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Wind Speed Affects Pollination Success in Blackberries

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Abstract

Pollination of wild plants and agricultural crops is a vitally important ecosystem service. Many landscape and environmental factors influence the pollination success of crops, including distance from natural habitat, wind speed, and solar radiation. Although there is a general consensus that increasing distance from forest decreases pollination success, few studies have examined the influence of specific environmental factors. In this study, we examined which environmental factors influence the pollination success of blackberries (*Rubus glaucus*). We measured the number of fruitlets per berry, a proxy for pollination success, as well as the weight and sweetness of each berry. Our results indicate that number of fruitlets is positively correlated with wind speed, but number of unripe red berries per bush is negatively correlated with wind speed. In addition, sweetness increased with increasing numbers of red berries per bush but was lower when flowers and berries were present, though this result should be considered with caution due to methodological limitations. Our findings suggest that a little studied environmental factor, wind, has a large impact on the number of fruitlets in blackberries. Although our findings should be confirmed in other locations to draw broader conclusions, they suggest that producers should consider the effect of wind on blackberry yield to optimize blackberry production.

Introduction

Ecosystem services represent the goods and services derived from the functioning of ecosystems and utilized by humans (Constanza et al., 1997). Pollination is a clear example of an ecosystem service, with the majority of all animal-mediated pollination provided by bees (Roubik, 1995; Klein et al., 2007). It is estimated that 87.5% of the angiosperm species in the world depend on animal-mediated pollination (Ollerton et al., 2011). Similarly, 87 of the leading global crops are dependent on animal pollination (Klein et al., 2007), with pollinators contributing about 9.5% of the total value of the production of human food worldwide (Gallai et al., 2009). Pollination is therefore important for both biodiversity and human food security (Hadley & Betts, 2012). However, pollination is currently threatened by anthropogenic changes such as deforestation and agricultural intensification (Kremen et al., 2002; Chacoffet al., 2008; Brown & Paxton, 2009; Hadley & Betts, 2012). Because of this threat, understanding the factors that influence the pollination success of crops, mediated by bees, is critical to protect global biodiversity and food security (Klein et al., 2007; Chacoff et al., 2008; Hadley & Betts, 2012).

A number of recent studies have indicated that large-scale landscape changes have profound impacts on pollinator communities and on their ability to successfully pollinate agricultural crops (Hadley & Betts, 2012; Boreux et al., 2013; Kennedy et al., 2013; Garibaldi et al., 2016). Because bees return to a fixed nest site after foraging, their foraging (and

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therefore pollinating) range is limited by their flight capacity (Ricketts et al., 2006). Factors that impact the flight ranges of bees therefore have large impacts on pollination success. Distance from natural or semi-natural habitat is one of the most important factors (Ricketts et al., 2006; Ricketts et al., 2008), as both the abundance and diversity of bee pollinators decreases with increasing distance from forest (De Marco & Coelho, 2004; Blanche et al., 2006; Carvalheiro et al., 2010), influencing pollination success in crops such as coffee, mango, and macadamia (Blanche et al., 2006; Vergara & Badano, 2009; Carvalheiro et al., 2010).

Although many studies have explored the relationship between distance to forest edge and bee abundance and diversity, few have examined how other environmental factors influence pollination success and crop yields (but see Vergara & Badano, 2009; Krishnan et al., 2012). Wind speed, for example, could also have large impacts on the ability of bees to successfully pollinate crops. For instance, wind speed influences the speed at which honeybees (*Apis mellifera*) fly (Wenner, 1963). A study on stingless bees showed that flight activity is reduced or even completely halted in high wind (Kleinert-Giovannini & Imperatriz-Fonseca, 1986). Thus, wind speed can potentially impact the amount of foraging and the provision of pollination services. Ambient temperature and solar radiation have also been shown to impact the foraging decisions of honey bees (Burrill & Dietz, 1981). Higher temperatures increased the number of foraging trips these bees made, while high levels of solar radiation strongly reduced the number of trips (Burrill & Dietz, 1981). It is therefore likely that the interaction of many environmental factors, and not only distance from natural habitat, influence pollination success.

Here we investigated how different environmental factors affect the pollination success of blackberries (*Rubus glaucus*) in Costa Rica by examining fruit production. Blackberries are a common crop in many Latin American countries, including Costa Rica, where they are produced for both local markets and for exportation to countries such as the United States, Holland, Canada, the United Kingdom, and Nicaragua (Castro & Cerdas, 2005). The blackberry industry in Costa Rica has grown 55% since 1995 and is expected to continue to increase (Strik et al., 2007). Increased agriculture, including that of blackberries, will likely be one of the biggest threats to tropical forests, ecosystems, and biodiversity this century (Laurance et al., 2014). This threat is exacerbated by the inefficiency of tropical agriculture, with most farmers producing significantly less than the full potential of their land for many crops (Tilman et al., 2002; Laurance et al., 2014). Hence, understanding how landscape factors influence pollination of crops such as blackberries is necessary to improve crop yields and help design more sustainable agricultural practices, which maximize production while reducing the need to deforest new land (Laurance et al., 2014).

Blackberries are an ideal model system in which to quantify pollination success because they produce a compound flower and fruit (Fig 1), which contains many pistils that must be individually pollinated to produce a fruitlet (the small fruits that make up compound berries (Cane, 2005)). Because each fruitlet must be individually pollinated, the number of fruitlets on a berry can be used as a direct proxy for pollination success. Although fruits such as blackberries are capable of limited self-pollination, the flower structure prevents complete self-pollination because only the outermost stigmata can be reached by the stamen, which leads to small, malformed berries made up of few fruitlets (Cane, 2005). Adequate bee pollination is therefore vital to blackberry production.

We hypothesized that blackberry fruitlet set is strongly dependent on environmental and landscape factors that influence bee foraging ability, and predicted that distance from the forest edge and wind speed would have the strongest effects on pollination success compared to other factors such as slope, tree height, canopy cover, and flower production. Specifically, we predicted that fruit-set would decrease with both wind speed and distance to forest edge. To our knowledge, this study is the first to examine the influence of environmental factors on blackberry pollination success. Our results provide preliminary management recommendations to producers regarding how to optimize pollination of blackberry crops and maximize yields.

Fig 1. Structure of blackberry flowers and fruits. Each blackberry flower has multiple stigmata that are individually pollinated (see leftmost flower). The number of fruitlets in each berry depends on the number of stigmata successfully pollinated (Photograph by Pilar Gómez).

Materials and methods

This study was conducted in a blackberry field (about 10 ha) owned by the Cuericí Biological Station in the Orosi District of Cartago, Costa Rica from July 7 – 8, 2016. We selected 62 blackberry bushes that had more than 5 ripe (hereafter referred to as "black") blackberries on the bush, and were at least 20 meters apart from each other (Fig 2). Ideally bushes with more than 5 black blackberries would have been used in this study, but black berries are harvested weekly at Cuericí Biological Station. This weekly harvesting prevented us from measuring bushes with large numbers of intact ripe berries. Distance was estimated using GPS waypoints (GPS map 60CSx Garmin). Wind speed was measured once for each blackberry bush over a period of 10 minutes to account for gusts of wind. For each bush, we recorded several landscape predictor variables summarized in Table 1. In addition, we recorded the number of fruitlets per berry and berry weight as proxies of pollination success of the blackberry bush for a minimum of 3 black blackberries per bush. Weight of each black berry was first recorded, and then number of fruitlets per berry was counted. In addition, we measured sweetness of each sampled black blackberry through a taste test. A score for sweetness was assigned to each berry independently (see Table 1). Because black berries were picked weekly, we also recorded the number of unripe (hereafter referred to as "red") berries per bush to compare fruit set across bushes (Table 1).

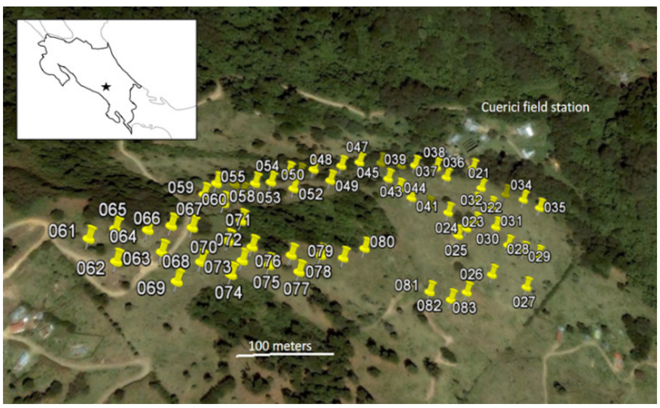

Fig 2. Distribution of sampled blackberry bushes surrounding Cuericí Biological Station, Costa Rica ($N = 63$) and location of Cuericí on a map of Costa Rica (inset). Bushes were located more than 20 meters apart (~10 ha area).

We analyzed the data using linear models and linear mixed models, using the "lme4" R (3.1.0) package. For each model, we performed model selection using the *drop1* function. We modeled the number of fruitlets per berry, weight of each berry, number of red berries per bush, and sweetness of black berries as response variables in 4 separate models (Table 2). For number of fruitlets, weight, and sweetness we included all environmental variables and bush characteristics as predictor variables in initial models, and bush identity as a random effect to account for the fact that some samples came from the same bush. For the number of red berries per bush we included only environmental (not landscape) variables. We used four tasters to assess the sweetness of the berries, and included taster ID as a random factor in the sweetness model to account for differences in taste preference. We also fit Poisson generalized linear mixed models (GLMM) for the continuous response variables, but excluded these models because they failed to converge.

Results

We found that the number of fruitlets per berry was best explained by wind speed (Table 2), with the number of fruitlets positively correlated with wind speed (estimate = 4.3, p= 0.0312, df = 59.78; Fig 3A). In contrast, the number of red berries per bush was best explained by slope and wind speed (Table 2), so that the number of red berries was negatively correlated with both wind speed (estimate = -12.9, p = 0.031, df= 59; Fig 3B) and slope (estimate = -1.0, p= 0.036, df= 59). Black berry sweetness was best explained by the number of red berries per bush and the presence of flowers on the bush (Table 2), such that black berries were sweeter on bushes with more red berries (estimate = 0.0044, p = 0.043, df= 194.06; Fig 4A) and in the absence of flowers (estimate = -0.64, p= 0.00016, df= 181.64; Fig 4B). Berry weight was best explained by a null model containing no predictor variables. However, berry weight was strongly correlated to number of fruitlets per berry (estimate = 0.021, p = < 2e-16, df = 196). In addition, wind speed was found to be correlated with slope (estimate = 0.013, p= 0.0251, df = 196) and distance to forest edge (estimate = 0.010, p= 1.04e-8, df = 196).

Table 1. Description of measured variables and their respective data collection methods.

Variables		**Data Collection Method**
Predictor	Distance to forest edge	Rangefinder
	Canopy cover	Densitometer
	Slope	Inclinometer
	Wind speed	Measured directly above top of bush using paper anemometer, categorized 1: no wind, 2: flagging tape moves, 3: anemometer moves slowly, 4: anemometer moves quickly
	Presence of other flowering plants	Visual inspection of surrounding 1 meter, recorded presence or absence
	Presence of ferns	Visual inspection of surrounding 1 meter, recorded presence or absence
	Number of black blackberries	Visual inspection of bush
	Presence of flowers on blackberry bush	Visual inspection of bush
	Height of sampled berry	Measuring tape
	Height of bush	Measuring tape
	Distance to nearest blackberry bush	Measuring tape
	Distance to nearest blackberry bush with fruit	Measuring tape
Response	Number of red blackberries	Counted total number of unripe (red) berries per bush
	Number of fruitlets per berry	Individually counted fruitlets of 3-5 ripe (black) berries per bush
	Berry mass	Weighed 3-5 ripe (black) berries per bush
	Berry sweetness	Individually ranked 3-5 ripe (black) berries per bush from 1-5, where 5 is extremely sweet and 1 is extremely sour

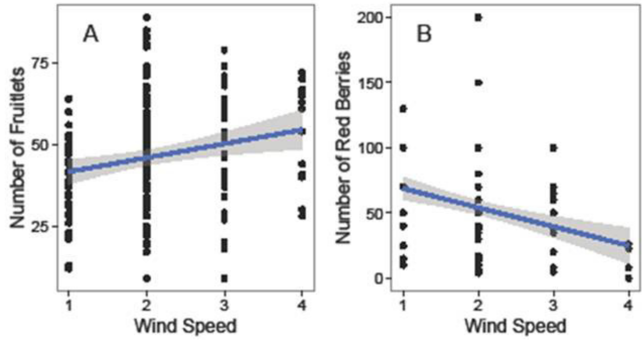

Fig 3. Effect of wind speed on (A) the number of fruitlets per berry and (B) the number of red berries per bush at a blackberry farm in Cuericí, Costa Rica.

Discussion

Our study aimed to determine how environmental factors influence fruit production and sweetness in blackberries (*R. glaucus*). We found that the pollination success of blackberries, as indicated by the number of fruitlets per berry, was positively related with wind speed. Conversely, the number of red berries per bush was negatively associated with wind speed. Also, blackberries were sweeter on bushes with more red berries and no flowers. We found no direct evidence linking blackberry weight to any of the assessed environmental variables, but did find a strong correlation between number of fruitlets per berry and berry weight.

We predicted that wind speed would reduce fruitlet set, but actually found the opposite effect. A positive effect of wind speed on the number of fruitlets could be explained by the pollination syndrome of *R. glaucus*, because some species of *Rubus* can self-pollinate with the assistance of wind (Jennings, 1988; as reviewed by Cane, 2005). A previous study found that increased visitation by pollinators can decrease fruitlet set in raspberries (Saez et al., 2014), a crop with similar reproductive biology. If this also applies to blackberries, the positive effect of wind on fruitlet number could indicate that windy conditions are reducing flower visitation rates. Windy conditions could also exclude the smallest pollinators, which usually have the shortest foraging ranges (Greenleaf et al., 2007), and/or increase the amount of time pollinators spend on flowers (Brown & McNeil, 2009). Although we did not collect flower visitors, we observed that honeybees and bumblebees were the most common bees visiting blackberry flowers in our study site (smaller native bee species are also known to occur in the region (Jarau & Barth, 2008)). Our results could suggest that windy conditions are favoring pollination by larger bees (i.e. honeybees and bumblebees), but future studies are needed to experimentally test the effect of wind on bee-mediated blackberry pollination.

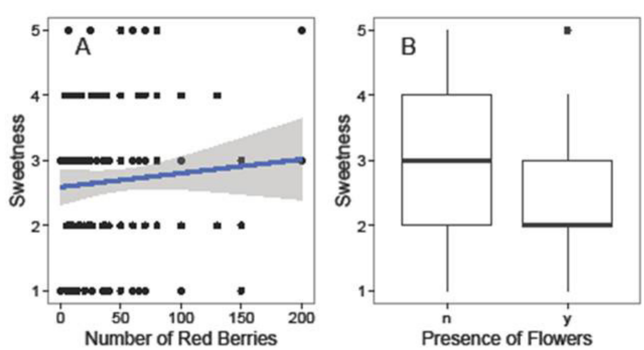

Fig 4. Effects of (A) the number of red berries and (B) the presence of flowers (where 'y' means present and 'n' means absent') on the sweetness of the berries at a blackberry farm in Cuericí, Costa Rica.

One major limitation of our study was that we only measured wind speed once for each blackberry bush, at the time of our measurements of berry production not at flower anthesis. Wind speed is variable, so it is possible that wind speed might have been different during flowering than at the time of data collection. However, wind was significantly correlated with slope and distance to forest edge in this experiment, suggesting that the terrain plays a large part in determining wind speed in this environment regardless of time of day or season. Wind speed can therefore be viewed as a measure of how sheltered blackberry bushes are. If some bushes are more sheltered than others, that would suggest there might be differences in pollinator visitation due to landscape differences, mediated through their effects on wind speed. That a significant relationship was found between wind and fruitlet set despite the confounding factors of terrain and time of year, highlights the importance of the wind effect found in this study.

We found no significant effect of distance to forest on our response variables, similar to the findings of Chacoff et al. (2008). These results contradict those of other studies, which found that fruit yields decreased with increasing distance from forest (De Marco & Coelho, 2004; Blanche et al., 2006; Carvalheiro et al., 2010). We posit that the lack of an effect is probably due to the limited distance gradient we measured in

Table 2. Likelihood ratio test results for final models chosen for each of the four tested variables: number of fruitlets per berry, berry weight, black berry sweetness, and number of red berries per bush. The null model was selected as the best model for berry weight based on the AIC values.

Response Variable	Number of observations	Predictor Variable(s)	Chi-square value	p-value
Number of fruitlets per berry	198	Wind	4.8385	0.02783
Berry weight	198	None	N/A	N/A
Berry sweetness	198	Flowers	14.0627	0.0001768
	198	Number of red berries	4.4381	0.0351444
Number of red berries	198	Slope	-4.168	4.61e-05
		Wind speed	-3.998	9.06e-05

this study. We only sampled bushes scattered across a distance gradient of 2-120 m to the forest edge, which is a fraction of a bee's flight range. Honey bees, for example, usually forage between 1-2 km from their nest (Steffan-Dewenter & Kuhn, 2003; Greenleaf et al., 2007). Even smaller bees, such as stingless bees, have flight ranges between 540 m and 2,000 m depending on their body size (Araújo et al., 2004). All of the blackberry bushes we measured could therefore be easily reached by native bees.

We found no effect of the environmental variables measured on blackberry weight, contradicting previous studies that found factors such as number of fruit per bush (Link, 2000; Whiting et al., 2005) and wind exposure (Dry et al., 1988) influence fruit weight. However, a strong positive correlation between berry weight and number of fruitlets per berry was found, suggesting that environmental factors have an indirect effect on berry weight that is mediated through number of fruitlets per berry. A positive correlation between fruitlet number and berry weight has been found in other cultivars of blackberries (Strik et al., 1996), supporting our finding.

In our study, we found that blackberries were sweeter in bushes that had more red berries, likely due to high resource investment in fruits on a given bush. We also found that blackberries were less sweet on bushes with flowers. These results should be considered with caution, though, as sweetness is usually measured using ˚Brix, which gives the sugar content of an aqueous solution (as seen in Jayasena & Cameron, 2008). Measuring sweetness based on human subjects will likely be biased due to differences in taste receptors and preference. However, by taking into account taster ID as a random factor in our model some of that bias was removed, providing support to our findings. Our results, if true considering the limited methods, could be explained as the consequence of a trade-off between resources investment in the production of berries and flowers on the bush at a given point in time. Investments in a particular type of structure can limit resources investment in other functions and structures in plants (Bazzaz et al., 1987). Alternatively, it is possible that bushes without flowers began producing fruits earlier in the year, and so had fruits with a higher sugar content; sugar is known to increase with ripeness in blackberries (Tosen et al., 2008). However, sugar levels in a similar compound fruit, raspberries, are not significantly different between harvested fruit that is 50% mature and that which is 100% mature (Wang et al., 2009). As all of the berries tested in this experiment were visibly mature and ripe, this issue likely did not play a large role in our results.

Our results suggest that wind speed has implications for the blackberry farming industry. With crops such as blackberries, which have long been a favorite wild fruit, common in several countries, and picked for commercial use (Strik et al., 2007), knowledge about the environmental factors that affect yield could improve fruit production. As of 2005, the blackberry industry has grown 55% since 1995 (Strik et al., 2007) and continues to grow, making it an important crop for many Costa Rican farmers. For local production in small Costa Rican farms, improvements to the field conditions related to wind speed could enhance blackberry production. Because factors such as slope and wind speed, as likely indicators of how sheltered bushes are, impact the number of fruitlets per berry, the number of berries produced, and (indirectly) the weight of the berries, farmers could determine the best market for their blackberry yield based on the structure of their fields, or possibly even manipulate how sheltered bushes are to produce more berries. Though this work is too preliminary to produce extensive recommendations, it can serve as a starting point for further research into how environmental factors impact blackberry production.

Supplementary information may be found online:
http://periodicos.uefs.br/index.php/sociobiology/rt/suppFiles/1620/0

Appendix I. Raw data
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Appendix II. R script used for analysis
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Author Contributions

All authors were involved in designing and performing the study. All authors except R. J. wrote an initial draft of the manuscript, which A. M. Y. then revised and finalized. R. J. assisted with data analyses and writing of the manuscript.

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