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RESEARCH ARTICLE

Phenological resistance of grapes to the green June beetle, an obligate fruit-eating scarab

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Abstract

Changes in fruit characteristics associated with ripening increase the vulnerability of crops to insect depredation, making it difficult for growers to protect cultivated fruits from pest injury close to harvest. This study evaluated phenological resistance, the use of cultivars that ripen before or after peak pest activity, for reducing injury to grapes (*Vitis* spp.) by the green June beetle (GJB) (*Cotinis nitida*), an obligate feeder on soft, ripe fruits. Accumulation of sugars, softening of berry skins and recruitment of GJB feeding aggregations were monitored on replicated vines of early-, mid- and late-season ripening cultivars that require from 85 to 125 growing days from bloom to harvest. GJB flight peaked in late July and early August coinciding with later stages of veraison of early-season ripening cultivars which recruited numerous GJB feeding aggregations resulting in >95% crop loss. Small (1–2 weeks) phenological differences between mid-season ripening cultivars and peak GJB flight translated to marked differences in injury, whereas cultivars that ripened in mid-August or later, after GJB flight had waned, sustained little or no damage. Trapping experiments confirmed that the tougher berries and low sugar content of less-ripe fruit clusters inhibited beetle feeding and induction of yeast-mediated volatiles responsible for GJB host-location. Implications of these findings for sustainable or organic management of GJB and other near-harvest fruit pests are discussed.

Introduction

Changes in fruit characteristics associated with ripening have traditionally been viewed as adaptations to encourage seed dispersal by birds and other vertebrates (Herrera, 1982*a*,*b*; Howe & Smallwood, 1982; Willson & Whelan, 1990; Levey *et al*., 2002; Saxton *et al*., 2009). Non-ripe fruits commonly are green, hard, relatively low in sugars and contain bitter, astringent or toxic chemicals, traits that may deter premature removal by vertebrate and invertebrate frugivores (Stiles, 1989; Willson & Whelan, 1990). During ripening, levels of secondary chemicals decline, sugar content increases and fruit skins thin, soften and change in colour or contrast which advertises the fruit is edible (Herrera, 1982*a*,*b*; Willson & Whelan, 1990). Ripening, however, also appreciably increases susceptibility to damage by bacteria, fungi and insects (Howe & Smallwood, 1982; Willson & Whelan, 1990, Cazetta *et al*., 2009), so timing of ripening reflects adaptive trade offs between the need to deter damaging agents until the seed is mature without deterring dispersers (Janzen, 1971; Herrera, 1982*a*,*b*; Stiles, 1989).

Growers of grapes and other edible fruits must protect them from pathogens, insects and vertebrate frugivores. Following the onset of veraison, or berry ripening of grapes, hexose sugars accumulate, titratable acidity decreases, the berries swell, soften and their skins become thinner and often change in colour (Mullins *et al*., 1992; Potter & Hotchkiss, 1995). Grape producers commonly use bird netting, electronic bird calls and other tactics to deter vertebrate predation prior to harvest. Such methods are not effective, however, in preventing attack by invertebrate pests that are attracted to ripe grapes.

In the southeastern United States, where viticulture is an emerging industry (Fisher, 2002; SERA, 2003; Woods & Mansfield, 2006), many growers are impacted near harvest by the green June beetle (GJB) (*Cotinis nitida* L.), a univoltine scarab pest of ripe and over-ripened grapes, blackberries, peaches and figs, as well as other tree and vineyard fruits (Garman, 1904; Davis & Luginbill, 1921; Chittenden & Fink, 1922; Fig. 1). The beetles are strong fliers and proximity of pasture and other grassy habitats, in which the larvae feed and overwinter, leads to high numbers of GJB in vineyards. Aggregations of GJB can devour nearly an entire crop (Garman, 1904), and also taint partially eaten fruit clusters with odorous secretions. Damaged fruits and the beetles themselves may be inadvertently harvested, contaminating the crop. GJB is the most severe harvest-time insect pest of grapes in Kentucky (Hammons *et al*., 2008, 2009).

Green June beetle host-location and aggregation on fruits is mediated by yeast-induced fermentation volatiles (Domek & Johnson, 1988; Hammons *et al*., 2009). The beetles have bluntly spatulate, non-opposable mandibles specialised for feeding on fruit pulp and plant exudates, so they have difficulty biting through the skins of all but

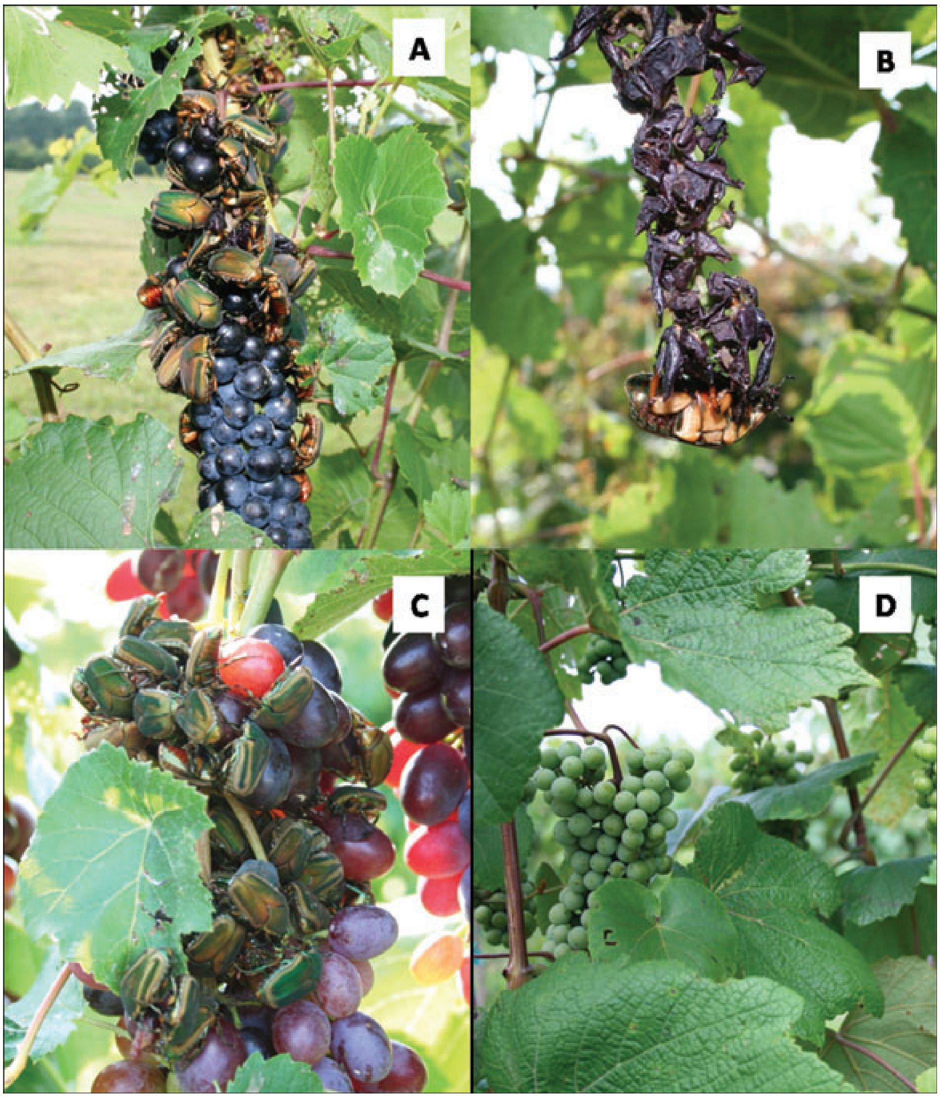

Figure 1 Variation in ripening phenology and susceptibility of grapes to green June beetle (GJB) on 29 July 2008. (A) Feeding aggregation on early-season ripening Marechal Foch, (B) totally consumed cluster of Marechal Foch, (C) feeding aggregation on early-season ripening Jupiter, (D) late-season ripening Norton is phenologically resistant to GJB.

the softest of intact fruits (Hammons *et al.*, 2008). GJB damage is exacerbated, however, by another abundant vineyard pest, the Japanese beetle (JB) (*Popillia japonica* Newman), that readily bites ripe grapes with its sharp mandibles, exposing the fruit pulp and eliciting the same fermentation volatiles that attract GJB (Hammons *et al.*, 2008, 2009). Feeding aggregations on fruit clusters often contain both beetle species (Hammons *et al.*, 2008). The prevailing management strategy for GJB relies on weekly sprays with carbaryl (Bordelon *et al.*, 2009). Labels of carbaryl and many other insecticides prohibit spraying close to harvest, which for some grape cultivars coincides with or occurs shortly after peak GJB flight (Hammons *et al.*, 2008). Little information exists on non-chemical tactics for managing GJB.

The growing season in the Southeast is relatively long and grape growers are capable of producing several cultivars (Kurtural & Wilson, 2008) that vary in berry ripening phenology (McIntyre *et al.*, 1982; Dami *et al.*, 2005). Anecdotes in the early literature suggest that the timing of veraison may determine cultivar susceptibility to GJB feeding (Garman, 1904; Chittenden & Fink, 1922), but that hypothesis has not been tested. In Kentucky, flight of the GJB peaks in mid-summer coincident with the later stages of veraison for early-season and mid-season ripening grape cultivars (Hammons *et al.*, 2008). This study evaluated phenological resistance, i.e. use of grape cultivars that ripen outside of the window of peak pest activity, as a strategy for reducing GJB injury to ripe fruit clusters close to harvest. Olfactory response of GJB to beetle-exposed fruit clusters, and crop injury in relation to berry ripeness of selected cultivars was documented. Prospects for exploiting phenological resistance for sustainable and organic management of GJB and other near-harvest fruit pests are discussed.

Materials and methods

Site and plant material

A research vineyard consisting of six grape cultivars varying in ripening phenology and timing of harvest was established on a Maury silt loam (a fine, mixed, semiactive, mesic and typic Paleudalfs; 314 m elevation) at the University of Kentucky Horticulture Research Farm in Lexington, KY, USA. The site was cultivated and a cover crop of perennial ryegrass (*Lolium perenne* L.) and KY 31 fescue [*Schedonorus arundinaceus* (Schreb.) Dumort]. was established in 2005. Vines were planted in early May 2006 in a randomised complete block (RCB) design with eight replications for each cultivar and two vines per experimental unit.

The six cultivars and their approximate days from bloom to harvest (Dami *et al.*, 2005) were: early-season: 'Jupiter' (*V. labrusca* × *V. vinifera*) (85 days) and 'Marechal Foch' (*Vitis* sp., interspecific hybrid) (90 days); mid-season: 'St. Croix' (*Vitis* sp., interspecific hybrid) (99 days) and 'Chancellor' (*Vitis* sp., interspecific hybrid) (100 days); and late-season: 'Chambourcin' (*V. vinifera* × *V. riparia*) (115 days) and 'Norton' (*V. aestivalis*) (125 days). Cultivars only having blue-black fruits were used to eliminate potential confounding effects of fruit colour. Vines were trained to a 1.8 m high, single high-wire bilateral cordon system with 2.4 m × 3.0 m (vine × row) spacing.

During the first (2006) and second (2007) growing seasons' vines were de-fruited and not cropped. The young vines were trained to two primary shoots in 2006 to establish trunks. Following the second growing season, the canes were trained to cordons and the shoots on cordons were spur-pruned (pruned to ≤ 4 buds every 10 cm along the cordon) during dormancy in mid-February 2008 to retain 36 buds per vine, and not balance-pruned. Vines were managed according to University of Kentucky recommendations (Brown *et al.*, 1997; Dami *et al.*, 2005), except that no insecticides or fungicides were applied after late June in 2008, about 2 weeks before the start of GJB flight.

Green June beetle flight and berry phenology

Seasonal emergence and flight of GJB was monitored to assess berry phenology and harvest in relation to adult beetle activity. Traps were operated near plantings of grapes and other fruit crops at the UK Horticultural Research Farm, Lexington, KY, USA, from 24 June 2008 until 2 weeks after last catch. Traps and lures were from Trécé (Adair, OK, USA); lures were replaced weekly. GJBs were monitored with JB Xpando traps, which have a larger funnel opening than standard JB traps, and TRE-8643 experimental food-type lures at two sites. Traps were emptied several times per week to prevent overflowing. Samples were frozen and counted to evaluate total weekly catch per trap.

Berry ripening was evaluated during GJB flight beginning 17 July until the cultivars' respective harvest date. For each sample, 50 berries (rachis intact) per replicate of each cultivar were collected into plastic bags, placed in a cooler in the field and evaluated the same day. Relative toughness of 10 intact berries per replicate was assessed with an electronic digital force gauge (MARK-10 Model EG-2; Hicksville, NY, USA) which measured the force (g) required to penetrate the skin with a pointed punch. Berries were then crushed by hand and a 5 mL sample of juice was used to determine the percentage total soluble solids (TSS), which are mostly sugars (Mullins *et al.*, 1992; Potter & Hotchkiss, 1995). Total soluble solids were measured as degrees Brix using a PAL-1 Digital Refractometer (ATAGO, Bellevue, WA, USA).

Green June beetle aggregation on clusters and crop damage

Aggregations of GJB on field-ripening clusters in the vineyard were evaluated on six dates from 18 July to 14 August. For each cultivar and vine, the total initial number of clusters, the number of clusters bearing aggregations of >10 GJB and the number of clusters with >90% of the berries damaged or consumed to date were recorded. Harvest dates were based on commercial ripeness standards for desirable TSS levels. At harvest, the remaining clusters per vine were counted and the percentage that had sustained ≥90% berry damage or loss from GJB was determined.

Olfactory attraction of green June beetle to beetle-exposed grape clusters of differing ripeness

Field trapping was conducted to test beetle capacity to feed on grape clusters of different cultivars varying in degree of ripeness and thereby attract additional GJB. The trials were conducted in plantings of grapes and blackberries at the University of Kentucky Horticultural Research Farm, Lexington, KY, USA, during July and August. Traps were designed to allow baiting with grape clusters and beetles while denying incoming beetles' access to the fruit. They consisted of intersecting vanes (31 × 31 cm) of green corrugated plastic (Coroplast, Dallas, TX, USA) atop a galvanised steel tractor funnel (25.4 cm top diameter) with a standard ventilated metal JB trap container (Ellisco, Philadelphia, PA, USA) attached underneath to hold captured beetles. A central cut out (9.5 cm wide, 11.5 cm deep) in the vanes accommodated a slightly smaller cylindrical screened cage containing the baits. Traps were suspended by monofilament fishing line from plant hangers attached to 1.8 m steel fence posts so that the baits were 1 m above the ground. Traps were spaced 10 m apart in rows; and treatments were replicated five times in each trial.

Trap baits were prepared with representative clusters of about 25 intact grape berries attached to a single stem that had been collected from each cultivar tested on a given date. Clusters used in the first two trials came from vines in the aforementioned research vineyard. Mixed cohorts of GJB and JB were confined with the grape clusters allowing them the opportunity to feed upon and damage the fruits (Hammons *et al.*, 2009). JBs were included because they are better able to bite through the skins of intact grapes, elicit GJB host-locating response to grapes and because feeding aggregations on fruit clusters often contain both beetle species (Hammons *et al.*, 2008, 2009). Beetles used to prepare the baits were hand-collected from grape foliage (JB) or grape, blackberry and peach fruits (GJB) the day before each trial. Only female JB were used to obtain more consistent feeding on the baits (males do not feed while mating). GJBs are about four times heavier than JB and their feeding aggregations consist of both sexes with little mating (Hammons *et al.*, 2008), hence 5 male and 5 female GJB plus 20 female JB were used for baits in each replicate. Male and female beetles were separated using morphological differences in the foretibiae (Fleming 1972; Pszczolkowski *et al.*, 2008). Beetles and grapes were preloaded into covered 1-L translucent plastic containers and held at 29°C with photoperiod of L15:D9 for 24 h before being taken to the field and transferred to the bait cages. This allowed some feeding injury before the start of the trial.

In trial 1 (22–24 July) and trial 2 (26–28 July), the six original cultivars described above were used. By early August the early-season ripening cultivars Marechal Foch and Jupiter had been very heavily damaged by GJB (Fig. 1), so for trial 3 (1–3 August), which coincided with peak GJB flight, we substituted two additional mid- to late-season ripening cultivars 'Concord' (*V. labrusca* L.) and 'Sunbelt' (*Vitis* sp.), to further test the phenological resistance hypothesis. Each trial was run in the field for about 48 h.

The traps were not 100% efficient in capturing attracted beetles so they were examined about every 1–2 h from 09:00 to 20:00 hours and any beetles clinging to the outside of bait cages or vanes were knocked into the funnel. Trap captures were frozen and later sorted to compare the number of GJB attracted to the beetle-exposed clusters of each cultivar. Sexes of captured GJB were separated and confirmed by squeezing the abdomen to expose the genitalia (Pszczolkowski *et al.*, 2008).

Statistical analyses

The number of GJB attracted to the traps were compared by analysis of variance (ANOVA) for a RCB design, and preplanned single degree of freedom linear contrasts comparing response to early-season, mid-season and late-season ripening cultivars. TSS and force levels were analysed between cultivars by ANOVA for repeated measures and within individual dates by ANOVA followed by a posteriori linear contrasts using Sheffe's F method which controls experiment-wise error rate (Analytical Software, 2008). Percentage crop loss was arcsine square-root transformed and GJB trap catches were log-transformed to meet requirements for normality and homogeneity of variances. The non-parametric

Kruskal–Wallis test was used in subsequent trials when ANOVA assumptions could not be met because of all zeros in some treatments. All data are presented as original means ± standard error (SE). Statistix 9 (Analytical Software, Tallahassee, FL, USA) was used for all analyses.

Results

Green June beetle flight and berry phenology

The first GJB were captured in the week of 10–17 July (Fig. 2). Flight peaked in late July and early August, and then rapidly declined by mid-August. TSS levels differed among cultivars during peak GJB flight (Fig. 3; d.f. = 5,29 and 5,28; $F = 92.6$ and 56.9 for 31 July and 7 August, respectively; $P < 0.001$; ANOVA) with Foch > Jupiter = St. Croix > Chancellor = Chambourcin > Norton (linear contrasts by Scheffe's F, $P < 0.05$). Mean force (g) required to penetrate representative berries, or berry toughness, also differed significantly on both dates (Fig. 3; d.f. = 5,29 and 5,28; $F = 39.9$ and 113.6 for 31 July and 7 August, respectively; $P < 0.001$; ANOVA) with St. Croix ≤ Jupiter < Foch < Chancellor = Chambourcin < Norton (linear contrasts by Scheffe's F, $P < 0.05$). St. Croix and Chancellor, both regarded as mid-season ripening cultivars, nevertheless differed in phenology during peak GJB flight. St. Croix ripening coincided more closely with early-season ripening Foch and Jupiter, whereas ripening of Chancellor was closer to that of late-season ripening Chambourcin and Norton (Fig. 3).

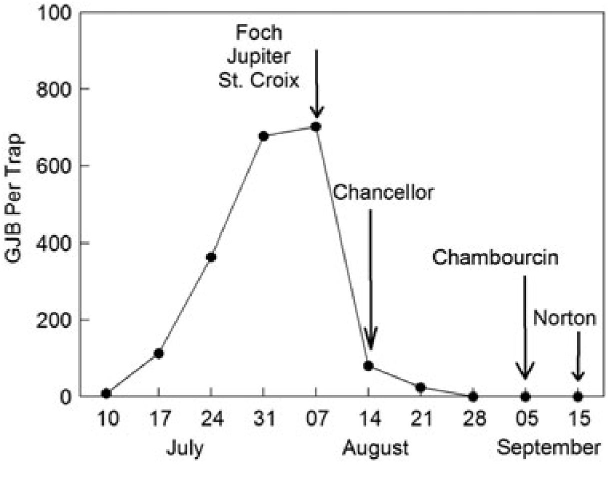

Figure 2 Weekly trap catches of green June beetles (GJBs) in 2008 in Lexington, KY. Arrows indicate harvest dates for the respective cultivars to which GJB response was evaluated. Foch and Jupiter are early-season ripening; St. Croix and Chancellor are classified as mid-season ripening; and Chambourcin and Norton are late-season ripening cultivars.

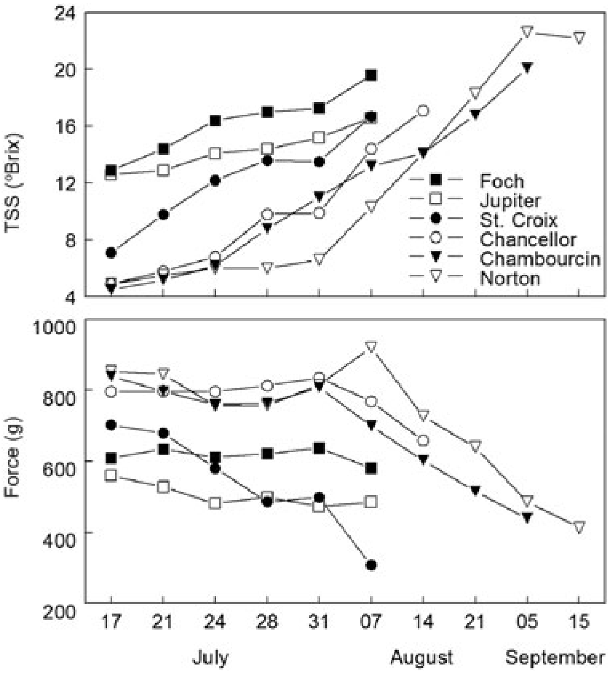

Figure 3 Total soluble solids (TSS; as degrees Brix) and force needed to penetrate ripening berries of the six grape cultivars evaluated for phenological resistance to green June beetles. From 17 July to 7 August 2008, main effects of cultivar, and cultivar X date interaction, respectively, were significant for both TSS ($F = 334, 4.82$; $p < 0.001$) and force ($F = 143, 5.89$; $p < 0.001$); repeated measures ANOVA.

Green June beetle aggregation on clusters and crop damage

The first GJB feeding aggregations were observed on clusters of Foch on 17 July 2008. Aggregations and crop damage increased on the early-season ripening cultivars, and on St. Croix, throughout GJB flight with the highest percentages of clusters with aggregations on 31 and 6 August. Nearly all Foch, Jupiter and St. Croix fruit clusters had been consumed by GJB by those cultivars' harvest date (7 August), with >95% crop loss (Table 1; Fig. 1). Mid-season ripening Chancellor, which had not sustained any crop damage by 6 August, nevertheless was heavily fed upon in the subsequent week preceding its harvest date on 14 August (Table 1). Late-season ripening Chambourcin, harvested on 5 September, received little damage from GJB feeding, whereas Norton, the last cultivar harvested, did not elicit any aggregations of GJB or associated crop loss (Table 1; Fig. 1).

Olfactory attraction of green June beetle to beetle-exposed grape clusters of differing ripeness

Early-season ripening Foch and Jupiter, which had similarly high TSS and low berry toughness, were heavily

Table 1 Percentage of fruit clusters on third-year vines of selected early-, mid- and late-ripening grape cultivars having green June beetle (GJB) aggregations and injury and total crop loss from GJB by each cultivar's respective harvest date[a]

		% Clusters with >10 GJB				% Clusters Eaten to Date			
Cultivar (Type)	Clusters per Vine	21 July	24 July	31 July	6 Aug	24 July	31 July	6 Aug	% Crop Loss[b]
Foch (E)	51 ± 3	5 ± 3	18 ± 6	37 ± 9	47 ± 14	10 ± 5	42 ± 12	94 ± 3	96 ± 1
Jupiter (E)	42 ± 3	6 ± 3	13 ± 5	35 ± 7	51 ± 18	2 ± 1	7 ± 3	90 ± 5	95 ± 2
St. Croix (M)	49 ± 2	0 ± 0	1 ± 1	31 ± 5	77 ± 14	0 ± 0	5 ± 1	98 ± 1	99 ± 1
Chancellor (M)	45 ± 3	0 ± 0	0 ± 0	0 ± 0	3 ± 1	0 ± 0	0 ± 0	0 ± 0	28 ± 10
Chambourcin (L)	60 ± 6	0 ± 0	0 ± 0	0 ± 0	2 ± 1	0 ± 0	0 ± 0	0 ± 0	8 ± 1
Norton (L)	36 ± 4	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Kruskal-Wallis (*P*)		<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

[a] Data are means ± SE . Types E, M and L denote early-, mid- and late-season ripening cultivars, respectively.

[b] Percentage (%) crop loss by harvest for individual cultivars. Harvest dates were 7 August (Foch, Jupiter and St. Croix), 14 August (Chancellor), 5 September (Chambourcin) and 15 September (Norton).

Table 2 Berry total soluble solids (TSS; as degrees Brix) and force to crack the berry skin of early-season (E), mid-season (M) and late-season (L) ripening grape cultivars and numbers of green June beetles (GJBs) attracted to fruit clusters that were pre-exposed to GJB and Japanese beetles[a]

		Trial 1			Trial 2		
Cultivar	Type	TSS	Force (g)	GJB	TSS	Force (g)	GJB
Foch	E	14 ± 1	635 ± 29	129 ± 9	16.4 ± 1.3	612 ± 48	163 ± 38
Jupiter	E	13 ± 1	530 ± 20	118 ± 21	14.4 ± 0.6	481 ± 12	189 ± 61
St. Croix	M	10 ± 1	680 ± 26	54 ± 33	12.2 ± 0.5	581 ± 32	73 ± 10
Chancellor	M	6 ± 1	798 ± 21	9 ± 1	6.9 ± 0.6	797 ± 21	4 ± 2
Chambourcin	L	5 ± 1	798 ± 22	5 ± 2	6.2 ± 0.3	760 ± 14	6 ± 2
Norton	L	6 ± 1	845 ± 19	3 ± 1	6.0 ± 0.3	757 ± 23	1 ± 1
ANOVA: $F =$		41.45**	19.11**	27.8**	57.01**	14.3**	58.14**
Contrasts (t)							
E versus L		12.73**	9.01**	11.5**	14.73**	6.68**	14.69**
E versus St. Croix		4.86**	3.02**	3.89**	4.28**	0.95	2.36*
St. Croix versus Chancellor		4.63**	3.32**	2.39*	6.23**	4.88**	7.94**
Chancellor versus L		0.54	0.75	2.72*	0.98	0.91	0.47

[a] Data are means ± SE. For F and t statistics from ANOVA and single degree of freedom linear contrasts, ** and * denote $P \leq 0.01$ and 0.05, respectively. For ANOVA, d.f. = 5, 20 for trapping experiments; d.f. = 5, 31 for TSS and force.

fed upon in the bait cages and attracted the greatest numbers of GJB in trials 1 and 2 (ANOVA, linear contrasts, Table 2). Mid-season ripening St. Croix, which had intermediate TSS levels and berry toughness, attracted some GJB, but less-ripe Chancellor and late-ripening Chambourcin and Norton attracted few GJB in those late-July trials. St. Croix was nearly ripe by early August and it attracted the greatest numbers of GJB, by far, in trial 3 (Table 3). Notably, it ripened earlier, coinciding with still-heavy GJB flight, and attracted more GJB than did Chancellor, the other mid-season cultivar, in all three trapping experiments. Late-season ripening cultivars were relatively unattractive to GJB in all three trials (Tables 2 and 3). Both sexes of GJB were attracted; females and males represented 54% and 46%, respectively, of the total captured beetles for the three most attractive baits in trials 1–3.

Discussion

This study confirms that phenological differences in veraison among grape cultivars, particularly berry toughness and sugar content, are major determinants of susceptibility to the GJB, an important harvest pest. During late July and August the thin, soft skins of ripening grapes are more easily damaged, or may rupture naturally with berry swell, exposing sugar-rich pulp and making it easily accessible to GJB (Hammons *et al.*, 2008). In grape production, where native yeasts are commonly associated with the berry skin (Rosini *et al.*, 1982), natural berry crack or insect injury may facilitate microbial activity, inducing fermentation volatiles that make the fruits increasingly attractive to foraging GJB (Hammons *et al.*, 2009). During GJB flight, the still-hard berries of late season-ripening cultivars, however, are difficult for GJB or associated JB to bite into (Hammons *et al.*, 2008).

Table 3 Berry total soluble solids (TSS; as degrees Brix), force to crack the berry skin and number of green June beetles (GJBs) attracted to grape clusters of early-ripening (E), mid-ripening (M) and late-ripening (L) cultivars that were pre-exposed to GJB and Japanese beetles (trial 3)[a]

Cultivar	Type	TSS	Force (g)	GJB
St. Croix	M	13.6 ± 0.6	499 ± 30	253 ± 46
Chancellor	M	9.9 ± 0.5	835 ± 22	57 ± 17
Chambourcin	L	10.9 ± 0.3	808 ± 19	25 ± 10
Norton	L	6.6 ± 0.3	815 ± 23	2 ± 1
Concord	L	7.6 ± 0.2	836 ± 51	7 ± 3
Sunbelt	L	5.8 ± 0.1	844 ± 50	6 ± 2
ANOVA: F =		71.7^{**}	16.9^{**}	28.9^{**}
Contrasts (t)				
M versus L		12.8^{**}	5.38^{**}	10.5^{**}
St. Croix versus Chancellor		7.1^{**}	7.0^{**}	3.6^{**}
Chancellor versus L		5.2^{**}	0.3	5.8^{**}

[a] For test statistics from ANOVA (F) and single degree of freedom linear contrasts (t), ** denote $P < 0.01$; d.f. = 5, 20 for trapping experiments; d.f. = 5, 31 for TSS and force. For TSS and force, 50 and 10 berries, respectively, per replicate were evaluated.

Even if the berry skin is damaged, low sugars and high acidity may limit the complex multitrophic interaction that produces the volatiles involved in GJB host-location and aggregation from occurring (Hammons *et al*., 2009).

Phenology of veraison is a critical attribute for adaptation of cultivated grapevines to their growing environment. Timing of veraison, length of the ripening period and harvest date are target traits in viticulture (Constantini *et al*., 2008). Grapevines respond to a number of environmental variables, management practices and pest pressures which may act independently or integrate and alter the timing of phenological events. However, with non-climatic factors held constant, individual cultivars tend to develop at consistent rates relative to others (McIntyre *et al*., 1982). Knowledge of climatic requirements for specified cultivars and regional climate conditions for a vineyard can improve growers' success. In Kentucky the long growing season and regional differences in climatic conditions provide opportunity for growers to produce many table and wine cultivars (Kurtural & Wilson, 2008) that vary in berry ripening phenology including so-called early-, mid-, or late-season ripening cultivars (McIntyre *et al*., 1982; Dami *et al*., 2005; Constantini *et al*., 2008). Being able to produce multiple cultivars is desirable for staggering harvests across the growing season, expanding production periods, and potentially targeting high-value market opportunities (McIntyre *et al*., 1982; Dami *et al*., 2005; Constantini *et al*., 2008). However, the timing of events such as veraison and harvest of grape cultivars within a particular region may determine the vines' susceptibility to destructive insects and pathogens.

Carbohydrates for energy are the main nutritional reward to birds and other vertebrates for dispersing enclosed seeds (Stiles, 1989). Free-living adult insects also have high caloric requirements (Waldbauer & Friedman, 1991). For beetles, wasps (e.g. Vespidae) and other insects having mandibulate mouthparts non-suited to nectar feeding, sugar-rich fruit pulp can be a rich source of carbohydrates. Adults in the scarab subfamily Cetoniinae (fruit and flower chafers), to which GJB belongs, have weakly developed mandibles specialised for feeding on flower nectar and pollen, plant exudates or juices and soft pulp of ripening or overripe fruits (Ritcher, 1958). They, and other bulky day-active scarabs, have high energetic requirements because they must attain and maintain elevated thoracic temperatures to power their flight (Chappell, 1984; Heinrich & McClain, 1986; Kreuger & Potter, 2001; Held & Potter, 2004). Females must have sufficient energy reserves to fly to oviposition sites, enter the soil and lay eggs there for 1–3 days, and then fly back to patchily distributed food resources to refuel and repeat the process multiple times, and males engage in vigorous diurnal mating flights (Chittenden & Fink, 1922). Thus, GJB are morphologically and energetically dependent on soft fruits or other sources of sugary plant exudates.

Our results also experimentally validate historical anecdotes that GJB are capable of 'utterly destroying the fruit of whole bunches and even whole vines . . . clinging to the berries, in some cases a dozen on a bunch, greedily devouring the pulp and leaving them in an unsightly and utterly ruined condition' (Garman, 1904). Indeed, GJB accounted for >95% crop loss of both early-season ripening cultivars (Marechal Foch and Jupiter) and of the relatively early mid-season ripening cultivar St. Croix in our research vineyard (Fig. 1). GJB also severely damages other early- and mid-season ripening cultivars of table and wine grapes, e.g. 'Reliance' and 'Seyval Blanc', in Kentucky (authors' observations). In contrast, late-season ripening cultivars in our research vineyard sustained almost no injury from GJB and yielded good crops despite having received no insecticidal sprays during GJB flight. The trapping experiments confirmed that once damaged by GJB and JB, berries of early-season cultivars attract many additional GJB, whereas the beetles' inability to feed on late-season ripening clusters results in little or no recruitment. Both beetles contaminate the wounded grapes with yeasts that elicit fermentation volatiles that the GJB exploits as aggregation kairomones (Hammons *et al*., 2009).

Grape growers must protect their crop from pathogens, insects and vertebrate frugivores until it is ready to harvest. Many insecticide labels have preharvest spray interval restrictions that limit their use, leaving cultivars that ripen during peak GJB and JB activity vulnerable to damage. Residual effectiveness of insecticides that require ingestion may provide only limited protection against GJB, because the berry skin is usually torn and only the untreated pulp is consumed. Furthermore, most synthetic insecticides are unacceptable in certified organic production systems, and organic alternatives (e.g. pyrethrins) are more expensive and short-lived. Netting that growers apply over rows to protect the ripening crop from birds is generally too coarse to exclude GJB.

In conclusion, planting cultivars that ripen after peak beetle flight offers a viable management option for GJB. In contrast, only a few cultivars recommended for Midwestern grape growers (Dami *et al*., 2005) ripen any earlier than Jupiter, which was heavily damaged in our study. Of those, the earliest-ripening ones require an estimated 75 or 80 days from bloom to harvest, only 5 or 10 days less than Jupiter and still within the early peak of GJB activity. Many growers, nonetheless, will still choose to produce GJB-susceptible cultivars to expand production periods and target high-value market opportunities. This study may help grape growers to predict which cultivars will suffer most from GJB and require the highest degree of protection. Such information will allow new growers to better match their cultivar choice with their desired intensity of management, and help growers to focus GJB management where it is most needed. Understanding and exploiting the phenological resistance of plants, is a sustainable approach that supports integrated pest management and organic agriculture production.

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