BEARING FRUIT:
POSSIBLE TRADE-OFFS IN BLACK RASPBERRY FRUIT BEHAVIOR

by

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Abstract:

Black raspberry (*Rubus occidentalis*) has recently been highlighted in numerous research studies for its purported health benefits, its market potential as a crop, and its role in native ecosystems. However, we currently understand little about where the species grows and fruits best, how variable its fruiting behavior is, and how its fruit behaviors are influenced by its environment. I compared light, soil pH, soil organic matter, soil texture, and soil nitrogen measurements with data from fruits harvested from 49 black raspberry stands in southeastern Michigan. Linear mixed-effect regressions (LMERs) were used to determine whether any fruit traits show significant relationships with any of these environmental factors. My data suggest black raspberry is a very tolerant species; its ecological role may be broader than originally thought. The plant's fruit traits appear to be highly variable, and this flexibility may have adaptive significance. Canes were significantly more likely to successfully fruit in environments with higher midday light availability and in environments with more neutral, more finely-textured, and less organic matter-rich soils. Light availability and soil texture were strongly positively correlated with fruits and fruit mass produced, and soil texture was also significantly correlated with a taller and narrower average fruit shape and higher average water content. My research suggests that fruiting success may be the most appropriate metric to use when characterizing a fruiting plant's niche. Also, black raspberry appears well-suited for use as a model organism to study life-history ecology in angiosperms.

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Introduction:

Health professionals, agriculturalists, and wildlands managers have recently been paying closer attention to black raspberry (*Rubus occidentalis*) for a number of reasons. Recent research suggests that the very antioxidant-rich black raspberry fruit may possess potent health benefits (Graham & Woodhead 2009, Weber 2007, Dossett *et al.* 2008, Seeram *et al.* 2006, Ozgen *et al.* 2008, Johnson *et al.* 2011). As consumer demand for fresh, healthy berries has increased, prospective and current growers are considering, or considering expanding, black raspberry cultivation (Dossett *et al.* 2008, Feldhake 2002, Dossett & Finn 2010, Weber 2007, Graham & Woodhead 2009).

Black raspberry, while it provides important food and protection to wildlife, also aggressively invades new areas, impeding successful restoration and management (Eastman 1992, B. Grese, per. comm., Hedtcke *et al.* 2009, Krojerova-Prokesova *et al.* 2010, D'hondt *et al.* 2011, Pellerin *et al.* 2010, Taylor 1980, Harmer *et al.* 2010). Native to the Midwestern US and common in disturbed and transitional field and woodland habitats, black raspberry is labeled as, among other things, an early-successional weed, like many of its relatives (Suzuki 1987, Feldhake 2002, Caplan & Yeakley 2006, Dossett & Finn 2010, Bazely *et al.* 1991, Whitney 1984, Fotelli *et al.* 2005, Eastman 1992, Gleason & Cronquist 1963, Hughes & Fahey 1991, Roberts & Gilliam 1995, Krojerova-Prokesova *et al.* 2010, Nowinksa 2010, Caplan & Yeakley 2010, Harmer *et al.* 2010). Despite renewed interest in its fruits, we know little about black raspberry's ecology in the wild beyond such cursory labels.

While natural history texts and other sources frequently delineate "typical" or "ideal" black raspberry habitat (Gleason & Cronquist 1963, Eastman 1992), we lack quantitative information on what that "ideal" habitat is or what range of conditions black raspberry can tolerate (its niche). Moreover, these ideal habitat descriptions are often, though not always, based on presence/absence rather than establishment, survival, growth, or reproduction, most likely because relevant data is unavailable or incomplete. Still, habitats where a species *can grow* and where it *prefers* to grow may not be identical. Similarly, habitats where a species *grows* best and where it *fruits* best may differ. For fleshy-fruiting species like black raspberry, whose ecology depend so heavily on successful fruiting, conditions that impact fruiting success may be *most* salient for defining the species' ideal habitat or tolerance range, and yet we lack data on what factors lead to successful fruiting for black raspberry in the wild. We also lack data on how variable individual black raspberry fruits are in size, shape, or content. Without these data, we cannot know with certainty what environmental factors, if any, influence fruit trait expression. This study is, to my knowledge, the first to quantify black raspberry's tolerance range as measured by where it is able to thrive and fruit successfully.

Fruiting behavior & fitness in Rubus

Fruiting success, I suspect, relates strongly to trade-offs in investment experienced by plants in different environments. For example, *R. vestitus* trades off between investment in growth and in defense in environments with differing resource availabilities by allocating more energy to growth and less to prickles under intense browsing pressure and nutrient scarcity (Gibson *et al.* 1993). Within both physiological and evolutionary limits, every organism trades off throughout its lifetime between competing uses of limited energy and resources. Traits are the result of this differential investment, and we often observe trait variation commensurate with the flexibility inherent in this differential investment. Because variants aren't always equally fit, trade-offs, and the factors that envelop them, likely drive a species' evolution and ecological role.

A few researchers have studied trade-offs in this or other *Rubus* species (Gibson *et al.* 1993, Stapanian 1982, McDowell & Turner 2002, Bazely *et al.* 1991, Funk 2008), but their work focused on trade-offs in growth versus survival or versus non-fruit reproductive outcomes like flowering. However, because fruiting is pivotal (Whitney 1984), and because fruits are energetically expensive to produce (Stapanian 1982), understanding how trade-offs occur during fruiting is paramount to managing a fruiting species like black raspberry successfully. This study sought to discover what factors influence how much energy is invested toward producing fruits, into what that energy gets invested, and how this investment affects the traits of the fruits produced.

A plant's environment largely determines and constrains the plant's physiological condition; unless the local environment has recently changed substantially, we predict a plant will respond to its environment by investing its energy and resources in ways that are most likely to maximize fitness. If resources or energy are highly limited, plants may respond by cutting back investments into otherwise-useful structures or strategies. For example, raspberries may respond to stress by producing fewer fruits (Weber 2007), becoming pricklier (Bazely *et al.* 1991), not growing as tall (Caplan & Yeakley 2006), or aborting fruits or canes (McDowell & Turner 2002). However, the number of "options" available with respect to each trade-off is not unlimited (Funk 2009). If an option is consistently less successful than others, we would expect natural selection to decrease the frequency of or eliminate that option over time. Conversely, substantial variation for a trait may be evidence that natural selection is maintaining a variety of options, each well-suited to certain environmental contexts over evolutionary time. Another aim of this study was to discern what options, or alternative strategies, black raspberry has available for how and how much it will produce fruits.

A plant's physiological state is determined by both biotic factors, such as its genotype (*e.g.* Graham & Woodhead 2009), competition (*e.g.* Bazely *et al.* 1991), herbivory (*e.g.* Krojerova-Prokesova *et al.* 2010) and disease (*e.g.* Weber 2007), and by abiotic factors, such as weather (*e.g.* Weber 2007), light (*e.g.* Feldhake 2002), and soil chemistry (*e.g.* Sikiric *et al.* 2011). We might assume, *a priori*, that all abiotic and biotic factors in a plant's environment exert some influence on how that plant will fruit and what those fruits will be like. However, I hypothesize a relatively small subset of factors will be predominate in importance. This study sought to identify and quantify these dominating factors.

Linking environment to fruiting behavior

In this study, I quantified five abiotic factors that I predicted would be among the most influential factors for determining how black raspberry fruits: irradiance (hereafter "light"), soil pH, soil organic matter (SOM), soil texture, and soil nitrogen. These factors are often-cited determinants of overall *Rubus* well-being, and they are relatively stable, reliably measureable, and diagnostic components of typical *Rubus* environments. Many studies report a possible relationship between these environmental factors and a trend in *Rubus* establishment, survival, growth, or reproduction. However, few have quantified the relationship or have established a causal mechanism, and even fewer have studied these factors' relationship with fruiting success specifically. This study is, as far as I know, the first to assess black raspberry's flexibility in fruiting behavior and to attempt to relate specific behaviors to specific environmental conditions.

When other resources are not limiting, higher light availability is linked to enhanced growth and photosynthetic capacity (Funk 2008, Fotelli *et al.* 2005), water stress and sunscald (Weber 2007, Feldhake 2002), altered establishment or survival (Eastman 1992, Caplan & Yeakley 2006, Weber 2007, Taylor 1980, Fedlhake 2002, Marshall 1937, Bazely *et al.* 1991, Kirby 1980, Roberts & Gilliam 1995, Falkengren-Grerup 1990, Krojerova-Prokesova *et al.* 2010), and enhanced reproductive capacity (McDowell & Turner 2002).

Many studies suggest mildly acidic soils improve *Rubus* establishment (Morrison 1998, Taylor 1980, Hedtcke *et al.* 2009, Pancer-Koteja *et al.* 1998, Hughes & Fahey 1991, Roberts & Gilliam 1995, Sikiric *et al.* 2011, Falkengren-Grerup 1990, Eastman 1992, Pellerin *et al.* 2010; but see Harmer *et al.* 2010, Roberts & Gilliam 1995, Caplan & Yeakley 2006). However, very acidic soils may foster *Rubus* pathogens, cause root damage, or disrupt nutrient balance (Sikiric *et al.* 2011).

Too much or too little soil organic matter may also cause nutrient imbalances in *Rubus*, as well as water stress (Sikiric *et al.* 2011); several studies suggest richer soils support better *Rubus* establishment (Morrison 1998, Caplan & Yeakley 2006, Roberts & Gilliam 1995, Sikiric *et al.* 2011). The right soil texture—sandy, well-drained, but with some water retention—is also widely cited as important for *Rubus* establishment and for proper water and nutrient balance (Morrison 1998, Suzuki 1987, Caplan & Yeakley 2006, McDowell & Turner 2002, Marshall 1937, Hedtcke *et al.* 2009, Weber 2007, Hughes & Fahey 1991, Kirby 1980, Roberts & Gilliam 1995, but see Sikilic *et al.* 2011 and Stapanian 1982).

Finally, nitrogen availability appears to be associated with many *Rubus* traits, such as cane growth rates (Gibson *et. al.* 1993), biomass accumulation (Sikiric *et al.* 2011, Funk 2009), photosynthetic capacity (McDowell & Turner 2002, Fotelli *et al.* 2005), fruit yield (Collison & Slate 1943), internode length and prickle density (Bazely *et al.* 1991), and establishment (Hughes & Fahey 1991).

The black raspberry fruit traits I chose to quantify were: number of fruits produced, fruit mass produced, average fruit size, average fruit shape, and average fruit water content. I predict that these five traits—whose outcomes likely interest prospective black raspberry growers—result from trade-offs encountered by plants. These traits influence fruiting success directly, as measures of fecundity (production and mass production), and indirectly as measures of fruit physical characteristics (average fruit size, shape, and content) that may influence consumption and dispersal likelihood. Because *Rubus* are semi-obligate colonizers, consumption and dispersal are their keys to long-term success (Whitney 1984, Pancer-Koteja *et al.* 1998, Stapanian 1982, D'hondt *et al.* 2011). Plants that trade off investments toward producing more fruits and fruit mass will likely be fitter because they will more successively attract frugivores (fruit-eating organisms). Additionally, plants that can adjust fruit size, shape, and content to maximize their fruits' attractiveness to frugivores relative to the costs of doing so will also be more fit. These traits' relevance to fitness make them particularly important to study.

I sought to answer four questions with this study:

1. In what southern Michigan environments can black raspberry thrive?

2. Does a black raspberry cane's likelihood of successfully fruiting depend on its environment?

3. To what degree are black raspberry fruit traits plastic and thus possibly the result of trade-offs in investment of limited energy and resources?

4. Are black raspberry fruit traits correlated with any environmental factors, providing evidence for an association between environment and fruiting behavior?

Methods:

Site selection and field methods:

In May, 2011, I chose 49 black raspberry stands of comparable size, containing between 75-125 second-year canes, across five University of Michigan properties in southeastern Michigan. Large stands take years to develop, so growing conditions within stands must have been accomodating to *Rubus* establishment. Because stands had similar densities, it is unlikely that intraspecific competition varied substantially between stands. All stands were at least 50 meters apart, as measured by a handheld GPS unit (Garmin 12XL), for two reasons. First, this distance ensured more varied between-stand environmental conditions. Second, because *Rubus* reproduce vegetatively via stolons, including close stands could have led to an overrepresentation of certain genotypes (Bazely *et al.* 1991, Caplan & Yeakley 2010). At the beginning of June, I chose, at random, 12 canes to harvest fruits from within each stand (588 canes total). Care was taken to avoid choosing two canes from the same root mass to avoid non-independent data points (McDowell & Turner 2002). I replaced any canes that died back prior to the end of the flowering season (end of June) with the nearest cane, root collar to root collar (the root collar is the portion of the stem that is even with the soil's surface).

Environmental factors:

I used a handheld light meter (Extech Instruments Light Meter #401025) to estimate light intensity (in footcandles, 1fc=approx. 10.76lux) for each cane. Considerable effort was taken to standardize measurements; all readings were taken directly above a cane's highest leaves, and readings were only taken on clear days between 10am and 2pm, and between 6/6 and 7/5, 2011. Due to frequent, cloudy conditions, I only obtained one light measurement per cane.

Five soil samples (~2kg total) were taken from within each stand in late May by blind-throwing an object into the stand multiple times and taking samples where the object landed. Sample locations were altered slightly, if necessary, to avoid damaging root masses. Soils were air-dried and sieved using a 2.0mm mesh—coarse material (>2.0mm) was removed from subsequent analyses. Unlike light, which was measured for each cane individually, soil characteristics were analyzed at the stand level and applied to all canes within that stand.

A digital-read pH meter (Fisher Scientific Accumet pH meter 915) was used to determine each stand's soil pH. Both a deionized water solution and calcium chloride solution were used, but the two solutions produced highly correlated values (R^2=0.903, p=<0.001), so here I report only the deionized water values, as those seem to be the more typical to report (*e.g.* Sikiric *et al.* 2011). Soil organic matter content was determined using a modified Walkley-Black wet combustion method (Schumacher 2002). Potassium dichromate ($K_2Cr_2O_7$) solution and hydro-sulfuric acid (H_2SO_4) were used to oxidize organic matter within a soil subsample, generating free dichromate ions (Cr_2^+) in proportion to the amount of organic matter present. Dichromate ion concentrations were then measured using a spectrophotometer (Spectronic 20 Genesys).

Each soil's texture was assessed using a soil suspension method similar to Sur & Kukal (1992) and Caplan & Yeakley (2006). Soil subsamples were hydrated with detergent (sodium hexametaphosphate), agitated, and suspended in a glass column. At 40 seconds, and again at two hours, buoyancy readings were taken from each column using a glass hydrometer (Ertco ASTM 152H). Once corrected for ambient conditions, these hydrometer readings were used to calculate the percent of sand (>0.05mm), silt (between 0.002 and 0.05mm), and clay (<0.002mm) particles in each soil (*cf.* Caplan & Yeakley 2006). Because *Rubus* are considered sandy-soil species

(Morrison 1998, Weber 2007), I use the percentage of fine soil particles (silt + clay) as my metric of soil texture (*cf.* Caplan & Yeakley 2006).

Lastly, soil nitrogen availability (in parts per million) was estimated using an automated chemistry analyzer (OI Analytics Flow Solutions 3000) from soil subsamples hydrated with concentrated potassium chloride (KCl) solution. Whether black raspberry shows an uptake preference for nitrate versus ammonium is unclear. Metcalfe *et al.* (2011) found *R. spectabilis* in British Columbia to prefer nitrate strongly, and Hart *et al. (*1992, cited in Caplan & Yeakley 2006) suggest all *Rubus* might share this same preference. However, Nordin *et al.* (2001) observed *R. ideaus* in Sweden taking up equal amounts of both nitrogen forms, and Fraterrigo *et al.* (2011) similarly found no form preference for a Georgian forest community in which *Rubus* were present. I have chosen to represent soil nitrogen in my model as nitrate plus ammonium as though black raspberry has no strong form preference, as has been done in studies of other *Rubus* (*e.g* Caplan & Yeakley 2006, Sikiric *et al.* 2011).

Fruit collection and traits:

I harvested all ripe fruits from each randomly-selected cane three times over the course of the fruiting season (roughly 7/4 through 7/31 in Michigan) (Stapanian 1982, Morden-Moore & Willson 1982, Weber 2007). I did not collect any aborted fruits, because these are unlikely to contribute to fitness as they offer no reward to frugivores (McDowell & Turner 2002, Stapanian 1982). I am certain I was unable to collect all fruits produced for several reasons. First, black raspberry stagger their fruit production, so many fruits probably became available when I was not there to collect them (Morden-Moore & Willson 1982, Stapanian 1982). Also, some ripe fruits were probably consumed by frugivores, although fleshy fruit removal rates are probably low (30% to 3% or less) (Morden-Moore & Willson 1982 and Stapanian 1982). Lastly, physical disturbances, such as wind, can dislodge ripe fruits.

To assess whether I had obtained a comparable number of fruits from each cane, I compared the number of fruits collected from each cane with each cane's number of empty fruit receptacles, which I counted after the third collection period. Black raspberry fruits detach cleanly from their receptacles, which are persistent and recognizable after fruit removal (Eastman 1992). However, aborted fruits sometimes leave their receptacles, receptacles are sometimes broken off by disturbances, and weather-beaten flowers occasionally resemble empty receptacles, so this metric may itself overestimate or, rarely, underestimate true fruit production. Nevertheless, the number of fruits I collected and the number of empty fruit receptacles per cane were strongly correlated (R^2=0.697, p=<0.001), so while the number of fruits collected from each cane may underestimate that cane's true level of fruit production, the metric should allow for fair comparison between canes.

Canes that had no ripe fruits to collect during any collection period were considered non-productive. The total number of fruits collected from each cane served as that cane's measurement of fruit production (# of fruits produced). Collected fruits were stored in Ziploc bags in a chilled, insulated container while in the field to prevent premature decomposition and transpiration weight loss (McDowell & Turner 2002, Feldhake 2002). I weighed each cane's fruits while still in the bag and then subtracted off the weight of the bag to get a total fruit mass produced (in grams) for each cane, which I summed across all three collection periods (McDowell & Turner 2002, Feldhake 2002, Funk 2008). Stapanian (1982) found that average fleshy fruit weight decreases throughout the fruiting season, a pattern I also observed (1st period average=0.422g, 2nd period average= 0.325g, 3rd period average=0.280g). However, any bias created by summing up fruit mass across collection dates is probably minor because most fruits were harvested early in the season (1st date=2,811, 2nd date=1283, 3rd date=145).

I divided each cane's fruit mass produced by the number of fruits produced to obtain an average fruit size (grams/fruit/cane). Total fruit diameter (in millimeters) was measured by lining fruits up, side edge to side edge, on a ruler. For this measurement, black raspberries were assumed to be approximately gumdrop-shaped and approximately circular when viewed from the top-down. I then divided each cane's total fruit mass produced by its total fruit diameter to obtain an average fruit shape (grams/millimeter diameter/cane). Lastly, fruits were oven-dried and reweighed to allow for the dry weight of fruits to be subtracted off the total weight. This difference, the fruit water weight, was divided by fruit total weight, following Funk (2008), to produce an average fruit water content for each cane.

Statistical analyses:

Data were compiled and graphs produced in Microsoft Excel 2010 and R, and statistical analyses were also performed in R (Ver. 2.12.1). I used a General Linear Mixed-Effects Logistic Regression (GLMER) (*glmer* function, binomial link function, package:lme4) to assess whether environmental conditions differed significantly for productive versus non-productive canes (for more information on these types of linear models, see Bolker *et al.* 2008). Stand was included as a random factor to exclude any genetic non-independence caused by including possibly genetically identical individuals as separate data points (D. Childers, pers. comm.). This model included data from all 588 canes.

I also used Linear Mixed-Effects Regressions (LMER, *lmer* function) to assess whether any of the five environmental factors I've quantified are significantly related to any of the five black raspberry fruit traits I measured. These regressions include only canes that successfully fruited (n=343). Light, fruit production, and fruit mass production were log-transformed to better meet linear model assumptions. Results are statistically significant or marginally statistically significant at $p<0.05$ and $0.1>p>0.05$, respectively. Post-hoc influence tests for undue model influence were run on the “stand” random factor using the R influence.ME package (see Nieuwenhuis *et al.* 2009). Influence tests assess the extent to which any one stand influences the parameterization of the entire model. Stands with extreme values draw the model towards their data points considerably more than other stands do and thus may bias the results of a model. One stand was removed from Model 5 (fruit shape) because it failed the influence test (n= 334) (Nieuwenhuis *et al.* 2009). I damaged this stand’s fruits during transport during the first collection period, leading to very irregularly-shaped fruits.

Results

This study's first question asked: "In what southern Michigan environments can black raspberry thrive?" Black raspberry successfully established in areas ranging from full daylight (1325fc, 1fc=approx. 10.76lux) to very heavy shade (4fc), with a median of 48fc (Figure 1A). Black raspberry establishment was most common in mildly acidic soils (median pH ~6.31), but raspberries tolerated a wider range of 5.34-7.63 (Figure 1B). Soils in which black raspberry were observed thriving were generally organic matter rich (minimum 4.2%), with a median of ~7%, although soils as rich as 12.3% were observed (Figure 1C).

In this study, black raspberry only thrived in sandy loam and loamy sand soils; however, soils ranged from very sandy (15.9% silt and clay) to much more finely-textured (65.9% silt and clay) with a median value in the middle of this range (~41.5%) (Figure 1D). Finally, black raspberry appeared tolerant of a range of nitrogen availabilities, establishing successfully in areas with low (2.48ppm nitrate + ammonium) to high nitrogen levels (11.88ppm), with a median value of 5.32ppm nitrogen (Figure 1E).

My study's second question was: "In what southern Michigan environments can black raspberry successfully fruit?" An average cane's log-odds of successfully producing fruits (Table 1A) were significantly higher as light levels increased (between 10am-2pm) (Figure 1A, $B=0.7866$, $p<0.001$), as soil pH became more neutral (Figure 1B, $B=1.0233$, $p=0.002$), and as soil organic matter (SOM) decreased (Figure 1C, $B=-19.9039$, $p=0.023$). Additionally, canes were marginally more likely to fruit as soil texture became finer (Figure 1D, $B=2.894$, $p=0.087$). Whether canes fruited successfully was completely unresponsive to soil nitrogen ($B=-0.0113$, $p=.913$). A cane's probability of fruiting (Figure 3A) could be reasonably predicted to increase, based on my model results, as much as 43% as midday light levels increase from 4fc to 1325fc, 48% as soil pH rises from 5.3-7.6, 38% as SOM concentrations decline from 12.3% to 4.2%, and 33% as soil silt plus clay increases from ~16% to around 66%, assuming all other environmental factors are held constant at their median values in each case.

My third question asked: “To what degree are black raspberry fruit traits plastic?” Canes differed substantially in their fecundity. I harvested between 1 and 105 fruits per cane, with a median value of about 8 fruits (Figure 2A). Likewise, I received 54.28g of fruit mass from one cane, while the median value was just 2.59g of fruit mass per cane, and the minimum observed fruit mass was just 0.08g (Figure 2B). However, both ranges likely underestimate the true variability for these two traits in black raspberry (for details, see Methods). Average fruit size varied from 0.01g to over 1g, with a median fruit size of 0.39g (Figure 2C). Fruit shape varied from relatively flat and wide (0.78mg/mm) to relatively tall and narrow (85.92mg/mm), with the median fruit being about 38mg/mm (Figure 2D). Lastly, fruits ranged from seedy (~41% water by mass) to juicy (~95% water by mass), with the median fruit being about 75% juice (Figure 2E).

This study’s last question asked: “Are black raspberry fruit traits significantly correlated with light or soil conditions?” To assess whether any such correlations exist, linear mixed-effects regressions (LMERs) were run using environmental factors as fixed effects and each fruit trait as a dependent variable. For fruiting canes, light was significantly (B= 0.1136, p=0.009) and soil texture marginally significantly (B=0.6659, p=0.093) positively correlated with the number of fruits produced by canes in this study (Table 1B). Fruit production is predicted by my model to increase by about 5 fruits, on average, as light increases from 4fc to 1325fc and soil silt plus clay increases from ~16% to ~66% (Figure 3B), all other factors held constant at their medians. SOM

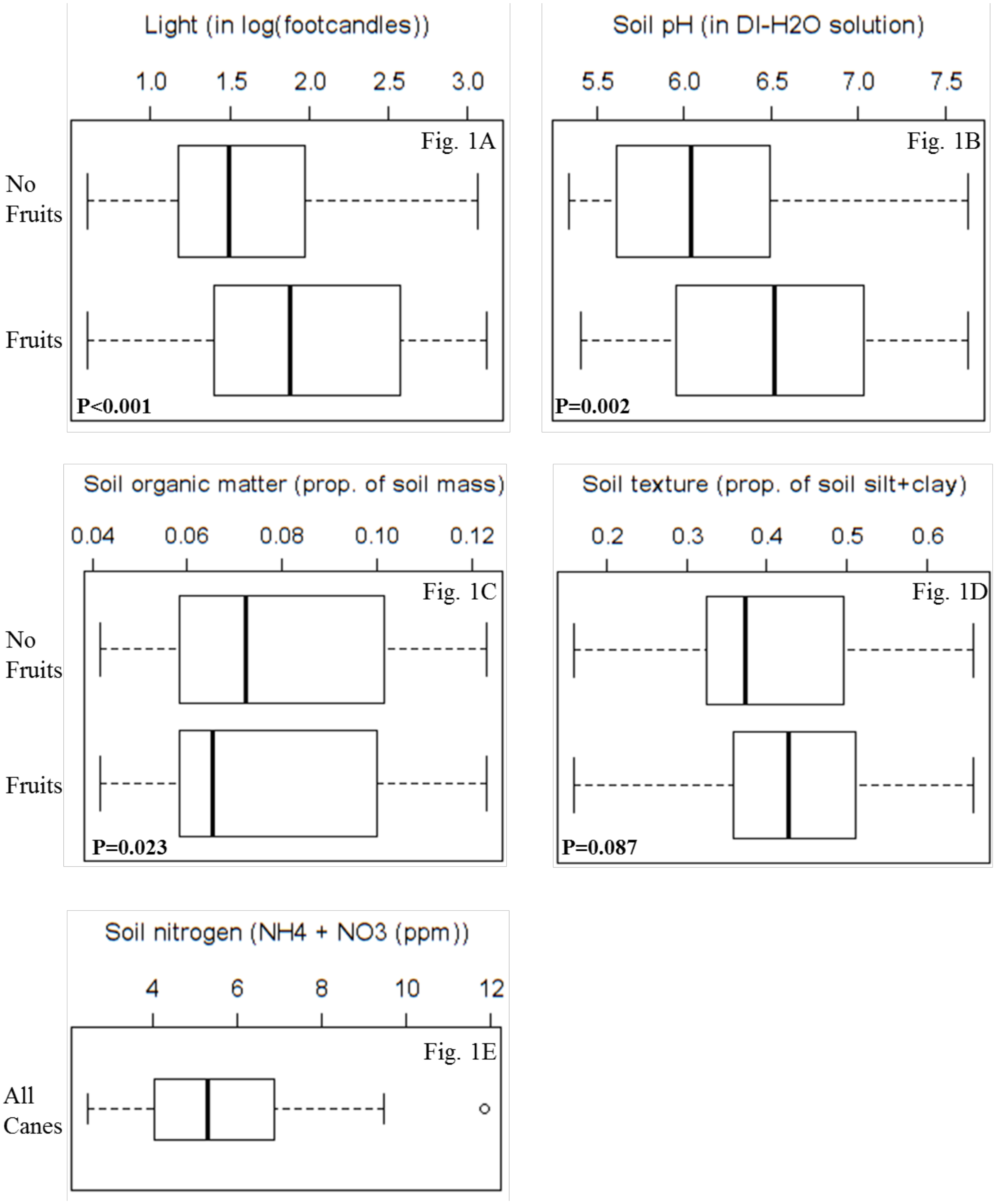
(B=-1.4432, p=.49), soil nitrogen (B=.0222, p=.95) and soil pH (B=-0.0006, p=.994) were uncorrelated with fruit production (Table 1B).

Model 3's results (Table 1C) for fruit mass produced were similar to those for fruits produced; light was significantly (B=.1235, p=0.008) and soil texture marginally significantly (B=.8615, p=0.083) positively correlated with fruit mass produced. The model suggests fruit mass per cane might be increased by up to 1.5g as light levels increase from 4fc to 1325fc and by up to 2.0g as soil silt plus clay proportions increase from 16% to 66 (Figure 3C). SOM (B=-1.405, p=0.59), nitrogen (B=.0161, p=0.565), and soil pH (B=-0.0141, p=.876) were unpredictive of fruit mass produced (Table 1C).

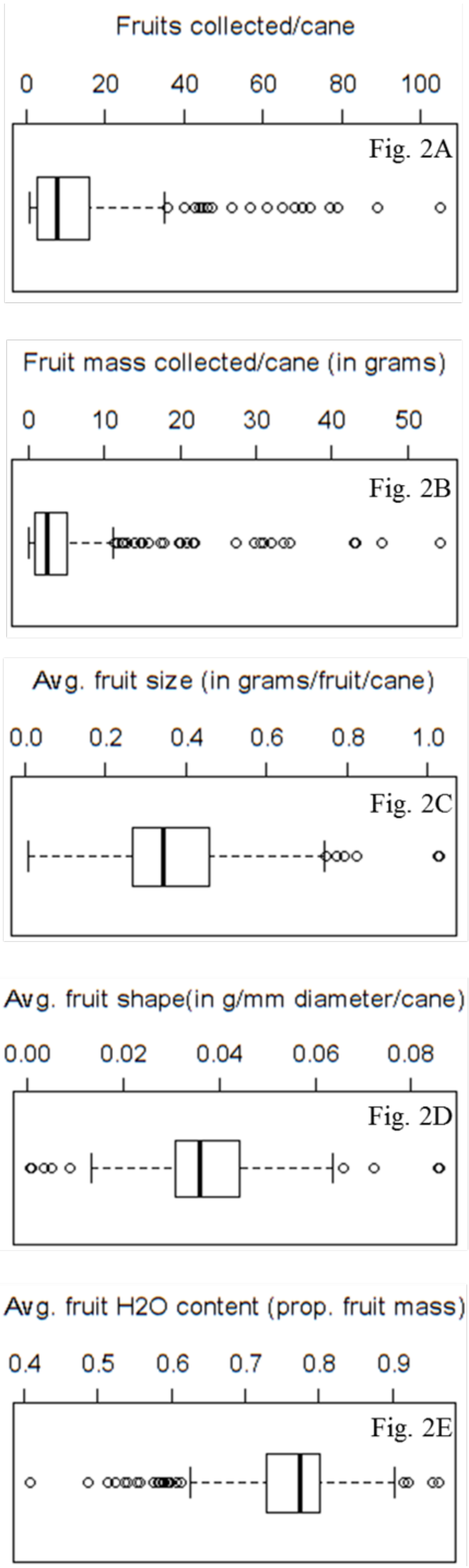
Although no factors were significant (p<0.1), Model 4's results (Table 1D) show some evidence for a positive relationship between average fruit size and soil nitrogen (B=.0124, p=.151), and soil texture (B=.1932, p=.203). The model suggests that increases of up to 11cg in average fruit size might be possible as soil nitrogen increases from ~2.8ppm to 11.88ppm, and a similar increase of up to 10cg is possible as soil texture increases from 16% silt plus clay to 66% (Figure 3D). However, these results are by no means conclusive. Light (B=0.0105, p=.381), soil pH (B=.0144, p=.603) and SOM (B=-.4455, p=.576) were unrelated to average fruit size.

Fruit shape (Table 1E) is marginally significantly positively related to soil texture (B=0.0172, p=0.1), with fruit shape predicted to become taller and narrower by up to 9mg/mm as soil texture increases from 16% to 66% silt plus clay (Figure 1E). However, the model also suggests that soil pH, while not significant (B=.0027, p=.183), may also be moderately predictive of fruit shape. Predicted increases of up to 6mg/mm may be possible as soil pH increases from ~5.5 to ~7.5 (Figure 3E), but this is not a conclusive result. Light (B=.0009, p=.28), SOM (B=.0555, p=.285), and soil nitrogen (B=.0005, p=.434) were not statistically well-correlated with fruit shape.

Lastly, a fruit's average water content (Table 1F) is significantly positively correlated with soil texture (B=0.1528, p=.032), with fruits predicted to become up to 8% wetter by mass as soil texture increases from 16% to 66% silt plus clay (Figure 3F). Additionally, soil pH (B=0.019, p=.142), and soil nitrogen (B=0.0047, p=.246) are moderately, though not quite significantly, correlated with fruit water content, with predicted increases of up to 4% each as soil pH rises from 5.5-7.5 or as nitrogen increases from 2.8pmm to 11.9ppm (Figure 3F). Light (B=0.0003, p=.966) and SOM (B=-0.1006, p=.787) are uncorrelated with average fruit water content.



Figures 1A-E: Canes that successfully produced at least one fruit were observed growing in environments with significantly higher light availability than unproductive canes (A). Productive canes were also observed growing in significantly more neutral (B), more finely-textured (C), and less organic matter-rich (D) soils than canes that did not produce any fruits. Nitrogen availability did not differ significantly between the two groups (E). Overall, black raspberry is highly tolerant of a range of environments. P-values were generated using a General Linear Mixed-Effects Logistic Regression (GLMER, Table 1A). 1 footcandle=approx.. 10.76 lux. DI stands for "Deionized."



Figures 2A-E: Black raspberry fruiting behavior appears to be highly plastic. Canes differ substantially in their fecundity, both in terms of fruit mass produced (B) and in terms of number of fruits produced (A). Canes also differ considerably in the average size (C), shape (D), and water content (E) of their individual fruits. This plasticity may be of adaptive significance. Each data point in each of these boxplots is an individual cane (n=588).

Table 1A:

Environmental Factors	B estimate	Standard Error	Z Statistic	p-value
Intercept	-7.0472	2.039	-3.456	<0.001
Log(light)	0.7866	0.1993	3.947	**<0.001**
Soil pH	1.0233	0.3239	3.16	**0.002**
Soil organic matter	-19.904	8.7747	-2.268	**0.023**
Soil texture	2.894	1.6895	1.713	*0.087*
Soil nitrogen	-0.0113	0.1031	-0.11	0.913

Fruit trait: Log(odds of producing at least one fruit)
(GLMER, Model 1, n=588)

Table 1B:

Environmental Factors	B estimate	Standard Error	T Statistic	p-value
Intercept	0.3999	0.4541	0.881	0.379
Log(light)	0.11364	0.0423	2.648	**0.009**
Soil pH	-0.0006	0.0715	-0.008	0.994
Soil organic matter	-1.4432	2.0858	-0.692	0.49
Soil texture	0.66592	0.3956	1.683	*0.093*
Soil nitrogen	-0.0014	0.0222	-0.063	0.95

Fruit trait: Fruits produced
(log(# of fruits collected)) (LMER, Model 2, n=343)

Table 1C:

Environmental Factors	B estimate	Standard Error	T Statistic	p-value
Intercept	-0.214	0.5684	-0.376	0.707
Log(light)	0.1235	0.0463	2.668	**0.008**
Soil pH	-0.0141	0.09	-0.157	0.876
Soil organic matter	-1.405	2.604	-0.54	0.59
Soil texture	0.8615	0.4958	1.738	*0.083*
Soil nitrogen	0.0161	0.0279	0.575	0.565

Fruit trait: Fruit mass produced
(log(grams of fruit/cane)) (LMER, Model 3, n=343)

Table 1D:

Environmental Factors	B estimate	Standard Error	T Statistic	p-value
Intercept	0.1295	0.174	0.744	0.457
Log(light)	0.0105	0.0119	0.877	0.381
Soil pH	0.0144	0.0276	0.521	0.603
Soil organic matter	-0.4455	0.7954	-0.56	0.576
Soil texture	0.1932	0.1516	1.274	0.203
Soil nitrogen	0.0124	0.0086	1.44	0.151

Fruit trait: Average fruit size
(grams of fruit mass/fruit/cane) (LMER, Model 4, n=343)

Table 1E:

Environmental Factors	B estimate	Standard Error	T Statistic	p-value
Intercept	0.0132	0.0122	1.079	0.281
Log(light)	0.0009	0.0008	1.082	0.28
Soil pH	0.0027	0.002	1.333	0.183
Soil organic matter	-0.0595	0.0555	-1.071	0.285
Soil texture	0.0172	0.0104	1.652	*0.1*
Soil nitrogen	0.0005	0.0006	0.783	0.434

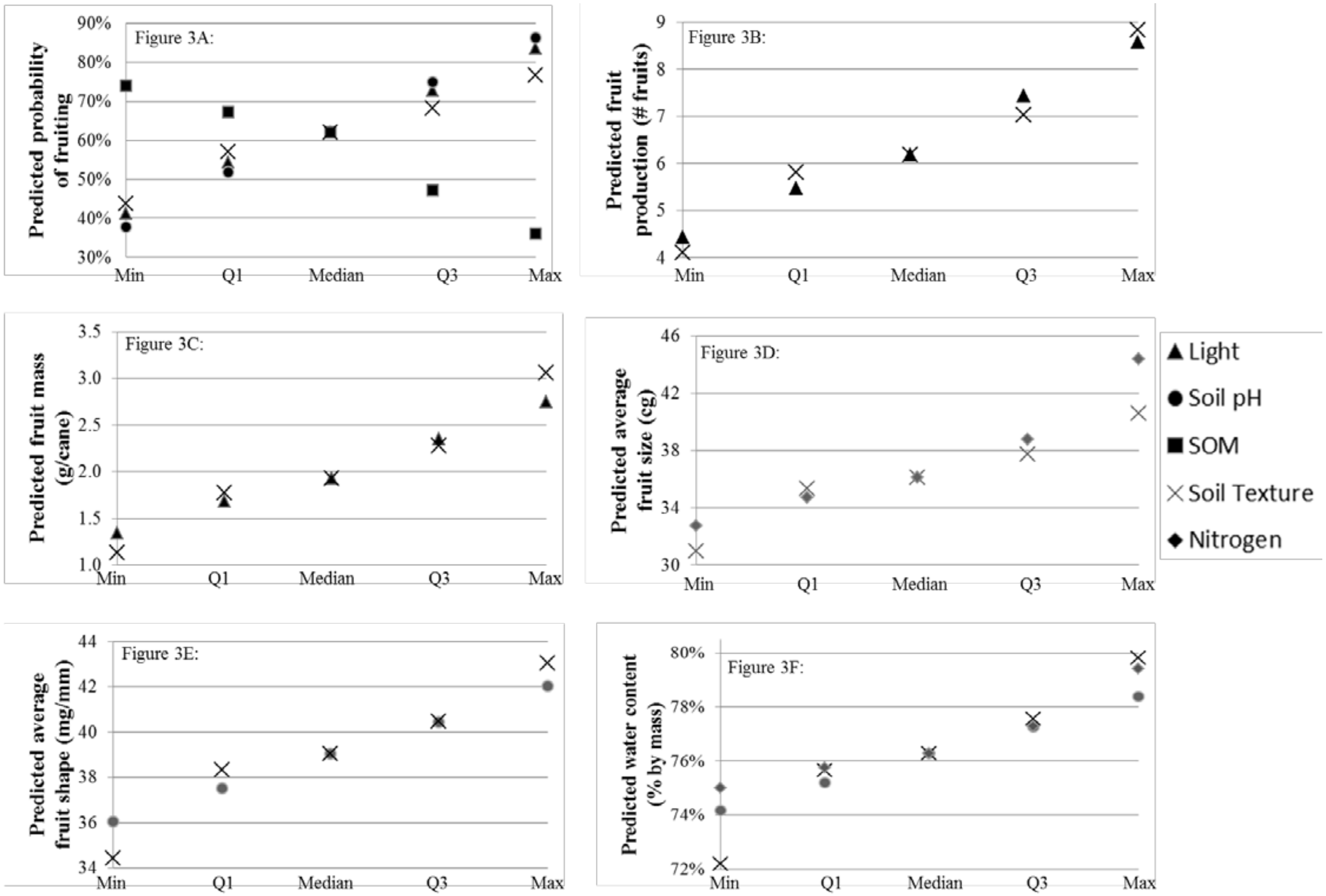
Fruit trait: Average fruit shape
(grams of fruit mass/mm fruit diameter/cane) (LMER, Model 5, n=334)

Table 1F:

Environmental Factors	B estimate	Standard Error	T Statistic	p-value
Intercept	0.5552	0.0814	6.818	<0.001
Log(light)	0.0003	0.006	0.043	0.966
Soil pH	0.019	0.0129	1.474	0.142
Soil organic matter	-0.1006	0.3726	-0.27	0.787
Soil texture	0.1528	0.071	2.152	**0.032**
Soil nitrogen	0.0047	0.004	1.161	0.246

Fruit trait: Fruit water content
(% of fruit mass) (LMER, Model 6, n=343)

Tables 1A-F: Light, pH, organic matter, and soil texture were all significantly correlated with a cane's log-odds of fruiting (A). Black raspberry fruit production increased significantly as light and soil texture (soil silt plus clay) increased (B). Fruit mass was significantly positively correlated with light and soil fineness as well (C). Average fruit size was not strongly correlated with any of the environmental factors assessed here (D). Black raspberry fruits became significantly taller and narrower as soil fineness increased (E). As soils became finer, water constituted a significantly larger percentage of black raspberry fruit mass (F). Overall, soil texture was the single best predictor for black raspberry fruiting behavior of the factors studied here. Bolded p-values are significant at alpha=0.05. Italicized p-values are marginally significant at alpha=0.1. GLMER stands for "General Linear Mixed-Effects Logistic Regression." LMER stands for "Linear Mixed-Effects Regression." Beta estimates are unstandardized.



Figures 3A-F:When all other environmental factors are held constant at their medians, a raspberry cane's probability of fruiting is predicted to increase as light, soil texture (soil silt plus clay) , and soil pH increase, and as soil organic matter (SOM) decreases (A). Fruit production per cane is predicted to increase substantially in sites with finer soil texture and more light (B). Fruit mass per cane is expected to rise significantly in sites with higher light levels and finer soil texture (C). Average fruit size is predicted to increase with increasing soil nitrogen and soil fineness, but these patterns are not significant (D). Fruits are expected to be significantly taller and narrower in finer soils. Fruit shape is also predicted to increase with soil pH, though not significantly so (E). Fruit water weight is expected to increase significantly with soil fineness and non-significantly with soil pH and nitrogen (F). Q1 and Q3 stand for "Quartile 1" and "Quartile 3." The x-axes are based on observed environmental values; extrapolation outside of the range of environmental contexts reported here is not advisable. Darkened symbols are significant at alpha=0.1. Grayed symbols are non-significant but have p-values<0.25.

Discussion

I sought to answer four questions with this research: 1. Where is black raspberry able to thrive in southern Michigan? 2. Do black raspberry plants fruit more successfully in certain habitats? 3. Is black raspberry fruiting behavior flexible? and 4. Is black raspberry fruiting behavior associated with environmental factors and, if so, how?

Question 1: In what southern Michigan environments can black raspberry thrive?

To my knowledge, I am the first researcher to assess black raspberry's realized niche quantitatively in southeastern Michigan for light, soil pH, soil organic matter, soil texture, and soil nitrogen availability. Across all stands, I observed black raspberry growing in environments ranging from open and well-lit (1325fc, 1fx=approx. 10.76lux, light levels as of between 10am-2pm in June) to very heavily shaded (4fc); the median light condition (~48fc) was characteristic of a closed forest understory. These results corroborate other researchers' observations that *Rubus* are generally well-adapted to shady environments like forest edges and interiors (Eastman 1992, Taylor 1980, Caplan & Yeakley 2006, Feldhake 2002, Gleason & Cronquist 1963, Nowinska 2010, Harmer *et al.* 2010). Also, while black raspberry does not appear to require a sunny environment, my data suggest it can tolerate high light levels, like many other *Rubus* (Suzuki 1987, Falkengren-Grerup 1990, Fotelli *et al.* 2005, Roberts & Gilliam 1995, Kirby 1980, Marshall 1937, Feldhake 2002, Krojerova-Prokesova *et al.* 2010).

With our collective knowledge of *Rubus* responses to light, including my data, in mind, I question whether a broad label of "early-successional species" for black raspberry is appropriate. The species appears to cope, at least, with life in the mature forest understory. Feldhake (2002) argued black raspberry's diagnostic and adjustable glaucous coating on its stems and leaves help protect the plant from excessive light, suggesting to me that the plant is adapted to a wide range of light levels. That cultivated black raspberry plants will occasionally suffer sunscald from full sun exposure further suggests that black raspberry is even better-suited to lower, rather than higher, light levels (Weber 2007). Eastman (1992) agreed, writing that black raspberry is ideally well-adapted to moderate light levels.

If these assertions are true, black raspberry may be more like its mid-successional relatives in *Rubus* than its early-successional ones. Taylor's (1980) *R. vestitus* grew predominantly in heavily shaded areas (no greater than 70% of full sunlight) in Britain, *R. palmatus* prospered in secondary forests in Japan (Suzuki 1987), and Caplan & Yeakley (2006) even observed the invasive and shade-intolerant *R. armeniacus* regularly growing in Oregon forests with greater than 50% canopy cover. Black raspberry may be just as ecologically important as an understory shrub as it is as an early colonizer, like these other *Rubus*.

Black raspberry appears to grow successfully only in mildly acidic to neutral soils (pH 5.3-7.6) in southeastern Michigan, matching qualitative assessments reported elsewhere (Eastman 1992, Hedtcke *et al.* 2009, Morrison 1998). This range is somewhat smaller than those reported for other *Rubus*, but that may be simply a sampling artifact of my study. Still, I tentatively hypothesize a preference for a soil pH between roughly 5.5 and 7.5 may be a genus-wide characteristic, although little quantitative data is available to support this notion (but see Harmer *et al.* 2010). Caplan & Yeakley (2006) observed *R. armeniacus* in Oregon only in soils with a pH of 4.2-6.3, but this species appeared to prefer soils toward the higher end of this range. Other studies only note a correlation between *Rubus* presence/absence and soil acidity. *R. vestitus* in Britain grew in soils with a pH of 3.8-7.6 but preferred the more mildly acidic soils in this range (Taylor 1980), and *R. hirtus* in Poland grew predominantly on mildly acidic soils (Pancer-Koteja *et al.* 1998), as did *R. ideaus* and *R. allegheniensis* in New Hampshire (Hughes &

Fahey 1991), *R. ideaus* in Sweden (Falkengren-Grerup 1990), and *R. ideaus* and *R. fructicosus* in eastern France (Pellerin *et al.* 2010). Also, Roberts & Gilliam (1995) found *Rubus* spp. preferentially colonized sites in northern Michigan that were the most neutral (pH ~5.5) of those studied, and Sikiric *et al.* (2011) report that *R. ideaus* in Serbia suffer from disrupted water balance, nutrient deficiencies, and decreased productivity when grown in soils below pH 5.6. These proposed links between soil pH and *Rubus* physiology may be true for black raspberry as well.

Michigan black raspberries appear to establish best in organic matter-rich soils (~4% to ~12.5% of soil mass). The literature suggests *Rubus* are effective colonizers of disturbed sites, which tend to be high in soil organic matter (SOM) (Sikiric *et al.* 2011, Morrison 1998, Caplan & Yeakley 2006, Roberts & Gilliam 1995), and I conclude that black raspberry is not substantially different in this regard. *Rubus* spp. preferentially colonized disturbed, mesic sites rich in soil carbon in northern Michigan (Roberts & Gilliams 1995) and *R. armeniacus* significantly preferred soils richer in SOM than reference sites in Oregon (Caplan & Yeakley 2006). However, Caplan & Yeakley (2006) thought that *R. armeniacus* may have produced this high level of organic matter itself, so I can’t conclude that high SOM is a cause, not an effect, of black raspberry presence. Interestingly, because SOM contributes to soil acidity (Birkeland 1999, cited in Caplan & Yeakley 2006), *Rubus* may occur more often in mildly acidic soils partially *because* their detritus acidifies soils, possibly providing evidence of a plant-soil feedback. SOM improves nutrient retention and soil aggregation, so richer soils may also improve resource availability and water retention for *Rubus* (Sikiric *et al.* 2011, Feldhake 2002, Weber 2007, Morrison 1998, Boynton & Wilde 1959, McDowell & Turner 2002), which may mechanistically explain the correlation between high *Rubus* establishment and high SOM.

My samples of black raspberry grew exclusively in sandy loam and loamy sand soil, as predicted by some sources (Morrison 1998, Marshall 1937, Hedtcke *et al.* 2009, Weber 2007). I conclude that black raspberry prefers well-drained, water-poor soils. The literature broadly suggests that this preference is also genus-wide, but quantitative evidence is scant. Caplan & Yeakley (2006) found *R. armeniacus* to prefer soils significantly coarser than reference soils in Oregon (Caplan & Yeakley 2006). They also note that water acquisition and transpiration rates for *R. parviflorus*, *R. spectabilis*, and *R. armeniacus* are high compared to other shrubs in the Pacific Northwest. These shrubs are adapted, it seems, to cope with low soil water availability. Additionally, Weber (2007) added that some virulent *Rubus* pathogens like *Verticillium* (blue stem wilt) can thrive in poorly-drained soils. Stapanian (1982) hypothesized that species like black raspberry fruit in the early, wetter portion of summer to limit water stress associated with fruiting. Lastly, a few studies (Roberts & Gilliam 1995, Hughes & Fahey 1991) parenthetically note a preference for coarser soils for their studies' *Rubus* species.

Conversely, a number of studies suggest that water stress is actually a serious concern for *Rubus*. Black raspberry grew better when water was not limiting in a study by Morrison (1937), and Suzuki (1987) reported that *R. palmatus* and *R. crataegifolius* in Japan spread more rapidly in wetter sites. McDowell & Turner (2002), summarizing multiple studies, noted that water stress and reproductive potential are negatively correlated in *Rubus*, even when photosynthetic rates are controlled for. In their study, *R. discolor* was forced to abort flowers and fruits under water stress. *R. ideaus* is, apparently, ideally cultivated in Serbia on more finely-textured clay loam soils (silt + clay ~ 70%) (Sikiric *et al.* 2011), and Kirby (1980) observed no difference in cane density or biomass of *R. vestitus* in Britain on clay-loam versus sandy-loam soils. My own black raspberries grew in soils approximately normally distributed between ~16% to ~66% clay plus silt by volume, so I conclude that while black raspberry generally prefers coarse-textured soils like some its congeners, it may be more tolerant of finer soils than previously thought.

Finally, I observed black raspberry in relatively nitrogen-poor (2.48ppm) to relatively nitrogen-rich (11.88ppm) sites, with a median of about 5.3ppm. Nitrogen, as a constituent of proteins like chlorophyll, drives photosynthetic capacity, so, *a priori*, most plants should benefit from more available nitrogen. Some literature on *Rubus* is suggestive to this end (McDowell & Turner 2002, Sikiric *et al.* 2011, Kirby 1980, Stapanian 1982). Both Morrison (1998) and Collison & Slate (1943) suggested cultivated black raspberry will grow and fruit more effectively when fertilized with nitrogen. In a study assessing Midwestern shrub digestibility, Hedtcke *et al.* (2009) discovered that black raspberry biomass is relatively rich in crude protein, suggesting high nitrogen content. Further, Stapanian (1982) hypothesized that early-fruiting species like black raspberry may need higher fruit protein levels than mid-season fruiting species to compete with protein-rich insects as a food source. Additionally, many studies have reported that nitrogen additions enhance *Rubus* performance (Morrison 1998, Gibson *et al.* 1993, Funk 2009, Collison & Slate 1943, Sikiric *et al.* 2011). These studies all suggest a high need for, as well as a high capacity to use, additional nitrogen. However, some sources contend *Rubus* tolerate low nitrogen conditions well because they colonize disturbed sites where nutrient retention may be poor (Caplan & Yeakley 2006, Hughes & Fahey 1991, Roberts & Gilliam 1995), and it seems black raspberry can perform adequately without abundant nitrogen, if my data are representative.

I conclude that black raspberry is a highly versatile species, even within the relatively narrow geographic range studied here, able to thrive in environments with substantially different light levels, as well as levels of soil richness, pH, texture, and nitrogen availability. That said, the species seems less well-adapted to cope with soil pHs outside the range of 5.5-7.5 and in soils that are not sandy loams or loamy sands.

Question 2: Under what conditions is black raspberry able to successfully produce fruits?

Successfully fruiting canes tended to live in slightly different habitats than unproductive canes. Canes that successfully produced fruits experienced, on average, higher light availability during midday in June (366.51fc to 188.85fc), more neutral soil pH (6.46 to 6.15), lower SOM concentrations (7.39% to 7.83%), more finely-textured soil (42.87% to 40.07%), and higher soil nitrogen availability (5.62ppm to 5.40ppm). Contrary to suggestions in the literature, black raspberry seems to reproduce more successfully in soils less rich in organic matter and that are more finely-textured than those in which it establishes and survives best (Morrison 1998, Caplan & Yeakley 2006, Roberts & Gilliam 1995, Sikiric *et al.* 2011, Hedtcke *et al.* 2009, Weber 2007, Hughes & Fahey 1991, Kirby 1980). Additionally, black raspberry seems to more often fruit successfully in better-lit environments, which the literature suggests is reasonable (Falkengren-Grerup 1990, Fotelli *et al.* 2005, Roberts & Gilliam 1995, Kirby 1980, Marshall 1937, Caplan & Yeakley 2006, Funk 2008).

In Model 1 (Table 3A and Figure 1A), I assessed whether a cane's environment was strongly correlated with its chances of fruiting successfully. I found that a cane's log-odds of fruiting significantly increased as light, soil texture, and soil pH increase and as SOM decreases.

Based on these results, I conclude that not all environments that foster successful black raspberry establishment, survival, and growth lead to successful sexual reproduction as well. Some studies report possible links between environment and reproductive success in this and other *Rubus* (McDowell & Turner 2002, Palmer *et al.* 1987, cited in Feldhake 2002, Braun *et al.*

1989, cited in Feldhake 2002, Collison & Slate 1943, Dossett *et al.* 2010, Whitney 1984), but I believe my study is the first to do so quantitatively for black raspberry.

My research suggests that important environmental factors for successful reproduction in one species of *Rubus* may not be important for all *Rubus*. While McDowell & Turner (2002) found a possible link between fruiting success and water availability in *R. ursinus*, *R. ursinus* also fruited more successfully with higher nitrogen availability while my black raspberry did not. Current and prospective growers may be able to use my results to decide whether their land is ideally suited to black raspberry reproductive success. More studies are needed, though, before we can better discern what black raspberry's "ideal" reproductive habitat might be like.

To summarize, I believe that black raspberries are not equally fit within their entire realized niche. Black raspberries can successfully establish, survive, and grow in environments that they cannot necessarily fruit successfully in. In particular, raspberries fruit more successfully in environments that are sunnier, and that have more finely-textured, less organic-matter rich, and more neutral soils than those it successfully establishes in. Because of the importance of fruiting to this species' ecology, I propose we opt to characterize its niche quantitatively using reproductive metrics in the future.

Question 3: How plastic is black raspberry fruiting behavior?

Substantial trait plasticity is evidence of possible alternative strategies that plants may trade off between to maximize fitness under certain circumstances. Producing more fruits or more fruit mass may allow plants to more successfully attract frugivores, but both strategies have considerable costs as well. More fruits produced means more numerous, costly flowers and seeds to produce, while more fruit mass often means higher water requirements and more stress on stems. Additionally, the benefits of more fruit or fruit mass produced may have diminishing returns relative to their fixed costs.

Black raspberry's fruit production ranged from 1 to 105 fruits per cane (median: 8 fruits, Figure 2A); others have published much higher values for cultivated varieties (Weber 2007, Dossett *et al.* 2010). Fruit mass produced per cane in this study ranged from 0.08g to 54.28g (median: 2.59g, Figure 2B). These values are also low relative to published values for domestic black raspberry (Weber 2007, Dossett *et al.* 2010). However, my values for both metrics are likely underestimates of true fruit production in wild black raspberry. Comparing my values with those of cultivated black raspberry is likely inappropriate anyhow because domesticated raspberries are specifically bred to maximize yield and production (Graham & Woodhead 2009, Dossett *et al.* 2008, Weber 2007).

Individual black raspberry fruits appear to be highly plastic. Average fruit size ranged from 1-103cg (median: 34cg, Figure 2C); these are smaller values than those reported by Weber (2007) or Stapanian (1982) for cultivated and wild black raspberries in Kansas, respectively. However, cultivated black raspberries are bred for large fruit size, and these raspberries are often heavily irrigated to maintain plant water balance (Graham & Woodhead 2009, Dossett *et al.* 2008, Weber 2007, McDowell & Turner 2002, Stapanian 1982, Boynton & Wilde 1959, Morrison 1998). Because fruits are predominantly water by weight, my raspberries may have been small from natural water stress. Too few studies report individual *Rubus* fruit weights to discipher whether my values differ significantly from "true" values. Still, growers are likely keen on producing large fruits, so I think future studies on this fruit behavior are warranted.

Fruit shape varied from very flat and wide (0.74mg/mm) to very tall and narrow (85.92mg/mm, median: 35.89mg/mm, Figure 2D). I conclude that plasticity in black raspberry fruit shape does exist, so different fruit shapes may represent alternative strategies with adaptive significance. One hypothesis is that if wider fruits were more conspicuous and thus attractive to frugivores than taller fruits, black raspberry would produce wider fruits in most situations. My data suggest this hypothesis is false, so perhaps wide fruits have hidden costs I did not anticipate, such as greater transpiration rates or greater ease of dislodgement (Stapanian 1982, Morden-Moore & Willson 1982). The transpiration loss hypothesis seems the most plausible to me, as moderately-shaped fruits would have a minimal surface-to-volume ratio, and most of the fruits I observed were moderately-shaped. I could not find any other study that assessed dynamics in *Rubus* fruit shape, so we need more studies to discern what adaptive significance, if any, alternate fruit shapes may have.

Fruit water content—following Stapanian (1982), the “reward” portion of fruit mass—varied from very low (~40%) to very high (~95%) in this study, with fruits typically about 75% water by weight (Figure 2E). Black raspberry appears to have great control over the juiciness of its fruits. That raspberries are typically more, not less, juicy matchs Stapanian’s (1982) prediction that early-fruiting species will need highly attractive fruits to woo consumers away from protein-rich insects. Black raspberry’s apparently evolved tendency toward juicier fruits might make the plant more attractive to growers (Graham & Woodhead 2009, Weber 2007, Dossett *et al.* 2008).

I conclude from my results that: 1) on average, fecundity is highly variable and asymmetric in wild black raspberry populations; 2) the average cane only produces a very modest amount of fruits (~8) and fruit mass (~2.5g); 3) considerable flexibility exists in black raspberry fruit traits and behaviors, so there may be adaptive significance underlying this flexibility 4) average fruit size for all canes is relatively small compared to its range of variability, suggesting black raspberries may prefer to produce many smaller fruits (a "quantity" strategy) rather than fewer bigger fruits (a "quality" strategy) in a majority of circumstances; 5) average fruit shape is moderate, on average, so perhaps fruits with extreme shapes are often unsuccessful; 6) black raspberry appears to produce fruits that are juicy for their weight much of the time.

Question 4: Are black raspberry fruit behaviors correlated with environmental factors?

To assess whether tendencies in black raspberry fruit traits correlate with environmental factors, I ran five linear mixed-effects regression models with each fruit trait as a dependent variable and environmental factors as independent variables (LMERs).

Model 2 (Table 1B and Figure 3B) suggests that canes in better-lit, more finely-textured soils will produce, on average, significantly more fruits. As I mentioned earlier, that raspberries would be more productive in finer-textured soils conflicts with what we might expect given where *Rubus* tend to live (Eastman 1992, Caplan & Yeakley 2006, Feldhake 2002, Taylor 1980). I am unsure whether cultivated black raspberry varieties would perform similarly well in well-lit, finely-textured soils. Certainly, we tend to cultivate black raspberry in full sun, but it's possible that black raspberry could manage in areas half or less as well-lit with no substantial production drop (Taylor 1980, Suzuki 1987, Feldhake 2002). As Feldhake (2002) saliently argued, if true, this would make black raspberry ideally suited to agro-forestry systems. Fruit mass produced (Table 1C and Figure 3C) is, like fruit production, strongly positively correlated with light and soil texture.

That nitrogen, soil organic matter, and pH would be unpredictive of fecundity is surprising. Some literature has suggested a strong link between nitrogen fertilization and increased yields (Morrison 1998, Collison & Slate 1943). Nitrogen, it is argued, is instrumental in biomass acquisition (Sikiric *et al.* 2011, Funk 2009), vegetative reproduction (Kirby 1980), establishment and growth (Hughes & Fahey 1991), internode length (Bazely *et al.* 1991), biomass protein content (Hedtcke *et al.* 2009), and photosynthetic capacity (McDowell & Turner 2002) in *Rubus* species. Moreover, some researchers have suggested nitrogen remobilization to reproductive structures can cause significant plant stress if nitrogen is limiting (Taylor 1980, McDowell & Turner 2002, Sikiric *et al.* 2011, Stapanian 1982). As for organic matter, carbon-rich soils better hold water, which may foster raspberry pests (Weber 2007), and these soils may also be those in which competition is most fierce. Lastly, Sikiric *et al.* (2011) present a number of compelling reasons why soil pH should be relevant to fruit and fruit mass production in raspberries. However, while it was reasonable to hypothesize that these environmental factors are important to the amount of fruits or fruit mass produced by black raspberry, my data provide no evidence for any such relationship.

Different fruit sizes may be more or less attractive to specific frugivores, depending on these frugivores' preference for "quantity" (more fruits) versus "quality" (fewer big fruits). Model 4 (Table 1D and Figure 3D) suggests that none of the factors included in this study are highly predictive of average fruit size. Average fruit size is expected to be somewhat higher in environments with more finely-textured and nitrogen-rich soils, but these patterns are not statistically significant ($0.25>p>0.1$). It is reasonable, I think, to predict these factors may influence fruit size, but more detailed studies are required to substantiate any such relationship.

Fruits with certain shapes may be more conspicuous to frugivores, but these same fruits may be costly in that they may be too easy to dislodge, too energy-inefficient to produce, or too water-inefficient to maintain. Model 5 (Table 1E and Figure 3E) provides evidence that fruit shape is influenced by soil texture. Additionally, the model predicts increases in soil pH could lead to taller and narrower fruits, but this result is by no means conclusive. Again, perhaps future research can resolve more definitively whether soil pH is related to fruit shape.

Finally, juicier fruits likely contain more sugar, water, vitamins, and other rewards for frugivores, which may increase a fruit's dispersal chances; however, juicier fruits may also be more costly to produce, may be too heavy to stability support, may rot more quickly, or may transpire too much water (Stapanian 1982). Fruit water content (Table 1F and Figure 3F) was positively related with soil texture, as well as with soil nitrogen and soil pH to a lesser and non-significant degree. Generally speaking, fruits could become more juicy and attractive as soils get finer, and they may get juicier still in environments with a more neutral and nitrogen-rich soil, but these latter results would need more robust testing to be convincing.

Based on my model results and predictions (Tables 1A-F and Figures 3A-F), I tentatively conclude that black raspberries will tend to 1) fruit, 2) produce more fruits, 3) produce more fruit mass, 4) produce taller and narrower fruits, and 5) produce juicier fruits as their environment becomes better lit and their soil becomes finer and, to a much less certain degree, more nitrogen-rich and neutral.

I also tentatively conclude that there are several possible linkages between a plant's environment and its fruiting behavior. More light might positively coincide with an increase in a cane's chances of fruiting and its fruit and fruit mass production. Soil pH (>5.5) potentially positively correlates with a cane's odds of successfully fruiting, and it may also correlate with the shape and water content of black raspberry fruits. SOM, my results suggest, has a definitively negative relationship with a cane's likelihood of fruiting.

My data implicate soil texture as the single most important environmental factor studied thus far for predicting black raspberry fruiting behavior. As soil texture get finer, canes are predicted to become more likely to fruit, to produce more fruits and fruit mass, and to make taller and narrower, juicier fruits. Soil texture may even be associated with larger fruit size as well, although this notion will need more conclusive testing. Lastly, though nitrogen is a strong determiner of plant physiology overall, it may only positively relate to fruit size and juiciness in black raspberry, and even these linkages are not strongly supported by my data.

Study limitations and future directions

This study had a number of limitations that future research could better account for. First, without prior knowledge of prospective black raspberry stand locations, my stand selection process was limited and *ad hoc*. Most stands were in accessible areas over a relatively narrow geographic range and so may not be representative of black raspberry's complete tolerance range. Second, because I had no prior data on environmental conditions within my stands, I could not choose diverse stands intentionally, which may make the observed range of conditions reported here too narrow. Generalizing my results outside of Michigan, or outside of the Midwestern US, may not be appropriate as different climatic or evolutionary processes are at work.

Third, I was unable to obtain more frequent light, soil, or fruit measurements, so my power for establishing associations between environment conditions and fruit behaviors may be relatively weak. Fourth, I acknowledge that genetics, competition, herbivory, parasitism, weather, and other environmental factors beyond those I studied here may also play substantial roles in determining fruit behavior, but I was constrained to assessing just a few factors in this study. Finally, my study was observational. As such, I emphasize that my results are strictly correlational. Future studies may be able to establish the causal mechanisms, if any, behind these correlations.

I found only a few studies that explicitly examined *Rubus* reproductive trade-offs (McDowell & Turner 2002, Stapanian 1982, Morden-Moore & Willson 1982). However, understanding these trade-offs is vital to successful management of *Rubus*, as well as for our understanding of *Rubus* community ecology, reproductive biology, and evolutionary biology. We could benefit from understanding how plant physiology and environmental conditions interact to result in successful fruiting.

To arrive at that understanding, though, we will need to fill many current knowledge gaps. In black raspberry, for example, we lack information on fruit consumption rates, on what animals consume black raspberry fruits, and with what criteria these frugivores choose among available fruits (Eastman 1992, Stapanian 1982, Morden-Moore & Willson 1982). We also do not know how pollinator or frugivore competition between black raspberry shrubs, or between black raspberry and other native and non-native plants, might affect fruit traits and reproductive success in black raspberry. Further, some researchers have drawn potential links between climatic factors and *Rubus* reproductive success (Marshall 1937, Weber 2007, Feldhake 2002, Suzuki 1987, Rajappan & Boynton 1960, Boynton & Wilde 1959), but how anthropogenic influences on climate (*e.g.* global climate change) or resource availability (*e.g.* acid precipitation) might affect black raspberry fruit behavior into the future is unknown.

I believe my study is the first to assess black raspberry fruit traits quantitatively from a life-history perspective. Black raspberry is, in my opinion, an ideal model organism in which to study plant life-history, especially with regard to fruiting behavior, trade-offs, and alternative strategies. The plant is common, hardy, easily recognizable, easy to propagate, and relatively fecund, and it has ample complexity in its life-history strategies and life-cycle. As black raspberry research becomes timelier, I would argue we have much to gain from a better understanding of what trade-offs black raspberry must negotiate to successfully fruit. Future researchers may be able to use my results to generate predictions related to black raspberry fruit trade-offs, and current and prospective black raspberry growers may be able to use my results to enhance their crop’s productivity.

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