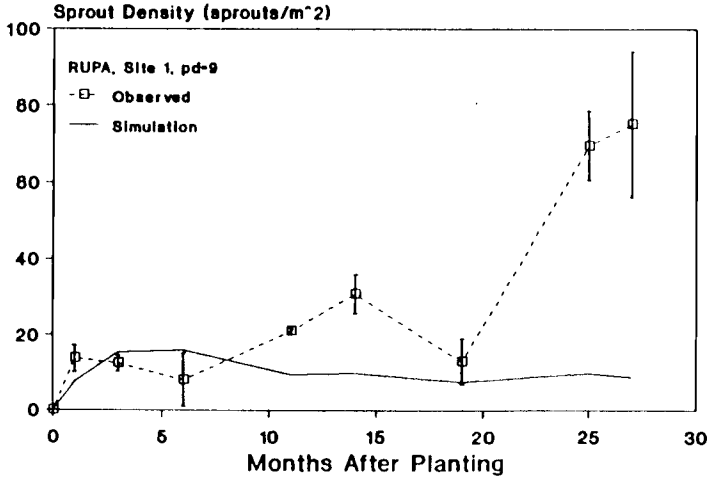

Veg. Shoot Density (veg. shoots/m^2)
RUPA, Site 2, pd-81
Observed
Simulation
100
80
60
40
20
0
0
5
10
15
20
25
30
Months After Planting

Fig. A5.6.

Figure A5.7. Simulated thimbleberry ramet density (top left), basal bud density (top right), sprout density (bottom left) and vegetative shoot density (bottom right) over the first three growing seasons plotted with mean and 1 standard deviation of observed populations planted with 9 cuttings/m^2 at Woods Creek (Site 1).


Ramet Density (total shoots/m^2)
RUPA, Site 1, pd-9
Observed
Simulation
120
100
80
60
40
20
0
0
5
10
15
20
25
30
Months After Planting


Bud Density (buds/m^2)
RUPA, Site 1, pd-9
Observed
Simulation
60
50
40
30
20
10
0
-10
0
5
10
15
20
25
30
Months After Planting


Sprout Density (sprouts/m^2)
RUPA, Site 1, pd-9
Observed
Simulation
100
80
60
40
20
0
0
5
10
15
20
25
30
Months After Planting

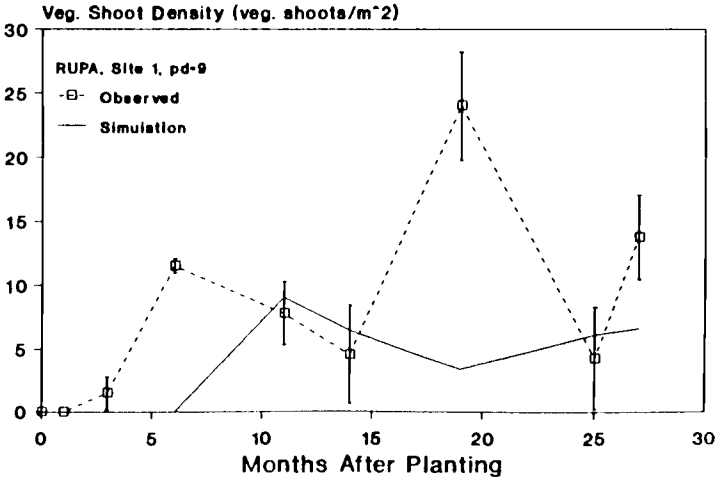
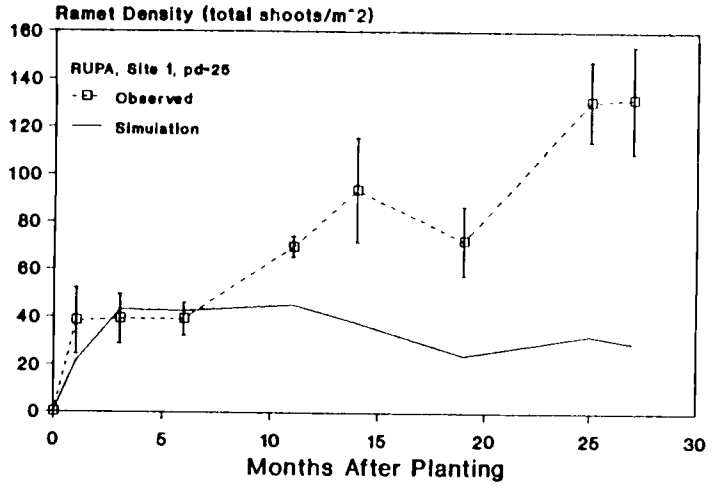
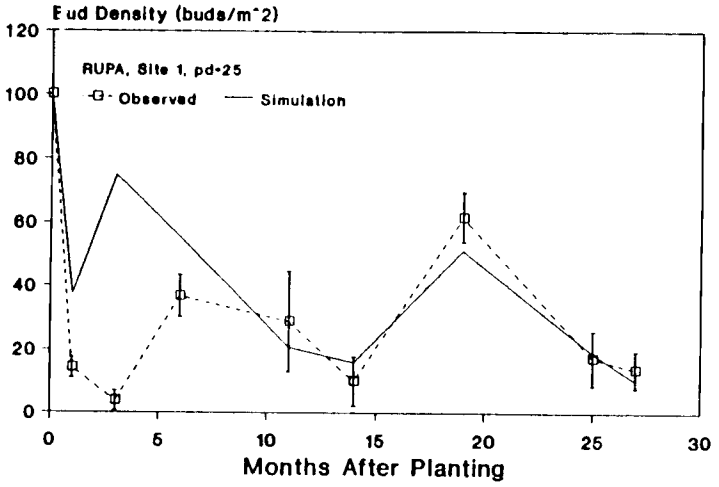
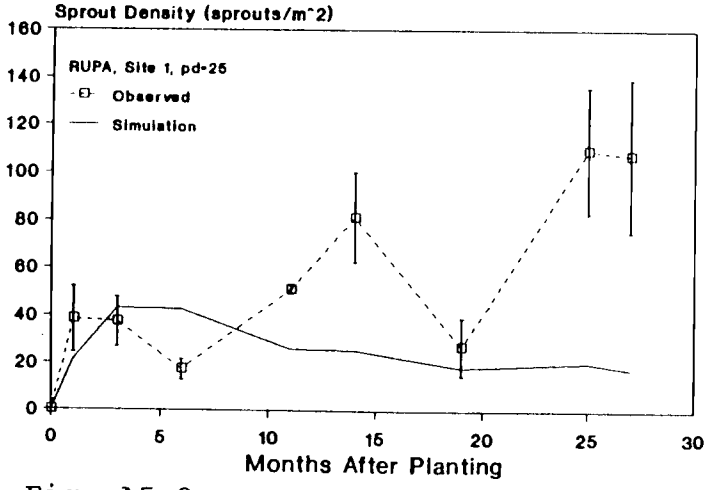

Veg. Shoot Density (veg. shoots/m^2)
RUPA, Site 1, pd-9
Observed
Simulation
30
25
20
15
10
5
0
0
5
10
15
20
25
30
Months After Planting

Fig. A5.7.

Figure A5.8. Simulated thimbleberry ramet density (top left), basal bud density (top right), sprout density (bottom left) and vegetative shoot density (bottom right) over the first three growing seasons plotted with mean and 1 standard deviation of observed populations planted with 25 cuttings/m^2 at Woods Creek (Site 1).


Ramet Density (total shoots/m^2)
RUPA, Site 1, pd-25
Observed
Simulation
160
140
120
100
80
60
40
20
0
0
5
10
15
20
25
30
Months After Planting


Bud Density (buds/m^2)
RUPA, Site 1, pd-25
Observed
Simulation
120
100
80
60
40
20
0
0
5
10
15
20
25
30
Months After Planting


Sprout Density (sprouts/m^2)
RUPA, Site 1, pd-25
Observed
Simulation
160
140
120
100
80
60
40
20
0
0
5
10
15
20
25
30
Months After Planting

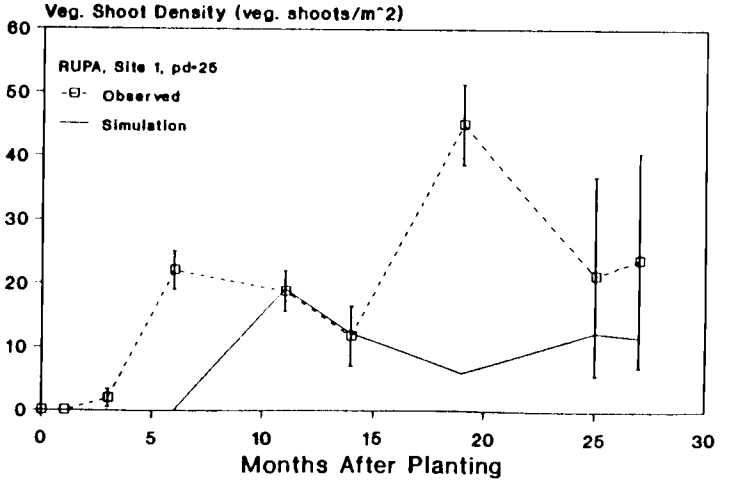

Veg. Shoot Density (veg. shoots/m^2)
RUPA, Site 1, pd-25
Observed
Simulation
60
50
40
30
20
10
0
0
5
10
15
20
25
30
Months After Planting

Fig. A5.8.

Table A5.1. Mean and maximum demographic parameter value ransition matrices.

Transition Matrix Parameters

$$\begin{bmatrix} R0 & 0 & 0 & 0 & 0 & F6 & 0 \\ 0 & R2 & 0 & 0 & V5 & V6 & V7 \\ G1 & 0 & R3 & 0 & 0 & 0 & 0 \\ 0 & G2 & 0 & R4 & 0 & 0 & 0 \\ 0 & 0 & G3 & G4 & R5 & 0 & 0 \\ 0 & 0 & 0 & 0 & G5 & R6 & 0 \\ 0 & G7 & 0 & 0 & 0 & 0 & R7 \end{bmatrix}$$

Mean Matrices

Establishment

$$\begin{bmatrix} 0.90 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.39 & 0 & 0 & 0.37 & 0.02 & 0.50 \\ 0.05 & 0 & 0.09 & 0 & 0 & 0 & 0 \\ 0 & 0.42 & 0 & 0.24 & 0 & 0 & 0 \\ 0 & 0 & 0.02 & 0.29 & 0.65 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.01 & 0.01 & 0 \\ 0 & 0.10 & 0 & 0 & 0 & 0 & 1.00 \end{bmatrix}$$

Reproduction

$$\begin{bmatrix} 0.95 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.27 & 0 & 0 & 0.17 & .008 & 0.50 \\ 0.05 & 0 & 0.12 & 0 & 0 & 0 & 0 \\ 0 & 0.37 & 0 & 0.76 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.08 & 0.53 & 0 & 0 \\ 0 & 0 & 0 & 0 & .007 & 0.05 & 0 \\ 0 & 0.05 & 0 & 0 & 0 & 0 & 0.70 \end{bmatrix}$$

Senescence

$$\begin{bmatrix} 0.64 & 0 & 0 & 0 & 0 & 53 & 0 \\ 0 & 0.23 & 0 & 0 & 1.21 & 0.04 & 1.00 \\ 0 & 0 & 0.09 & 0 & 0 & 0 & 0 \\ 0 & 0.17 & 0 & 0.32 & 0 & 0 & 0 \\ 0 & 0 & 0.07 & 0.48 & 0.39 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.03 & 0 \\ 0 & 0.05 & 0 & 0 & 0 & 0 & 1.00 \end{bmatrix}$$

Maximum Matrices

Establishment

$$\begin{bmatrix} 0.64 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.33 & 0 & 0 & 2.30 & 2.00 & 2.00 \\ 0.36 & 0 & 0.19 & 0 & 0 & 0 & 0 \\ 0 & 0.33 & 0 & 0.50 & 0 & 0 & 0 \\ 0 & 0 & 0.81 & 0.50 & 0.32 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.68 & 1.00 & 0 \\ 0 & 0.33 & 0 & 0 & 0 & 0 & 1.00 \end{bmatrix}$$

Reproduction

$$\begin{bmatrix} 0.95 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.45 & 0 & 0 & 2.00 & 1.00 & 1.00 \\ 0.05 & 0 & 1.00 & 0 & 0 & 0 & 0 \\ 0 & 0.45 & 0 & 0.37 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0.63 & 0.82 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.18 & 1.00 & 0 \\ 0 & 0.10 & 0 & 0 & 0 & 0 & 1.00 \end{bmatrix}$$

Senescence

$$\begin{bmatrix} 1.00 & 0 & 0 & 0 & 0 & 65 & 0 \\ 0 & 0.45 & 0 & 0 & 3.00 & 3.00 & 2.00 \\ 0 & 0 & 0.50 & 0 & 0 & 0 & 0 \\ 0 & 0.45 & 0.50 & 0.50 & 0 & 0 & 0 \\ 0 & 0 & 0.02 & 0.50 & 1.00 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1.00 & 0 \\ 0 & 0.10 & 0 & 0 & 0 & 0 & 1.00 \end{bmatrix}$$

Table A5.2. Density dependent functions and mean values for salmonberry (RUSP) and thimbleberry (RUPA) demographic parameters for each measurement time at the establishment (EST), reproductive (REP), and senescence (SEN) phenology stages included in the model.

Parameter	Stage	Time	Equation		n
G1	EST	G1 =	.030	RUSP	60
			.040	RUPA	60
G1	REP	G1 =	.000	RUSP	-
			.000	RUPA	-
G1	SEN	G1 =	.000	RUSP	-
			.000	RUPA	-
R1	EST	R0 =	.480	RUSP	200
			.474	RUPA	200
R1	REP	R0 =	1.00	RUSP	-
			1.00	RUPA	-
R1	SEN	R0 =	1.00	RUSP	-
			1.00	RUPA	-
M1	EST	M1 =	.490	RUSP	200
			.486	RUPA	200
M1	REP	M1 =	.000	RUSP	-
			.000	RUPA	-
M1	SEN	M1 =	.000	RUSP	-
			.000	RUPA	-

Table A5.2 cont'd. Density dependent functions and mean values for salmonberry (RUSP) and thimbleberry (RUPA) demographic parameters for each measurement time at the establishment (EST), reproductive (REP), and senescence (SEN) phenology stages included in the RUBSM simulation model. (continued)

Parameter	Stage	Time	Equation		n	MSE	F	r^2
G2	EST	11	G2 = .400	RUSP, site 1	14			
			.007	RUSP, site 2	12			
			.388	RUPA, site 1	16			
			.350	RUPA, site 2	12			
G2	EST	25	G2 = .854	RUSP, site 1	15			
			.190	RUSP, site 2	12			
			.641	RUPA, site 1	16			
			$.542/(1 + .001RamD^{(1.244X22)})$	RUPA, site 2	12	.085	73.8	.024
G2	REP	3	G2 = .341	RUSP, site 1	15			
			.612	RUSP, site 2	11			
			$.411/(1 + .001RamD^{(1.606X12 + 1.507X22)})$	RUPA	25	.091	26.1	.055
G2	REP	14	G2 = .542	RUSP, site 1	14			
			.459	RUSP, site 2	12			
			$.475/(1 + .001RamD^{(1.793X12)})$	RUPA, site 1	16	.059	77.5	.128
			.535	RUPA, site 2	12			
G2	REP	27	G2 = .330	RUSP, site 1	8			
			$.325/(1 + .001RamD^{(1.595X21)})$	RUSP, site 2	12	.027	79.7	.167
			.380	RUPA, site 1	16			
			.288	RUPA, site 2	12			
G2	SEN	6	G2 = $.677/(1 + .001RamD^{(3.474X11 + 1.838X12 + 1.763X21 + 2.279X22)})$		34	.137	6.7	.194
G2	SEN	19	G2 = .113	RUSP, site 1	10			
			G2 = $.180/(1 + .001RamD^{(1.317X12 + 1.335X21 + 1.390X22)})$		40	.041	6.8	.073

Indicator variables: X11 = Site 1, RUSP X12 = Site 1, RUPA X21 = Site 2, RUSP X22 = Site 2, RUPA
r^2 values are approximate for nonlinear equations.

Table A5.2 cont'd. Density dependent functions and mean values for salmonberry (RUSP) and thimbleberry (RUPA) demographic parameters for each measurement time at the establishment (EST), reproductive (REP), and senescence (SEN) phenology stages included in the RUBSM simulation model. (continued)

Parameter	Stage	Time	Equation		n	MSE	F	r^2
R2	EST	11	R2 = .876 / (1 + .001RamD$^{(1.696X11 + 1.473X12 + 1.390X22)}$)	RUSP, site 2	12			
					42	.070	57.8	.131
R2	EST	25	R2 = .053	RUSP, site 1	15			
			.169	RUSP, site 2	16			
			.279/(1 + .001RamD$^{(1.411X12)}$)	RUPA, site 1	12	.041	43.2	.066
			.425	RUPA, site 2	12			
R2	REP	3	R2 = .030	RUSP, site 1	11			
			.110/(1 + .001RamD$^{(1.280X21)}$)	RUSP, site 2	11	.039	7.7	.002
			.191	RUPA, site 1	14			
			.163	RUPA, site 2	11			
R2	REP	14	R2 = .480 / (1 + .001RamD$^{(1.349X11 + 1.473X12 + 1.476X22)}$)	RUSP, site 2	12			
					42	.049	28.8	.112
R2	REP	27	R2 = .813 / (1 + .001RamD$^{(1.647X11 + 1.754X12 + 1.497X22)}$)	RUSP, site 2	12			
					36	.041	75.1	.514
R2	SEN	6	R2 = .063	RUSP, site 1	8			
			.090	RUSP, site 2	6			
			.178	RUPA, site 1	13			
			.193	RUPA, site 2	8			
R2	SEN	19	R2 = .613 / (1 + .001RamD$^{(2.579X11 + 1.565X12 + 1.589X22)}$)	RUSP, site 2	12			
					38	.083	25.8	.138

Indicator variables: X11 = Site 1, RUSP X12 = Site 1, RUPA X21 = Site 2, RUSP X22 = Site 2, RUPA
r^2 values are approximate for nonlinear equations.

Table A5.2 cont'd. Density dependent functions and mean values for salmonberry (RUSP) and thimbleberry (RUPA) demographic parameters for each measurement time at the establishment (EST), reproductive (REP), and senescence (SEN) phenology stages included in the RUBSM simulation model.

Parameter	Stage	Time	Equation		n	MSE	F	r^2
M2	EST	11	M2 =	.216 RUSP, site 1	14			
				.116 RUSP, site 2	12			
				.149 RUPA, site 1	16			
				.168 RUPA, site 2	12			
M2	EST	25	M2 =	$.393/(1 + 1000RamD^{(-1.414X11 - 1.470X12 - 3.374X21 - 1.486X22)})$	55	.017	30.9	.346
M2	REP	3	M2 =	.629 RUSP, site 1 $.552/(1 + 1000RamD^{(-2.680X21)})$ RUSP, site 2 .566 RUPA, site 1 .520 RUPA, site 2	15 11 14 11	.116	22.7	.340
M2	REP	14	M2 =	.221 RUSP, site 1 $.400/(1 + 1000RamD^{(-1.100X21 - 1.800X22)})$ .448 RUPA, site 1	14 25 16	.048	15.5	.290
M2	REP	27	M2 =	.238 RUSP, site 1 .361 RUSP, site 2 .047 RUPA, site 1 .290 RUPA, site 2	8 12 16 12			
M2	SEN	6	M2 =	.706 RUSP, site 1 .567 RUSP, site 2 .405 RUPA, site 1 .498 RUPA, site 2	8 6 13 8			
M2	SEN	19	M2 =	$.644/(1 + 1000RamD^{(-3.379X11 - 4.059X12 - 1.443X21 - 2.352X22)})$	51	.057	46.6	.522

Indicator variables: X11 = Site 1, RUSP X12 = Site 1, RUPA X21 = Site 2, RUSP X22 = Site 2, RUPA
r^2 values are approximate for nonlinear equations.

Table A5.2 cont'd. Density dependent functions and mean values for salmonberry (RUSP) and thimbleberry (RUPA) demographic parameters for each measurement time at the establishment (EST), reproductive (REP), and senescence (SEN) phenology stages included in the model.

Parameter	Stage	Time	Equation			n
				.000	RUSP	2
G3	EST	11	G3 =	.200	RUPA, site 1	4
				.107	RUPA, site 2	7
				.000	RUSP	5
G3	EST	25	G3 =	.000	RUPA	4
				.000	RUSP	-
G3	REP	3	G3 =	.000	RUPA	9
				.000	RUSP	2
G3	REP	14	G3 =	.000	RUPA	6
				.000	RUSP	8
G3	REP	27	G3 =	.000	RUPA	4
				.000	RUSP	8
G3	SEN	6	G3 =	.520	RUPA, site 1	12
				.100	RUPA, site 2	5
				.000	RUSP	4
G3	SEN	19	G3 =	.000	RUPA	12

Table A5.2 cont'd. Density dependent functions and mean values for salmonberry (RUSP) and thimbleberry (RUPA) demographic parameters for each measurement time at the establishment (EST), reproductive (REP), and senescence (SEN) phenology stages included in the model.

Parameter	Stage	Time	Equation			n
				.000	RUSP, site 1	-
R3	EST	11	R3 =	.335	RUSP, site 2	2
				.465	RUPA, site 1	4
				.179	RUPA, site 2	7
				.000	RUSP, site 1	-
R3	EST	25	R3 =	.600	RUSP, site 2	5
				.000	RUPA, site 1	1
				.600	RUPA, site 2	3
				.000	RUSP	-
R3	REP	3	R3 =	.857	RUPA, site 1	7
				.750	RUPA, site 2	2
				.000	RUSP, site 1	-
R3	REP	14	R3 =	.500	RUSP, site 2	2
				.917	RUPA, site 1	3
				.667	RUPA, site 2	3
				.000	site 1	2
R3	REP	27	R3 =	.316	RUSP, site 2	8
				.700	RUPA, site 2	2
				.000	RUSP, site 1	2
R3	SEN	6	R3 =	.500	RUSP, site 2	4
				.111	RUPA, site 1	12
				.700	RUPA, site 2	5

Table A5.2 cont'd. Density dependent functions and mean values for salmonberry (RUSP) and thimbleberry (RUPA) demographic parameters for each measurement time at the establishment (EST), reproductive (REP), and senescence (SEN) phenology stages included in the RUBSM simulation model.

Parameter	Stage	Time	Equation			n
R3	SEN	19	R3 =	.000	RUSP, site 1	-
				.250	RUSP, site 2	4
				.200	RUPA, site 1	5
				.089	RUPA, site 2	7
M3	EST	11	M3 =	1.00	RUSP, site 1	-
				.665	RUSP, site 2	2
				.335	RUPA, site 1	4
				.714	RUPA, site 2	7
M3	EST	25	M3 =	1.00	RUSP, site 1	-
				.400	RUSP, site 2	5
				.700	RUPA	4
M3	REP	3	M3 =	1.00	RUSP	-
				.143	RUPA, site 1	7
				.250	RUPA, site 2	9
M3	REP	14	M3 =	.500	RUSP	2
				.083	RUPA, site 1	3
				.333	RUPA, site 2	3
M3	REP	27	M3 =	1.00	RUSP, site 1	-
				.684	RUSP, site 2	2
				.650	RUPA	4

Table A5.2 cont'd. Density dependent functions and mean values for salmonberry (RUSP) and thimbleberry (RUPA) demographic parameters for each measurement time at the establishment (EST), reproductive (REP), and senescence (SEN) phenology stages included in the RUBSM simulation model.

Parameter	Stage	Time	Equation		n
			.750	RUSP	6
M3	SEN	6	M3 = .369	RUPA, site 1	12
			.200	RUPA, site 2	5
			.750	RUSP	4
M3	SEN	19	M3 = .800	RUPA, site 1	5
			.911	RUPA, site 2	7

Table A5.2 cont'd. Density dependent functions and mean values for salmonberry (RUSP) and thimbleberry (RUPA) demographic parameters for each measurement time at the establishment (EST), reproductive (REP), and senescence (SEN) phenology stages included in the RUBSM simulation model.

Parameter	Stage	Time	Equation		n	MSE	F	r^2
G4	EST	11	G4 =	.564 RUSP, site 1	15			
				$.536/(1 + .001RamD^{(6.281X12 + 1.520X21 + 1.988X22)})$	40	.050	41.6	.398
G4	EST	25	G4 =	.199 RUSP, site 1	15			
				.403 RUSP, site 2	12			
				$.271/(1 + .001RamD^{(1.781X12)})$ RUPA, site 1	16	.040	41.1	.096
				.299 RUPA, site 2	12			
G4	REP	3	G4 =	.000 RUSP, site 1	15			
				.001 RUSP, site 2	12			
				.083 RUPA, site 1	16			
				.017 RUPA, site 2	12			
G4	REP	14	G4 =	.039 RUSP, site 1	14			
				.300 RUSP, site 2	12			
				.031 RUPA, site 1	16			
				$.116/(1 + .001RamD^{(1.801X22)})$ RUPA, site 2	12	.021	15.5	.025
G4	REP	27	G4 =	$.165/(1 + .001RamD^{(1.335X11 + 1.370X12 + 1.566X21 + 1.849X22)})$	55	.013	11.1	.129
G4	SEN	6	G4 =	$.603/(1 + .001RamD^{(2.040X11 + 1.486X12 + 1.220X21 + 1.365X22)})$	56	.049	60.4	.179
G4	SEN	19	G4 =	$.507/(1 + .001RamD^{(2.142X11 + 1.251X21)})$ RUSP	27	.030	122	.284
				.105 RUPA, site 1	16			
				.062 RUPA, site 2	12			

Indicator variables: X11 = Site 1, RUSP X12 = Site 1, RUPA X21 = Site 2, RUSP X22 = Site 2, RUPA
r^2 values are approximate for nonlinear equations.

Table A5.2 cont'd. Density dependent functions and mean values for salmonberry (RUSP) and thimbleberry (RUPA) demographic parameters for each measurement time at the establishment (EST), reproductive (REP), and senescence (SEN) phenology stages included in the RUBSM simulation model. (continued)

Parameter	Stage	Time	Equation		n	MSE	F	r^2
R4	EST	11	R4 = .148	RUSP, site 1	15			
			.516	RUSP, site 2	12			
			$.284/(1 + .001RamD^{(0.354X12 + 0.192X22)})$	RUPA	28	.055	21.4	.095
R4	EST	25	$.244/(1 + .001RamD^{(1.418X11)})$	RUSP, site 1	15	.067	23.5	.005
			.470	RUSP, site 2	12			
			.059	RUPA, site 1	16			
			.304	RUPA, site 2	12			
R4	REP	3	$.760/(1 + .001RamD^{(1.658X11 + 1.123X12)})$	site 1	31	.043	222	.118
			.808	RUSP, site 2	12			
			.811	RUPA, site 2	12			
R4	REP	14	.889	RUSP, site 1	14			
			$.876/(1 + .001RamD^{(1.343X21)})$	RUSP, site 2	12	.016	121	.234
			.874	RUPA, site 1	16			
			.907	RUPA, site 2	12			
R4	REP	27	.707	RUSP, site 1	15			
			.865	RUSP, site 2	12			
			$.775/(1 + .001RamD^{(1.038X21)})$	RUPA, site 1	16	.035	451	.058
			.824	RUPA, site 2	12			
R4	SEN	6	R4 = .406	RUSP, site 1	16			
			.297	RUSP, site 2	12			
			.273	RUPA, site 1	16			
			$.319/(1 + .001RamD^{(1.231X22)})$	RUPA, site 2	12	.037	74.0	.009

Indicator variables: X11 = Site 1, RUSP X12 = Site 1, RUPA X21 = Site 2, RUSP X22 = Site 2, RUPA
r^2 values are approximate for nonlinear equations.

Table A5.2 cont'd. Density dependent functions and mean values for salmonberry (RUSP) and thimbleberry (RUPA) demographic parameters for each measurement time at the establishment (EST), reproductive (REP), and senescence (SEN) phenology stages included in the RUBSM simulation model. (continued)

Parameter	Stage	Time	Equation	n	MSE	F	r^2
			.497 RUSP, site 1	15			
R4	SEN	19	R4 = .406 RUSP, site 2	12			
			$.379/(1 + .001RamD^{(1.185X12 + 2.008X22)})$	28	.034	59.6	.198
M4	EST	11	$M4 = .712/(1 + 1000RamD^{(-1.890X11 - 7.547X12 - 1.320X21 - 2.352X22)})$	56	.089	24.7	.287
M4	EST	25	$M4 = .723/(1 + 1000RamD^{(-10.12X11 - 1.249X21 - 2.123X22)})$	40	.078	47.4	.401
			.127 RUPA, site 1	16			
			.379 RUSP, site 1	8			
M4	REP	3	M4 = .191 RUSP, site 2	6			
			.231 RUPA, site 1	13			
			.173 RUPA, site 2	8			
			.072 RUSP, site 1	14			
M4	REP	14	M4 = .008 RUSP, site 2	12			
			.094 RUPA, site 1	16			
			.016 RUPA, site 2	12			
M4	REP	27	$M4 = .242/(1 + 1000RamD^{(-1.728X11 - 2.716X12 - 1.594X22)})$	43	.005	45.3	.559
			.017 RUSP, site 2	12			
M4	SEN	6	$M4 = .339/(1 + 1000RamD^{(-4.507X11 - 1.917X12 - 1.434X21 - 2.073X22)})$	56	.035	11.9	.147
M4	SEN	19	$M4 = .287/(1 + 1000RamD^{(-7.153X11 - 3.119X12 - 1.772X21)})$	41	.043	15.3	.545
			.302 RUPA, site 2	15			

Indicator variables: X11 = Site 1, RUSP X12 = Site 1, RUPA X21 = Site 2, RUSP X22 = Site 2, RUPA
r^2 values are approximate for nonlinear equations.

Table A5.2 cont'd. Density dependent functions and mean values for salmonberry (RUSP) and thimbleberry (RUPA) demographic parameters for each measurement time at the establishment (EST), reproductive (REP), and senescence (SEN) phenology stages included in the model.

Parameter	Stage	Time	Equation		n
G5	EST	11	G5 = .000	RUSP, site 1	15
			.000	RUSP, site 2	12
			.000	RUPA, site 1	16
			.000	RUPA, site 2	12
G5	EST	25	G5 = .002	RUSP, site 1	15
			.058	RUSP, site 2	12
			.000	RUPA, site 1	15
			.057	RUPA, site 2	12
G5	REP	3	G5 = .000	RUSP, site 1	-
			.000	RUSP, site 2	1
			.000	RUPA, site 1	13
			.000	RUPA, site 2	1
G5	REP	14	G5 = .003	RUSP, site 1	14
			.014	RUSP, site 2	12
			.010	RUPA, site 1	15
			.000	RUPA, site 2	12
G5	REP	27	G5 = .000	RUSP, site 1	14
			.010	RUSP, site 2	12
			.029	RUPA, site 1	16
			.018	RUPA, site 2	12

Indicator variables: X11 = Site 1, RUSP X12 = Site 1, RUPA X21 = Site 2, RUSP X22 = Site 2, RUPA
r^2 values are approximate for nonlinear equations.

Table A5.2 cont'd. Density dependent functions and mean values for salmonberry (RUSP) and thimbleberry demographic parameters for each measurement time at the establishment (EST), reproductive (REP), and senescence (SEN) phenology stages included in the RUBSM simulation model. (continued)

Parameter	Stage	Time	Equation		n	MSE	F	r^2
G5	SEN	6	G5 = .000	RUSP, site 1	14			
			.000	RUSP, site 2	12			
			.000	RUPA, site 1	16			
			.000	RUPA, site 2	12			
G5	SEN	19	G5 = .000	RUSP, site 1	15			
			.000	RUSP, site 2	12			
			.000	RUPA, site 1	16			
			.000	RUPA, site 2	12			
R5	EST	11	R5 = .863	RUSP, site 1	15			
			.920	RUSP, site 2	12			
			$.840/(1 + .001RamD^{(1.485X12 + 1.794X22)})$		28	.066	153	.306
R5	EST	25	$R5 = .708/(1 + .003RamD^{(1.185X11 + 1.597X12 + 1.104X22)})$		42	.055	90.4	.354
			.850	RUSP, site 2	12			
R5	REP	3	R5 = .000	RUSP, site 1	-			
			.000	RUSP, site 2	1			
			.000	RUPA, site 1	13			
			.000	RUPA, site 2	1			

Indicator variables: X11 = Site 1, RUSP X12 = Site 1, RUPA X21 = Site 2, RUSP X22 = Site 2, RUPA
r^2 values are approximate for nonlinear equations.

Table A5.2 cont'd. Density dependent functions and mean values for salmonberry (RUSP) and thimbleberry (RUPA) demographic parameters for each measurement time at the establishment (EST), reproductive (REP), and senescence (SEN) phenology stages included in the RUBSM simulation model. (continued)

Parameter	Stage	Time	Equation		n	MSE	F	r^2
R5	REP	14	R5 = .904	RUSP, site 1	15			
			.984	RUSP, site 2	12			
			$.912/(1 + .001RamD^{(1.455X12 + 0.794X22)})$	RUPA	27	.014	902	.647
R5	REP	27	R5 = .802	RUSP, site 1	14			
			.972	RUSP, site 2	16			
			$.865/(1 + .001RamD^{(1.245X12 + 0.943X22)})$	RUPA	24	.042	278	.210
R5	SEN	6	R5 = .000	RUSP, site 1	14			
			.000	RUSP, site 2	12			
			.781	RUPA, site 1	16			
			.000	RUPA, site 2	12			
R5	SEN	19	R5 = .848	RUSP, site 2	12			
			$.686/(1 + .001RamD^{(1.588X11 + 1.586X12 + 1.495X22)})$		43	.067	69.1	.230

Indicator variables: X11 = Site 1, RUSP X12 = Site 1, RUPA X21 = Site 2, RUSP X22 = Site 2, RUPA
r^2 values are approximate for nonlinear equations.

Table A5.2 cont'd. Density dependent functions and mean values for salmonberry (RUSP) and thimbleberry (RUPA) demographic parameters for each measurement time at the establishment (EST), reproductive (REP), and senescence (SEN) phenology stages included in the RUBSM simulation model. (continued)

Parameter	Stage	Time	Equation		n	MSE	F	r^2
M5	EST	11	M5 = .080	RUSP, site 2	12			
			.486/(1 + 1000RamD$^{(-1.197X11 - 3.700X12 - 4.544X22)}$)		43	.069	16.5	.297
M5	EST	25	M5 = .512/(1 + 1000RamD$^{(-4.329X11 - 1.192X21 - 3.634X22)}$)		39	.059	3.5	.396
			.686	RUPA, site 1	15			
			1.00	RUSP, site 1	-			
M5	REP	3	M5 = 1.00	RUSP, site 2	1			
			1.00	RUPA, site 1	13			
			1.00	RUPA, site 2	1			
M5	REP	14	M5 = .002	RUSP, site 2	12			
			.417/(1 + 1000RamD$^{(-1.325X11 - 2.846X12 - 1.353X22)}$)		42	.016	35.0	.628
M5	REP	27	M5 = .380/(1 + 1000RamD$^{(-1.575X11 - 2.242X12 - 0.933X21 - 1.482X22)}$)		54	.045	10.6	.178

Indicator variables: X11 = Site 1, RUSP X12 = Site 1, RUPA X21 = Site 2, RUSP X22 = Site 2, RUPA
r^2 values are approximate for nonlinear equations.

Table A5.2 cont'd. Density dependent functions and mean values for salmonberry (RUSP) and thimbleberry (RUPA) demographic parameters for each measurement time at the establishment (EST), reproductive (REP), and senescence (SEN) phenology stages included in the RUBSM simulation model.

Parameter	Stage	Time	Equation		n	MSE	F	r^2
M5	SEN	6	M5 = 1.00	RUSP	24			
			.219	RUPA, site 1	16			
			1.00	RUPA, site 2	12			
			.505	RUSP, site 1	15			
M5	SEN	19	$M5 = .542/(1 + 1000RamD^{(-1.466X21 - 3.786X22)})$	site 2	28	.052	47.4	.409
			.560	RUPA, site 1	16			
V5	EST	11	V5 = .215 - .0014RamD + .238Site + 0.0Spp		53	.074	6.1	.193
			.145	RUSP, site 1	15			
V5	EST	25	V5 = .239	RUSP, site 2	12			
			.238	RUPA, site 1	15			
			.213	RUPA, site 2	12			
			.000	RUSP, site 1	-			
V5	REP	3	V5 = .000	RUSP, site 2	1			
			.337	RUPA, site 1	13			
			.000	RUPA, site 2	1			
V5	REP	14	V5 = .500 - .003GenD - .276Site - .183Spp		54	.040	11.6	.406
V5	REP	27	V5 = .132 - .001GenD + .175Site - 0.0Spp		54	.031	7.3	.220
V5	SEN	6	V5 = 1.44 - .005GenD - 0.0Site - .138Spp		53	.106	2.2	.079
V5	SEN	19	V5 = 1.41 - .001RamD - 0.0Site - .543*Spp		54	.097	21.1	.448

Indicator variables: X11 = Site 1, RUSP X12 = Site 1, RUPA X21 = Site 2, RUSP X22 = Site 2, RUPA
r^2 values are approximate for nonlinear equations.

Table A5.2 cont'd. Density dependent functions and mean values for salmonberry (RUSP) and thimbleberry (RUPA) demographic parameters for each measurement time at the establishment (EST), reproductive (REP), and senescence (SEN) phenology stages included in the model.

Parameter	Stage	Time	Equation			n
R6	EST	11	R6 =	.000		1
R6	EST	25	R6 =	.188		8
R6	REP	3	R6 =	.000		-
R6	REP	14	R6 =	.000		5
				1.00	RUSP	9
R6	REP	27	R6 =	.000	RUPA	8
R6	SEN	6	R6 =	.000		-
R6	SEN	19	R6 =	.688		4
M6	EST	11	M6 =	1.00		1
M6	EST	25	M6 =	.813		8
M6	REP	3	M6 =	1.00		-
M6	REP	14	M6 =	1.00		5
				.000	RUSP	9
M6	REP	27	M6 =	1.00	RUPA	8
M6	SEN	6	M6 =	1.00		-
M6	SEN	19	M6 =	.313		4