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Reproductive effort in invasive and non-invasive Rubus

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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 $\delta^{13}C$, 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], $\delta^{13}C$, 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 cane lifetime. 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.

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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 that 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 escape 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 1999; Galen et al. 1999). Foliage typically responds to water stress with stomatal closure, which forces a decline in photosynthetic rates.

The objective of 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?

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 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 ($\delta^{13}C$) were also measured from collected foliage. Field gas exchange measurements and local meteorological data were used to model gross photosynthesis (A_{gross}) over the 2-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}.

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 terminal apex of each lateral shoot.

Field measurements were made at three sites in the McDonald-Dunn Research Forest near Corvallis, Ore. (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, Mass.) and Li-Cor PAR sensors (LI 190SA, Li-Cor, Lincoln, Neb.) 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.

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:

$$\mathrm{RE} = \frac{(B\mathrm{r} + B\mathrm{rv} + R_{\mathrm{ra}}) - Pr}{(B\mathrm{v} + R_{\mathrm{va}}) - Pr} \quad (1)$$

where *B*r is the reproductive biomass, *B*rv is the vegetative biomass attributed to reproduction (e.g., pedicels), R_{ra} is total respiration of flowers and fruit, *P*r is the change in photosynthesis due to reproduction, *B*v is the vegetative biomass, and R_{va} is respiration from the vegetative organs, with each of these input values expressed in g C.

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 Forest sites. Leaf area of all foliage was determined using a video image recorder and AgVision software (Decagon Devices, Pullman, Wash.). 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, first 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 first 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:

$$\mathrm{gCseed}^{-1} = \frac{B\mathrm{r} + B\mathrm{rv} + R_{\mathrm{ra}} - Pr}{\mathrm{no.seeds}} \quad (2)$$

for each of the collected canes.

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 hours. The F_{net} from flowers and fruit during the day was often zero or negative. Reproductive *A*, in units of μmol m^{-2} s^{-1}, was calculated from

$$F_{\mathrm{net}} = A - R_{\mathrm{r}} \quad (3)$$

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*.

Reproduction effects on foliage

We used field measurements and a photosynthesis model to calculate *P*r 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 2 h 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 3–7 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, Ore.).

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 3–6 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 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 μmol m^{-2} 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 s, and then verifying cuvette [CO_2] had stabilized (i.e., coefficient of variation for [CO_2] inside the cuvette <2%) before logging measurements. Measurements were made every 10 s for a total of three measurements per leaf at each of the following cuvette [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 [CO_2]=36.5 Pa (A_{max}) was calculated using non-linear regression between *A* and cuvette [CO_2]. Respiration (*R*) and photosynthetic capacity, which is defined by both the maximum rate of carboxylation (Vc_{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 Vc_{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 hours, 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 laboratory. 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 $\delta^{13}C$ 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 $\delta^{13}C$ 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 Laboratory (Moscow, Idaho). The stable carbon isotope composition was calculated as:

$$\delta^{13}C = (R_{sample}/R_{standard} - 1) \times 1{,}000 \quad (‰) \tag{4}$$

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

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., Vc_{max} and J_{max}).

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:

$$1/E = 1/a(\mathrm{VPD}) + b \tag{5}$$

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:

$$g_s = \frac{g_m}{(1 + g_m \cdot \mathrm{VPD}/E_m)} \tag{6}$$

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.

Photosynthesis biochemistry

The original equations for the photosynthesis model are outlined in Farquhar et al. (1980), with net CO_2 assimilation expressed as:

$$A = V_c - 0.5V_o - R \tag{7}$$

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 Vc_{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 Vc_{max} and J_{max} were calculated following Harley et al. (1992) and Leuning (1997). An average instantaneous A_{gross} in units of μmol m^{-2} s^{-1} was calculated for each day by adding R to Eq. (7).

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} (μmol m^{-2} day^{-1}) was calculated by adding the instantaneous A_{gross} over all daylight hours except for approximately 1.5 h following sunrise and before sunset. Since Vc_{max}, J_{max}, and g_s changed with development stage, the model was run separately for each of those stages (first-year, second-year preflowering, 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 $cane^{-1}$ $lifespan^{-1}$). *P*r 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.

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 RE. A/C_i curves of reproductive and non-reproductive canes were compared with paired *t*-tests of Vc_{max} and J_{max}, where Vc_{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 (α=0.05) was used.

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 1). The [N] in fruit was higher in *R. ursinus* than *R. discolor* (X±SE= 1.80±0.11 g g^{-1} and X±SE=0.87±0.09 g g^{-1}, respectively; t=6.52, P <0.001). However, due to its larger fruit (X±SE=0.08±0.01 g for *R. ursinus* and X±SE= 0.44±0.02 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 1). The fruit of *R. discolor* also contained a greater amount of H_2O than fruit of *R. ursinus* (Table 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 (Fig. 1; F=3.33, P=0.11; F=1.96, P=0.20; F=0.05, P=0.83, respectively). During fruiting, however, afternoon Ψ of reproductive plants fell below that of non-reproductive plants (Fig. 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 (Fig. 1; F=0.78, P=0.40; F=0.12, P=0.74; F=1.41, P=0.36, respectively) or fruiting (Fig. 2; F=0.86, P=0.38; F=0.23, P=0.65; F=0.04, P=0.84, respectively).

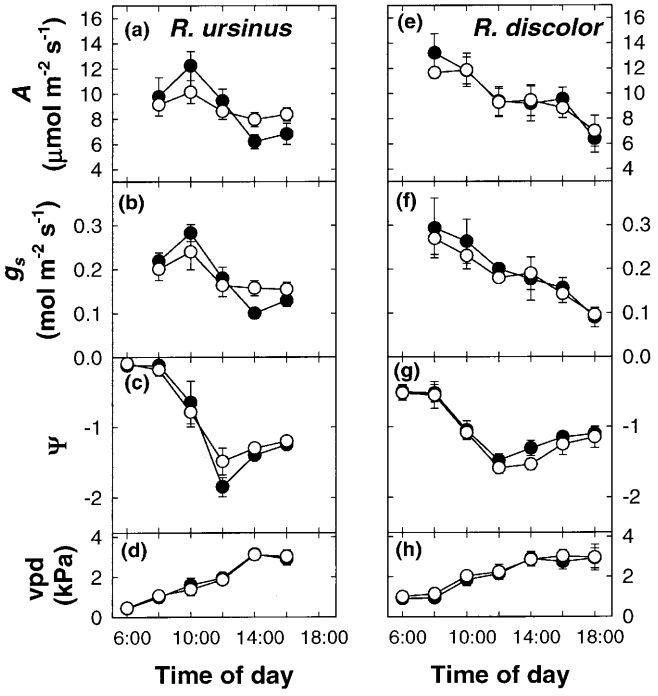

Fig. 1a–h Average diurnal values of *A*, g_s, Ψ, and VPD during the flowering stage for reproductive (*filled circles*) and non-reproductive (*open circles*) canes of *Rubus ursinus* and *R. discolor*. *Error bars*=1 SE

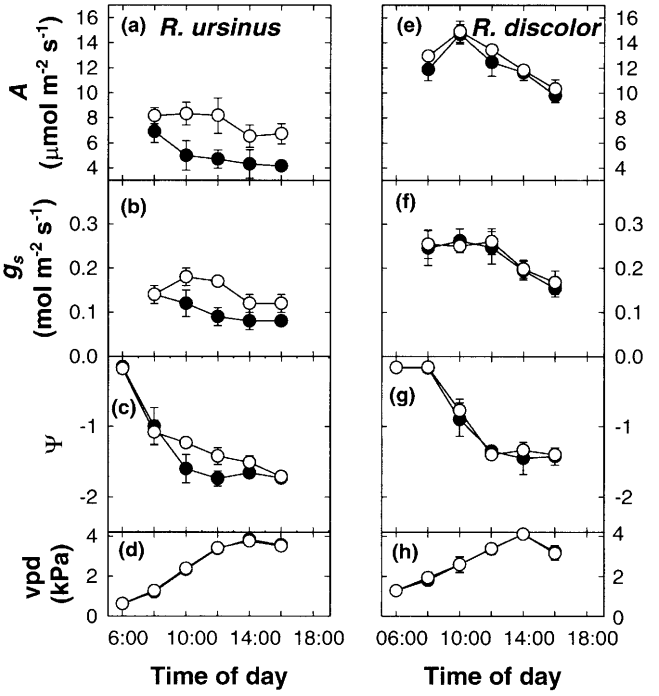

Fig. 2a–h Average diurnal values of *A*, g_s, Ψ, and VPD during the fruiting stage for reproductive (*filled circles*) and non-reproductive (*open circles*) canes of *R. ursinus* and *R. discolor*. *Error bars*= 1 SE

Table 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±1 SE

	Rubus ursinus	*R. discolor*	*t*	*P*
Leaf area per cane (m^2)	0.03±0.004	2.96±0.31	13.80	<0.001
Cane development stages (~ weeks)				
Juvenile	44	44		
Pre-flowering 2nd year	2	8		
Flowering	3.5	3		
Fruiting	6	11.5		
Fruit no. per cane	23.5±4.4	720.3±123.9	–8.25	<0.001
Fruit and flower biomass per cane (g)	2.3±0.4	331.3±56.9	–8.02	<0.001
Fruit and flower biomass per plant biomass (g g^{-1})	0.22±0.03	0.36±0.02	–2.68	0.01
N (g $fruit^{-1}$)	0.16±0.01	0.38±0.04	–5.85	<0.001
H_2O (g $fruit^{-1}$)	0.54±0.05	1.97±0.06	18.33	<0.001
Total reproductive respiration (R_{ra}) (g C $cane^{-1}$ cane $lifespan^{-1}$)	0.56±0.07	58.46±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±0.03	0.007±1.1×10^{-5}	–2.54	0.006
Reproductive effort	0.15±0.002	0.13±0.01	–1.96	0.03

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*=2.41 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.

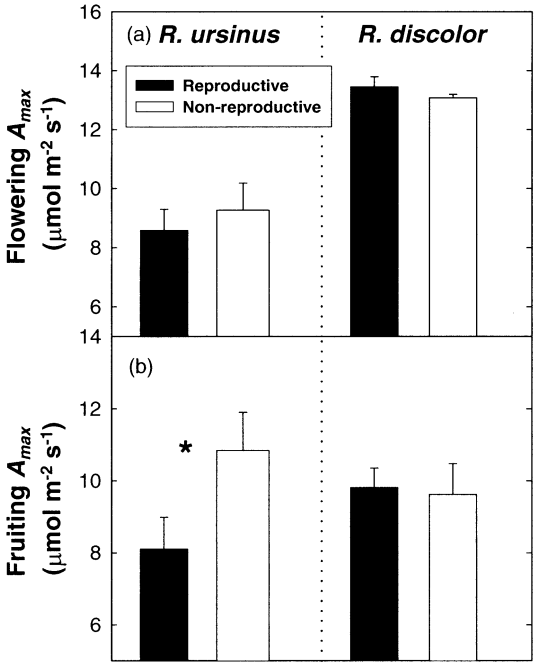

Fig. 3 Average foliar A_{max} for *R. ursinus* and *R. discolor* during flowering (**a**) and fruiting (**b**). The *asterisk* indicates a significant difference at the 0.05 level of significance. *Error bars*=1 SE

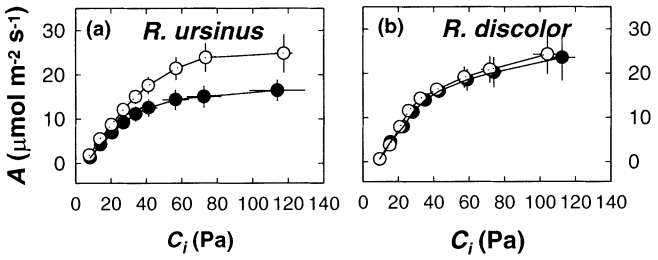

Fig. 4 **a** Average A/C_i curves for reproductive (*filled circles*) and non-reproductive (*open circles*) canes of *R. ursinus* during fruiting stages. **b** Average A/C_i curves for reproductive (*filled circles*) and non-reproductive (*open circles*) canes of *R. discolor* during fruiting stages. *Error bars*=1 SE

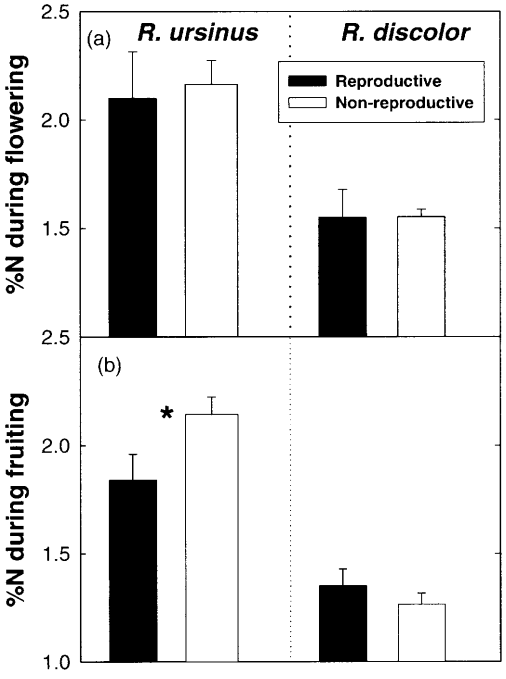

Fig. 5 Average foliar leaf [N] of *R. ursinus* and *R. discolor* during flowering (**a**) and fruiting (**b**). The *asterisk* indicates a significant difference at the 0.05 level of significance. *Error bars*=1 SE

Fruiting 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 (Fig. 3; t=–0.58 and P=0.30). During fruiting, however, A_{max} was significantly lower in reproductive canes of the non-invasive species than in non-reproductive canes (Fig. 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 (Fig. 4). Both Vc_{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 Vc_{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 (Fig. 3; t=–1.03 and P=0.17). However, unlike *R. ursinus*, fruiting had no effect on A/C_i curves of *R. discolor* (Fig. 4) or A_{max} (Fig. 3; t=0.18 and P=0.43). Both Vc_{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 Vc_{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 (Fig. 5; t=–0.26 and P=0.40). However, during fruiting, leaf [N] was lower in foliage of reproductive canes than in non-reproductive canes (Fig. 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 (Fig. 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 $\delta^{13}C$ of reproductive and non-reproductive canes for either *R. ursinus* or *R. discolor* (Fig. 6;

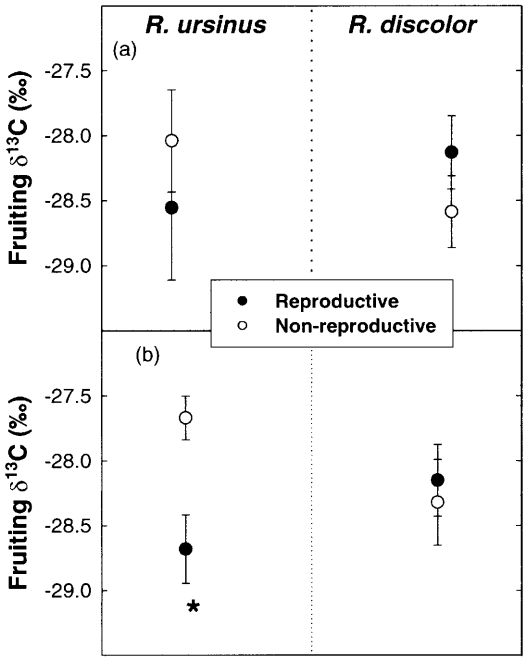

Fig. 6 Average $\delta^{13}C$ values for *R. ursinus* and *R. discolor* foliage during flowering (**a**) and fruiting (**b**). *Filled circles* represent reproductive canes and *open circles* represent non-reproductive canes. The *asterisk* indicates a significant difference at the 0.05 level of significance. *Error bars*=1 SE

t=0.756 and P=0.23; t=–1.16 and P=0.14, respectively). However, during fruiting, $\delta^{13}C$ was significantly higher in non-reproductive than reproductive canes of *R. ursinus* (Fig. 6; t=–3.23 and P=0.005). Reproductive and non-reproductive canes of *R. discolor* shared similar $\delta^{13}C$ during fruiting (Fig. 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 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 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 cane (Table 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 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 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 1). Therefore, reproduction in the non-invasive species diverts relatively more carbon from vegetative activity than in the invasive species.

Discussion

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 few 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 $\delta^{13}C$ 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 $\delta^{13}C$ 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.

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 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 2-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.

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 RE 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 Vc_{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 ranges of 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 photosynthet-

ic 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 process 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* (S. McDowell and S. Radosevich, unpublished data). 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, personal observation). 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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References

Almeida-Cortez JS, Shipley B, Arnason JT (1999) Do plant species high relative growth rates have poorer chemical defenses? Funct Ecol 13:819–827

Antonovics J (1980) Concepts of resource allocation and partitioning in plants. In: Staddon JER (ed) The allocation of individual behavior. Academic Press, New York, pp 1–25

Ashman TL (1994) A dynamic perspective on the physiological cost of reproduction in plants. Am Nat 144:300–316

Bazzaz FA (1986) Life history of colonizing plants: some demographic, genetic, and physiological features. In: Mooney HA, Drake JA (eds) Ecology of biological invasions of North America and Hawaii. Springer, Berlin Heidelberg New York, pp 96–110

Bazzaz FA, Ackerly DD (1992) Reproductive allocation and reproductive effort in plants. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford, pp 1–26

Bazzaz FA, Carlson RW, Harper JL (1979) Contribution to reproductive effort by photosynthesis of flowers and fruits. Nature 279:554–555

Bazzaz FA, Chiarello NR, Coley PD, Pitelka LF (1987) Allocating resources to reproduction and defense. BioScience 37:58–67

Bloom AJ, Chapin FS III, Mooney HA (1985) Resource limitation in plants – an economic approach. Annu Rev Ecol Syst 16:363–392

Blossey B, Notzold R (1995) Evolution of increased competitive ability in invasive non-indigenous plants: a hypothesis. J Ecol 83:887–889

Cohen D (1971) Maximizing final yield when growth is limited by time or by limiting resources. J Theor Biol 33:299–307

Dawson TE, Ehleringer JR (1993) Gender-specific physiology, carbon isotope discrimination, and habitat distribution in box elder, *Acer negundo*. Ecology 74:798–815

Delph LF (1990) Sex-differential resource allocation patterns in the subdioecious shrub *Hebe subalpina*. Ecology 71:1342–1351

Delph LF, Lu Y, Jayne LD (1993) Patterns of resource-allocation in a dioecious *Carex* (Cyperaceae). Am J Bot 80:607–615

Ehleringer JR (1993) Carbon and water relations in desert plants: an isotopic perspective. In: Ehleringer JR, Hall AE, Farquhar GD (eds) Stable isotopes and plant carbon-water relations. Academic Press, San Diego, Calif. pp 155–172

Eis S, Garman EH, Ebell LF (1965) Relation between cone production and diameter increment of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco], grand fir [*Abies grandis* (Dougl.) Lindl.], and western white pine (*Pinus monticola* Dougl.). Can J Bot 43:1553–1559

El-Kassaby YA, Barclay HJ (1992) Cost of reproduction in Douglas-fir. Can J Bot 70:1429–1432

Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London

Farquhar GD, von Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta 149:78–90

Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. Annu Rev Plant Physiol Mol Biol 40:503–537

Field CB, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In: Givnish TJ (ed) On the economy of plant form and function. Cambridge University Press, Cambridge, pp 25–55

Fox JF, Stevens GC (1991) Costs of reproduction in willow: experimental responses vs natural variation. Ecology 72:1013–1023

Galen C (1999) Why do flowers vary? BioScience 49:631–640

Galen C, Dawson TE, Stanton ML (1993) Carpels as leaves: meeting the carbon cost of reproduction in an alpine buttercup. Oecologia 95:187–193

Galen C, Sherry RA, Carroll AB (1999) Are flowers physiological sinks or faucets? Costs and correlates of water use by flowers of *Polemonium viscosum*. Oecologia 188:461–470

Geber MA (1990) The cost of meristem limitation in *Polygonum arenastrum*: negative genetic correlations between fecundity and growth. Evolution 44:799–819

Gehring JL, Monson RK (1994) Sexual differences in gas exchange and response to environmental stress in dioecious *Silene latifolia*. Am J Bot 81:166–174

Gross HL (1972) Crown deterioration and reduced growth associated with excessive seed production by birch. Can J Bot 50:2431–2437

Harley PC, Thomas RB, Reynolds JF, Strain BR (1992) Modeling photosynthesis of cotton grown in elevated CO_2. Plant Cell Environ 15:271–282

Huxman TE, Hamerlynck EP, Smith SD (1999) Reproductive allocation and seed production in *Bromus madritensis* ssp. *rubens* at elevated atmospheric CO_2. Funct Ecol 13:1769–777

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170

Laporte MM Delph LF (1996) Sex-specific physiology and source-sink relations in the dioecious plant *Silene latifolia*. Oecologia 106:63–72

Leuning R (1997) Scaling to a common temperature improves the correlation between the photosynthesis parameters J_{max} and Vc_{max}. J Exp Bot 48:345–47

Marshall JD, Dawson TE, Ehleringer JR (1993) Gender-related differences in gas exchange are not related to host quality in the xylem-tapping mistletoe, *Phoradendron juniperinum* (Viscaceae). Am J Bot 80:641–645

McDowell SCL, McDowell NG, Marshall JD, Hultine K (2000) Carbon and nitrogen allocation to male and female reproduction in Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca*, Pinaceae). Am J Bot 87:539–546

Monteith JL (1995) A reinterpretation of stomatal responses to humidity. Plant Cell Environ 18:357–364

Nicotra AB (1999) Reproductive allocation and the long-term costs of reproduction in *Siparuna grandiflora*, a dioecious tropical shrub. J Ecol 87:138–149

Phillips N, Bond BJ (1999) A micro-power precision amplifier for converting the output of light sensors to a voltage readable by miniature data loggers. Tree Physiol 19:547–549

Reekie EG, Bazzaz FA (1987) Reproductive effort in plants. 1. Carbon allocation to reproduction. Am Nat 129:876–896

Roy J (1990) In search of the characteristics of plant invaders. In: di Castri F, Hansen AJ, Debussche M (eds) Biological invasions in Europe and the Mediterranean Basin. Kluwer Academic, Dordrecht, pp 335–352

Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford

Stephenson AG (1981) Flower and fruit abortion: proximate causes and ultimate functions. Annu Rev Ecol Syst 12:253–279

Tezara W, Mitchell VJ, Driscoll SD, Lawlor DW (1999) Water stress inhibits plant photosynthesis by decreasing coupling factor and ATP. Nature 401:914–917

Thornton P (1998) Regional ecosystem simulation: combining surface-and satellite-based observations to study linkages between terrestrial energy and mass budgets. PhD Dissertation. University of Montana, Montana

Ward JK, Dawson TE, Ehleringer JR (2002) Responses of *Acer negundo* genders to interannual differences in water availability determined from carbon isotope ratios of tree ring cellulose. Tree Physiol 22:339–346

Willis AJ, Thomas MB, Lawton JH (1999) Is the increased vigor of invasive weeds explained by a trade-off between growth and herbivore resistance? Oecologia 120:632–640

Zinselmeier C, Jeong BR, Boyer JS (1999) Starch and the control of kernel number in maize at low water potentials. Plant Physiol 121:25–35