

AN ABSTRACT OF THE DISSERTATION OF

Susan C. McDowell for the degree of Doctor of Philosophy in Environmental Sciences presented on May 22, 2002.

Title: Life-history and Physiological Trade-offs to Reproduction of Invasive and Noninvasive *Rubus*

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Abstract approved: _____

Steven R. Radosevich

The goal of this dissertation was to improve our understanding of the physiology and life-history of invasive plants and of the mechanisms underlying life-history trade-offs. I compared invasive and noninvasive species of *Rubus* (blackberry) that grow together in the Pacific Northwest. Three hypotheses were investigated: (1) Invasive *Rubus* have higher photosynthetic capacity and lower leaf-level resource costs of photosynthesis than native, noninvasive species; (2) The physiological effects of reproduction on foliage result in higher reproductive effort for noninvasive *Rubus* than for an invasive species, in spite of the greater number and size of fruit produced by the invasive species; and (3) Reproduction produces greater trade-offs to growth for noninvasive *Rubus* because of its higher reproductive effort, and these trade-offs affect the population demographics of these species.

I found that two invasive species, *R. discolor* and *R. laciniatus*, had higher photosynthetic capacities and maintained these rates for a longer portion of the year

than two noninvasive species, *R. ursinus* and *R. leucodermis*. Furthermore, the two invasive species had higher rates of photosynthesis per unit resource investment, such as carbon, nitrogen, and water, than the noninvasive *Rubus*. I found that these photosynthetic characteristics could be used to distinguish between the noninvasive and invasive species using discriminant analysis.

I compared reproductive effort for one of the invasive, *R. discolor*, and one of the noninvasive, *R. ursinus*, species. I found that, although the invasive *Rubus* allocated more resources directly to reproduction than the noninvasive species, it had lower reproductive effort because it did not have the significant decline in leaf nitrogen and photosynthetic capacity and significant increase in mid-day water stress that were associated with reproduction in the noninvasive species.

I also observed that sexual reproduction in the noninvasive species was associated with trade-offs to growth both within and between generations, but these were not observed in the invasive species. These trade-offs in the noninvasive species resulted in an almost complete dependence on clonal growth rather than sexual reproduction for population growth. The invasive *Rubus* relied on sexual reproduction for population growth relatively more than the noninvasive species and, therefore, reproductive effort influenced the demographics of these species.

Life-history and Physiological Trade-offs to Reproduction
of Invasive and Noninvasive *Rubus*

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Susan C. McDowell

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Susan C. McDowell, Author

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Life-history and Physiological Trade-offs to Reproduction
of Invasive and Noninvasive *Rubus*

CHAPTER 1. INTRODUCTION

1.1 WHY STUDY INVASIVE PLANTS?

The spread of invasive species is now considered to be the second largest cause of biodiversity loss globally (Heywood 1989; Vitousek et al. 1996). In addition to the threat invasive species pose to native species and to ecosystem structure and function, invasive species can have severe effects on commercial industries such as agriculture, fisheries, and forestry. The economic impacts of invasive species are considerable. It has been estimated that invasive species cost the United States billions of dollars annually (Pimentel et al. 2000). Few regions of the earth remain sheltered from invasive species, and the scope of their impact is expected to grow as international trade increases the number of species introductions (Keane and Crawley 2002) and previously introduced species become established in new locations (OTA 1993; Sakai et al. 2001). In an effort to address these current and future impacts of invasive species in the United States, Executive Order 13112 was issued in February 1999 to direct federal agencies to prevent the introduction of new invasive species and control and limit the impacts of established invasive species (Federal Registry 64 (25): 6183-86). The National Invasive Species Council was established to develop a coordinated Invasive Species

Management Plan, which provides specific guidelines for implementing the Executive Order. One of the stated goals of the Management Plan is to conduct research on invasive species, methods to prevent future introductions, and methods for the environmentally sound control of invasive species.

The potential impacts of invasive plant species have been recognized for decades and have stimulated the development of several theoretical ideas about invasiveness and invasibility (Elton 1958; Baker 1965). Such theories have been the basis of our understanding of invasive plants and for some methods of controlling their spread. However, some of these theories have not been directly tested and the connection between several of these ideas and quantitative field data has yet to be made (Parker 2000; Kolar and Lodge 2001; Keane and Crawley 2002). There is increasing recognition of the need for quantitative data to test theories of invasiveness and for research on the biology and ecology of invasive plant species in order to better understand and control them (Radosевич et al. 1997; Sakai et al. 2001).

An additional motivation for the study of invasive plants is the application of such research to evolutionary and life-history studies. Invasive plants have arrived in their new settings relatively recently, where they are exposed to new and varied selective pressures. They offer an opportunity to observe and study the basic processes of population biology (Sakai et al. 2001) and natural selection (Mack et

al. 2000), which may be occurring and changing at a more rapid pace than for native species.

1.2 WHAT IS AN INVASIVE PLANT SPECIES?

1.2.1 Definition

There are several stages a plant species must undergo before it is considered invasive. The process begins when a plant is transported from its native habitat, across geographical barriers to new locations (Mack et al. 2000; Richardson et al. 2000). At this stage, these species are referred to as “alien,” “exotic,” “introduced,” “non-indigenous,” or “non-native” (Mack et al. 2000). Relatively few introduced species survive and reproduce in their new habitats, but those that form self-sustaining populations are considered “naturalized” (Mack et al. 2000; Richardson et al. 2000). Naturalized species become invasive when they overcome barriers of dispersal to reach new regions away from their sites of introduction and are able to persist, reproduce, and spread, often at very high rates (Richardson et al. 2000). It has been estimated that as few as ~0.1% (Williamson and Fitter 1996a) and as many as 13% (Lonsdale 1994) of introduced species survive to become invasive in their new ranges. Although the term “weed” is sometimes applied to invasive plants, weeds are any plant species, introduced or native, that grows where it is not wanted (Radosevich et al. 1997; Richardson et al. 2000).

1.2.2. Characteristics of invasive plants.

Ever since Asa Gray (1879) compiled a list of traits of invasive species, ecologists have been interested in identifying characteristics common to all invasive plants in an effort to identify and predict future invaders. Perhaps the most well known list of traits is Baker's characteristics of the "ideal weed" (1965, 1974). Traits listed include the ability to reproduce both sexually and asexually, rapid development to sexual maturity, continuous and abundant seed production, and a "general purpose genotype" with high levels of phenotypic plasticity that enables "weeds" to grow under a range of environmental conditions. Although many of the world's most successful invasive plants share several of these discrete, readily identifiable traits, there are many others that have few or even none (Roy 1990; Mack 1996; Sakai et al. 2001). Several noninvasive species also share some of these traits (Barrett and Richardson 1986).

New lists of characteristics of invasive plants have been compiled since Baker with a similar objective of predicting invasiveness (e.g. Bazzaz 1986; Roy 1990, Pyšek et al. 1995). Such lists, however, have had generally low predictive value for several reasons. Baker's list (1965) and the similar list proposed by Bazzaz (1986) name characteristics for weeds or colonizing species that invade recently disturbed sites. Such lists are appropriate for only a subset of invading species and would not apply to plants invading other habitats, such as relatively undisturbed forests (Mack 1996). Secondly, the characteristics typically listed for

invasive plant species are often related to the initial colonization and naturalization of an invasive population, such as self-fertility or clonal spread capabilities.

However, the difference between the introduced species that become invasive and those that do not may be dependent upon an entirely different suite of characteristics, such as the ability to exploit local resources more rapidly than non-invading introduced species (Thébaud et al. 1996) or having allelopathic effects on native species (Ridenour and Callaway 2001). Finally, these lists are based on the theoretically ideal weed, but there are relatively few empirical data available to either refute or support this list of characteristics for successful invasive plant species or for characteristics associated with unsuccessful invasions (Kolar and Lodge 2001).

More recent analyses have limited their scope from identifying a list of predictive characteristics of all invasive species to isolating characteristics that are more common among invasive than noninvasive species within a functional group, within a genus, or for species invading similar habitats or ranges. For example, pines considered invasive in the Southern Hemisphere have lighter seeds, a shorter interval between large seed crops, and a shorter juvenile period than noninvasive, introduced pines in the same region (Rejmánek and Richardson 1996). In contrast, large seeds, tall stature, and extended seed dormancy are traits found more commonly among invasive than noninvasive species in Great Britain (Crawley et al. 1996). Another analysis in Britain found that morphological characters, such as

height and leaf area, characterized invasive species better than life history and reproductive characters (Williamson and Fitter 1996b). Invasive woody plants in North America are characterized by vegetative reproduction, a lack of pre-germination seed treatment requirements, and a short interval during which fruit remains on the plant (Reichard and Hamilton 1997). Daehler (1998) compiled a global list of nearly 3,000 plant species, including those that are agricultural weeds as well as those that are natural area invaders. He identified that invaders into natural areas were represented by aquatic or semi-aquatic species, grasses, nitrogen-fixers, climbers, and clonal trees that had abiotic pollination and dispersal mechanisms. In contrast, the agricultural weeds used in his study had attributes similar to those proposed by Baker, such as herbaceousness, rapid reproduction, and abiotically dispersed seeds (Daehler 1998). These analyses, based on retrospective examinations of species that have become invasive, have been able to distinguish among invasive and noninvasive species in particular environments or for particular groups of plants with a relatively high degree of resolution.

1.2.3 Theories of invasiveness and plant invasion.

There are several theories that attempt to explain plant invasiveness and the process of plant invasions by focusing primarily on the factors that enable invasive species to outcompete natives. Perhaps the first of these theories was proposed by Darwin (1859) and attributes invasion success for some plant species to

membership in genera that are not found in the invaded areas. He stated, “the struggle will generally be more severe between [species of the same genus]... than between the species of distinct genera” (p. 84). The distributions of some current invasive species, such as the genera of European Poaceae and Asteraceae that are invasive in California, appear to support this idea (Rejmánek 1996). However, it is difficult to prove this pattern was not produced by introductions skewed toward new genera, rather than by a competitive advantage of a given genus.

An extension of this theory relating to the invasibility of communities states that more diverse communities are less readily invaded than communities with few species. This classic theory, which is based on the work of Elton (1958) and MacArthur (1955, 1972), suggests that diverse communities are more stable and resistant to invasion than less diverse ones because, in part, of the combined competitive abilities of the resident species that may exclude invaders. Theoretical studies support this theory as well as some (Knops et al. 1997; McGrady-Steed et al. 1997), but not all (Robinson and Dickerson 1984; Palmer and Maurer 1997), research in microcosms and controlled environments. However, spatial analyses at the community level suggest that invasibility is positively correlated with native species diversity (Levine and D’Antonio 1999; Lonsdale 1999; Parker 1999; Stohlgren et al. 1999; Levine 2000). A recent study has directly addressed this apparent contradiction and made a link between theory and quantitative field data. Levine (2000) showed that, while controlled environment studies uncover

neighborhood and local effects of diversity on invasibility, the relationship between diversity and invasibility becomes obscured at the community level by other factors that vary with diversity, such as propagule supply. These results suggest that invasive plant species respond to environmental conditions similarly to native species and are more like the native species around which they invade than formerly believed.

An additional theory related to the relationship between diversity and invasion is the concept that invasive species require disturbed habitats for establishment (Elton 1958). The theory assumes that human-related disturbance can alter the environment enough to reduce the competitive ability of native plant species, thus conferring a competitive advantage to invasive species (Mack 2000). Recent spatial analyses identifying the positive relationship between native species diversity and invasibility across a range of habitats call this theory into question. Invasive plants are found in nearly all natural areas in many habitats on all continents except for Antarctica (Usher 1988). Population studies designed specifically to link this theory with empirical analyses of *Cytisus scoparius* (scotch-broom) showed that it invaded more rapidly in intact, species-rich communities in Washington than into disturbed communities with lower species diversity (Parker 1999), while disturbance increased establishment of the same species in California (Bossard 1991). Similarly, other studies have shown invasion success of particular invasive species following disturbance is variable, and may depend on site

characteristics, such as nutrient availability (D'Antonio 1993; Harrison 1999; Smith and Knapp 1999). Some disturbances, such as fire, can significantly reduce species invasions (Smith and Knapp 1999).

While Darwin suggested that invasiveness was related to novelty of the invasive species, several recent theories aim to predict invasiveness based on similarities. For example, many regions have invasive flora that originated from similar latitudes or climates (Baker 1974). Of course, there are exceptions to this idea, such as the invasion of the tropical *Eichhornia crassipes* into the California Central Valley (Mack 1996), but climate-matching accurately predicts invasiveness for some groups of species, such as those in Poaceae, Asteraceae, and Fabaceae invasions in North America (Rejmánek 1996) and some *Opuntia* invasions in Australia (Johnston 1924). Another approach to predicting whether a species will be invasive is based on the notion of "guilt by association." If a species is invasive in another region or is closely related to species that are invasive, then it is likely to be a future invader (Holm et al. 1977; Daehler and Strong 1993). While some plant families (e.g., Poaceae, Fabaceae, Asteraceae) appear to contain more invasive species than others, a recent probability analysis showed that these families appear to be over represented in the invasive plant flora because of their size, not necessarily because of invasive qualities of the family (Daehler 1998). Additionally, Heywood (1989) identified 44 families that have only one invasive member. Similarly, while some genera contain several invasive plant species (e.g.,

Bromus, *Cirsium*, *Centaruea*, *Opuntia*, *Rubus*, *Acacia*, and *Tamarix*), congeners of some of the most successful invaders, such as *Eichhornia* and *Robinia*, are not invasive (Mack 1996). Therefore, close relationship to an invasive species is not a reliable indicator of invasiveness. However, several analyses have shown that species invasiveness in one area of the world is a reliable indicator that a species will become invasive in other parts of the world, as well (Williamson and Fitter 1996b; Reichard and Hamilton 1997).

Perhaps the most commonly accepted hypothesis for the success of invasive species is that of enemy release. This hypothesis states that plant species removed from their native ranges are also removed from the pressure of natural enemies such as herbivores and pathogens, conferring a competitive advantage for them over native species, and enabling them to grow, reproduce, and spread at high rates (Elton 1958; Blossey and Notzold 1995). This hypothesis, which has served as a basis for biological control of invasive plant species, is based on the assumptions that local enemies have a relatively greater impact on native than on introduced species and that the introduced species are able to take advantage of this release, shifting allocation patterns away from defense and toward resource acquisition, growth, and/or reproduction (Keane and Crawley 2002). There are few quantitative data to support or refute the assumption that enemies affect native species more than invasives. Invasive species are subject to attack by generalist enemies, by specialist natural enemies that affect congeners in their introduced range, and by

specialist enemies that were introduced along with the invasive plant (Keane and Crawley 2002). The assumption that invasive plants take advantage of this release and allocate fewer resources to defense is based on life-history theory that predicts plants make trade-offs when allocating limited resources among different fitness-related functions, such as growth, reproduction and defense. Support for this assumption, however, is mixed (Daehler and Strong 1997; Almeida-Cortez et al. 1999; Willis et al. 1999). In general, the theory of enemy release is supported by the success of several introduced biological control methods that rely on introducing natural enemies to control invasive species. However, the low probability of introduced species becoming invasive appears to conflict with the notion that enemy release is the sole mechanism for invasiveness. As for most of the current theories and ideas about invasions and invasiveness, it is likely that enemy release plays a role in some invasions, but that its potential to explain invasiveness varies across species and habitats (Keane and Crawley 2002). In general, relatively little is known about resource allocation and life-history trade-offs in invasive plants. More research is needed to address how life-history and resource allocation may relate to invasion success (Mack et al. 2000; Sakai et al. 2001)

1.3 ECOPHYSIOLOGY AND RESOURCE ALLOCATION OF INVASIVE SPECIES

The characteristics and theories summarized above illustrate several ways by which invasive species fail to be characterized by generalizations. The ecological physiology of invasive plant species has similarly defied generalizations, but recent research is making advances. A predominant assumption has been that invasive plants have higher photosynthetic rates than noninvasive species (Bazzaz 1986). Indeed, comparisons among groups of invasive and noninvasive species growing in similar habitats have shown that some invasive species do have higher instantaneous photosynthetic rates (Pavlik 1983; Baruch and Goldstein 1999; Durand and Goldstein 2001). However, similar comparisons made between congener invasive and noninvasive species have revealed that more closely related species have similar instantaneous photosynthetic rates (Caldwell et al. 1981; Pammenter et al. 1986; Schierenbeck and Marshall 1993). Instead, different allocation patterns, such as invasive species maintaining photosynthetically active leaves longer throughout the year (Schierenbeck and Marshall 1993) or allocating less nitrogen and biomass per unit photosynthetic area such that grazed foliage is replaced more rapidly (Caldwell et al. 1981), enable invasive species to assimilate more carbon per resource investment and grow more rapidly than closely related noninvasive species within a given environment. Such comparisons among congeners have enabled researchers to identify probable mechanisms of success for specific invasive species. An emerging pattern in recent analyses is that invasive

species have higher photosynthetic rates per unit resource investment, such as higher photosynthetic nitrogen-use efficiency and water-use efficiency, than noninvasive species (Pattison et al. 1998; Baruch and Goldstein 1999; Durand and Goldstein 2001; McDowell, In press), indicating that total resource allocation, and not merely rates of resource acquisition, plays a role in the success of some invasive plant species.

1.4 LIFE-HISTORY THEORY AND RESOURCE ALLOCATION WITHIN PLANTS

The life-history traits of plants are those that pertain directly to survival and reproduction, such as the number and size of offspring, the amount of reproductive investment, or the length of an individual plant's lifespan. These traits are linked by trade-offs, which are fundamental to the study of life-history theory. A basic assumption underlying life-history theory is that plants have a limited amount of resources to allocate among different traits or functions. Therefore, trade-offs are observed as correlations between traits that have direct fitness consequences, such as between current reproduction and survival or current and future reproduction.

There are several levels at which trade-offs may occur within plants. Physiological trade-offs are those that are caused by allocation to two or more processes that compete directly with each other for resources (Stearns 1992). An example of a physiological trade-off is reduced growth, such as decreased leaf area or stemwood production, associated with increased reproduction (Eis et al. 1965;

Tappeiner 1969; El-Kassaby and Barclay 1992; Nicotra 1999). Physiological trade-offs can constrain the optimization of allocation among life history traits or functions (Cohen 1967, 1976; Charnov 1982; Stearns 1992).

Microevolutionary trade-offs are broader in scale and are a population-level response to selection on variation in physiological trade-offs (Stearns 1992).

Microevolutionary trade-offs include resource allocation trade-offs within individuals or between generations, such as the relationship among seed size, seed number, and seedling survival (Stanton 1984, 1985; Marshall 1985; Stock et al. 1990; Vaughton and Ramsey 1998) or between the size of the parent plant and the number or size of offspring produced (Geber 1990; Moegenburg 1996; Nicotra 1999). These trade-offs are also referred to as demographic trade-offs or costs (Horvitz and Schemske 1988; Fox and Stevens 1991; Nicotra 1999). Physiological and demographic trade-offs have been observed in many plant species. However, such trade-offs associated with reproduction are not always observable, such as when resources are not limiting, when different traits draw on a different resource pools, or when reproduction does not affect the plant's ability to develop meristems or acquire resources in the future (Bloom et al. 1985; Bazzaz et al. 1987; Horvitz and Schemske 1988; Geber 1990; Stearns 1992). Relatively little is understood about the mechanisms that lead to or enable a plant to avoid such trade-offs.

1.5 REPRODUCTIVE EFFORT AND THE MECHANISMS PRODUCING TRADE-OFFS OF RESOURCE ALLOCATION TO REPRODUCTION

1.5.1 Currency of the direct costs of reproduction.

The most evident source of trade-offs associated with reproduction is the direct resource cost of reproduction. Reproductive biomass is typically used to estimate resource costs because of the assumption that it reflects partitioning of other resources, particularly carbon (Bazzaz et al. 1987). Carbon is a desirable currency of allocation because it is an indirect measure of energy allocation within a plant, and rates of carbon assimilation often limit plant growth (Chapin 1989). However, direct measurements of carbon allocation to reproduction can be difficult, so biomass is often used as a substitute (Reekie and Bazzaz 1987).

Several factors confound the use of biomass to estimate resource costs of reproduction. First, although reproductive structures are typically comprised of resource-expensive compounds, such as aromatics or lipid-rich pollen and endosperm, they generally lack other expensive compounds such as structural carbohydrates and lignin. Therefore, the carbon cost per gram of reproductive tissue is relatively similar to that of vegetative tissue for some plant species (Poorter and Villar 1997), but the degree to which biomass accurately predicts allocation to reproduction is highly variable among species (Goldman and Willson 1986). Secondly, reproductive structures frequently can photosynthesize, contributing to their own carbon demands (Flinn and Pate 1970; Bazzaz et al. 1979;

Werk and Ehleringer 1983; Williams et al. 1985; Whiley et al. 1992; Galen et al. 1993; Ogawa et al. 1995; Ogawa and Takano 1997; McDowell et al. 2000).

Although the amount of carbon assimilated by reproductive structures varies between species, reproductive photosynthesis may satisfy as much as 50% of their own carbon costs (Bazzaz et al. 1979). Furthermore, the time during which biomass is measured can affect estimates of reproductive allocation. The components and, therefore, biomass of reproductive tissues can change daily. For example, pollen and nectar are ephemeral features of flowers or cones. They can virtually disappear within a day, resulting in very different estimates of reproductive allocation over a short period (McDowell et al. 2000). Additionally, some resources allocated to reproductive structures are translocated to neighboring foliage following flower or fruit development (Ashman 1994). Biomass measurements, which are typically collected before the translocation that occurs during senescence, would incorrectly include those resources as net costs to the plant. Finally, reproduction has varying effects on the capacity of a plant to capture resources and these effects are not necessarily detectable with biomass measurements. These effects will be described in Section 1.5.2.

Reproductive effort is defined as the total amount of resources that are allocated to reproduction and are diverted from vegetative activity (Reekie and Bazzaz 1987; Bazzaz and Ackerly 1992; Stearns 1992). The estimate of reproductive effort includes the net costs of reproductive structures, including net

respiration of reproductive structures, as well as effects of reproduction on foliar photosynthesis. The estimation of reproductive effort has been proposed as a method of calculating a meaningful estimate of resource allocation in terms of demographic trade-offs and plant evolution (Reekie and Bazzaz 1985, 1987). However, the difficulty in assessing its components, such as the photosynthetic contributions of reproductive structures or the effects of reproduction on foliar photosynthesis, has limited its use.

1.5.2 Effects of reproduction on vegetative tissues

Although reproduction poses net resource costs to plants, development of reproductive structures can also have positive impacts on the vegetative activity of a plant. Sink-induced photosynthesis is the term for elevated photosynthetic rates observed in foliage neighboring a rapidly developing sink, such as reproductive tissues. Various processes, such as the rate at which photosynthetic end-products (*e.g.*, sucrose) are synthesized or the carbon/nitrogen balance within the plant, regulate the rate at which photosynthesis can occur for the optimal use of resources and to avoid “feast or famine” conditions in developing sink tissues (Paul and Foyer 2001). Therefore, if the necessary resources are available, both photosynthetic and reproductive rates increase. Sink-induced photosynthesis and its effects have been observed in many crop species (Choma et al. 1982; Fujii and Kennedy 1985; DeJong 1986; Roper et al. 1988; Giuliani et al. 1997; Palmer et al.

1997; Klages et al. 2001), and knowledge of the relationship between optimal resource use and reproduction has been used to increase crop yield (Paul and Foyer 2001). Sink-induced photosynthetic rates have also been observed in greenhouse studies in which resource availability is controlled (Reekie and Bazzaz 1987). However, sink-induced photosynthesis is observed less commonly in the field, perhaps because plants in these settings are generally not irrigated or fertilized. In those few studies where sink-induced photosynthesis has been observed in field settings, it has been limited to the morning hours when leaf stomata are wide open (Dawson and Ehleringer 1993; McDowell et al. 2000; McDowell and Turner 2002). By afternoon in these studies, the photosynthetic rates of foliage near reproductive sinks was lower than that of foliage lacking or with smaller neighboring reproductive sinks. Some studies that have followed photosynthesis patterns in horticultural crops throughout the afternoon have observed a similar decline (Giuliani et al. 1997).

Reproduction can also have negative impacts on foliar photosynthetic rates, primarily through the effects of reproduction on plant water status. There appears to be a positive relationship between size of reproductive structures and plant water stress (Dawson and Ehleringer 1993; Galen et al. 1999; McDowell and Turner 2002). There are at least two possible explanations for this relationship. Flowers, fruits, and cones may all lose water. While some of these structures have stomata (Galen et al. 1993; McDowell et al. 2000), it is not clear whether they play any role

in regulation of water loss from these structures or whether they are vestigial remnants from the foliage progenitors of these structures. Additionally, sink-induced photosynthesis in field settings during the morning appears to lead to greater water stress and earlier stomatal closure in the afternoon relative to that of foliage not experiencing sink-induced photosynthesis (Dawson and Ehleringer 1993; McDowell and Turner 2002). This response may be due to the higher stomatal conductance associated with sink-induced photosynthesis, leading to increased water loss from foliage neighboring reproductive sinks (McDowell and Turner 2002).

The effect of reproduction on plant water status is further revealed by studies of water-use efficiency. Water-use efficiency is the ratio of carbon gained to water lost and can be estimated from instantaneous measurements of photosynthesis and transpiration or from integrated measurements of $\delta^{13}\text{C}$ of tissues. For plants growing in field settings, most studies quantifying water-use efficiency in relation to reproduction have utilized male and female plants of dioecious species. Female plants, which have larger reproductive sinks, have lower water-use efficiency, indicating less conservative water use, than male plants (Dawson and Bliss 1989; Dawson and Ehleringer 1993; Retuerto et al. 2000; Ward et al. 2002). The relationship among plant water status, flower production, and plant yield has been recognized and studied in several crop plants (Syvertsen and Albrigo 1980; Gucci et al. 1991; Passioura 1994; Bindraban et al. 1998; Fishman

and Génard 1998; Ntare and Williams 1998; Zinselmeier et al. 1999; Dickson et al. 2000; Gaudillère et al. 2002). However, this relationship has not been well explored in ecological studies, where it has many implications, including for the selection and evolution of floral size and form (Galen 1999, 2000) and for responses of plant reproduction to drought or elevated temperatures (McDowell et al. In review).

Development of reproductive tissues can also impede the development of vegetative tissues within a plant. As already discussed, the resource requirements of reproduction can limit the availability of resources for growth. In some plant species, these resource costs are observed in reduced leaf area in reproductive plants as compare with non-reproductive plants, which reduces the capacity of a plant to acquire resources in the future (Bloom et al. 1985). Furthermore, in some plant species, such as *Polygonum*, the commitment of meristems to reproductive tissues terminates their potential for developing into vegetative shoots, reducing the plant's overall growth and future reproduction, irrespective of resource availability (Geber 1990).

1.6 OBJECTIVES

This dissertation is consists of three studies. The principle objectives of this dissertation are described below.

1. Identify differences in photosynthetic capacity and resource costs for photosynthesis among two invasive and two native, noninvasive species of *Rubus* that grow coexist in the Pacific Northwest.
2. Quantify, in detail, the reproductive effort, including the physiological effects of reproduction on foliage, for one of the invasive and one of the noninvasive species of *Rubus* used in the previous study.
3. Assess the implications of the differences in physiology and reproductive effort for demographic trade-offs and life-history traits of the same two species used in the previous study.

CHAPTER 2. PHOTOSYNTHETIC CHARACTERISTICS
OF INVASIVE AND NONINVASIVE SPECIES OF *RUBUS* (Rosaceae)

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2.1 ABSTRACT

The prolific growth and reproduction of invasive plants may be achieved by greater net photosynthesis and/or resource-use efficiency. I tested the hypotheses that leaf-level photosynthetic capacity and resource-use efficiency were greater in two invasive species of *Rubus* than in two noninvasive species that have overlapping distributions in the Pacific Northwest. The invasive species had significantly higher photosynthetic capacity and maintained net photosynthesis (A) over a longer period of the year than the noninvasive species. The construction cost (CC) of leaf tissue per unit mass was comparable among the four species, but the invasive species allocated less nitrogen (N) per unit leaf mass. On an area basis, both leaf CC and N were higher for the invasive species. The specific leaf area (SLA) was also lower in the invasive species, indicating less photosynthetic area per gram leaf tissue. The invasive species achieve high A at lower resource investments than the noninvasive species, including having higher maximum photosynthetic rate (A_{max}) per unit dark respiration (R_d), greater A_{max} per unit leaf N (photosynthetic nitrogen-use efficiency), and greater water-use efficiency as measured by instantaneous rates of A per unit transpiration (A/E) and by integrated A/E inferred from stable carbon isotope ratios ($\delta^{13}C$). Using discriminant analysis, these photosynthetic characteristics were found to be powerful in distinguishing between the invasive and noninvasive *Rubus*. A_{max} and A/E were identified as the

most useful variables for distinguishing between the species and, therefore, may be important factors contributing to the success of these invasive species.

2.2 INTRODUCTION

The spread of invasive plants threatens native biodiversity, the structure and function of ecosystems, and the productivity of industries such as agriculture and forestry (Walker and Vitousek, 1991; D'Antonio and Vitousek, 1992; Hobbs and Mooney, 1998; Mack et al., 2000). In spite of the serious impacts of invasive plants, the mechanisms that confer their vigor are not adequately explained by current theories and hypotheses (Bazzaz, 1986; Mack, 1996). The magnitude of the threats imposed by invasive plants have motivated much research on invasions, particularly on predicting additional invasions and developing control methods. However, we still lack a fundamental understanding of the mechanisms by which invasive plants succeed, an understanding that may eventually improve predictive and control capabilities (Baruch and Goldstein, 1999; Mack et al., 2000).

Several characteristics common to invasive plants have been identified to facilitate recognition and prediction of future invaders, such as high reproductive allocation, rapid vegetative growth rates, and high potential for acclimation (Bazzaz, 1986; Rejmanek, 1996). Physiological characteristics of invasive plants have also been identified by contrasting invasive species with unrelated noninvasive species (Pattison, Goldstein, and Ares, 1998; Baruch and Goldstein, 1999). One effective approach to identify mechanisms of invasive plant success

may be through the comparison of closely related invasive and noninvasive congeners that overlap in range and share morphological and life-history traits (Schierenbeck and Marshall, 1993; Mack, 1996). The advantage of comparing congeners rather than unrelated species is that it may provide more insight into which traits actually play a role in the invasiveness of a species and which are merely coincidental (Mack, 1996). The mechanisms that underlie the success of the invasive species may be found among those characteristics that distinguish them from similar species that are not considered invasive.

One mechanism by which invasive plants may achieve success is through maximizing photosynthesis (Baruch and Goldstein, 1999; Durand and Goldstein, 2001). High photosynthetic rates may be obtained by maximizing the biochemical capacity for photosynthesis. The biochemical capacity to photosynthesize can be assessed by relating net photosynthesis (A) to varying internal leaf CO_2 concentrations (C_i), also known as A/C_i curves (Wullschlegel, 1993). The components of photosynthetic capacity that may be determined from A/C_i curves include the carboxylation capacity (V_{cmax}), which is constrained by the amount and activity of the enzyme ribulose 1,5-bisphosphate carboxylase-oxygenase (Rubisco), and the chloroplast electron transport capacity (J_{max}), which is constrained by the amount of thylakoid membranes.

Photosynthesis can be limited by low nitrogen or water availability. Therefore, maximizing A relative to nitrogen and water costs may be another mechanism of invasive plant success. Both Rubisco and thylakoid-bound electron

transport carriers represent a major investment in leaf nitrogen (N), so there is typically a positive relationship between photosynthetic capacity and leaf N. The ratio of A to leaf N, or photosynthetic nitrogen-use efficiency (PNUE), is an indicator of resource capture per unit investment (Field and Mooney, 1986). Additionally, a high rate of photosynthesis per unit water loss (water-use efficiency, WUE) is a mechanism by which invasive plants may increase the efficiency of resource capture. The ratio between rates of A and transpiration (E) provides an instantaneous measure of WUE. Measurements of integrated WUE are obtained from the relative abundance of the stable isotopes of ^{13}C and ^{12}C in plant tissue ($\delta^{13}\text{C}$). During photosynthesis, plants discriminate against ^{13}C due to a combination of diffusional and enzymatic processes. Increases in A/E reduce the concentration of CO_2 within the leaf due to increased consumption of CO_2 relative to the supply, thereby forcing photosynthesis to consume relatively more ^{13}C and resulting in increased $\delta^{13}\text{C}$ of plant tissue. The positive relationship between A/E and $\delta^{13}\text{C}$ is well established for many species (Farquhar, O'Leary, and Berry, 1982; Johnson et al., 1990; Knight, Livingston, and Van Kessel, 1994).

An additional possible mechanism contributing to invasive plant success is the minimization of carbon costs associated with photosynthesis, leaving more carbon available for growth and reproduction. For example, leaf area per unit leaf mass (specific leaf area, SLA) is an indicator of photosynthetic surface area per unit investment in leaf tissue and is often positively associated with rapid growth rates

(Lambers and Poorter, 1992; Reich, Ellsworth, and Walters, 1998; Walck, Baskin, and Baskin, 1999). In one comparative study between invasive and noninvasive congeners in which both species had similar photosynthetic rates, the greater success of the invasive species was partly attributed to its thinner leaves and, therefore, lower carbon cost per unit photosynthetic area (Pammenter, Drennan, and Smith, 1986). Lower carbon costs of leaf construction (CC) (Baruch and Goldstein, 1999; Nagel and Griffin, 2001) and higher A relative to dark respiration rates (R_d) (Pattison, Goldstein, and Ares, 1998) have also been found for invasive species in comparison with noninvasive species from other genera. One study also observed a negative correlation between species abundance and leaf CC for one invasive and several noninvasive species growing together along pond banks (Nagel and Griffin, 2001).

The objective of this research was to compare physiological characteristics of four similar noninvasive and invasive *Rubus* (blackberry) species, two of which are prolific and vigorously invasive species. All of the species share similar morphologies and life history, and they often occupy the same sites in the Pacific Northwestern United States (PNW), but the two invasive species have strikingly greater rates of growth and reproduction. Given the similarities among the *Rubus* species in the PNW, the differences among their growth and reproductive rates become even more remarkable. The physiological mechanisms that underlie these differences may play a role in the success and vigor of these invasive species. This study focuses on instantaneous measurements of photosynthesis and resource costs.

An additional, simultaneous study examines how these rates and costs translate into annual carbon gain, reproductive effort, and growth (McDowell and Turner, in press). The following hypotheses were tested: (1) invasive *Rubus* species have higher photosynthetic capacity than similar noninvasive species, and (2) invasive *Rubus* species achieve these rates at a lower resource investment than the noninvasive species. The rate and efficiency at which these invasive species acquire carbon may contribute to their vigor, and thus invasiveness, in the PNW.

2.3 MATERIALS AND METHODS

2.3.1 Species and site descriptions

All four of the *Rubus* species used in this study share many morphological and ecological characteristics. The two invasive species are native to Europe, but are considered invasive outside of their native range because they grow, reproduce, and spread prolifically following introduction to new regions. The most prominent of the invasives is *R. discolor* Weihe and Nees (also *R. procerus* or *R. fruticosus*; Himalayan blackberry), individual canes of which may grow up to 10 m (Pojar and MacKinnon, 1994) and produce over 700 fruits in a single year (McDowell and Turner, in press). *Rubus laciniatus* Willd. (lace-leaf blackberry), also an invasive species, is similar in size and fruit production to *R. discolor*, but may be distinguished by its highly dissected leaves. These two species contrast with the noninvasive *R. ursinus* Cham. and Schlect. (trailing blackberry) and *R. leucodermis*

Dougl. (black raspberry). The latter two species are considered noninvasive in their native range of the PNW where this study took place. Canes of these species grow to merely 2 m and produce only about 50-100 fruits per cane per year (McDowell and Turner, in press). Aside from differences of size and reproductive allocation, these species share similar morphologies. All have perennial roots with arching and sprawling biennial canes (i.e., canes reproduce sexually only in the second year). First-year canes emerge in the spring. Foliage is maintained on these canes until the following spring, when second-year foliage emerges, except for *R. leucodermis*, which sheds first-year foliage in the fall. All second-year foliage and canes senesce after reproduction is completed in the second growing season. These species often inhabit the same sites throughout the PNW, growing in open areas and forests, predominantly at low elevations.

Gas exchange was measured on all four species growing together at three sites within 10 km of each other in the McDonald-Dunn Research Forest near Corvallis, Oregon (44° 40' N, 123° 20' W; 210-360 m elevation). Measurements were made on one fully exposed leaf per cane and all leaves of all species were of similar age and position on the canes. Vapor pressure deficit (vpd) was calculated using humidity and temperature data taken concurrently from a nearby (<5 km) meteorological station. The diurnal patterns of instantaneous WUE of each species were examined with respect to diurnal patterns of vpd. Additionally, five leaves of *R. discolor* and *R. ursinus* were collected from each of three other sites in western Oregon to assess how foliar $\delta^{13}\text{C}$ varies for these species across a wider range of

sites. These sites included Jack Creek (43° 41' N, 123° 24' W; 207 m elevation), Alsea Fish Hatchery (44° 24' N, 123° 45' W; 69 m elevation), and Kiser Creek (44° 29' N, 123° 30' W; 500 m elevation) and cover a range of approximately 100 km.

2.3.2 Gas exchange measurements

Rates of A in relation to varying internal leaf CO_2 concentrations (A/C_i curves) were measured in the field with an LI-6400 infrared gas-exchange system (LI-COR, Lincoln, Nebraska, USA). Measurements were made on 6-9 leaves per species per month during spring and summer (April - August), and less frequently during fall and winter (September - March). All measurements were made before 1000 on overcast days to minimize effects of increasing ambient vpd and temperature. The order of species measured was random. During all measurements, temperature was $23^\circ \pm 4^\circ\text{C}$ and vpd was 1.1 ± 0.3 kPa inside the cuvette. Photon flux density within the cuvette was held at approximately $1500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Enough time was allowed for the cuvette $[\text{CO}_2]$ to stabilize before logging measurements (i.e., coefficient of variation for $[\text{CO}_2]$ inside the cuvette $< 2\%$). Three measurements per leaf were made at each of the following cuvette $[\text{CO}_2]$ s: 10, 20, 30, 40, 60, 80, 100, and 150 Pa.

The A/C_i curves for each species were used to calculate biochemical photosynthetic capacity and R_d . Parameters of photosynthetic capacity include the maximum carboxylation rate (V_{cmax}), maximum electron transport rate (J_{max}), and the maximum rate of net photosynthesis measured under saturating light, optimal

ambient temperature and humidity, and ambient CO₂ concentration of 36.5 Pa (A_{\max}). Light saturation levels for each species were determined by measuring A in relation to varying levels of radiation for each species (data not shown). V_{\max} , J_{\max} , and R_d were estimated by using nonlinear least squares regression to calculate the values of these parameters that best fit the equations of the von Caemmerer and Farquhar photosynthesis model (1981; Harley et al., 1992; Wullschleger, 1993). Measured values of V_{\max} and J_{\max} were adjusted to a common temperature of 25°C following Harley et al. (1992) and Leuning (1997).

Diurnal measurements of A and E were made on three plants each of *R. ursinus* and *R. discolor*, alternating between the species, on six days during May and early June 2000. Measurements were made on each plant approximately every 2 h from 0630 to 1830. Temperature and vpd within the leaf cuvette were allowed to vary with ambient conditions. Instantaneous water-use efficiency was calculated as A/E (in micromoles of CO₂ per millimoles of H₂O) for each measurement.

2.3.3 Leaf analyses

Following field measurements, each leaf was collected, placed in a plastic bag, and kept in cold storage until laboratory analyses were performed, which was typically within 48 h of collection. Leaf area was determined using a video image recorder and AgVision software (Decagon Devices, Pullman, Washington, USA). Leaves were then dried for 48 h at 65°C and mass was measured to the nearest

0.01g immediately upon removal from the oven. SLA (in square centimeters per gram) was calculated as area per unit mass for each leaf.

Dried leaves of all four species collected from the McDonald-Dunn Forest and of *R. discolor* and *R. ursinus* collected from three other sites were ground for elemental analysis. Leaf N and carbon content (C_{om}) were measured on a subsample of finely ground material from each leaf using a NC2500 elemental analyzer (CE Instruments, Milan, Italy). Instantaneous PNUE (in micromoles of CO_2 per mole of N per second) was calculated as A_{max} per leaf N. The construction cost (CC) of leaf tissue (grams of glucose necessary to synthesize 1 g leaf tissue) was calculated according to the equation developed by Vertregt and Penning de Vries (1987):

$$CC = \frac{5.39(C_{om}) - 1191}{1000} \quad (1)$$

where C_{om} is the C content of the tissue in grams per kilogram as measured with the elemental analyzer.

The $\delta^{13}C$ (‰) for leaves of *R. ursinus* and *R. discolor* was measured on 2.0 ± 0.1 mg ground subsamples of leaves collected from the McDonald-Dunn Forest and from the three other sites in western Oregon using a Finnigan MAT stable isotope mass spectrometer (Bremen, Germany) at the Idaho Stable Isotope Lab (Moscow, Idaho). The stable carbon isotope composition was calculated as:

$$\delta^{13}C = (R_{sample} / R_{standard} - 1)1000 \quad (2)$$

where R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ of the leaf samples and of the standard, respectively, using the international standard of Pee Dee belemnite (Farquhar, Ehleringer, and Hubick, 1989). In plant tissues, the values of $^{13}\text{C}/^{12}\text{C}$ are less than those of the standard and therefore, $\delta^{13}\text{C}$ is negative. When comparing $\delta^{13}\text{C}$ values between plant samples, those that are less negative have relatively more ^{13}C , which indicates higher WUE (Farquhar, O'Leary, and Berry, 1982; Johnson et al., 1990; Knight, Livingston, and Van Kessel, 1994).

2.3.4 Discriminant analysis

Discriminant analysis was used to examine whether the measured photosynthetic characteristics may be used to distinguish between invasive and noninvasive species. This analysis was performed for these data by first grouping each of the four species into either an invasive or a noninvasive species category. Then, a classification function was developed for each of the two categories using A_{max} , J_{max} , V_{cmax} , SLA, and leaf N and leaf CC on a leaf area basis for individual plants to calculate a discriminant score. Integrated and instantaneous WUE data were available for only two species, so those parameters were used in a subsequent discriminant analysis along with the ratio of A to R_d and PNUE to classify individuals of *R. ursinus* and *R. discolor*. Using the classification functions developed for each group, an individual case was grouped into the category for which its discriminant score was highest. An approximate F test was calculated from a transformation of Wilks' lambda to test the equality of group centroids and,

therefore, test the distinctness of groups (SYSTAT, 1999). An F -to-remove statistic can be used to determine the relative importance of the input variables of the classification function for predicting group membership (SYSTAT, 1999). To examine this discriminant analysis graphically, Mahalanobis distances from the category centroid were calculated for each case, given the posterior probability of group membership. The pair of these distances was then plotted for each case, where similar data points (i.e., those that are grouped in the same category by the discriminant analysis) will have a similar pair of distances and will therefore be plotted together as a group (SYSTAT, 1999).

2.4 RESULTS

Photosynthetic capacity of the invasive species appears to be higher than that of the noninvasive species, as shown by the relationship between A and C_i (Figure 2.1). Both invasive *Rubus* species had higher A_{\max} than the noninvasive species ($F_{3,44} = 14.87$, $P < 0.001$) (Figure 2.2). The higher A_{\max} of the invasive species are supported by greater rates of V_{cmax} and J_{\max} ($F_{3,44} = 5.716$, $P = 0.009$ and $F_{3,44} = 4.73$, $P = 0.004$, respectively; Figure 2.2). However, for *R. laciniatus* V_{cmax} and J_{\max} were not statistically greater than those of the noninvasive *R. ursinus* (Tukey's HSD, $P = 0.68$ and $P = 0.63$, respectively) or *R. leucodermis* (Tukey's HSD, $P = 0.45$ and $P = 0.38$, respectively; Figure 2.2).

The higher A_{\max} of both invasive *Rubus* in the spring and early summer was maintained throughout the year. In late summer and early fall, average A_{\max} of both

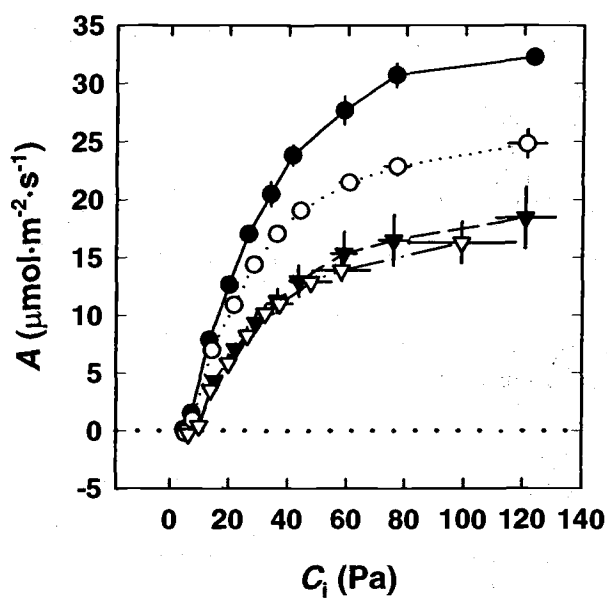


Figure 2.1: Average A/C_i curves for the invasive *R. discolor* (filled circles) and *R. laciniatus* (open circles) and for the noninvasive *R. ursinus* (filled triangles) and *R. leucodermis* (open triangles) measured during May and June. Each curve is an average of six to nine measured curves. The maximum photosynthetic (A_{max}), carboxylation ($V_{c_{max}}$), and electron transport rates (J_{max}) and dark respiration (R_d) for each species were calculated from these curves (see Methods). Error bars = 1 SE.

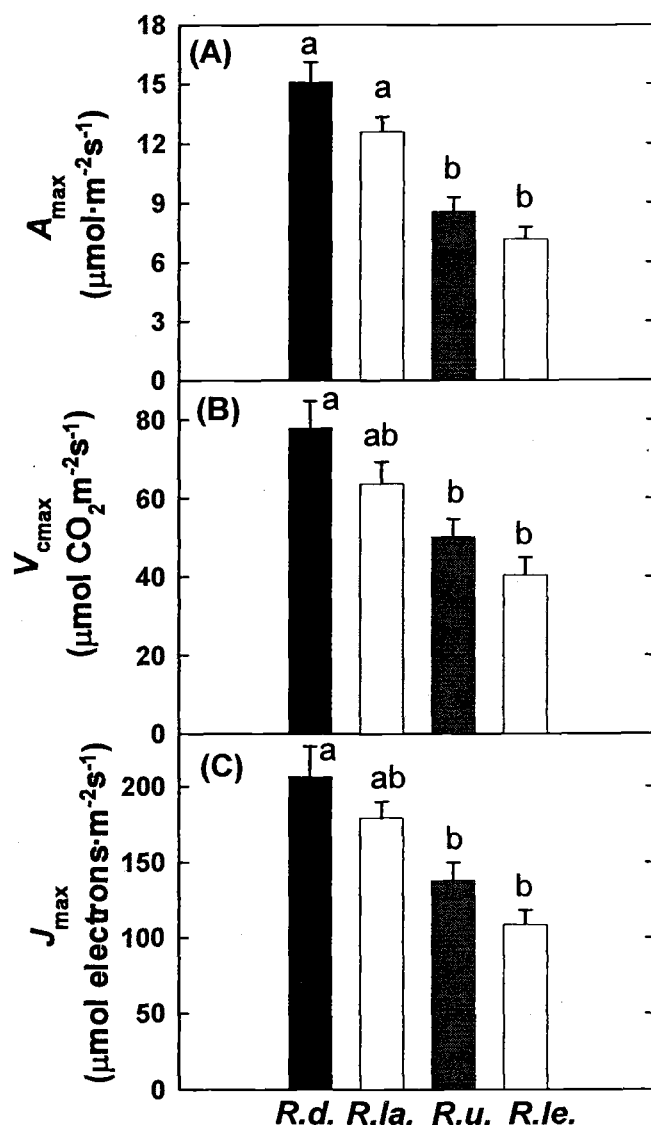


Figure 2.2: (A) Average maximum photosynthetic rate (A_{\max}), (B) carboxylation rate ($V_{c\max}$), and (C) rate of electron transport (J_{\max}) for each of the two invasive species of *Rubus* (*R.d.* = *R. discolor* and *R.la.* = *R. laciniatus*) and the two noninvasive species (*R. u.* = *R. ursinus* and *R. le.* = *R. leucodermis*) measured during May and June at the McDonald-Dunn Forest sites. Error bars = 1 SE. Means with a common letter do not differ from each other at the $\alpha = 0.05$ level of significance based on Tukey's HSD pairwise comparisons.

invasive species was $12.93 \pm 1.31 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ while the average A_{max} of both noninvasive species was $10.38 \pm 0.69 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ($F_{3,28} = 5.98$, $P = 0.058$). In the winter and early spring, A_{max} of the invasive species was significantly higher than that of the noninvasive species ($F_{3,20} = 10.35$, $P = 0.005$). Average A_{max} of the invasive *Rubus* was $9.45 \pm 0.56 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and was $7.74 \pm 0.35 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for the noninvasive species during the winter and spring.

In both of the invasive *Rubus* species, SLA was lower than the noninvasive species ($F_{3,70} = 27.34$, $P < 0.0001$; Table 2.1). The CC per gram of leaf was very similar among all four species ($F_{3,50} = 0.136$, $P = 0.94$; Table 2.1). However, on an area basis, values of CC were higher in the invasive species ($F_{3,50} = 3.165$, $P = 0.03$; Table 2.1). Leaf N was significantly different among the four species at the McDonald-Dunn site ($F_{3,50} = 3.54$, $P = 0.02$; Table 2.1). The noninvasive *R. ursinus* had the highest leaf N of the four species, although its leaf N was not significantly higher than that of *R. discolor*. At the three other sites from which leaves were collected, *R. ursinus* had higher leaf N than *R. discolor*, and these differences were also not statistically significant (data not shown). Leaf N per unit leaf area was higher in the invasive species, although the values for the invasive *R. discolor* and noninvasive *R. ursinus* were not significantly different ($F_{3,50} = 12.16$; $P < 0.001$; Table 2.1).

At all levels of leaf N, A_{max} per unit leaf mass of invasive *Rubus* were higher than those of the noninvasive species (Figure 2.3). For both species types,

Table 2.1: Average specific leaf area (SLA), leaf nitrogen concentration per unit leaf mass (N), leaf nitrogen per unit leaf area, photosynthetic nitrogen-use efficiency (PNUE), leaf carbon construction costs (CC) on both a leaf dry mass and leaf area basis, and respiration rates (R_d) for each of the four *Rubus* species at the McDonald-Dunn sites. Values are means \pm 1 SE. For each variable, means labeled with the same letter are not significantly different from other means for the same variable according to Tukey's HSD pairwise comparison procedure at the $\alpha = 0.05$ level of significance.

	Invasive		Noninvasive	
	<i>R. discolor</i>	<i>R. laciniatus</i>	<i>R. ursinus</i>	<i>R. leucodermis</i>
SLA (cm ² /g)	126.65 \pm 5.86 ^a	127.89 \pm 5.04 ^a	156.21 \pm 4.59 ^b	221.02 \pm 12.91 ^c
Leaf N (%)	1.87 \pm 0.13 ^{ab}	1.71 \pm 0.23 ^b	2.14 \pm 0.10 ^a	1.65 \pm 0.13 ^b
Leaf N (g/m ²)	1.61 \pm 0.09 ^a	2.10 \pm 0.15 ^b	1.61 \pm 0.10 ^a	0.78 \pm 0.11 ^c
PNUE (μ mol CO ₂ mol ⁻² ·s ⁻¹)	117.74 \pm 7.27 ^a	96.38 \pm 14.4 ^{ab}	83.45 \pm 6.39 ^b	98.26 \pm 12.09 ^{ab}
CC (g glucose / g dry mass)	1.22 \pm 0.03 ^a	1.26 \pm 0.02 ^a	1.22 \pm 0.03 ^a	1.19 \pm 0.01 ^a
CC (g glucose/ cm ²)	0.011 \pm 0.001 ^a	0.010 \pm 0.001 ^{ab}	0.009 \pm 0.001 ^b	0.006 \pm 0.001 ^b
R_d (μ mol·m ⁻² ·s ⁻¹)	0.23 \pm 0.03 ^a	0.28 \pm 0.03 ^a	0.31 \pm 0.04 ^a	0.34 \pm 0.04 ^a

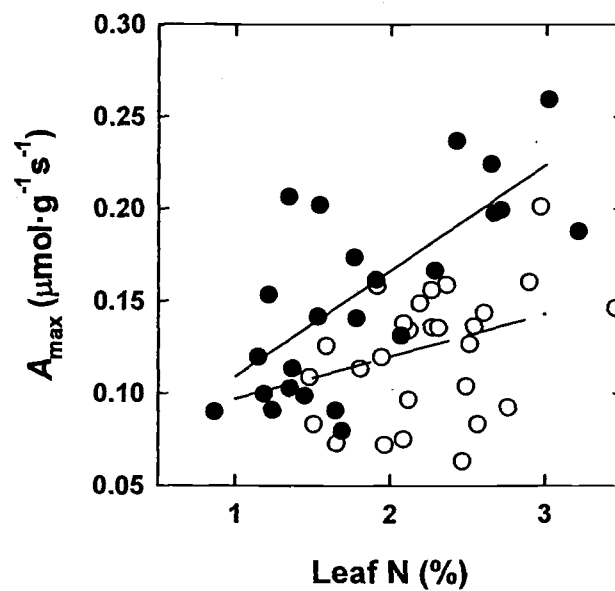


Figure 2.3: The relationship between maximum photosynthetic rate per unit leaf dry mass (A_{\max}) and leaf nitrogen concentration per unit leaf mass (N) for the two invasive (filled circles) and two noninvasive (open circles) *Rubus* species measured during May and June. The regression equation for the invasive species (solid line) is $A_{\max} = 0.0456 + 0.058N$ ($r^2 = 0.52$, $P < 0.001$). The regression equation for the noninvasive (dashed line) is $A_{\max} = 0.074 + 0.023N$ ($r^2 = 0.12$, $P = 0.09$).

there was a positive relationship between A_{\max} and leaf N. The intercept and slope of the relationship between A_{\max} and N were different between the two groups of species ($F_{1,45} = 18.22$, $P < 0.0001$ and $F_{1,44} = 3.458$, $P = 0.06$; Figure 2.3). PNUE, calculated as a ratio of A_{\max} to leaf N, was highest for the invasive *R. discolor* ($F_{3,44} = 3.915$, $P = 0.01$; Table 2.1), although it was not statistically different from the noninvasive *R. leucodermis*.

The relationship between A_{\max} and R_d gives a measure of the metabolic efficiency of leaves. A_{\max} per unit R_d was consistently higher for the invasive relative to the noninvasive species (Figure 2.4). The slope of the relationship between A_{\max} and R_d was not significantly different between the invasive and noninvasive *Rubus* ($F_{1,44} = 1.385$, $P = 0.24$). However, the intercept was significantly greater for the invasive species ($F_{1,45} = 36.3$, $P < 0.001$). Therefore, at a given R_d , values of A_{\max} of the invasive species were higher than that of the noninvasive species. Average R_d of the noninvasive species were higher than those of the invasive species, but this difference was not significant ($F_{3,44} = 1.511$, $P = 0.23$; Table 2.1).

During the early morning, both *R. ursinus* and *R. discolor* had similar instantaneous WUE (Figure 2.5). As vpd increased, however, the invasive *R. discolor* maintained a higher WUE than *R. ursinus* (Figure 2.5). The $\delta^{13}\text{C}$ values of *R. discolor* further demonstrate that this species tends to have higher WUE than the noninvasive species (Figure 2.6). At all four sites from which leaves were

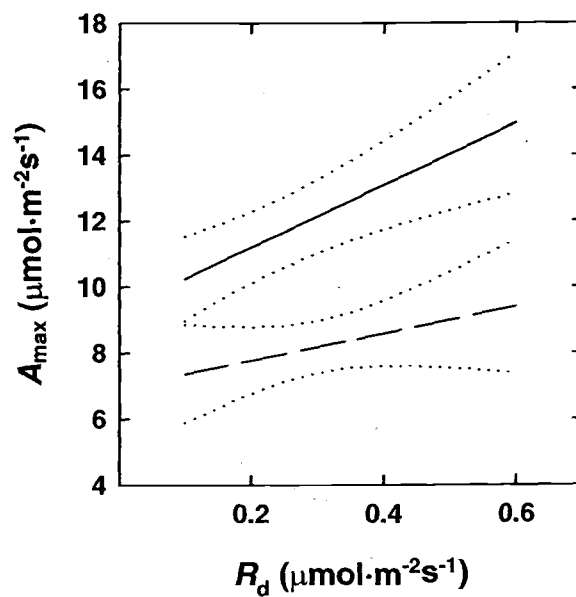


Figure 2.4: The relationship between maximum photosynthetic (A_{\max}) and dark respiration (R_d) rates from May and June measurements. The regression for the two invasive species (solid line) is $A_{\max} = 8.72 + 11.81R_d$ ($r^2 = 0.25$, $P = 0.01$) and for the two noninvasive species (dashed line) is $A_{\max} = 6.51 + 5.30R_d$ ($r^2 = 0.17$, $P = 0.09$). Dotted lines are the $\pm 95\%$ confidence intervals for each regression.

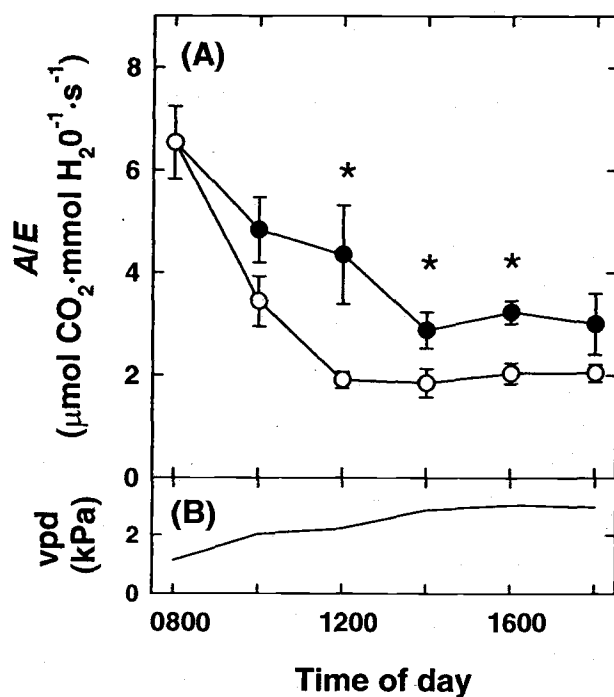


Figure 2.5: (A) Diurnal course of instantaneous water-use efficiency (A/E) of the invasive *R. discolor* (filled circles) and the noninvasive *R. ursinus* (open circles) measured over the same diurnal periods in June. Each point is an average of all measurements made within 1h of the time shown on the x-axis over all days for which measurements were made. Error bars = 1 SE. Measurements labeled with an asterisk were significantly different from each other at the $\alpha = 0.05$ level ($t = -2.5$, $P = 0.02$ at 1200; $t = -1.99$, $P = 0.04$ at 1400; $t = -4.66$, $P < 0.001$ at 1600). At 1000 and at 1800, measurements were significantly different from each other at the $\alpha = 0.10$ level ($t = -1.63$, $P = 0.08$ and $t = -1.54$, $P = 0.09$, respectively). (B) Average vapor pressure deficit (vpd) over the same diurnal periods.

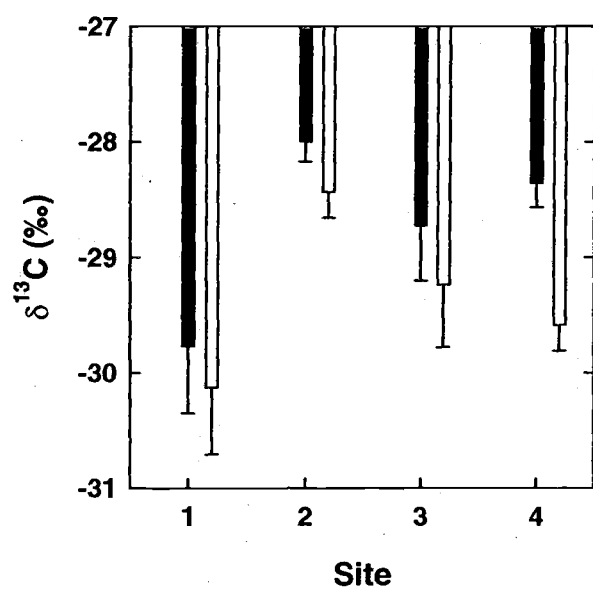


Figure 2.6: $\delta^{13}\text{C}$ of the invasive *R. discolor* (filled circles) and the noninvasive *R. ursinus* (open circles) for leaves collected from four sites. Site 1 = Jack Creek, Site 2 = McDonald-Dunn Forest, Site 3 = Alsea Fish Hatchery, and Site 4 = Kiser Creek. Error bars = ± 1 SE.

collected, *R. discolor* had less negative $\delta^{13}\text{C}$ values, indicating higher integrated WUE (randomized block ANOVA $F_{1,45} = 5.50$, $P = 0.02$).

The first discriminant analysis, which included data from all four species, clearly differentiated between the groups of invasive and noninvasive species (approximate $F_{6,41} = 17.459$, $P < 0.0001$). The variables included in this analysis were A_{max} , J_{max} , V_{cmax} , SLA, and leaf N and leaf CC on a leaf area basis. Only two out of 48 cases were misclassified with this discriminant analysis; two noninvasive individuals that had high A_{max} were grouped with the invasive *Rubus*. The variable A_{max} was the most powerful for discriminating between invasive and noninvasive species (F -to-remove = 21.51). For these *Rubus* species, the data fall into two relatively distinct groups, with the exception of the two misclassified individuals (Figure 2.7).

An additional discriminant analysis was performed and plotted to determine whether the efficiency at which resources are captured (water- and nitrogen-use efficiency and the ratio of A to R_d) can be used to distinguish between the invasive and noninvasive *Rubus*. Only *R. discolor* and *R. ursinus* were included in this analysis because some data (e.g., $\delta^{13}\text{C}$) were available for only these two species. Only two out of 36 cases were misclassified in this analysis; one noninvasive and one invasive case (data not shown). The most important variable in discriminating between the two species was instantaneous A/E (F -to-remove = 4.81). In spite of the misclassifications, there was good discrimination between *R. discolor* and *R.*

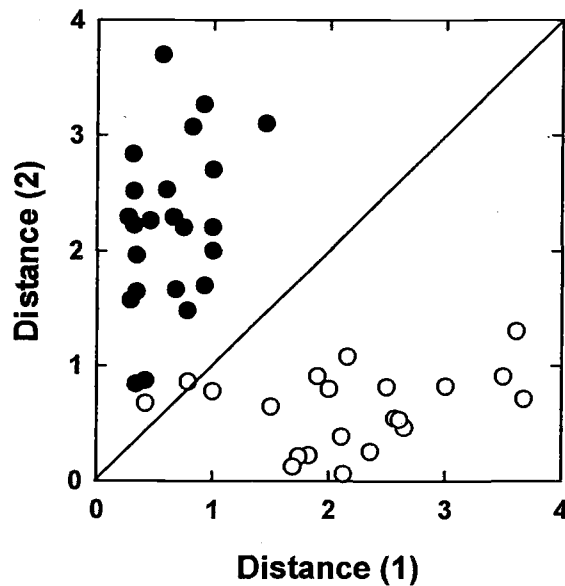


Figure 2.7: Mahalanobis distances calculated from a discriminant analysis where individuals from all four species were classified into either an “invasive” or “noninvasive” category using A_{\max} , $V_{c\max}$, J_{\max} , SLA, and leaf N as input variables. The symbol indicates the true group membership for the invasive (filled circles) and noninvasive (open circles) *Rubus* species. The line separates the two predicted categories. Individuals that are classified together by the discriminant analysis share similar Mahalanobis distances and are, therefore, plotted near each other. See text for further explanation.

ursinus when using these variables of resource capture efficiency as inputs (approximate $F_{4,43} = 8.3511$, $P < 0.0001$).

2.5 DISCUSSION

2.5.1 Rates of resource capture

The invasive *Rubus* species exhibited much greater biochemical capacity for photosynthesis than the noninvasive species. Both V_{cmax} and J_{max} were highest in the two invasive species, leading to their higher A_{max} values. This relatively higher photosynthetic capacity was maintained throughout the year. During the spring and summer, A_{max} values of the invasive species were up to 46% higher than those of similarly aged leaves of the noninvasive species, while during the fall and winter, A_{max} rates range from 22 to 25% higher for the invasive species. These higher rates of A_{max} give the invasive *Rubus* a larger pool of available carbon to allocate to reproduction, growth, and respiration. When used in the discriminant analysis, A_{max} was the most powerful variable in discriminating between invasive and noninvasive *Rubus* species.

In addition to having higher A_{max} , leaves of the invasive species remained on the canes for longer, enabling them to have an extended period of carbon gain. Second-year foliage of the noninvasive *R. ursinus* senesces in early July, while that of both invasive species does not senesce until September or October.

Furthermore, unlike the three other species in this study, the noninvasive *R.*

leucodermis completely sheds all first-year foliage in the fall, and therefore has no net carbon gain during the winter. The higher photosynthetic capacity maintained over a longer period of the year enabled these invasive species to fix significantly more carbon over their two-year lifespan than the noninvasive species (McDowell and Turner, in press). The accumulated carbon may be translocated to the perennial roots following cane senescence and stored for future cane and fruit production.

2.5.2 Cost of resource capture

While leaf CC per unit dry mass was similar among the *Rubus*, SLA was lower in the invasive species for foliage collected from the same light environment on the same sites as the noninvasive species, resulting in the higher CC per unit leaf area for the invasive species. Therefore, the invasive species allocated a greater amount of carbon to leaf tissue per unit of light-absorbing surface. These results contrast with those from a study of leaf characteristics of invasive and noninvasive species growing along pond banks in New York (Nagel and Griffin, 2001) and from two Hawaiian studies comparing groups of invasive and noninvasive species (Baruch and Goldstein, 1999; Durand and Goldstein, 2001). These other studies found that SLA was generally higher and area-based leaf CC was lower in invasive species than noninvasive species. In one of these studies, Baruch and Goldstein (1999) compared 34 invasive and noninvasive species from different genera in Hawaii, including one invasive and one noninvasive species of *Rubus*. In contrast

to the general pattern of SLA for species in that study, the SLA of the invasive *Rubus* was lower than that of the noninvasive, similar to the patterns observed for *Rubus* in this study. These results highlight that comparisons of average patterns across invasive and noninvasive species of different genera does not necessarily lead to generalizable conclusions regarding mechanisms of success for particular invasive species.

Although the SLA results from this study were not expected, the results for leaf N on a leaf area basis are consistent with the higher A_{\max} observed for the invasive species. For a given N concentration, plants with a low SLA will have higher N per unit leaf area. Most leaf N is allocated to photosynthetic pigments and enzymes, and, therefore, a higher N per leaf area should translate into higher photosynthetic capacity, as was observed for invasive as compared with noninvasive *Rubus*. However, studies examining the relationship among SLA, leaf N, and A_{\max} across species show that species with low SLA generally have a lower PNUE and a smaller change in A_{\max} per unit leaf N (Field and Mooney, 1986; Reich and Walters, 1994; Reich, Ellsworth, and Walters, 1998). The invasive species used in this analysis deviate from this pattern by having high A_{\max} per unit investment in leaf N in spite of low SLA, suggesting that invasive species may have different combinations of leaf characteristics than those plant species considered noninvasive.

The low SLA of the invasive species may also have aided in increasing WUE. Thicker, denser leaves (i.e., lower SLA) increase the distance through

which water must diffuse to leave the leaf, leading to water conservation (Van den Boogaard and Villar, 1998). Therefore, the thicker leaves of the invasive *Rubus* may have contributed to their greater integrated and instantaneous WUE. Although the value of $\delta^{13}\text{C}$ varied within each species across the sites from which samples were taken, this level of variation is commonly observed with changes in elevation and precipitation for a given species (Marshall and Zhang, 1994; Panek and Waring, 1997). The relative pattern of greater WUE for the invasive species held across all sites, indicating that WUE may be an important contributing factor to the success of this invasive *Rubus* species. This same pattern of low SLA and high WUE has been observed for an invasive dune grass as compared with a closely related noninvasive species in northern California, where water conservation is also likely to be important for invasive plant success (Pavlik, 1983). In this study, discriminant analysis identified A/E (instantaneous WUE) as a powerful variable for distinguishing between the invasive and noninvasive *Rubus* species, providing further support that WUE may be an important contributing factor to invasive *Rubus* success in the PNW.

Another indicator of the carbon costs of resource gain is the relationship between A_{max} and R_d . All species exhibited a positive relationship between these two values, indicating a trade-off between rates of A_{max} and respiration costs. Across all ranges of R_d , the A_{max} values of the invasive species were higher than those of the noninvasive species. Therefore, the respiratory trade-off to high net photosynthetic rates is lower in the invasive *Rubus* relative to the noninvasive

species. These results are consistent with those of another study examining the relationship between A and R_d in invasive and noninvasive plant species of different genera (Pattison, Goldstein, and Ares, 1998).

The high values of PNUE in the invasive *R. discolor* in conjunction with high instantaneous rates of WUE demonstrates that this species is able to assimilate carbon at a relatively lower nitrogen and water investment than noninvasive *R. ursinus*. However, plants typically exhibit a trade-off between WUE and PNUE (Van den Boogaard and Villar, 1998). That is, plants that achieve high WUE by closing their stomata may be expected to have high leaf N allocated to photosynthetic enzymes in order to maintain high A under a reduced supply of CO_2 . However, if high WUE is achieved without reduced stomatal conductance, then the trade-off between WUE and PNUE may not be observed (Hikosaka et al., 1998; Van den Boogaard and Villar, 1998). Stomatal conductance of *R. discolor* remains high relative to that of *R. ursinus* throughout diurnal and seasonal periods of drought (McDowell and Turner, in press). Therefore, the WUE observed in *R. discolor* is probably due to its high photosynthetic capacity, and not due to reduced stomatal conductance. The maintenance of stomatal conductance through drought by the invasive *Rubus* may relate to its root allocation. Roots of *R. discolor* can descend more than 1.5 m into the soil, while those of the *R. ursinus* are relatively shallow and remain in the upper 0.5 m of soil (S. McDowell, personal observation). Therefore, *R. discolor* may be able to access water that is unavailable to *R. ursinus*, and therefore leave its stomata open throughout periods of high vpd. Analysis of *R.*

discolor in Europe shows that it maintained high WUE, as inferred from $\delta^{13}\text{C}$, when exposed to a variety of drought treatments, and this was apparently correlated with its high ratio of root to shoot biomass and ability to access soil water at the expense of neighboring plants (Fotelli et al., 2001). Therefore, WUE is a trait that is important to the success of *R. discolor*, even in its native range.

2.5.3 Discriminant analysis

The discriminant analysis summarizes the data from this study. The characteristics measured in this study proved to be very powerful in discriminating between invasive and noninvasive *Rubus* and, therefore, may be important factors contributing to their success. In particular, A_{max} and A/E were identified as the most powerful variables in the discriminant analysis. This combination of high photosynthetic capacity and high photosynthetic rates relative to water loss may be critical to the acquisition of carbon and tolerance of summer drought in the PNW for these species, leading to their high rates of growth and reproduction. While observations of other invasive species have also identified lower resource costs of photosynthesis relative to co-occurring noninvasive species, the particular combination of traits associated with invasive plants appears to vary with species and environmental conditions. This study, to my knowledge, is the first to use discriminant analysis to distinguish between physiological traits of invasive and noninvasive species. Further studies using discriminant analysis may help identify mechanisms of success for other invasive species or, if developed using a larger set

of species, may prove useful for predicting invasiveness within particular environments.

2.6 ACKNOWLEDGEMENTS

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CHAPTER 3. REPRODUCTIVE EFFORT
IN INVASIVE AND NON-INVASIVE *RUBUS*

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3.1 ABSTRACT

We quantified the physiological costs and the total amount of resources allocated to reproduction in two closely related species of *Rubus*, one of which is invasive. These two species share several morphological and life-history characteristics and grow together in the Pacific Northwestern United States. Reproductive effort was manipulated in canes of both species by removing flower buds. The non-invasive species, *R. ursinus*, exhibited significantly greater water stress in the reproductive canes, as indicated by lower leaf water potential (Ψ) and reduced stomatal conductance (g_s). This species also showed a reduction in leaf nitrogen concentration ([N]) associated with reproduction. Combined, these factors led to reduced photosynthesis (A) on a diurnal basis; lower water-use efficiency, as inferred from $\delta^{13}\text{C}$; and reduced photosynthetic capacity. All of these effects were more pronounced during the fruiting stage than in the flowering stage. The invasive species, *R. discolor*, showed no changes in water stress, [N], $\delta^{13}\text{C}$, or A associated with reproduction. A model was used to estimate total gross photosynthesis (A_{gross}) for reproductive and non-reproductive canes of both species over the growing season. Reproduction was associated with a greater decline in A_{gross} for the non-invasive *R. ursinus* than for the invasive *R. discolor*. Although *R. discolor* allocated more resources directly to flowers and fruit than *R. ursinus*, the invasive species had significantly lower reproductive effort, or total amount of resources diverted from vegetative activity to reproduction, than the non-invasive

species. By minimizing the reduction of photosynthesis associated with reproduction, this invasive species may be able to minimize the trade-offs commonly associated with reproduction.

3.2 INTRODUCTION

A basic assumption of life history theory is that reproduction and growth compete for limited resources within a plant and, therefore, plants face trade-offs when allocating resources between these functions (Stearns 1992). These trade-offs have been observed as a negative correlation of current reproduction (i.e., fruit or seed number) with growth and future reproduction within a plant, implying physiological mechanisms underlie these trade-offs (Geber 1990; Fox and Stevens 1991; Stearns 1992). For example, plants commonly produce narrower annual growth rings, fewer leaves, and have reduced height growth in years of high as compared to low seed production (Eis et al. 1965; Gross 1972; Antonovics 1980; Fox and Stevens 1991; El-Kassaby and Barclay 1992; Nicotra 1999). These trade-offs between current reproduction and growth are referred to as the physiological or ecological trade-offs of reproduction and little is known about the mechanisms that produce them (Fox and Stevens 1991; Stearns 1992).

There is especially little known about trade-offs associated with reproduction in invasive plants. Many invasive plant species appear to avoid or minimize the trade-offs associated with allocating resources to reproduction and

growth, typically exhibiting both high reproductive and growth rates (Bazzaz 1986; Roy 1990). One theory suggests that invasive plants avoid this trade-off by allocating fewer resources to anti-herbivore defense than non-invasive species, and therefore having more resources available for both reproduction and growth (Elton 1958; Blossey and Notzold 1995). Available empirical data provide mixed support for this theory, although there have been few direct experimental tests of the relationship between growth and defense allocation in invasive plants (Almeida-Cortez et al. 1999; Willis et al. 1999; Keane and Crawley 2002).

An additional, but not mutually exclusive, explanation for the apparent lack of a trade-off between growth and reproduction in invasive plants is that the physiological costs associated with reproduction may be relatively low.

Reproductive effort is defined as the total amount of resources that are allocated to reproduction and are diverted from vegetative activity (Reekie and Bazzaz 1987; Bazzaz and Ackerly 1992; Stearns 1992). The measurement of reproductive effort includes the total amount of all resources directly allocated to reproductive structures as well as any effects reproduction may have on foliar photosynthesis, which are defined here as the physiological costs of reproduction. Direct manipulations of reproductive effort, either through enhancement or reduction of reproduction, provide the best evidence for trade-offs between reproduction and growth (Reekie and Bazzaz 1987; Fox and Stevens 1991). Most studies in which reproductive effort has been manipulated have focused on the fitness consequences

of reproduction, such as looking at changes in plant size or future reproduction. However, there has been little quantification of the physiological basis of the observed changes.

There are several ways by which reproduction may influence the physiological costs and, therefore, trade-offs within a plant. Generally, reproductive structures are carbon sinks within a plant. However, reproductive structures of several plant species photosynthesize and may contribute up to 50% of the reproductive carbon costs, and therefore reduce reproductive effort (Bazzaz et al. 1979; Galen et al. 1993; McDowell et al. 2000). Reproduction may also affect the available resource pool by altering foliar photosynthesis. In most field settings, where water and nitrogen are often limiting, the size of reproductive sinks is often negatively associated with rates of net foliar photosynthesis (Marshall et al. 1993; Gehring and Monson 1994; Galen et al. 1999; Huxman et al. 1999; but see Dawson and Ehleringer 1993; McDowell et al. 2000). However, when resources are not limiting, such as in greenhouses and irrigated horticultural crops, the sink strength of reproductive structures may increase the photosynthetic rates of neighboring foliage (Reekie and Bazzaz 1987; Laporte and Delph 1996); under such conditions, the evidence for trade-offs between growth and reproduction is weaker.

There are at least two causes of reduced foliar photosynthesis associated with reproduction. One cause is the translocation of nitrogen from leaves to reproductive structures (Bazzaz et al. 1987; Ashman 1994; Huxman et al. 1999).

Nitrogen is an essential component of photosynthetic enzymes and there is a well-documented positive relationship between photosynthetic capacity and foliar nitrogen concentration (Field and Mooney 1986). A second cause of reduced photosynthesis is the water cost of reproduction. Allocation of water to reproductive structures can induce mid-day water stress of neighboring foliage (Galen et al. 1999; Galen 1999). Foliage typically responds to water stress with stomatal closure, which forces a decline in photosynthetic rates.

The objective of the study described in this paper is to compare the physiological costs of reproduction of two closely related plant species, one of which is considered invasive, that grow together in the Pacific Northwestern United States (PNW). We directly manipulated the reproductive effort of individuals of both species to answer the following questions: 1) What are the physiological costs of reproduction? and 2) Do these costs differ between the invasive species and the closely related non-invasive species?

3.3 MATERIALS AND METHODS

In this study, reproductive effort (RE) was calculated for two species of *Rubus* (blackberry). Biomass and respiration (R_{ra}) of flowers and fruit were quantified for both of the species. Effects of reproduction on foliage were also assessed. Reproduction was prevented in several canes of each species. Diurnal measurements of photosynthesis (A), stomatal conductance (g_s), transpiration (E),

and leaf water potential (Ψ) were measured in the field on both reproductive and non-reproductive canes. Nitrogen concentrations ([N]) and stable carbon isotope ratios ($\delta^{13}\text{C}$) were also measured from collected foliage. Field gas exchange measurements and local meteorological data were used to model gross photosynthesis (A_{gross}) over the two-year lifetime for reproductive and non-reproductive canes of both species. RE for each species over the lifespan of a cane was calculated from the difference between A_{gross} of reproductive and non-reproductive canes, reproductive biomass, and R_{ra} .

3.3.1 Species and site descriptions

Rubus ursinus Cham. and Schlect. (trailing blackberry) is native to low and mid-elevations of the PNW where it is considered non-invasive. It has sprawling canes that may grow to 3 m in length. *Rubus discolor* Weihe and Nees (also *R. procerus*; Himalayan blackberry) is native to Europe and was introduced to the western United States via India for its fruit. It is considered an invasive species of the PNW. It has stout arching and sprawling canes that may reach 10 m in length. Both species have perennial roots that may simultaneously bear several biennial canes. During the first year, a cane remains entirely vegetative and growth is limited to elongation of the cane. In the spring of the second year, lateral shoots develop from buds in the leaf axils and the first-year leaves senesce. Growth during

the second year is limited to lateral shoot elongation. Inflorescences are borne in the axils of leaves and at the apex of each lateral shoot.

Field measurements were made at three sites in the McDonald-Dunn Research Forest near Corvallis, OR (44° 40'N, 123° 20'W; 210 – 360 m elevation). Temperature and photon flux density were recorded at the sites every 4 min for a year using Hobo temperature loggers (Onset Co., Pocasset, MA) and Li-Cor PAR sensors (LI 190SA, Li-Cor, Lincoln, NE) according to Phillips and Bond (1999). Loggers were placed approximately 1 m above ground level. Vapor pressure deficit (vpd) was calculated from humidity measurements made at a nearby (< 5 km away) meteorological station.

3.3.2 Reproductive effort

We calculated *RE* for each of the species, where *RE* is defined as the carbon invested in reproduction that is diverted from vegetative activities (Reekie and Bazzaz 1987; Bazzaz and Ackerly 1992). The equation for *RE*, which is a proportion, is:

$$RE = \frac{(Br + Brv + R_{ra}) - Pr}{(Bv + R_{va}) - Pr} \quad (1)$$

where *Br* is the reproductive biomass, *Brv* is the vegetative biomass attributed to reproduction (e.g., pedicels), *R_{ra}* is total respiration of flowers and fruit, *Pr* is the change in photosynthesis due to reproduction, *Bv* is the vegetative biomass, and *R_{va}*

is respiration from the vegetative organs, with each of these input values expressed in g C.

3.3.3 Size and resource content of tissues

Entire canes of each species were collected to estimate parameters of cane size and resource content. One cane was harvested from each of 10 randomly selected patches of *R. ursinus* and six patches of *R. discolor* during peak fruiting from one of the McDonald-Dunn Forest sites. Leaf area of all foliage was determined using a video image recorder and AgVision software (Decagon Devices, Pullman, WA). All foliage and stems were dried in an oven for 48 h at 65 °C and mass was measured immediately following removal from the oven. B_{rv} and B_v were estimated from the total dry mass of reproductive stems and of canes converted to g C using the average carbon concentration ([C]) of vegetative tissues (see below).

We also used these canes to estimate the total amount of biomass, water, carbon, and nitrogen directly allocated to reproductive structures and the proportion of total cane biomass that was reproductive tissue biomass. To estimate these parameters, all fruit were collected from the canes and the maturity of each was assessed by color and size. To measure the biomass and water content of reproductive tissues, the fresh weight of fruit was measured to the nearest 0.01 g as soon as possible following collection. Fruit were dried in an oven for 48 h at 65 °C

and mass was measured immediately following removal from the oven. Water content per fruit was calculated as the difference between the fresh and dry weights. Since not all fruit were mature at the time of harvest, the total mature fruit biomass per cane was estimated by calculating the average mass of mature fruit then scaling to the total number of fruit for that cane. This method may have overestimated total fruit biomass because some late developing fruit are smaller than earlier fruit. The number of seeds was counted from 75 mature fruit per species. Total flower biomass was estimated from the average biomass of flowers collected during floral respiration measurements (see below) scaled to the total number of flowers per cane. B_v was calculated from the total flower and fruit biomass per cane converted to g C using the average [C] of flowers and fruit (see below).

To measure the amount of nitrogen and carbon allocated to tissues, we ground the samples following oven drying. Then, [N] and [C] were measured on a subsample of ground material using a NC2500 elemental analyzer (CE Instruments, Milan, Italy). The total C cost (g) per seed was calculated as:

$$\text{g C seed}^{-1} = \frac{Br + Brv + R_{ra} - Pr}{\text{\#seeds}} \quad (2)$$

for each of the collected canes.

3.3.4 Reproductive respiration

To calculate R_{ra} , we first measured respiration of reproductive structures (R_r) with the Li-Cor 6400 on six flowers of each species during the flowering

period and on six fruit of each species during fruiting after shading plants for approximately 45 min. Measured values of R_r were standardized to a common temperature and then used to estimate total annual R_r of reproductive structures using a typical temperature response value ($Q_{10} = 2.0$), daily maximum and minimum temperature measured on site, and equations developed in McDowell et al. (2000).

Diurnal gas exchange measurements of reproductive structures were made to determine the net CO_2 flux (F_{net}) from flowers and fruit. Measurements were made on six flowers or fruit of each species during the flower, green-fruit, and mature-fruit stages. These measurements were made approximately every 2 h from 0700 to 1900 h. The F_{net} from flowers and fruit during the day was often zero or negative. Reproductive A , in units of $\mu\text{mol m}^{-2} \text{s}^{-1}$, was calculated from

$$F_{net} = A - R_r \quad (3)$$

where R_r is the estimated respiration at the ambient temperature at which F_{net} was measured. Total daily A was calculated by summing A over all daylight hours. All daily values were added to calculate annual reproductive A . The R_{ra} over the lifespan of a cane was calculated from total R_r minus reproductive A .

3.3.5 Reproduction effects on foliage

We used field measurements and a photosynthesis model to calculate Pr per cane lifespan. First, reproduction was prevented in 30-40 canes of each species

randomly selected throughout each of the three sites. All floral buds were removed from the entire cane immediately following bud emergence. Those canes from which the floral buds were removed will be referred to as non-reproductive.

Diurnal measurements of foliar A , g_s , and E were measured in the field approximately every two hours for one leaf on each of three reproductive and three non-reproductive individuals per species. Measurements were paired, so that each reproductive cane was located near a non-reproductive cane and their measured leaves shared similar aspects and position along the cane. These diurnal measurements were made three to seven days per month using different canes each day until the reproductive individuals senesced in July for *R. ursinus* and in September for *R. discolor*. Leaf Ψ measurements were measured following each gas exchange measurement using a pressure chamber (PMS Instruments, Corvallis, OR).

Photosynthetic capacity was quantified by measuring rates of A in relation to varying internal leaf CO_2 concentrations (C_i), or A/C_i curves. The A/C_i curves were measured on 3 to 6 leaves of reproductive and non-reproductive individuals for each species. These measurements were made on different canes once per month from March through September to include measurements at different developmental stages of the canes (first-year, second-year pre-flowering, flowering, and fruiting). Measured leaves within a species were paired as they were for the diurnal measurements. During all measurements, temperature within the cuvette

was 23 ± 4 °C and vpd was 1.1 ± 0.3 kPa. Photon flux density within the cuvette was held at approximately $1,500 \mu\text{mol m}^{-2} \text{s}^{-1}$ using a red-blue LED light. A/C_i curves were measured by changing ambient CO_2 levels inside the cuvette, waiting a minimum of 90 seconds, and then verifying cuvette $[\text{CO}_2]$ had stabilized (i.e., coefficient of variation for $[\text{CO}_2]$ inside the cuvette $< 2\%$) before logging measurements. Measurements were made every 10 seconds for a total of three measurements per leaf at each of the following cuvette $[\text{CO}_2]$'s: 10, 20, 30, 40, 60, 80, 100, and 150 Pa. The maximum net photosynthetic rate under saturating light levels, optimal ambient temperature and humidity, and $[\text{CO}_2] = 36.5$ Pa (A_{max}) was calculated using non-linear regression between A and cuvette $[\text{CO}_2]$. Respiration (R) and photosynthetic capacity, which is defined by both the maximum rate of carboxylation ($V_{\text{c}_{\text{max}}}$) and the maximum rate of electron transport (J_{max}), were also calculated from the A/C_i curves using non-linear regression following Harley et al. (1992). Measured values of $V_{\text{c}_{\text{max}}}$ and J_{max} were adjusted to a common temperature of 25 °C following Harley et al. (1992) and Leuning (1997).

To test whether there was a significant increase in photosynthesis during the mid-morning associated with reproductive sinks, A was measured on one leaf on each of six similar flowering canes of each species at approximately 1000 h, then all flowers were immediately removed from the canes, and A was measured again. The change in A between those two measurements was compared with the A measured at approximately the same times on the previous day.

Following field measurements, leaves were collected and kept in cold storage until they could be processed in the lab. First, area was determined for each leaf using the video image recorder. Next, foliage was dried for 48 h at 65 °C and mass was measured immediately upon removal from the oven to the nearest 0.01 g. Leaves were then ground and [N] and [C] were measured from a subsample using the elemental analyzer.

The $\delta^{13}\text{C}$ of plant material is a sensitive measure of photosynthesis per unit water loss (A/E), also known as integrated water-use efficiency (WUE ; Ehleringer 1993). Foliar $\delta^{13}\text{C}$ was measured on 2.0 ± 0.1 mg ground subsample using a Finnigan MAT stable isotope mass spectrometer (Bremen, Germany) at the Idaho Stable Isotope Lab (Moscow, ID). The stable carbon isotope composition was calculated as:

$$\delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{standard}} - 1) * 1000 \quad (\text{‰}) \quad (4)$$

where R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ of the leaf samples and of the standard, respectively, using the international standard of Pee Dee belemnite (Farquhar et al. 1989).

3.3.6 Photosynthesis model

To determine the effects of reproduction on total carbon gain over the lifespan of a cane for each species, a model of the biochemistry of photosynthesis was used to calculate annual gross photosynthesis per cane. The basis of the model

is the daily time step photosynthesis routine of the Biome-BGC model (version 4.1.1, Thornton 1998). Modifications were used here to calculate daily values of g_s , and to include average parameters for each stage of cane development calculated from measured A/C_i curves (i.e., $V_{c_{max}}$ and J_{max}).

3.3.6.1 Stomatal conductance

Using measurements of E and vpd , g_s was calculated for each day according to Monteith (1995). First, a linear regression between diurnal measurements of vpd and E was established:

$$1/E = 1/a(vpd) + b \quad (5)$$

From this equation, the extrapolated maximum value of g_s (g_m), which is equal to a , and the extrapolated maximum value of E (E_m), which is equal to $1/b$, were calculated. Daily values of g_s for H_2O were then calculated as:

$$g_s = \frac{g_m}{(1 + g_m \cdot vpd / E_m)} \quad (6)$$

using a daytime average value of vpd . The values of g_s for H_2O were then corrected to account for the difference in diffusivity between H_2O and CO_2 by dividing by 1.6.

3.3.6.2 Photosynthesis biochemistry

The original equations for the photosynthesis model are outlined in Farquhar et al. (1980), with net CO₂ assimilation expressed as:

$$A = V_c - 0.5V_o - R \quad (7)$$

where V_c and V_o are the carboxylation and oxygenation rates of Rubisco and R is respiration during the day excluding photorespiration. These parameters were calculated from the daily values of g_s , values of $V_{c_{max}}$, J_{max} , and R calculated from the measured A/C_i curves for each developmental stage of the canes, and biochemical constants from Thornton (1998). The temperature response of the constants and R were calculated following Thornton (1998) and the temperature response of $V_{c_{max}}$ and J_{max} were calculated following Harley et al. (1992) and Leuning (1997). An average instantaneous A_{gross} in units of $\mu\text{mol m}^{-2} \text{s}^{-1}$ was calculated for each day by adding R to Eq. (7).

3.3.6.3 A_{gross} , Pr , and R_{va} over cane lifespan

Estimates of A_{gross} were scaled over the lifetime and leaf area of a cane. Daily A_{gross} ($\mu\text{mol m}^{-2} \text{day}^{-1}$) was calculated by adding the instantaneous A_{gross} over all daylight hours except for approximately 1.5 hours following sunrise and before sunset. Since $V_{c_{max}}$, J_{max} , and g_s changed with development stage, the model was run separately for each of those stages (first-year, second-year pre-flowering, flowering, and fruiting). All daily values were scaled to total cane leaf area and

were added to calculate total A_{gross} over the lifespan of a cane (mol cane^{-1} lifespan $^{-1}$). Pr was determined for each species by calculating the difference between lifespan A_{gross} for reproductive and non-reproductive canes. R_{va} was calculated over the lifetime of each species as the difference between modeled A_{gross} and modeled A .

3.3.7 Analyses

Data from all three sites in the McDonald-Dunn Forest were pooled because there were no apparent differences among data from the sites. Paired t -tests were used to test for differences between reproductive and non-reproductive canes for A_{max} , $[N]$, and $\delta^{13}C$ for each species. Two sample t -tests were used to test for differences between each species for the different measures of the amount of resources allocated to reproduction and for reproductive effort. A/C_i curves of reproductive and non-reproductive canes were compared with paired t -tests of $V_{c_{max}}$ and J_{max} , where $V_{c_{max}}$ defines the initial slope of the curve and J_{max} defines the slope of the plateau region. Repeated measures analysis of variance was used to test for differences between diurnal measurements of A , g_s , and Ψ of reproductive and non-reproductive canes for each of the species during flowering and fruiting. In each analysis, the main effect of reproductive state (i.e., reproductive or non-reproductive) was tested as a between-subjects effect while site and interaction terms were tested as within-subjects effects. For all analyses, assumptions of

normality and homogeneity of variance were examined and met. A 5% level of significance ($\alpha = 0.05$) was used.

3.4 RESULTS

The invasive *R. discolor* allocated significantly more resources to reproduction than *R. ursinus*. Fruit number and fruit biomass relative to plant size were greater in *R. discolor* than *R. ursinus* (Table 3.1). The [N] in fruit was higher in *R. ursinus* than *R. discolor* ($\bar{x} \pm \text{SE} = 1.80 \pm 0.11 \text{ g g}^{-1}$ and $\bar{x} \pm \text{SE} = 0.87 \pm 0.09 \text{ g g}^{-1}$, respectively; $t = 6.52$, $P < 0.001$). However, due to its larger fruit ($\bar{x} \pm \text{SE} = 0.08 \pm 0.01 \text{ g}$ for *R. ursinus* and $\bar{x} \pm \text{SE} = 0.44 \pm 0.02 \text{ g}$ for *R. discolor*; $t = -12.03$, $P < 0.001$), the invasive *R. discolor* had a greater mass of N per fruit than *R. ursinus* (Table 3.1). The fruit of *R. discolor* also contained a greater amount of H_2O than fruit of *R. ursinus* (Table 3.1).

Reproduction had a greater impact on foliar Ψ , g_s , and A for the non-invasive *R. ursinus* compared with the invasive *R. discolor*. A , g_s , and Ψ were all reduced in reproductive plants of *R. ursinus* during flowering, although the reduction was not significant (Figure 3.1; $F = 3.33$, $P = 0.11$; $F = 1.96$, $P = 0.20$; $F = 0.05$, $P = 0.83$, respectively). During fruiting, however, mid-day Ψ of reproductive plants fell below that of non-reproductive plants in *R. ursinus* (Figure

Table 3.1: Leaf area, cane lifespan, the amount and proportion of resources allocated to reproduction, modeled annual gross photosynthesis (A_{gross}) for reproductive and non-reproductive canes, reproductive effort, and results of two-sample t -tests comparing the species. Total A_{gross} is an estimated average for each species because it was modeled using average values as input parameters. Values are means \pm 1 SE.

	<i>R. ursinus</i>	<i>R. discolor</i>	<i>t</i>	P
Leaf area per cane (m ²)	0.03 \pm 0.004	2.96 \pm 0.31	13.80	<0.001
Cane development stages (~weeks)				
Juvenile	44	44		
Pre-flowering (2 nd year)	2	8		
Flowering	3.5	3		
Fruiting	6	11.5		
Fruit # per cane	23.5 \pm 4.4	720.3 \pm 123.9	-8.25	<0.001
Fruit and flower biomass per cane (g)	2.3 \pm 0.4	331.3 \pm 56.9	-8.02	<0.001
Fruit and flower biomass per plant biomass (g g ⁻¹)	0.22 \pm 0.03	0.36 \pm 0.02	-2.68	0.01
N (g fruit ⁻¹)	0.16 \pm 0.01	0.38 \pm 0.04	-5.85	<0.001
H ₂ O (g fruit ⁻¹)	0.54 \pm 0.05	1.97 \pm 0.06	18.33	<0.001
Total reproductive respiration (R_{ra}) (g C cane ⁻¹ cane lifespan ⁻¹)	0.56 \pm 0.07	58.46 \pm 10.05	7.49	<0.001
A_{gross} (mol cane ⁻¹ cane lifespan ⁻¹)				
Reproductive	99.3	147.0		
Non-reproductive	110.1	153.4		
C (g C seed ⁻¹)	0.12 \pm 0.03	0.007 \pm 1.1 \times 10 ⁻⁵	-2.54	0.006
Reproductive effort	0.15 \pm 0.002	0.13 \pm 0.01	-1.96	0.03

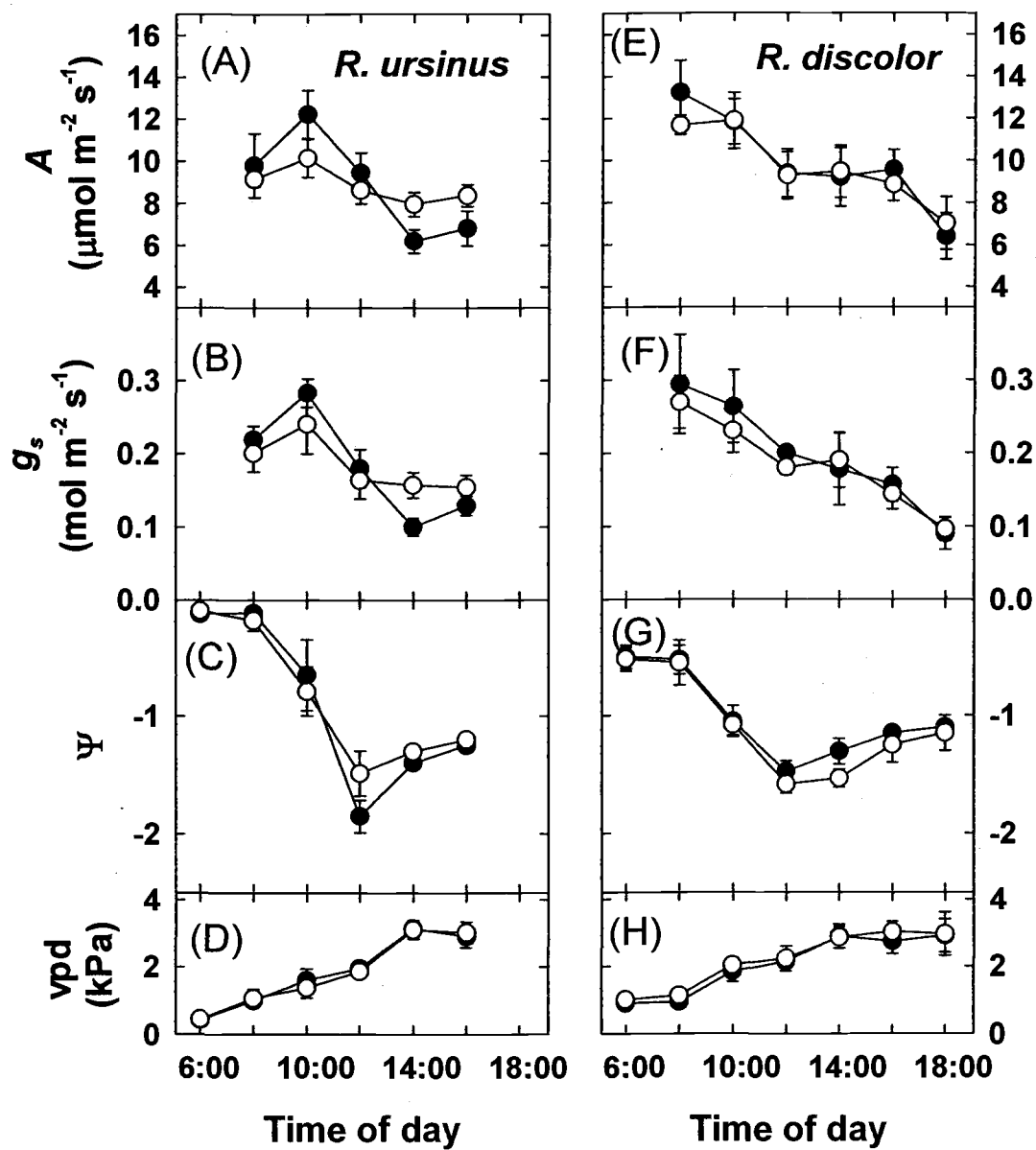


Figure 3.1: Average diurnal values of A , g_s , Ψ , and vpd during the flowering stage for reproductive (filled circles) and non-reproductive (open circles) canes of *R. ursinus* and *R. discolor*. Error bars = 1 SE.

3.2; $F = 4.48$, $P = 0.06$). This reduction was associated with simultaneous reductions in g_s and A ($F = 15.186$, $P = 0.005$ and $F = 24.88$, $P = 0.001$, respectively). The invasive *R. discolor* showed no significant change in A , g_s , or Ψ during flowering (Figure 3.1; $F = 0.78$, $P = 0.40$; $F = 0.12$, $P = 0.74$; $F = 1.41$, $P = 0.36$, respectively) or fruiting (Figure 3.2; $F = 0.86$, $P = 0.38$; $F = 0.23$, $P = 0.65$; $F = 0.04$, $P = 0.84$, respectively).

During the mid-morning, flowering canes of *R. ursinus* had slightly higher A than non-flowering canes. For *R. ursinus*, there was a significant reduction in A associated with flower removal ($t = 2.25$ and $P = 0.04$). Therefore, flowers of *R. ursinus* are associated with increased A during the mid-morning. However, that increase disappeared by mid-afternoon, when values of A and g_s were significantly lower in the reproductive canes than the non-reproductive canes ($t = 1.91$ and $P = 0.04$; $t = 2.4$ and $P = 0.02$, respectively). *Rubus discolor* showed no evidence for increases in mid-morning A in relation to reproduction ($t = -0.05$ and $P = 0.48$) and unlike *R. ursinus*, showed no significant decline in A during the afternoon associated with reproduction.

Fruiting in the non-invasive *R. ursinus* was associated with a reduction in photosynthetic capacity, while there were no apparent effects of reproduction on photosynthetic capacity of *R. discolor*. During flowering, A_{max} tended to be lower in reproductive canes of *R. ursinus* than in non-reproductive canes, although the difference was not significant (Figure 3.3; $t = -0.58$ and $P = 0.30$). During fruiting,

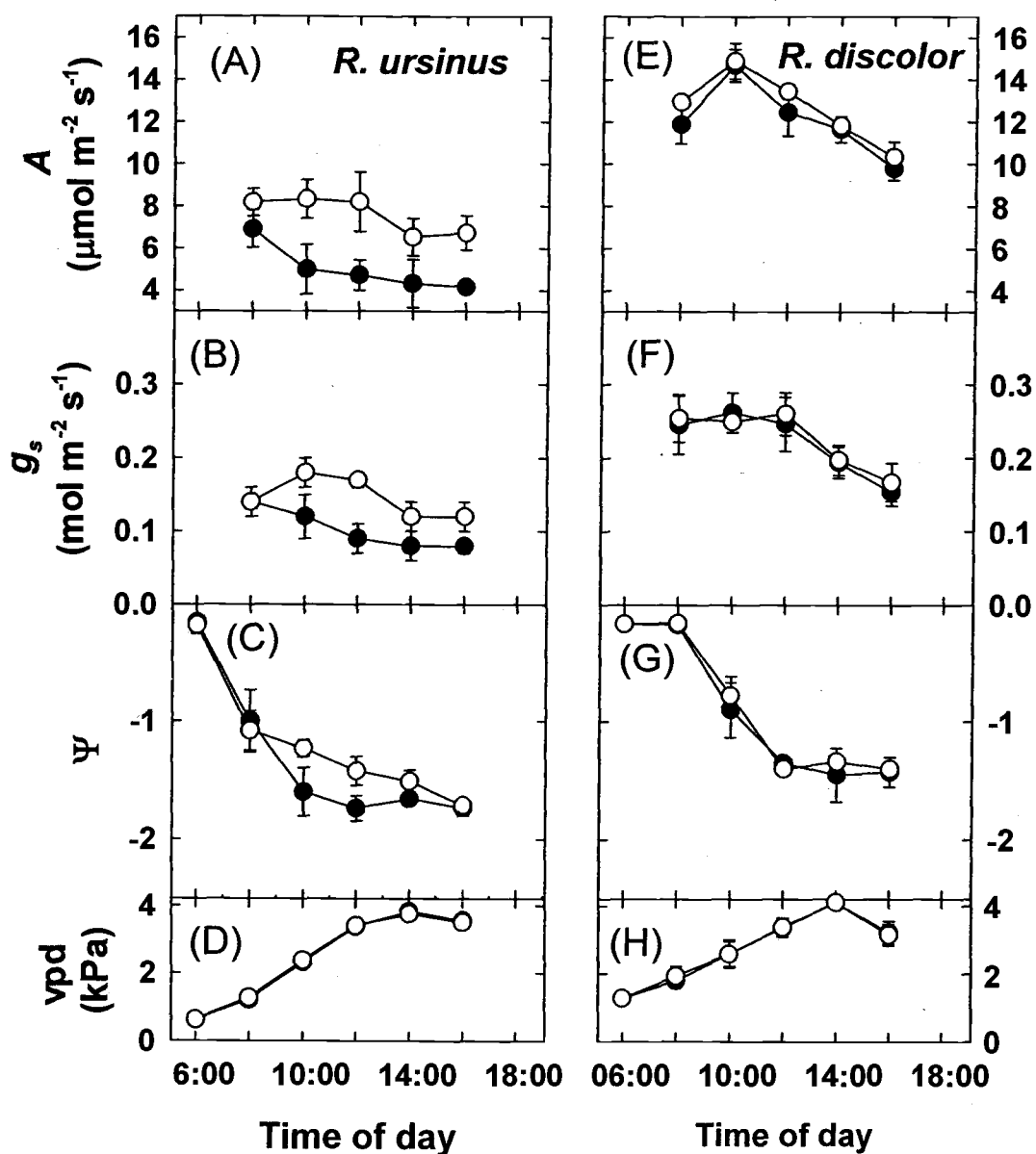


Figure 3.2: Average diurnal values of A , g_s , Ψ , and vpd during the fruiting stage for reproductive (filled circles) and non-reproductive (open circles) canes of *R. ursinus* and *R. discolor*. Error bars = 1 SE.

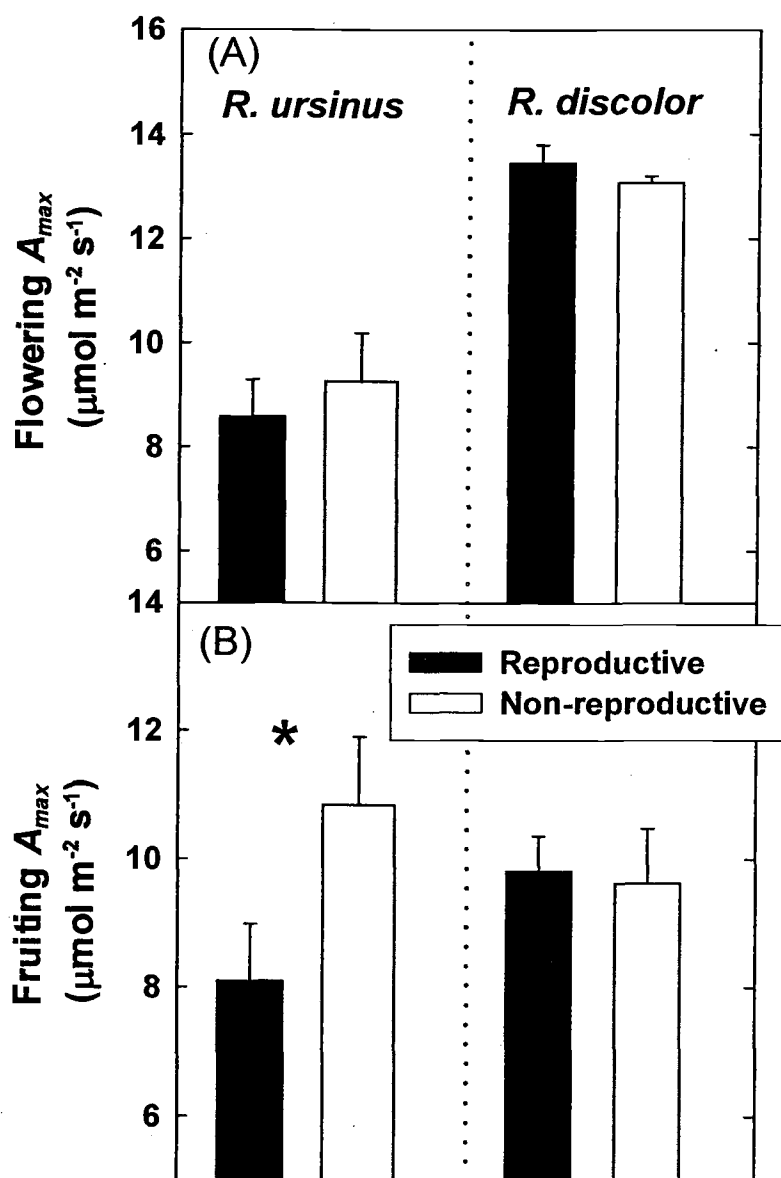


Figure 3.3: Average foliar A_{max} for *R. ursinus* and *R. discolor* during flowering (A) and fruiting (B). The asterisk indicates a significant difference at the 0.05 level of significance. Error bars = 1 SE.

however, A_{max} was significantly lower in reproductive canes of the non-invasive species than in non-reproductive canes (Figure 3.3; $t = -2.27$ and $P = 0.03$). The A/C_i curves of fruiting canes of the non-invasive *R. ursinus* were lower than those of non-fruiting individuals (Figure 3.4). Both $V_{c_{max}}$ and J_{max} were significantly lower in fruiting than in non-fruiting canes ($t = -2.17$ and $P = 0.03$; $t = -2.48$ and $P = 0.02$, respectively). For fruiting canes, average $V_{c_{max}}$ at 25 °C was 37.85 ± 5.38 and for non-fruiting canes, the average was 75.20 ± 14.91 . Average J_{max} at 25 °C for fruiting canes was 108.40 ± 18.10 and for non-fruiting canes was 213.21 ± 23.52 . As with *R. ursinus*, the invasive *R. discolor* showed no significant change in A_{max} associated with flowering (Figure 3.3; $t = -1.03$ and $P = 0.17$). However, unlike *R. ursinus*, fruiting had no effect on A/C_i curves of *R. discolor* (Figure 3.4) or A_{max} (Figure 3.3; $t = 0.18$ and $P = 0.43$). Both $V_{c_{max}}$ and J_{max} at 25 °C were also similar between fruiting and non-fruiting canes ($t = -0.72$ and $P = 0.25$; $t = -0.54$ and $P = 0.30$, respectively). The average $V_{c_{max}}$ for fruiting canes was 52.42 ± 6.83 and the average for non-fruiting canes was 63.83 ± 13.64 . Average J_{max} for fruiting canes was 137.73 ± 10.74 and for non-fruiting canes was 158.11 ± 29.42 .

The reduction in photosynthetic capacity in the non-invasive *R. ursinus* may be due in part to translocation of foliar N to flowers and fruits. During the flowering stage, leaf [N] for this species was not different between reproductive and non-reproductive canes (Figure 3.5; $t = -0.26$ and $P = 0.40$). However, during

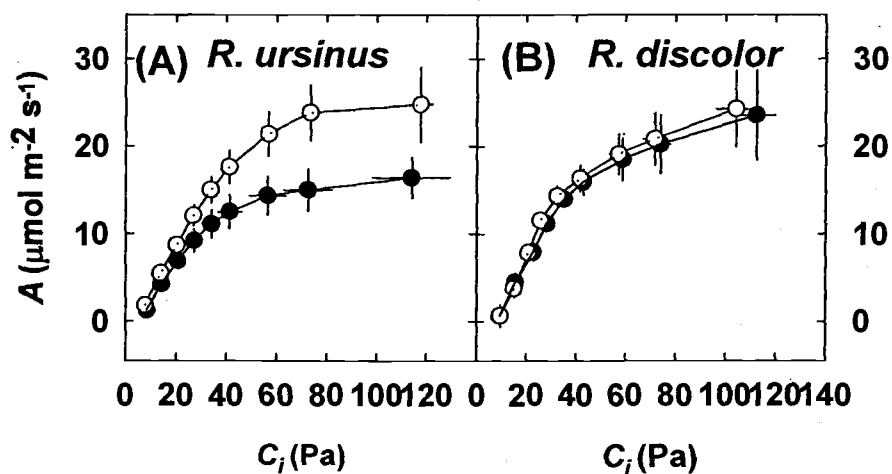


Figure 3.4: (A) Average A/C_i curves for reproductive (filled circles) and non-reproductive (open circles) canes of *R. ursinus* during fruiting stages. (B) Average A/C_i curves for reproductive (filled circles) and non-reproductive (open circles) canes of *R. discolor* during fruiting stages. Error bars = 1 SE.

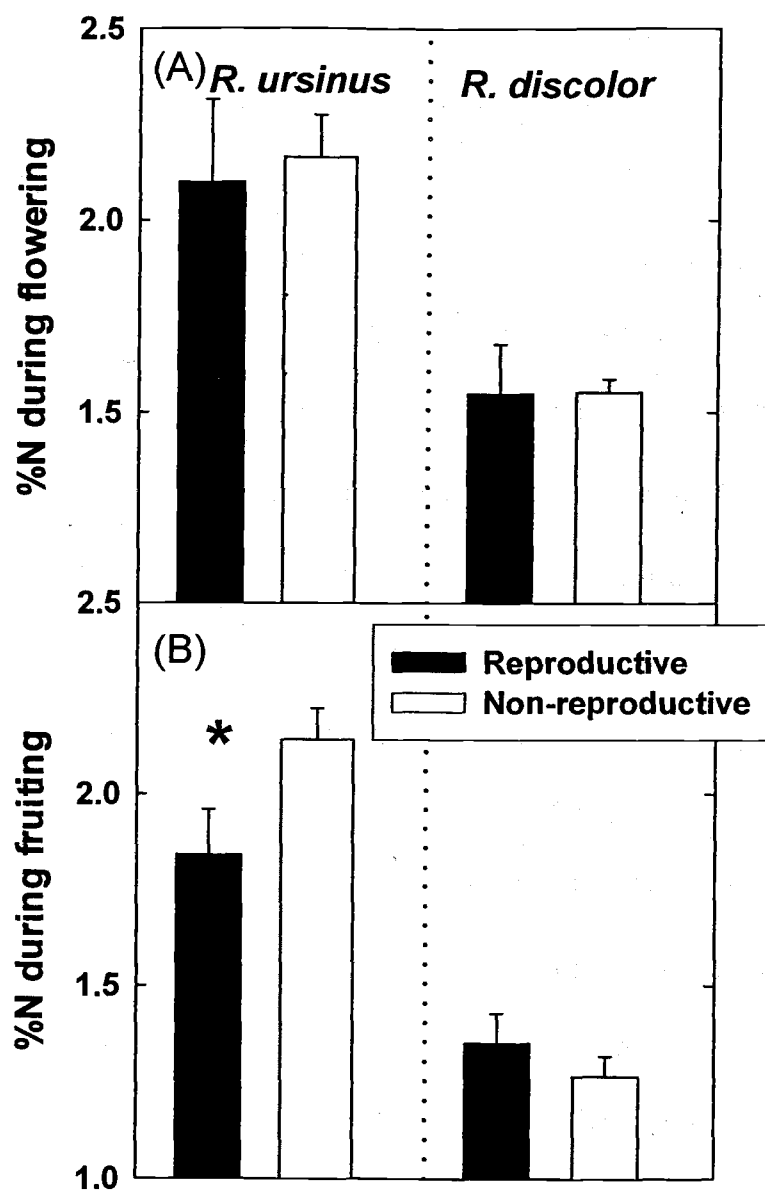


Figure 3.5: Average foliar leaf [N] of *R. ursinus* and *R. discolor* during flowering (A) and fruiting (B). The asterisk indicates a significant difference at the 0.05 level of significance. Error bars = 1 SE.

fruiting, leaf [N] was lower in foliage of reproductive canes than in non-reproductive canes (Figure 3.5; $t = -2.08$ and $P = 0.03$). The invasive *R. discolor*, which showed no difference in A_{max} between reproductive and non-reproductive canes, did not appear to have reduced foliar [N] in reproductive canes during either flowering or fruiting (Figure 3.5; $t = -0.03$ and $P = 0.49$; $t = 0.94$ and $P = 0.18$, respectively).

During flowering, there was no significant difference between foliar $\delta^{13}\text{C}$ of reproductive and non-reproductive canes for either *R. ursinus* or *R. discolor* (Figure 3.6; $t = 0.759$ and $P = 0.23$; $t = -1.16$ and $P = 0.14$, respectively). However, during fruiting, $\delta^{13}\text{C}$ was significantly higher in non-reproductive than reproductive canes of *R. ursinus* (Figure 3.6; $t = -3.23$ and $P = 0.005$). Reproductive and non-reproductive canes of *R. discolor* shared similar $\delta^{13}\text{C}$ during fruiting (Figure 3.6; $t = -0.39$ and $P = 0.35$).

The cumulative effect of lower g_s and A_{max} was that reproductive canes of the non-invasive *R. ursinus* had reduced A_{gross} over their lifetime (Table 3.1). This reduction was approximately 10% of the C assimilated over the 14-month lifespan of an individual cane, though reproduction lasts only about two and a half months. During only the months in which reproduction was taking place, the A_{gross} of reproductive *R. ursinus* was 33% lower than that of the non-reproductive canes. Although reproductive plants of the invasive *R. discolor* did not show a significant reduction in g_s or A_{max} , there was a slight reduction in A_{gross} over the lifespan of a

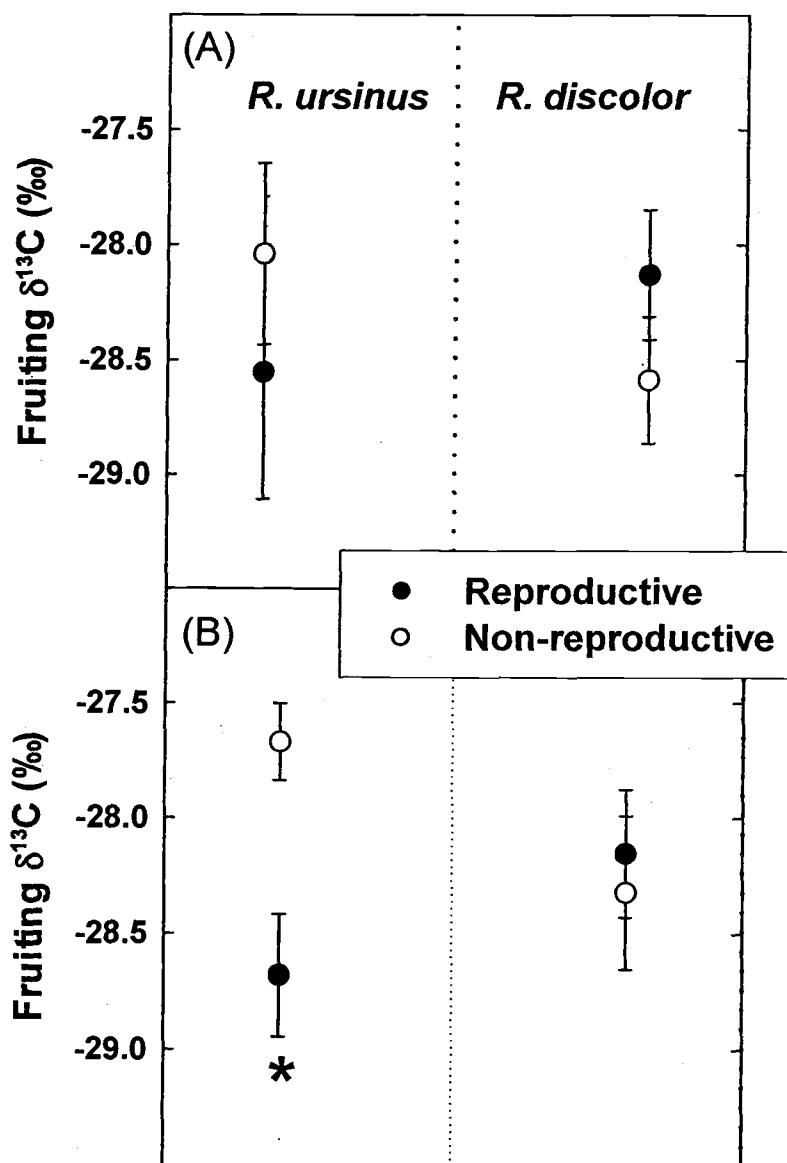


Figure 3.6: Average $\delta^{13}\text{C}$ values for *R. ursinus* and *R. discolor* foliage during flowering (A) and fruiting (B). Filled circles represent reproductive canes and open circles represent non-reproductive canes. The asterisk indicates a significant difference at the 0.05 level of significance. Error bars = 1 SE.

cane (Table 3.1). However, this reduction was only 4% of the C assimilated over the lifespan of a cane. Reproduction in *R. discolor* lasts nearly 4 months and during that period alone, overall A_{gross} may be reduced by up to 17%.

As a result of the reduction of A_{gross} in *R. ursinus*, the physiological cost of reproduction is higher relative to the invasive *R. discolor*. Reproductive R_r was much higher in *R. discolor* than in *R. ursinus*, in part because reproduction of *R. discolor* continues for a longer period (Table 3.1). However, the total g C per seed (including biomass of flowers, fruit, and support structures, respiration of flowers and fruit, and any change to foliar photosynthesis) was significantly higher in the non-invasive *R. ursinus* than in *R. discolor* (Table 3.1). Photosynthesis by flowers and fruit of each species compensated similar proportions of reproductive respiration; photosynthesis by reproductive structures of *R. ursinus* compensated for 41% of respiration and by *R. discolor* compensated for 39%. The greatest proportion of photosynthetic gain occurred while fruit were green. Furthermore, RE was significantly higher in *R. ursinus* than in *R. discolor* (Table 3.1). Therefore, reproduction in the non-invasive species diverts relatively more carbon from vegetative activity than in the invasive species.

3.5 DISCUSSION

3.5.1 Reproduction effects on water relations and photosynthesis

During the flowering phase, reproduction had no effect on diurnal patterns of A and g_s for the invasive *R. discolor*, but had a small effect on *R. ursinus*. During the mid-morning, flowering canes of *R. ursinus* had slightly higher g_s and A than non-flowering canes, suggesting that reproductive sinks may be inducing increased photosynthesis. Results of the experiment to test for sink-induced photosynthesis confirmed that it was occurring in the noninvasive *R. ursinus* but not in *R. discolor*. During the mid-afternoon, the flowering canes of *R. ursinus* had slightly lower A , g_s , and Ψ than non-flowering canes. Perhaps the higher g_s in reproductive canes during the morning depletes available moisture and, therefore, induces stomatal closure earlier in the afternoon than non-reproductive canes. Other evidence for increased photosynthesis in relation to reproductive sinks in field settings shows a similar pattern, where there is an apparent increase in A during morning, but that increase dissipates by mid-afternoon (Dawson and Ehleringer 1993).

Fruiting appears to cause greater water stress than flowering for *R. ursinus*, while the water status of *R. discolor* seems unaffected by fruiting. Leaf Ψ for fruiting canes and for non-fruiting canes of *R. ursinus* are similar in the morning and plateau in the afternoon at the same level. However, fruiting canes reach their

minimum leaf Ψ earlier in the afternoon than non-fruiting canes. This reduction in Ψ is associated with decreases in g_s and A , suggesting that water stress induced stomatal closure and reduced photosynthesis earlier in the day in the fruiting canes than in non-fruiting canes. The diurnal patterns for *R. ursinus* are consistent with the little data available concerning reproductive effects on plant water relations that suggests larger reproductive sinks are associated with lower mid-day Ψ (Dawson and Ehleringer 1993; Galen et al. 1999). However, the invasive *R. discolor* shows no such reduction in Ψ during any time of reproduction. Plants frequently abort flowers and fruit when under water stress (Stephenson 1981; Zinselmeier et al. 1999). By minimizing water stress associated with reproduction, *R. discolor* may avoid some abortion of flowers and fruit. These are the first data reporting the physiological costs of reproduction in an invasive species, so it is not possible to determine whether this is a property unique to *R. discolor* or is shared by other invasive species.

Integrated WUE , as inferred from $\delta^{13}C$, demonstrates the same relationships seen in the diurnal measurements. During flowering, there is no significant difference between reproductive and non-reproductive canes of either species. However, the $\delta^{13}C$ of *R. ursinus* of fruiting canes was significantly lower than that of the non-fruiting canes. Other research documenting the WUE of plants in relation to reproductive sinks have shown similar patterns. In dioecious species,

relatively low *WUE* is associated with the larger reproductive sinks of female plants compared to the small reproductive structures of male plants (Dawson and Ehleringer 1993; Marshall et al. 1993; Ward et al. 2002). The diurnal patterns for *R. ursinus* suggest that the reduction in $\delta^{13}\text{C}$ associated with fruiting is due to greater decline in *A* relative to the decline in *g_s*. In contrast, there was no difference between the $\delta^{13}\text{C}$ of fruiting and non-fruiting canes of *R. discolor*, which is supported by the diurnal gas exchange data in which there was no observed change in *A* or *g_s* associated with reproduction.

3.5.2 Reproduction effects on leaf [N] and photosynthetic capacity

Changes in leaf [N] during reproduction appeared to negatively affect photosynthesis in *R. ursinus*. Although there was no significant difference between leaf [N], *A/C_i* curves, or *A_{max}* of reproductive and non-reproductive canes of *R. ursinus* at the flowering stage, there were significant reductions in each parameter during fruiting. The decreased leaf [N] of reproductive canes during fruiting was probably due to translocation of N to fruit and was likely responsible for the lower photosynthetic capacity and *A_{max}*, since foliar N is essential to photosynthetic pigments and enzymes. Lower leaf [N] is frequently associated with greater reproductive sinks (Marshall et al. 1993; Ashman 1994; Laporte and Delph 1996).

Although there was no significant difference of leaf [N], photosynthetic capacity, or *A_{max}* between reproductive and non-reproductive canes of *R. discolor*,

there was a decline in these parameters between flowering and fruiting stages.

These declines may be due to the timing of reproduction for this species.

Flowering in *R. discolor* begins in late June and fruiting takes place late July through mid-September. Summers in the PNW are characterized by drought and by the time *R. discolor* is fruiting, the soil moisture availability has declined considerably below its level during flowering. Therefore, all plants, both reproductive and non-reproductive, may be under greater moisture stress during fruiting as compared with flowering. Moisture stress can lower photosynthetic capacity within a species (Tezara et al. 1999) and, therefore, moisture stress may underlie the reduction in photosynthetic capacity and A_{max} between the flowering and fruiting stages in *R. discolor*. Furthermore, the reduction in leaf [N] of both reproductive and non-reproductive canes of *R. discolor* between flowering and fruiting stages may also reduce photosynthetic capacity (Field and Mooney 1986). This reduction in leaf [N] may be due to the translocation of N toward root stores before two-year old canes senesce. *Rubus ursinus* reproduces early in the summer and has senesced by the time *R. discolor* is in fruit, thereby avoiding these effects of seasonal drought.

3.5.3 Reproductive effort

The cumulative effects of reproduction on water and nitrogen status of foliage increase the physiological costs of reproduction and, therefore, *RE* for the

non-invasive *R. ursinus* while having essentially no effect on the invasive *R. discolor*. Although *R. discolor* allocates more carbon to reproductive biomass and respiration than *R. ursinus*, the reduction of A_{gross} in *R. ursinus* counterbalances and slightly dominates that difference. Together, the results of the A/C_i curves, diurnal A and g_s , and $\delta^{13}C$ indicate that, although reproduction affects both the water relations and photosynthetic capacity of *R. ursinus*, it has a relatively greater impact on photosynthetic capacity than on stomatal conductance. Therefore, the reduction in A_{gross} is due primarily to the reduction in photosynthetic capacity. When RE is estimated including the physiological costs of reproduction, particularly the reduction in A_{gross} in reproductive plants, *R. ursinus* has higher reproductive effort than *R. discolor*. That is, this invasive species diverts relatively fewer resources from vegetative activity to support reproduction than the non-invasive species.

There are some potential limitations to the modeling approach utilized to calculate RE . The temperature response of the model parameters $V_{c_{max}}$ and J_{max} for *Rubus* were assumed to be similar to the temperature response of cotton from Harley et al. (1992). However, the temperature response of these parameters varies with species (Leuning 1997) and this assumption may have been a source for error. Additionally, daily average temperature and vpd values were used to scale instantaneous measurements to daily values. Therefore, the actual response and fluctuation of photosynthesis with temperature and g_s with vpd may have been oversimplified. However, measurements for both species were made at the same

time and over the same range temperature and vpd. These measurements were used to estimate gross photosynthesis over the same seasons, with the exception of the weeks during which the invasive *R. discolor* canes were alive following the senescence of *R. ursinus* canes. Therefore, this simplification affected both species similarly. Furthermore, photosynthetic capacity may be affected by soil water availability and will, therefore, vary seasonally (Tezara et al. 1999). In order to address the seasonal variation in soil moisture availability, we measured A/C_i curves monthly and used these measurements to calculate the seasonal variation in photosynthetic capacity. Finally, scaling from instantaneous measurements to annual whole-plant carbon gain is dependent on the assumption that the leaves we measured were typical of the plant. Leaves may vary, however, with light environment, position along the cane, amount of herbivory, or proximity to flowers or fruit. Although this modeling approach has some potential limitations, this simple and generalized representation of plant processes is an important tool used widely in fields of plant physiology and ecosystem processes. This study is the first extension of such a tool to life-history analysis or the study of invasive plant species, where it forms a valuable link between field measurements and theory.

Trade-offs between current reproduction and growth are commonly observed in plants. The current study quantifies the underlying mechanisms for observing, or not observing, such trade-offs. The lower physiological costs associated with reproduction in the invasive plant species result in fewer resources

being diverted from vegetative growth. The two species used in this study are capable of clonal growth as well as sexual reproduction and, therefore, costs of reproduction in one cane may influence growth and reproduction in other canes sharing the same roots. An additional study looking at the plant and population growth of these same two species determined that sexual reproduction significantly reduced growth of clonally connected ramets in the non-invasive *R. ursinus*, but not in the invasive *R. discolor* (McDowell and Radosevich, unpublished manuscript). Although population growth for both species was predominantly dependent on clonal growth rather than sexual reproduction, the invasive *R. discolor* had a relatively greater dependence on sexual reproduction than *R. ursinus*, enabling it to disperse to areas not previously colonized. Therefore, the physiological costs of reproduction appear to influence the rate of clonal spread within a population and dispersal for colonizing new populations for both of these species of *Rubus*. Further studies with other species are necessary to determine whether such mechanisms are actually associated with invasiveness, or merely reflect the life-history strategies and trade-offs of two different plant species.

The temporal separation of growth and reproduction within a cane of *R. discolor* may assist in lowering the physiological costs of reproduction. Leaves and shoots of *R. ursinus* are elongating concurrently with flowering. Therefore, reproductive and growth sinks may be competing for the same resources within canes of this species. This pattern of development contrasts with that of *R. discolor*

in which shoot and leaf growth is completed prior to flowering. Theoretical models of annual plant growth and fitness predict that the optimal strategy of resource allocation is to switch from purely vegetative to purely reproductive growth within a single growing season (Cohen 1971). This strategy would be optimal because vegetative tissues contribute to resource gain, so by increasing size prior to the onset of reproduction a plant will also increase the available pool of resources (Bloom et al. 1985; Geber 1990). This seasonal pattern of allocation has been observed in some dioecious, perennial species in which female plants have greater biomass allocation to reproduction than male plants, but do not have lower growth rates. Female plants accomplish this apparent lack of trade-off by increasing the size of their resource pool relative to that of the males by allocating early-season resources to vegetative growth and delaying reproduction (Delph 1990; Delph et al. 1993). Reduced physiological costs associated with reproduction may be particularly advantageous in species with long-lived roots, like *Rubus*, because excess resources are translocated to roots at the end of the growing season. Greater root storage and growth may facilitate late-season water and nutrient uptake, as well as growth and reproduction in future growing seasons. Although the extent to which this pattern is true for other invasive species is unknown, the majority of herbaceous species reproducing simultaneously with *R. discolor* on similar sites in the PNW are invasive (S. McDowell, pers. obs.). Therefore, perhaps the temporal separation of vegetative growth and reproduction is an important strategy to

accumulate resources early in the growing season, thereby reducing the physiological costs and trade-offs of reproduction, particularly where summer drought limits the growing season.

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CHAPTER 4. DEMOGRAPHIC DYNAMICS AND TRADE-OFFS
OF REPRODUCTION OF AN INVASIVE
AND NONINVASIVE SPECIES OF *RUBUS*

Susan C. L. McDowell and Steven R. Radosevich

4.1 ABSTRACT

Do trade-offs between growth and reproduction differ between invasive and noninvasive plant species and how do such trade-offs relate to population demographics? To answer these questions, we examined the population demographics for the invasive plant species *Rubus discolor* and the noninvasive *R. ursinus* in several populations across multiple stages of invasion. Removal of floral buds from mature canes significantly increased the size of sprouting canes in *R. ursinus*, suggesting a trade-off between current reproduction and growth. Removal of floral buds had no effect on growth of *R. discolor*. *R. ursinus* displayed trade-offs between reproduction (sexual and vegetative) and future growth based on negative correlations between leaf area production and both clonal sprout and seedling production during the previous year. *R. discolor* did not exhibit these trade-offs. We also examined population growth rates in relation to population density and the relative importance of sexual reproduction to population growth. Both species had high population growth rates in low-density populations, but exhibited no growth in high-density populations. A life table response experiment was used to determine the underlying cause for the effect of density on population growth. For *R. ursinus*, lack of population growth in high-density populations was due primarily to increased mortality of clonal sprouts, while for *R. discolor*, it was due to decreased clonal sprout production. Elasticity analysis revealed that clonal growth was much more important than sexual reproduction for population growth of both species. However, the elasticity values for sexual reproduction in *R.*

discolor were greater in high- than low-density populations. This suggests an increased reliance on sexual reproduction in populations that had reached stable sizes, which would enable *R. discolor* to disperse to new sites. Elasticity analyses were also used to simulate the efficacy of various control strategies for *R. discolor*. Control could be attained by reducing clonal sprout production within existing populations while reducing seed production to limit establishment of new populations. In conclusion, the costs of reproduction in the noninvasive *R. ursinus* lead to significant trade-offs between reproduction and growth, which results in almost complete dependence on clonal proliferation for the population growth of this species. Although the invasive *R. discolor* did not exhibit trade-offs between growth and reproduction, its population growth was also almost entirely dependent on clonal spread.

4.2 INTRODUCTION

Invasiveness in plant species has been correlated with the ability to reproduce abundantly and grow rapidly. Reproductive traits associated with invasiveness include the capacity for both sexual and vegetative reproduction, an ability to self-fertilize, a long period during which fruit remains on the plant, a lack of seed dormancy, and multi-seeded fruit (Baker 1965; Reichard and Hamilton 1997; Daehler 1998). Such traits have been related to invasiveness because they confer the capacity to rapidly colonize a site, which is the first stage of the invasion process (Bazzaz 1986; Sakai et al. 2001). Fast growth rates reflect rapid

acquisition and allocation of resources, which enable a species to swiftly establish a population following colonization. While life-history theory predicts a trade-off between high reproduction and growth rates (Stearns 1992), research examining growth, competitive ability, and reproduction in purple loosestrife (*Lythrum salicaria*), a noxious wetland invader, suggests that not all invasive plant species are subject to such trade-offs (Keddy et al. 1994). There is relatively little direct experimental evidence or observational data examining the life-history trade-offs of reproduction in invasive plant species.

The trade-offs between reproduction and growth are due to competition for limited resources within an individual (Stearns 1992). The mechanisms underlying these trade-offs are physiological, where reproductive effort may be expressed as the amount of resources (e.g., carbon) allocated to reproduction at the expense of other functions (Geber 1990; Fox and Stevens 1992; Stearns 1992). The consequences of allocation to reproduction, along with the constraints imposed by resource availability, are expressed at the demographic level and are called the long-term or demographic costs of reproduction (Fox and Stevens 1991; Nicotra 1999). It is at this level that the costs of reproduction may be observed as a decrease of growth or increase of mortality associated with increased reproduction. The balance among these demographic trade-offs of reproduction ultimately determines the population growth rate for a species.

Theory predicts that high allocation of resources to reproduction confers a competitive advantage during site colonization, but that allocation of resources

should shift to vegetative growth after colonization to facilitate population establishment (Sakai et al. 2001). Thus, density-dependent shifts in resource allocation between sexual reproduction and vegetative growth may be expected. However, relatively little is known about density effects on population growth rates of invasive plant species or how these effects compare with those found in native species (Parker 2000). Even less is known about the specific life-history factors that contribute to population growth at different densities as an invasion progresses.

Demographic matrix analysis can be used to assess population growth and the factors that contribute to it. Such analyses have been used to identify the relative contribution of various life-history parameters, such as growth, survival, sexual reproduction, or clonal spread to the population growth rate of a species (e.g., Silvertown et al. 1993; von Groenendal et al. 2000; Caswell 2001).

Furthermore, demographic analyses have valuable management applications. For example, they can be used to identify the most important life-history stage or process to the population growth of a species. Conservation biologists can use this information to guide management decisions with the objective of increasing or sustaining the population size of rare species (e.g., Charron and Gagnon 1991; Maschinski et al. 1997; Kaye et al. 2001), while weed managers can use it to target and decrease the population size of invasive species (e.g., Maxwell et al. 1989; Shea and Kelly 1998; McEvoy and Coombs 1999). A further application of demographic analyses to invasive plant study is they can provide valuable, but often ignored, insights into the connection between theories of plant invasions and

quantitative field data, such as determining whether population growth remains constant across disturbed and undisturbed habitats and throughout the stages of invasion (Parker 2000).

The native, noninvasive *R. ursinus* Cham. and Schlect. (trailing blackberry) and the invasive *R. discolor* Weihe and Nees (also *R. procerus*; Himalayan blackberry) share many life-history characteristics and often grow together in the same sites in the Pacific Northwest United States (PNW). A recent study compared the physiological costs associated with reproduction between these species (McDowell and Turner, 2002). Reproduction in the noninvasive species was associated with increased leaf water stress, which caused early stomatal closure, and with decreased leaf nitrogen concentration, which contributed to lower photosynthetic capacity. However, these physiological costs of reproduction were not observed in the invasive *Rubus*. The objective of the current study is to examine the implications of these physiological costs at the plant and populationscales. We used stage-based demographic models and field experiments and observations to address the following questions: (1) What are the demographic trade-offs between reproduction and growth within plants and how do they differ between invasive and noninvasive species? (2) How do these trade-offs affect the population demographics of these species? and 3) How do population demographics influence invasiveness and potential control strategies of *R. discolor*, the invasive species?

4.3 METHODS

4.3.1 Study species

Rubus ursinus is native to the PNW. Its canes typically grow to about 3 m in length and produce approximately 25 fruit per cane in a year (McDowell and Turner, 2002). *R. ursinus* is considered noninvasive in its native range, where this study took place. *R. discolor* was first introduced to the PNW from Europe via India for fruit production (Kent 1988) and is considered an invasive plant species outside of its native range because it can grow, reproduce, and proliferate following introduction. Canes of *R. discolor* can grow to 10 m in length and produce over 700 fruit in a year (McDowell and Turner, 2002).

Rubus ursinus and *R. discolor* share several morphological and ecological characteristics. They grow together in open to moderately shady sites at low- to mid-elevations in the PNW. Both species are described as biennial, although canes arising from seeds actually develop for three years. Seeds germinate in the winter or early spring and plants remain in a seedling stage for approximately one year. In the following year, canes remain vegetative while nearly all elongation occurs. In the spring of the next season, the canes shed their leaves and develop lateral reproductive shoots. The entire cane senesces following reproduction. Both species have perennial rhizomes that can produce and simultaneously support several clonal clusters that emerge and grow as vegetative canes for one year, and reproduce in the following year. Clonal spread may also occur in both species, as

in several other *Rubus* species, when the tip of a cane roots in the soil, forming a new perennial root crown from which multiple canes may arise (Heslop-Harrison 1959).

4.3.2 Study site

All research was conducted within the McDonald-Dunn Research Forest near Corvallis, OR (44° 40'N, 123° 20'W, ~350m elevation). In 1999, plots were established around existing populations of each species in a recent clearcut for demographic monitoring. Populations were selected to represent either early population colonization (presumed based on low density of the target species) or established populations (high density of the target species). Low-density populations for each species had approximately 6-12 canes each while high-density populations had approximately 45-55 canes each. Eight high- and low-density 5 x 5 m plots were established for *R. discolor* and six high- and low-density 2 x 2 m plots were established for *R. ursinus*. In 2001, six additional plots were established around populations of varying densities of each species to be used for an experiment manipulating sexual reproduction. All populations were located within 0.5 km of each other. Other plant species growing within and near the populations were primarily grasses, native and non-native forbs, poison oak (*Toxicodendron diversilobum*), and young (~10 years old) Oregon white oak (*Quercus garryana*) and Douglas-fir (*Pseudotsuga menziesii*).

4.3.3 Field and laboratory methods

We conducted one census of each population in fall 1999. Two censuses of each population were conducted per year in 2000 and 2001. At those times, one census was done in the spring, before growth of surrounding vegetation obscured seedlings, and another was done in the fall, after most mortality of seedlings and canes for both species occurred. In our initial census (1999), all canes were numbered and tagged, and their position within each plot was mapped. In subsequent censuses, we tagged and mapped new canes and recorded the mortality of previously identified canes.

During a census, canes were classified into one of four stages based on life-history. These stages were seedling, yearling, clonal sprout, or mature (sexually reproductive) canes (Figure 4.1). Yearlings were vegetative canes that had developed from seedlings, while clonal sprouts were vegetative canes that arose from either root sprouting or tip rooting of mature canes. Mature canes developed from both yearlings and from clonal sprouts. In the first census, clonal sprouts and yearlings were distinguished by their position relative to living or senesced mature canes. Our ability to make this distinction was validated by examining root connections in neighboring populations not used in the study. In all subsequent censuses, yearlings and clonal sprouts were easily distinguished because all seedlings were identified and labeled in a previous census. Over the course of this study, we followed the fate of approximately 600 canes of each species. The nonparametric Kruskal Wallis procedure was used to test for differences between



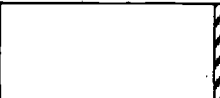







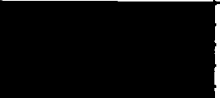
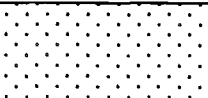


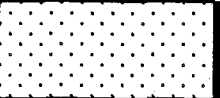

		Year t			
		Seedling	Yearling	Sprout	Mature
Year $(t + 1)$	Seedling				
	Yearling				
	Sprout				
	Mature				

Figure 4.1: A conceptual transition matrix for *R. ursinus* and *R. discolor* showing possible transitions from one year (t) to the next ($t + 1$). The dark shaded rectangles indicate the transitions (a_{ij}) associated with continuance in the same stage from one period to the next, stippled rectangles indicate a_{ij} associated with clonal sprouting and development, and hatched rectangles indicate a_{ij} associated with sexual reproduction and growth of canes originating from seeds. Transitions without shading were not observed.

the demographic parameters, such as production and survival rates of each life-history stage, for both species at each density.

In spring 2001, floral buds were removed from six entire populations of each species to determine the effects of current reproduction on current growth. Prior to bud removal, average cane length was measured to assess the degree of similarity between these six treatment and six control populations. The control populations were randomly selected from those used in the demographic analyses (three each from low- and high-density). Due to the length and the arching, sprawling growth form of *Rubus* canes, total cane length could be accurately measured only by harvesting canes. Therefore, we removed three senesced mature canes from each of the plots, which would not likely affect the growth or survival of plants remaining in the population. Average cane length per population was not significantly different between control and treatment populations (Wilcoxon Signed Ranks $Z = 0.280$, $P = 0.778$ for low-density and $Z = 0.294$, $P = 0.768$ for high-density *R. ursinus*; and Wilcoxon Signed Ranks $Z = 0.643$, $P = 0.530$ for low-density and $Z = 0.472$, $P = 0.647$ for high-density *R. discolor*) and, therefore, the populations were considered similar prior to the floral manipulation. To test for the effect of floral bud removal on growth of clonal sprouts, three randomly selected sprouts were removed from each of the control and manipulated populations in the fall. Total cane length of each sprout was measured in the field. Then, all leaves from each cane were harvested, brought to the lab, and kept in cold storage. Within ~48 hours of harvesting, leaf area of all foliage was determined using a video

image recorder and AgVision software (Decagon Devices, Pullman, WA). Three leaves per cane were randomly selected, placed in a 65 °C oven for 48 hours, and then weighed to the nearest 0.01g. Specific leaf area (SLA; leaf area per unit leaf mass) was calculated from these data. The non-parametric Wilcoxon Signed Ranks test was used to examine the difference between growth parameters of fruit-removal and control populations because these data did not meet the assumptions for a parametric analysis. Demographic and cane size parameters of control populations were used in a Pearson correlation matrix to examine life-history trade-offs between years.

4.3.4 Demographic analyses

The observations made during our field censuses were used to construct stage-based transition matrices with a time interval of one year using the four life-history stages previously described for the *Rubus* species. Separate transition matrices were constructed for each of the populations over each of the transition intervals to follow the form of projection matrix models

$$\mathbf{n}(t + 1) = \mathbf{A} \cdot \mathbf{n}(t)$$

where $\mathbf{n}(t)$ is a vector of the number of individuals in each of the four stages at time t , $\mathbf{n}(t+1)$ is a vector of the number of individuals in each stage at time $t+1$, and \mathbf{A} is a matrix of the transition probabilities (a_{ij}). The a_{ij} for all transitions except fecundity (seedling production) and clonal sprout production were calculated as the proportion of individuals in stage i at time t that contributed to stage j at time $t + 1$

(Figure 4.1). Occasionally, an individual remained in stage i over a transition interval (Figure 4.1), although this was rare. Several possible transition probabilities did not occur (e.g., seedlings in one year could not become mature canes in the next) and were, therefore, entered as 0's in the matrix.

Fecundity and clonal sprouting probabilities were calculated as the number of seedlings and clonal sprouts, respectively, produced in one year relative to the number of mature canes existing in the previous year. Our calculation for fecundity was based on the assumption that all seedlings germinated from seeds produced during the previous year and not from the seed bank. This assumption was reasonable based on the rapid disappearance of *Rubus* seeds from the soil due to predation (Maxwell 1990; Kollmann et al. 1998) and the low germination probability of seeds following long storage or desiccation (Amor 1972; S. McDowell, personal observation).

From each matrix, we calculated the finite rate of population growth, λ , which is the dominant eigenvalue of A . We calculated an average transition matrix for each species in both low- and high-density populations over each transition interval. A value of $\lambda > 1$ indicates a positive population growth rate, $\lambda < 1$ indicates the population is decreasing in size, and $\lambda = 1$ indicates a stable population size. We used an analytical approximation according to Caswell (2000, 2001) for the variance (V) of λ where

$$V(\lambda) \approx \sum_{ij} \sum_{kl} \text{Cov}(a_{ij}, a_{kl}) \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial \lambda}{\partial a_{kl}}$$

for each of these eight average matrices where Cov denotes the covariance between pairs of transition probabilities (a_{ij} and a_{kl}) and $\partial\lambda/\partial a_{ij}$ is a sensitivity term and denotes the effect of a change in a_{ij} on λ . We used t -tests to determine the significance of the difference between λ in low- and high-density populations over a transition interval for each species and between the species and densities for each transition interval.

Given a difference in λ between low- and high-density populations for both species, we used a life table response experiment (LTRE) to determine the contribution (c_{ij}) of each transition to the effect of population density on λ (Levin et al. 1996; Caswell 2000, 2001). The size of each c_{ij} relative to other c_{ij} indicates the relative effect of that transition on the reduction in population growth between low- and high-density populations. In this manner, the LTRE can be used to determine which transitions underlie the population-level effect of density. To calculate the c_{ij} for each species, we first calculated an average transition matrix for all populations at a given density. For *R. ursinus*, we averaged transitions from both transition intervals. However, for *R. discolor*, we only used the transitions from the 2000-2001 interval because we observed no effect of density on λ over the 1999-2000 interval for this species. We then calculated a matrix midway between the high- and low-density population matrices for each species where values in the midway matrix were averages of the corresponding values from the mean low-density and mean high-density matrices. Finally, we estimated the effect of density

on λ by calculating the c_{ij} of each vital rate using the difference between the average matrix elements of high- and low-density populations and using the equation

$$c_{ij} = (a_{ij}^{high} - a_{ij}^{low}) \left(\frac{\partial \lambda}{\partial a_{ij}} \right)$$

where $(a_{ij}^{high} - a_{ij}^{low})$ is the difference (d_{ij}) between the transition values in the low- and high-density matrices and the $\partial \lambda / \partial a_{ij}$ are the sensitivity terms calculated from the matrix midway between the high- and low-density matrices.

4.3.5 Elasticity analysis

The elasticity of each matrix element (e_{ij}) is a measure of the proportional sensitivity of λ to proportional changes in the a_{ij} (de Kroon et al. 1986; de Kroon et al. 2000; Caswell 2001). Using the same average matrices generated for the LTRE, we calculated the e_{ij} for each a_{ij} as

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}$$

for each of the four average matrices. The e_{ij} values for a single matrix sum to 1 and, therefore, it is possible to sum the e_{ij} for transitions associated with the same life-history process (e.g. sexual reproduction or clonal growth) to compare the relative importance of each life-history process to λ (Silvertown et al. 1993; van Groenendael et al. 1994; de Kroon et al. 2000). Using the transition matrix in Figure

4.1, we identified the characteristic life-history processes for the two *Rubus* species, denoting each with a different type of shading. The e_{ij} of all transitions sharing the same type of shading, and therefore, within the same life-history process, were added.

We used numerical manipulations of seedling and clonal sprout production to assess the contribution of these transitions to λ and to assess the impact of potential control strategies. For each of the four average transition matrices, new λ 's were determined by modifying the fecundity transition value by differing proportions (from -90 to + 50%), holding all other transition values constant. Similar analyses were repeated for manipulations of the transition value for clonal sprout production.

4.4 RESULTS

4.4.1 Trade-offs between growth and reproduction

Flower removal from all mature canes within a population only slightly increased cane length production by clonal sprouts for both species. Although the average cane length produced was higher for *R. ursinus* in the flower removal plots relative to the control plots, these differences were not statistically significant at $\alpha = 0.05$ (Table 4.1; low-density Wilcoxon Signed Ranks $Z = 1.244$, $P = 0.095$; high-density Wilcoxon Signed Ranks $Z = 0.524$, $P = 0.300$). Average cane length produced by clonal sprouts was more similar between flower removal and control

Table 4.1: Effects of floral bud removal on average cane length produced, leaf area produced per cane, and average specific leaf area in both low- and high-density populations of *R. ursinus* and *R. discolor*. Values are the mean \pm 1 SE. Tests for a significant treatment effect were made within a population density for each species with the nonparametric Wilcoxon Signed Ranks Test. A * indicates a significant treatment effect at the $\alpha = 0.10$ level of significance and a ** indicates significance at $\alpha = 0.05$.

		<i>R. ursinus</i>		<i>R. discolor</i>	
	Population density	Control	Floral bud removed	Control	Floral bud removed
Cane length produced (cm)	Low	145.5 \pm 23.2	228.2 \pm 45.7*	336.7 \pm 54.1	404.5 \pm 105.7
	High	106.9 \pm 16.5	133.9 \pm 16.9	345.1 \pm 41.9	475.4 \pm 135.0
Leaf area produced (cm ²)	Low	319.6 \pm 72.3	615.0 \pm 176.4**	3492.8 \pm 713.9	3964.6 \pm 939.0
	High	156.0 \pm 16.2	201.9 \pm 20.2*	2877.0 \pm 623.2	4018.6 \pm 1263.1
Specific leaf area (cm ² g ⁻¹)	Low	162.1 \pm 7.7	116.5 \pm 4.7**	88.8 \pm 2.6	64.6 \pm 4.0
	High	130.6 \pm 15.6	111.4 \pm 6.4*	87.1 \pm 3.4	93.8 \pm 2.2**

plots of *R. discolor* (Table 4.1; low-density Wilcoxon Signed Ranks $Z = 0.280$, $P = 0.389$; high-density Wilcoxon Signed Ranks $Z = 0.105$, $P = 0.459$).

In contrast to cane length, leaf growth responded significantly to the flower removal experiment. In low-density populations of *R. ursinus*, flower removal resulted in increased leaf area (Table 4.1; Wilcoxon Signed Ranks $Z = 1.718$, $P = 0.043$) and reduced SLA (Wilcoxon Signed Ranks $Z = 2.667$, $P = 0.004$) compared to control plots. There was a similar response in high-density populations of *R. ursinus*, but the differences were not significant at $\alpha = 0.05$ (Table 4.1; leaf area Wilcoxon Signed Ranks $Z = 1.363$, $P = 0.087$; SLA Wilcoxon Signed Ranks $Z = 1.373$, $P = 0.085$). Flower removal had no statistically significant impact on leaf area produced per cane for *R. discolor* (Table 4.1; low-density Wilcoxon Signed Ranks $Z = 0.280$, $P = 0.389$; high-density Wilcoxon Signed Ranks $Z = 0.943$, $P = 0.173$), but did significantly increase SLA for high-density populations (Wilcoxon Signed Ranks $Z = 2.694$, $P = 0.004$; low-density Wilcoxon Signed Ranks $Z = 1.234$, $P = 0.125$).

Correlations between growth, reproduction, and demographic parameters reveal differences between the species. For *R. ursinus*, leaf area produced per clonal sprout was negatively correlated with both the number of seedlings and the number of sprouts produced per mature cane in the previous year (Table 4.2; $P = 0.028$ and 0.050 , respectively), while there was no such relationship for *R. discolor* (Table 4.3; $P = 0.385$ and 0.695 , respectively). There was a positive correlation between seedling and yearling survival for both species ($P = 0.049$ for *R. ursinus*

Table 4.2: Pearson correlation values between demographic parameters of control populations of the non-invasive *R. ursinus*. All values except survival are per cane and all survival values are the average per plot. An * indicates a significant correlation at $\alpha = 0.05$ and a ** indicates a significant correlation at $\alpha = 0.01$.

	Cane length	Leaf area	Clonal sprouts	Seedlings	Seedling survival	Yearling survival	Clonal sprout survival
Leaf area	0.781**	—					
Clonal sprouts	-0.183	-0.576*	—				
Seedlings	-0.317	-0.630*	0.362	—			
Seedling survival	-0.006	-0.384	0.263	0.212	—		
Yearling survival	0.723**	0.313	-0.065	0.038	0.579*	—	
Clonal sprout survival	-0.226	0.069	-0.796**	-0.052	-0.073	-0.145	—

Table 4.3: Pearson correlation values between demographic parameters of control populations of the invasive *R. discolor*. All values except survival are per cane and all survival values are the average per plot. An * indicates a significant correlation at $\alpha = 0.05$ and a ** indicates a significant correlation at $\alpha = 0.01$.

	Cane length	Leaf area	Clonal sprouts	Seedlings	Seedling survival	Yearling survival	Clonal sprout survival
Leaf area	0.837**	—					
Clonal sprouts	0.347	0.242	—				
Seedlings	-0.111	-0.108	0.250	—			
Seedling survival	-0.516*	-0.465	0.190	0.081	—		
Yearling survival	—	-0.523*	0.270	0.288	0.573*	—	
Clonal sprout survival	0.665**	0.075	-0.147	0.309	0.509	-0.020	0.246

and $P = 0.026$ for *R. discolor*). For *R. discolor*, there was a negative correlation between cane length and both seedling and yearling survival ($P = 0.049$ and $P = 0.007$, respectively) and between leaf area and yearling survival ($P = 0.045$) while there was a positive correlation between cane length production and yearling survival for *R. ursinus* ($P = 0.008$). Leaf area and cane length were positively correlated for both species ($P = 0.003$ for *R. ursinus* and $P < 0.0001$ for *R. discolor*).

4.4.2 Demographic patterns

Populations of the two *Rubus* species exhibited differences in rates of clonal growth, sexual reproduction, and survival and advancement of individuals to the next stage of development. The noninvasive *R. ursinus* produced more seedlings per m² in both high- and low-density populations than the invasive *R. discolor* (Table 4.4; Kruskal Wallis $F = 22.89$, $P < 0.0001$), but the two species produced a similar number of seedlings per mature cane (Kruskal Wallis $F = 4.55$, $P = 0.208$). *R. ursinus* also produced more clonal sprouts per m² and per mature cane than *R. discolor* (Table 4.4; Kruskal Wallis $F = 31.32$, $P < 0.0001$ and $F = 12.04$, $P = 0.007$, respectively). Although *R. discolor* produced fewer seedlings and clonal sprouts, its clonal sprouts and yearlings tended to have higher survival rates than *R. ursinus* (Kruskal Wallis $F = 20.01$, $P < 0.001$ and Kruskal Wallis $F = 6.22$, $P = 0.102$, respectively). Seedling survival was similar between densities for a given species (Kruskal Wallis $F = 2.34$, $P = 0.505$).

Table 4.4: Average demographic parameters ± 1 SE for the non-invasive *R. ursinus* and the invasive *R. discolor*. Measured parameters include the number of seedlings and clonal sprouts produced m^{-2} and mature cane $^{-1}$, the percent of seedlings surviving to the yearling stage, and the percent of yearlings and of clonal sprouts surviving to the mature stage. Values of the same parameter sharing letters are not significantly different at $\alpha = 0.05$ as determined with the nonparametric Kruskal Wallis procedure.

	<i>R. ursinus</i>		<i>R. discolor</i>	
	Low density	High density	Low density	High density
Seedlings m^{-2}	2.0 ± 0.5^a	3.6 ± 0.6^b	0.3 ± 0.1^c	0.7 ± 0.2^c
Clonal sprouts m^{-2}	4.9 ± 0.7^a	14.7 ± 0.7^b	1.1 ± 0.2^c	1.5 ± 0.1^c
Seedlings per mature cane	1.1 ± 0.3^a	0.5 ± 0.1^a	0.3 ± 0.1^a	0.5 ± 0.2^a
Clonal sprouts per mature cane	3.1 ± 0.6^a	2.4 ± 0.3^{ab}	1.4 ± 0.2^{bc}	0.9 ± 0.2^c
Seedling survival (%)	68 ± 16^a	69 ± 9^a	79 ± 9^a	86 ± 7^a
Yearling survival (%)	41 ± 14^a	26 ± 13^a	58 ± 14^a	72 ± 9^a
Clonal sprout survival (%)	70 ± 7^a	41 ± 4^b	93 ± 4^c	98 ± 2^c

4.4.3 Population growth

Rubus ursinus exhibited positive population growth rates over both transition years in both low- and high-density populations (Figure 4.2). However, for high-density populations, λ was very close to 1, suggesting that population size in these established populations was fairly constant. The λ in low-density populations was higher than that of high-density populations over both transition years ($t = -2.144$, $P = 0.034$). The range in λ for low-density *R. ursinus* populations was 1.22 to 1.92 and for high-density populations was 0.72 to 1.22.

The average population growth rate of *R. discolor* was positive over both transition years in both low- and high-density populations, except in high-density populations in 2000-2001 (Figure 4.2). Like *R. ursinus*, *R. discolor* showed an apparently higher λ in low-density populations than in high-density populations in 2000-2001 ($t = -6.353$, $P = 0.003$), but in 1999-2000, λ was approximately equal between the two population densities ($t = 0.705$, $P = 0.262$). Values of λ for *R. discolor* ranged from 0.82 to 1.76 for low-density populations and from 0.70 to 1.41 in high-density populations.

Population growth rates were similar between the species. λ was not significantly different between the species over the 1999-2000 ($t = 0.437$, $P = 0.402$ for low-density and $t = 0.898$, $P = 0.251$ for high-density) or 2000-2001 transition intervals ($t = 1.428$, $P = 0.223$ for low-density and $t = 1.439$, $P = 0.206$ for high-density).

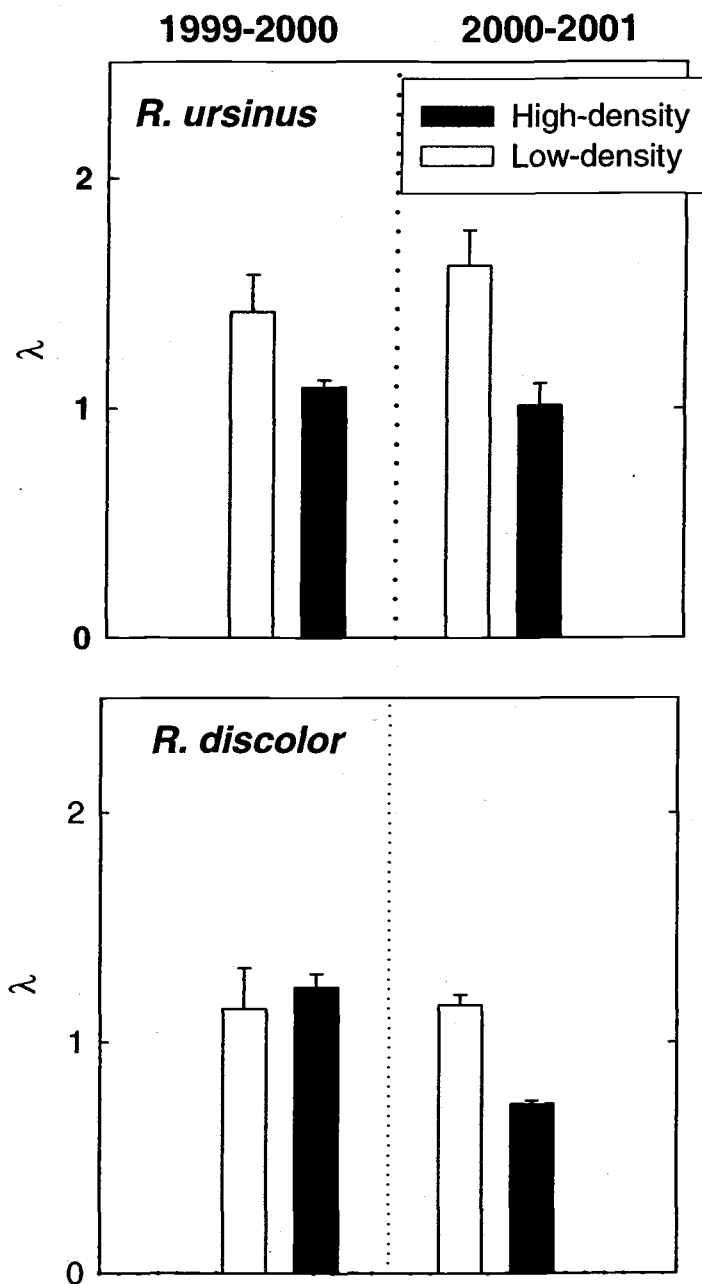


Figure 4.2: The finite rate of increase (λ) for low- (open bars) and high-density (shaded bars) populations of *R. ursinus* and *R. discolor* over each one-year transition interval. Error bars = 1 SE as calculated using an analytical approximation (discussed in the text).

The LTRE revealed that the factors underlying the effects of density on λ were different for each of the species. The transition that contributes the most to the density-dependent change in λ for each species has the largest c_{ij} . The c_{ij} for *R. ursinus* reveal that high population density caused reduced clonal sprout survival and, to a lesser degree, reduced sprout production because the c_{ij} for these transitions were largest (Figure 4.3C). For *R. discolor*, the reduction in λ in high- relative to low-density populations was due to reduced sprout production because this transition had the largest c_{ij} (Figure 4.3D). For *R. ursinus*, the transition elements that yielded the largest d_{ij} between high- and low-density populations did not produce the largest c_{ij} and, therefore, largest effect on λ (Figure 4.3). However, for *R. discolor*, the largest d_{ij} produced the largest c_{ij} (Figure 4.3).

4.4.4 Elasticity analysis

Comparison of the summed elasticity values for each life-history process indicated that clonal growth affected λ relatively more than sexual reproduction for both species in both low and high population densities (Table 4.5). For *R. ursinus*, the contribution of clonal growth and sexual reproduction to λ remained relatively constant between low- and high-density populations (Table 4.5). However, the relative importance of sexual reproduction to λ increased between low- and high-density populations of *R. discolor*. The summed elasticity values for sexual reproduction were slightly higher in *R. discolor* than *R. ursinus*, particularly in

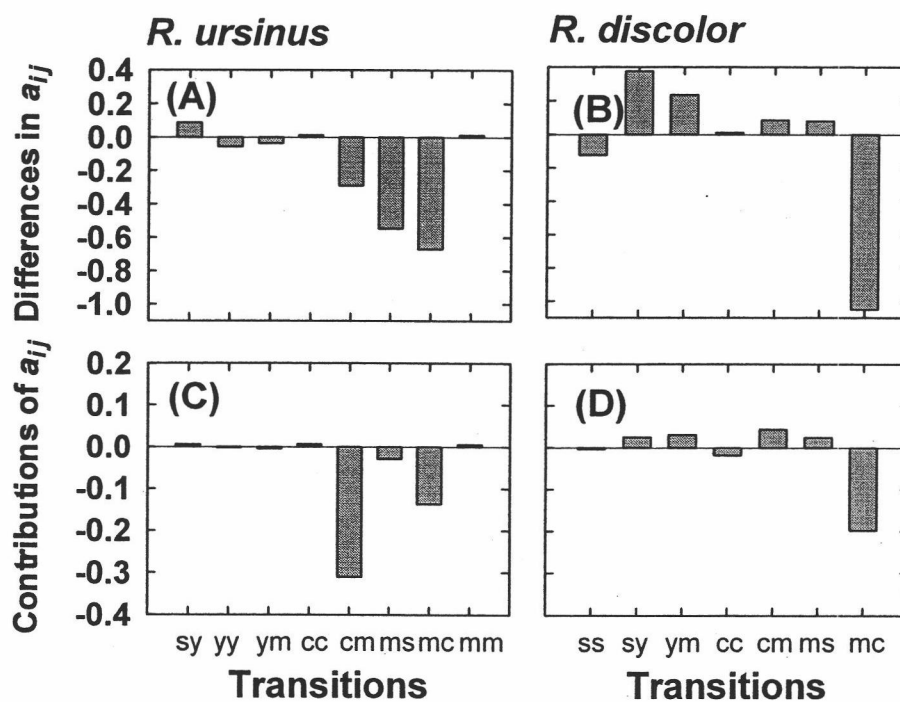


Figure 4.3: The differences (d_{ij}) between transition values (a_{ij}) from the mean low- and mean high-density populations of *R. ursinus* (A) and *R. discolor* (B), and the contribution (c_{ij}) of each of those differences to the density-dependent change in population growth (C and D). Abbreviations for transitions from one year to the next are ss (seedling to seedling), sy (seedling to yearling), yy (yearling to yearling), ym (yearling to mature), cc (clonal sprout to clonal sprout), cm (clonal sprout to mature), ms (fecundity), mc (clonal sprout production), and mm (mature to mature).

Table 4.5: Average summed elasticity values ± 1 SE for sexual reproduction and clonal growth transitions of all low- and high-density populations for each species over both transition years. Transitions included in the sum for sexual reproduction include those depicted with hatched lines in Figure 1 while transitions included in clonal growth include those with dots in Figure 1.

	Mode of reproduction	
	Sexual	Clonal
<i>R. ursinus</i>		
Low density	14 ± 10	85 ± 10
High density	13 ± 6	81 ± 6
<i>R. discolor</i>		
Low density	20 ± 8	71 ± 7
High density	28 ± 8	68 ± 8

high-density populations, but the differences were not significantly different ($t = 0.738$, $P = 0.239$ for low-density populations and $t = 1.243$ and $P = 0.121$ for high-density populations). Similarly, clonal growth contributed slightly more to population growth in *R. ursinus* relative to *R. discolor* ($t = -1.751$, $P = 0.050$ for low-density populations and $t = -1.544$, $P = 0.075$ for high-density populations).

For both species, changes in the average clonal growth transition value had a much larger effect on λ than proportional changes in the average sexual reproduction value, holding all other transition values constant (Figure 4.4). For *R. ursinus*, reducing sexual reproduction by as much as 90% had virtually no impact on λ in both low- and high-density populations while even small changes in clonal growth had a proportionately larger effect on λ . In low-density populations of *R. discolor*, the proportional effects of changes in reproduction and clonal growth on λ were similar to the effects observed in *R. ursinus* (Figure 4.4). However, in high-density populations of *R. discolor*, changes to the sexual reproduction and to the clonal growth transition value produced more similar effects on λ .

In order to effectively control *R. discolor*, population growth must be reduced to values of $\lambda < 1$. In low-density populations, only reductions in clonal sprouting could produce this effect (Figure 4.4). In high-density populations, sexual reproduction would have to be reduced by ~70% while reducing clonal sprouting by as little as 30% would lower λ sufficiently to control population growth within established populations (Figure 4.4).

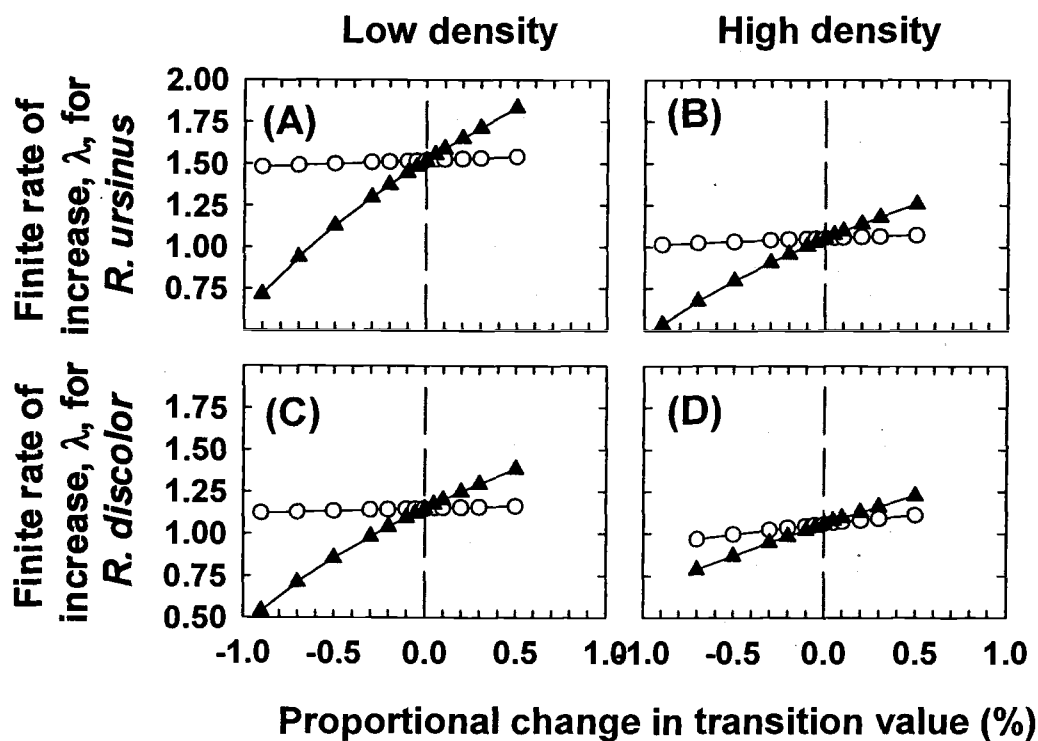


Figure 4.4: The finite rate of increase (λ) for a proportional change in the average transition value of fecundity (circles) and clonal sprout production (triangles) for *R. ursinus* in low- (A) and high-density (B) populations and for *R. discolor* in low- (C) and high- (D) density populations.

Figure 4.5 shows the percent change in λ given a 50% change in either the clonal growth or sexual reproduction transition values for each matrix of each species while holding all other transition values constant. For *R. ursinus*, a 50% reduction in sexual reproduction yielded a small change in λ (always less than 10% change), while a 50% change in clonal growth yielded a minimum 15% change in population growth (Figure 4.5). For *R. discolor*, although a 50% change in clonal growth generally had a larger impact on λ than a 50% change in sexual reproduction, the impact of these two transitions on λ were more similar to each other than their impacts on λ of *R. ursinus* (Figure 4.5). With a 50% change in fecundity, λ changed by as much as 14% while a proportional change in clonal growth changed λ by as little as 7%.

4.5 Discussion

4.5.1 Trade-offs between growth and reproduction

The demographic trade-offs between current sexual reproduction and growth of clonal sprouts within a clone are more evident in the noninvasive *R. ursinus* than in *R. discolor*. In *R. ursinus*, removal of floral buds increased cane length and leaf area produced per cane while decreasing SLA. Although there was a slight growth response of the invasive *R. discolor* clones to floral bud removal, his response was not as significant as that of *R. ursinus*. Trade-offs between current growth and reproduction are typically observed in studies with natural and

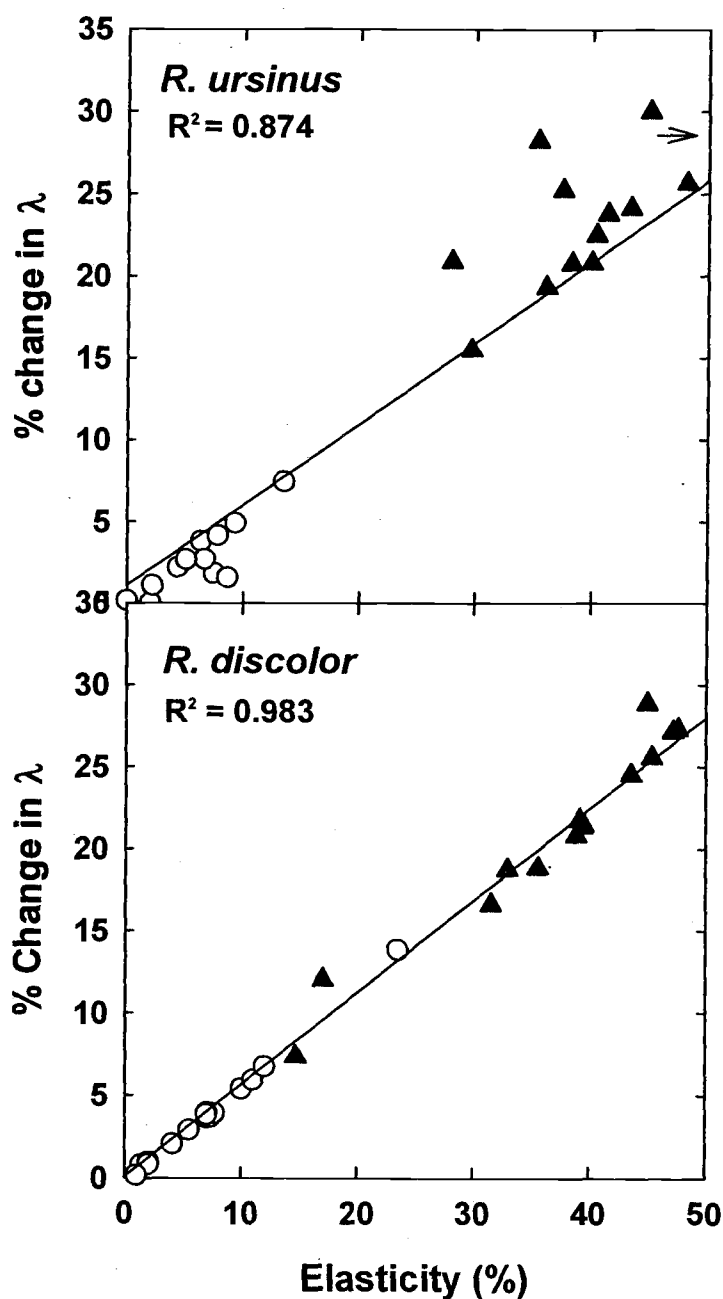


Figure 4.5: The percent change in the finite rate of increase (λ) for a 50% proportional change in fecundity (circles) and clonal sprout production (triangles) versus the elasticity value (e_{ij}) for each fecundity and clonal sprout transition for each matrix of *R. ursinus* and *R. discolor*. For *R. ursinus*, $\lambda = 1.06 + 0.49e_{ij}$ ($P < 0.0001$) and for *R. discolor*, $\lambda = 0.06 + 0.56e_{ij}$ ($P < 0.0001$).

manipulated levels of reproduction for noninvasive species (Fox and Stevens 1991; Newell 1991; Ashman 1992; Nicotra 1999). However, little is known about these trade-offs in an invasive plant species. The apparent trade-offs in *R. ursinus* were driven by the physiological costs associated with reproduction. A previous study of these same two species demonstrated that sexual reproduction caused increased foliar water stress and decreased photosynthetic capacity in *R. ursinus*, leading to a reduction in annual carbon gain (McDowell and Turner, 2002). These effects of reproduction on carbon gain, however, were not apparent in *R. discolor*, thus explaining the apparent lack of growth response to floral bud removal observed in this study. Therefore, the physiological costs of reproduction observed within canes of *R. ursinus* led to demographic trade-offs between reproduction and growth for clonally integrated genets.

In addition to the trade-off between current growth and reproduction, plants may also exhibit a negative relationship between current reproduction and future growth and reproduction. If current and future reproduction draw on the same pool of resources, then current reproduction may deplete available resources for future growth, flower, and fruit development (Stearns 1992). Furthermore, the negative effects of reproduction on current plant size may decrease a plant's capacity to acquire resources in the future (Bloom et al. 1985) or limit the number of meristems that may develop into inflorescences (Geber 1990). The negative correlation between leaf area per *R. ursinus* clonal sprout, which is an indication of the current year's growth, and seedling production, which is an indication of last

year's reproduction, suggests trade-offs may exist between generations in the noninvasive *Rubus*. However, in order for seedling production to have an effect on resource allocation to leaf area production of clonal sprouts, the seeds from which those seedlings germinated must have been produced by mature canes clonally connected to the affected sprouts. It was not possible to determine the seed source of the germinated seedlings and, therefore, this correlation may be spurious. More plausible evidence of trade-offs between generations for this species is the negative relationship between clonal sprout and leaf area production, both of which were produced from clonally integrated canes.

The demographic trade-offs between growth and reproduction within and between generations were not apparent in the invasive *R. discolor*. It is possible that such life-history trade-offs are not be apparent when resources are not limiting, when different life-history functions are dependent upon separate resource pools, or when current allocation does not affect the capacity of a plant to capture resources in the future (Geber 1990; Stearns 1992). The two *Rubus* species examined in this study grow in the same open sites and, therefore, have potential access to equivalent resources. However, *R. discolor* is able to achieve higher photosynthetic rates per unit resource investment of carbon, water, and nitrogen than *R. ursinus* (McDowell, 2002). Therefore, resource availability may be more limiting to carbon gain in *R. ursinus* than in *R. discolor*. Furthermore, the lack of effect of reproduction on carbon gain in *R. discolor* highlights a possible mechanism underlying the apparent lack of trade-offs for this species (McDowell

and Turner, 2002). Sexual reproduction in this environment does not significantly reduce this species' capacity to gain resources.

4.5.2 Demographic patterns

Rates of production and survival of canes within populations were different for the species. *R. ursinus* produced more seedlings and clonal sprouts than *R. discolor*. The higher rate of seedling and clonal sprout production on a ground area basis is due, at least in part, to the smaller size of *R. ursinus* canes; more small canes can grow in a given area than large canes. However, *R. ursinus* also produced more sprouts per mature cane, a value that was standardized for plant size. Although *R. discolor* produced fewer clonal sprouts, they had a higher survival rate than the clonal sprouts of *R. ursinus*. In fact, the noninvasive *R. ursinus* displayed a demographic trade-off between clonal sprout production and survival, as evidenced by the negative correlation between these two parameters. For *R. discolor*, there was a positive, although not significant, relationship between clonal sprout production and survival, suggesting there was no demographic trade-off between these two parameters. Both species demonstrated a positive relationship between seedling and yearling survival, which may indicate that comparable conditions favored survival of both of these life stages in both species.

4.5.3 Population growth and invasiveness

As plant populations become more dense, they eventually reach the site carrying capacity and are subject to density-dependent limits on recruitment of new individuals. In biennial species such as *Rubus*, recruitment may be expected to plateau so that each year, the population merely replaces senescing canes. Clonal plants commonly show constant rates of mortality and recruitment following population establishment so that ramet numbers remain relatively constant (Cook 1985; Hartnett and Bazzaz 1985; Meyer and Schmid 1999). For both *Rubus* species in this study, λ of the high-density populations was approximately equal to 1, suggesting that the populations had, on average, reached a plateau in population growth. Furthermore, λ was higher in low- than in high-density populations, with the exception of *R. discolor* over the 1999-2000 transition. This pattern of population growth is similar to that of other clonal plant species (Barkham 1980; Cooke 1985; Briske and Butler 1989) as well as that of the invasive, but non-clonal, *Cytisus scoparius* (Parker 2000), in response to increasing population density. The LTRE showed that for *R. ursinus*, the effect of density on λ was due to a reduction in clonal sprout survival with increasing population density, while in *R. discolor*, the difference was due to a reduction in clonal sprout production. Reduced clonal sprout production, rather than increased mortality, is a more commonly observed response to increased population density in other clonal plant species (Cook 1985; Briske and Butler 1989), perhaps because sprout mortality

generates a resource cost for the entire clone. The mortality of clonal sprouts in *R. ursinus* was particularly pronounced over the 2000-2001 transition interval, along with mortality of other life-history stages, and may have arisen due to the colder than normal conditions during the winter and much drier than normal spring. *R. discolor*, which is more tolerant of seasonal and diurnal drought than *R. ursinus* (McDowell, 2002; McDowell and Turner, 2002), may have been less adversely affected by the climate over that transition interval.

The elasticity analysis revealed that life stage transitions relating to clonal sprout production and survival were relatively more important to population growth of both species than transitions relating to sexual reproduction. Reducing rates of sexual reproduction of *R. ursinus* via numerical perturbations had essentially no impact on the population growth rate. The population growth rate of *R. discolor* responded similarly to changes of sexual reproduction transition values, particularly at low population densities. A reliance on predominantly clonal growth over sexual reproduction has been observed in other species of *Rubus* (Abrahamson 1975; Maxwell et al. 1993), as well as other plants that reproduce both sexually and clonally (Cook 1985). There are several advantages associated with the reliance on clonal growth for population expansion. Although clonal sprout production may require an initial investment of more resources than sexual reproduction, clonal sprouts eventually contribute positively to the resource balance of the clone (Cook 1985), increase the capacity of the clone to recover from stresses such as defoliation (Price et al. 1992), and increase the potential for the

clone to access unevenly distributed resources, such as light and water (Stuefer et al. 1996). Furthermore, production of clonal sprouts enables a clone to rapidly capture and dominate an area, competitively excluding other species (Pitelka and Ashmun 1985).

Population growth rates within existing populations were similar among the species across both densities and transition intervals. Therefore, invasiveness of *R. discolor* may be due to a greater capacity for dispersal and establishment of new populations than *R. ursinus*, where invasiveness is defined as the ability to rapidly colonize sites, reproduce, and spread to new sites outside of the species' previous range. We did not explicitly measure dispersal or establishment rates of new populations for these species, but we did observe a relative increase of importance of sexual reproduction with population density for *R. discolor*. This increase was due to seedlings germinating in locations within the high-density plots that had not been previously colonized by clonal spread. Sexual reproduction is essential to dispersal and, therefore, promotes colonization of new sites and invasion by this species. The minimal physiological costs associated with sexual reproduction for *R. discolor* (McDowell and Turner, 2002) mean that the importance of sexual reproduction in populations may increase without incurring negative effects on the current population. *R. ursinus* relied almost entirely on clonal spread for population growth and, therefore, had limited dispersal capacity.

4.5.4 Control of *R. discolor*

The elasticity analysis for *R. discolor* may be useful in determining methods for controlling this species. In order to control invasive plant species, population growth needs to be lowered to below $\lambda = 1$, so that population size will decrease. One biological control strategy suggested for several other invasive plant species is to utilize predators or pathogens to reduce flower or seed development (Shea and Kelly 1998; McEvoy and Coombs 1999; Parker 2000). Seed predation could reduce population growth of established populations of *R. discolor* by limiting dispersal, but only if fecundity is reduced by at least 70%. The most effective strategy for controlling population growth for existing populations of *R. discolor* would be to reduce clonal sprouting. The numerical simulations in this study showed that reducing sprout production by as little as 30% could reduce population growth adequately to bring about eventual extinction of existing populations. Control methods that involve mowing canes or applying herbicide to foliage have proven relatively ineffective at controlling this species (reviewed in Hoshovsky 2001), probably because such methods have failed to adequately affect allocation to the belowground portions of the plant. The most effective controls include the introduction of animals that graze canes to the roots from which clonal buds sprout (Amor 1974; Daar 1983) or the use of herbicides applied to cut or burned stems following fruit set (Hoshovsky 2001). The effectiveness of this latter approach is likely due to the translocation of nutrients and, therefore, herbicides from mature canes to the roots prior to senescence. Such management tactics, in addition to

reducing fecundity to limit dispersal and establishment of new populations, could be effective in controlling established populations of this invasive species in the PNW.

4.5.5 Conclusions

The native *R. ursinus* exhibited trade-offs between growth and reproduction both within and between years, while the invasive *R. discolor* showed no such trade-offs. The trade-offs observed in *R. ursinus* can be explained by physiological costs of reproduction, which are not apparent in *R. discolor*. At the demographic level, these trade-offs result in an almost complete reliance on clonal sprouting for population growth in *R. ursinus*. Although *R. discolor* also predominantly relied on clonal sprouting, sexual reproduction became relatively more important for population growth in high-density populations, when dispersal to new sites would be essential to its continued success as an invasive species. Effective control methods for *R. discolor* should focus on curtailing clonal growth within existing populations, but should also address sexual reproduction to minimize dispersal and establishment of new populations.

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CHAPTER 5. SUMMARY

This dissertation was conducted to look at closely related species of *Rubus*, some of which are invasive, to identify differences that may be related to invasive success. The foci of the three research chapters were to address the following questions: 1) What are the differences in photosynthetic capacity and in resource allocation to photosynthesis among the species, and can those differences be used to distinguish between invasive and noninvasive species?; 2) What are the physiological trade-offs to reproduction for one invasive and one noninvasive species and how do these affect reproductive effort?; and 3) Do the differences in leaf-level and whole-plant physiology and reproduction translate into differences in plant and population growth between species?

In Chapter 2, I observed that photosynthetic capacity and resource costs of photosynthesis were significantly different between the invasive and noninvasive species of *Rubus* and could be used to distinguish between the groups of species. The two invasive species used in this study were *R. discolor* (Himalayan blackberry) and *R. laciniatus* (laceleaf blackberry); the two noninvasive species were *R. ursinus* (trailing blackberry) and *R. leucodermis* (black raspberry). The two invasive species had higher photosynthetic capacities and maintained those rates over a longer period of the year than the noninvasive species. The invasive species achieved these higher photosynthetic rates with lower resource investments per unit

resource gain than the noninvasive species. Estimates of photosynthesis relative to resource investment included maximum photosynthetic rate (A_{max}) per unit dark respiration, greater A_{max} per unit leaf nitrogen (photosynthetic nitrogen-use efficiency, PNUE), and greater water-use efficiency as measured by instantaneous rates of A per unit transpiration (A/E) and by integrated A/E inferred from stable carbon isotope ratios ($\delta^{13}C$). On a leaf area basis, however, the invasive species had higher leaf construction costs (CC) and nitrogen content (N) than the noninvasive species. This pattern was probably due to the lower specific leaf area (SLA; leaf area per unit leaf mass) of the invasive species. Discriminant analyses were done to test whether the two invasive species could be distinguished from the two noninvasive species using the measured parameters. The first analysis used leaf characteristics, including CC, N, and SLA, and parameters of photosynthetic capacity estimated from measurements of A in relation to varying pressure of internal leaf CO_2 (A/C_i curves), including A_{max} , maximum carboxylation rate ($V_{c_{max}}$), and the maximum electron transport rate (J_{max}). This analysis clearly distinguished between the groups of species, and identified A_{max} as the most powerful variable for making this distinction. The second discriminant analysis used parameters of photosynthesis relative to resource investments measured in one invasive and one noninvasive species. These parameters included A/R_d , A/E , $\delta^{13}C$, and PNUE. This analysis also made a clear distinction between the species, and identified A/E as the most powerful variable distinguishing these species of *Rubus*.

In Chapter 3, I quantified reproductive effort of one invasive (*R. discolor*) and one noninvasive (*R. ursinus*) species. Reproductive effort is the total amount of resources (in this case, carbon) allocated to reproduction that is diverted from vegetative activity. Calculation of reproductive effort includes the carbon directly allocated to reproduction, as well as any effects of reproduction on foliar photosynthesis. To make these estimates over the lifespan of canes of each species, I removed flower buds from several canes of each species. Then, I made diurnal measurements of A , E , g_s , and leaf water potential (Ψ) on reproductive and non-reproductive canes of each species over the course of their development. I also measured A/C_i curves to estimate photosynthetic capacity, leaf N, and leaf $\delta^{13}\text{C}$ for the reproductive and non-reproductive canes. I used these field measurements to parameterize a photosynthesis model to calculate the effects of reproduction on carbon gain over the lifespan of a cane for each species. I also collected entire canes to measure reproductive and vegetative biomass; leaf area; and C, N, and H_2O allocated to reproductive tissues. I found that the invasive species allocated significantly more biomass, H_2O , C, and N directly to reproductive tissues than the noninvasive species. Canes of the invasive species are much larger than canes of the noninvasive species, so this difference could be due to differences in cane size. Therefore, I also calculated resource allocation relative to cane leaf area and cane biomass. These parameters were still much higher in the invasive species. However, the noninvasive species had significantly reduced leaf N, photosynthetic

capacity, and diurnal rates of A , E , g_s , and Ψ on reproductive relative to non-reproductive canes. The invasive species did not show this effect of reproduction. This reduction in photosynthesis in the noninvasive species was significant enough to result in a higher reproductive effort for this species than the invasive species.

In Chapter 4, I examined the components contributing to population growth for *R. discolor* and *R. ursinus* and the effect of sexual reproduction on cane growth for these two species. I removed floral buds from entire populations of each of these species and found that reproduction significantly reduced growth of clonally connected canes of the noninvasive *R. ursinus*, but had no effect on growth of *R. discolor*. Furthermore, populations of *R. ursinus* exhibited negative trade-offs between reproduction in one season and growth in the following year, as observed by negative correlations between leaf area production and both clonal sprout and seedling production. Populations of *R. discolor* did not exhibit these trade-offs. Elasticity analyses revealed that while clonal growth was much more important to population growth of both of these species than sexual reproduction, the relative importance of sexual reproduction was greater in *R. discolor* than *R. ursinus*. In dense populations of *R. discolor* that had reached stable size, sexual reproduction was relatively more important where it could increase the capacity of this species to disperse to new sites, which is an essential stage of the invasion process. The elasticity values for *R. discolor* were also used to simulate the efficacy of potential control methods for this species. Control methods that focus on reducing clonal

sprout production were predicted to be the most effective means of controlling spread within existing populations of *R. discolor*, while reducing seed production would limit its spread to new populations.

CHAPTER 6. CONCLUSIONS

This dissertation introduces new information to the literature of invasive plants and of reproductive effort. I used novel techniques to quantify reproductive effort in plants and made new observations about the differences between closely related invasive and noninvasive species.

The way in which traits identified for invasive species relate to each other, provide insight into invasiveness for *Rubus* in the PNW. High photosynthetic capacity and water-use efficiency, and low reproductive effort are all components of the resource acquisition and allocation patterns of invasive *Rubus* that probably contribute to their success. The low reproductive effort quantified in Chapter 3 was due, in part, to the high photosynthetic capacity and water-use efficiency quantified in Chapter 2. That is, reproduction did not significantly reduce photosynthetic capacity or water-use efficiency for the invasive *R. discolor* as it did for the noninvasive *R. ursinus*. The roots that enable *R. discolor* to access the nutrients and water necessary to maintain these rates of photosynthetic capacity and water-use efficiency are probably a key component of success of this species. Management and control of this species relies on methods that can affect these roots as well as seed production.

The difference between reproductive effort of the invasive *R. discolor* and the noninvasive *R. ursinus* is a new observation for differences between invasive

and noninvasive species. While there are data suggesting that invasive plants do not appear to be as subject to the trade-offs of allocation between growth and reproduction as noninvasive plants, there has been little elucidation of the mechanisms that may underlie this observation. The detailed quantification of reproductive effort and the effects of reproduction on foliar physiology enabled me to identify a possible mechanism for the success of invasive *Rubus*. Furthermore, my observations of leaf-level physiology related to my observations at the whole plant and population levels. The higher reproductive effort of the noninvasive species translated into reduced growth of clonally connected canes and minimal reliance on sexual reproduction for population growth. The lower reproductive effort of the invasive species resulted in minimal impact of reproduction on cane growth. These data link theory with quantitative field data that may explain those trade-offs.

I applied analyses in new ways to examine my data and to expand conclusions about invasive plants and reproductive effort. First, I used discriminant analysis to identify the most useful traits to distinguish between invasive and noninvasive *Rubus*. Additionally, I developed a method to quantify reproductive effort that overcomes previous difficulties that commonly prevented the calculation of this variable. By removing floral buds from entire plants, I was able to determine, in detail, the effects of reproduction on leaf-level traits relating to carbon acquisition. The application of a photosynthesis model to estimate the lifetime

effects of reproduction on carbon acquisition was a novel use for this type of model. Estimating the effects of reproduction on photosynthesis over long periods has been a challenge in the past, and the methods presented in this dissertation may prove useful to other scientists interested in quantifying reproductive effort.

The results of this dissertation may lead to further research in several areas. Costs of resource acquisition and rates of resource capture could be quantified for other invasive species in other regions. The traits identified with the invasive species in this study may confer success in the climate and conditions of the PNW, although other suites of traits may apply elsewhere. Furthermore, additional research is needed to quantify reproductive effort in both invasive and noninvasive species to determine the extent to which the effects of reproduction on foliar physiology relate to the magnitude of life history trade-offs between growth and reproduction.

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