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ORIGINAL PAPER

Trade-offs between defenses against herbivores in goldenrod (*Solidago altissima*)

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Abstract

In the goldenrod *Solidago altissima*, most stems are erect, but "ducking" genotypes bend the tip of the apical stem downward for much of the growing season, and this morphology protects against at least two gall-forming herbivore species. Despite this advantage to defense, ducking remains a rare strategy in goldenrod, yet the costs that prevent ducking genotypes from outcompeting erect genotypes remain unclear. We tested whether ducking (an architectural defense) trades off with chemical defense against aphids (*Uroleucon nigrotuberculatum*). We hypothesized that signaling related to the ducking defense might interfere with investment in chemical defenses, making ducking plants more susceptible to some herbivores. To test this hypothesis, we compared aphid survival and preference on ducking and erect genotypes. We also measured terpenoid concentration in *S. altissima* leaf tissue to determine whether plant investment in these compounds correlated with either ducking or aphid performance. Aphids had higher survival on all three ducking genotypes than their erect counterparts and preferred ducking to erect plants in two of three genotype pairings. However, terpenoid concentrations did not track with either ducking or aphid performance and cannot therefore explain the differences between ducking and erect host-plants. Although the mechanism remains unknown, the data supported the predicted trade-off in defenses against different herbivores, which may contribute to the distribution and abundance of these two defensive strategies.

Keywords Allelochemical · Aphid · Ducking · Goldenrod · Plant defense · Terpenoids

Introduction

A great deal of theoretical and empirical work has sought to explain patterns of defense against herbivores within and among plant species (Stamp 2003). A common assumption of plant defense theory is that investments in defense entail significant costs so that the allocation of scarce resources to defense requires trade-offs. While many such trade-offs are well documented (Herms and Mattson 1992; Koricheva 2002; Thaler et al. 2012; Pierik et al. 2014), other trade-offs predicted by theory are not reflected in the findings of empirical studies (e.g., Alba et al. 2011; Kempel et al. 2011), suggesting that there may be gaps in our understanding of the relevant fitness costs and benefits. For example, in tall goldenrod, *Solidago altissima* L. (Asteraceae), a minority of genotypes has a seemingly superior defensive strategy (Wise and Abrahamson 2008), and ecological costs to this strategy remain elusive or inconsistent (Wise 2009; Wise et al. 2010b).

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In the *S. altissima* system, there is a genetically controlled defense polymorphism: most stems remain erect throughout the life of the ramet, while a minority of genotypes are cernuous, with a "ducking" (also termed "candy-caning") tip that bends downward just below the bud (Wise and Abrahamson 2008). Ducking deters oviposition by the gall-inducing fly, *Eurosta solidaginis* Fitch (Diptera, Tephritidae); however, ducking stems that are attacked form galls at the same rate as erect stems (Wise and Abrahamson 2008; Wise et al. 2010a). Ducking also reduces galling by the midge *Rhopalomyia solidaginis* Loew (Diptera, Cecidomyiidae) although differences between galling and oviposition could not be distinguished for this species (Wise and Abrahamson 2008). Stems of ducking plants straighten to reach full height before flowering, and no differences in seed production were observed between stem morphs under greenhouse conditions (Wise 2009). Despite conferring resistance to at least two specialist herbivores and having no intrinsic trade-off with reproduction, ducking genotypes are a minority in all observed populations (2–10% of genets; Wise and Abrahamson 2008; Wise 2009), which suggests a cost to the ducking strategy that prevents it from outcompeting erect genotypes.

One cost to ducking might be trade-offs with other forms of defense that leave the plant vulnerable to some classes of herbivores. In field populations of *S. altissima*, ducking genotypes were no more vulnerable to a broad range of herbivores than erect genotypes (Wise 2009; Wise et al. 2010b). The only detectable cost of ducking was a 26% increase in attack by the non-galling, stem-boring lepidopteran *Dichomeris inserrata* Walsingham (Lepidoptera, Gelechiidae) but despite susceptibility to *D. inserrata*, ducking genotypes were slightly more likely than erect plants to have successfully flowered and set seed (Wise 2009). In addition, a subsequent study found that ducking and erect stems were equally attacked by *D. inserrata* (Wise et al. 2010b). We further investigated how costs of ducking might be explained, in least in part, by trade-offs with other types of defense; however, here we adopted a laboratory approach to control herbivore exposure and provide a more standardized test for trade-off mechanisms.

We hypothesized that ducking, as an architectural defense (Wise et al. 2010a), might impair chemical defense. Auxins are thought to regulate virtually all aspects of plant growth (Santner et al. 2009) and are therefore likely involved in *S. altissima* ducking. Auxin, among other hormones, can also suppress pathogen-defense and disrupt herbivore-defense signaling pathways (Grunewald et al. 2009; Huot et al. 2014), potentially creating a trade-off between ducking and resistance to some types of herbivores. To determine whether trade-offs with other defenses might contribute to the rarity of ducking genotypes, we tested whether ducking genotypes were more susceptible to the specialist aphid species *Uroleucon nigrotuberculatum* Olive (Hemiptera, Aphididae) which does not target the tip of the plant and whether any susceptibility was chemically mediated.

We examined terpenoids as potential defensive compounds as they represent one of the major chemical defenses in *Solidago* (Johnson et al 2007; Heath et al 2014). Terpenoids are the largest class of secondary plant metabolites (Langenheim 1994) and some of the most costly compounds that plants produce (Gershenzon 1994; Langenheim 1994), suggesting that trade-offs with other defenses or plant functions, such as growth, should be common. In addition, terpenoids are known to protect against aphids in several plant species (Manninen et al. 1998; Hagenbucher et al. 2013) and laboratory assays (Wang et al. 2008) and may also reduce aphid performance in *S. altissima*, a plant species with high concentrations of terpenoids and related compounds in aboveground tissues (Williams and Avakian 2015).

Given our hypothesis that ducking trades off with other defenses, we predicted that ducking plants would be better hosts for aphids and support higher aphid survivorship because phytohormone signaling for the architectural defense would suppress chemical defenses. Because the aphid *U. nigrotuberculatum* is a goldenrod specialist, we also predicted that aphids would correctly choose ducking plants as better host-plants than erect genotypes. Finally, we predicted that ducking genotypes would have reduced terpenoid content and that this would correlate with aphid performance.

Methods

Plant and insect material

Solidago altissima is a North American goldenrod, common in old-growth fields and other disturbed habitats (Abrahamson and Wies 1997). In addition to sexual reproduction, *S. altissima* also reproduces clonally through underground rhizomes (Abrahamson and Weis 1997). We collected rhizome tissue from three ducking ("CC17", "CC25", and "CCH") and three erect ("S110", "REI", and "Bell0") *S. altissima* genotypes (also referred to as "clones"); all rhizomes were collected in the vicinity of University Park, PA (USA; 40°49′9.87"N, 77°51′33.49"W) with all collections sites separated by no more than 17 km. No two ducking or erect clones were collected from the same field site to ensure each clone was distinct. To increase rhizome tissue and reduce any maternal effects, we grew in the greenhouse (27:21 °C D:N, 50%, RH, ambient spring/summer lighting) every clone through at least one generation before harvesting rhizomes and storing them bare-rooted at 4 °C until the experiments. We replicated each clone by cutting rhizomes into 5 cm lengths and planting them in shallow beds with Biomix

commercial potting mix (75% sphagnum moss, 25% perlite and vermiculite; Quakerstown, PA), without fertilizer. After two weeks, we transferred sprouts to pots (1 gal trade size; actual volume = 2.8 L), again without additional fertilizer. For aphid performance experiments, we planted one ramet per pot, while for choice experiments we planted two ramets (one ducking and one erect genotype). These two ramets were matched for size (by height of the sprouts) and were planted together about 6 cm apart. Ramets grew for another four weeks in a climate-controlled (conditions as above) and pest-free greenhouse before we conducted the experiments. During the four weeks, the sets of two ramets planted in one pot likely had a chance to compete with each other, but this competition inconsistently influenced plant height; in some pairings the ducking plants tended to be taller, in others the erect plants tended to be taller. Regardless, aphids did not show a preference for taller (more vigorous) plants (data not shown). We watered all plants to keep the soil moist.

The aphid *U. nigrotuberculatum* is a specialist that feeds mainly on *S. altissima* (Cappuccino 1988). This species is common in central Pennsylvania, but patchily distributed. Aphids used in experiments were maintained in a research laboratory at room temperature on *S. altissma* genotypes different from those used in the study. We collected aphid from *S. altissima* near University Park, Pennsylvania (USA; 40°49′9.87"N, 77°51′33.49"W).

Aphid survival

We assessed *U. nigrotuberculatum* survival on three pairs of randomly assigned erect and ducking genotypes. Not all experiments were conducted simultaneously, so to control for any time effects, we tested each ducking clone alongside an erect clone. CC17 was paired with REI; CC25 was paired with S110; and CCH was paired with Bell0. Ten pots of each clone were taken from the greenhouse into the laboratory, where they were kept on benchtops at room temperature (about 21 °C and 50% RH) with ambient lighting, but we also supplied additional lights (60 W incandescent bulbs, 12:12 L:D) with about one fixture per four pots. We placed ten aphid nymphs (1–3 days following nymphiposition) on each plant. Because removing young aphids from their host plants can easily damage their stylets, we placed aphids on our experimental plants by cutting stem segments of their original plant, removing all but ten nymphs, and placing the stem within the upper third of the stem of the new plant. This allowed aphids to disengage their stylets on their own and colonize their new host plant; most aphids colonized the new plant within 24 h, but a few took two days. We recorded the number of surviving aphids on each ramet every day for five days.

Aphid host-plant choice

To test aphid choice for ducking or erect host plants, we planted one erect and one ducking ramet into ten pots for each pairing. CC17 and CC25 were both paired with S110, and CCH was paired with Bell0. As in the aphid survival experiment, we placed plants in the laboratory (conditions as above) to perform the assays. For every pair, we carefully removed ten large aphids (adult or near-adult nymph of the final instar) off their original plants, using a fine brush, and placed them into plastic petri dishes (60 × 15 mm; Fisher Scientific, Hampton, NH, USA). We then placed the petri dishes with freely walking aphids on the soil in the center of each pot so that the stems of both clones touched the rim of the dish and counted the number of aphids on each plant at 30 min, 90 min, 18 h, and 48 h after release.

Terpenoid extraction and chemical analysis

To assess chemical defenses, nine days after aphids colonized the plants, we sampled one fully formed leaf (approximately 100 mg) from the upper third of each plant in the aphid survival experiment. We sampled ten replicates, i.e., one leaf from ten different plants of each clone, except CC25 for which we were only able to sample five. Because terpenoid concentrations can vary with leaf development (Crankshaw and Langenheim 1981; Heath et al. 2014), we took leaves that were all approximately the same size and age. We measured the exact weight of each cut leaf and then put each leaf in an Eppendorf tube (2.5 ml; Fisher Scientific) and placed it in a $^{-}$ 80 °C freezer until processing and analysis. We extracted terpenoids from frozen tissue by microwave extraction (Gómez and Witte 2001). In brief, we crushed tissue in 0.75 ml of *n*-hexane, containing 50 µg * ml^{-1} of *n*-octadecane. We then microwaved samples in a room-temperature water bath (200 ml) for 60 s on high (700 W microwave oven). After centrifuging samples (10,000 rpm for 1 min), we separated the supernatant into 1.5 ml glass vials and returned them to the freezer until analysis.

We identified terpenoid compounds using a gas chromatograph (Model 7890A, Agilent Technologies; Santa Clara, CA, USA) coupled with a mass spectrometer (Agilent model 5975C) in electron ionization mode, comparing retention times and mass spectra with that of known standards and libraries (Helms et al. 2014). We quantified compounds using gas chromatography-flame ionizing detection (GC-FID; Agilent model 7890A). We combined 150 µl of each sample with 400 ng of nonyl acetate as an internal standard and compared peak areas to measure µg of each identified the mass of terpenoid per g of leaf tissue. The gas chromatographs had splitless injectors held at 220 °C, were fitted with HP-1 columns (15 m × 0.25 mm × 0.25 µm film thickness; J&W Scientific, Folsom, CA), were maintained at 35 °C for

30 s, then ramped 2 °C min^{-1} to 130 °C, and ramped again at 20 °C min^{-1} to 220 °C.

Data analysis

We conducted all statistical analyses in R (version 3.5.1; R Core Team 2013). To compare aphid survivorship among clones, we tested for a significant interaction between time and ducking. If, as predicted, aphids perform better on ducking genotypes, then the decline in aphids over time should be more shallow for ducking than erect clones. We compared all six clones with each other with a linear mixed model, with time (day) and ducking as fixed effects, and individual plant as a random effect to account for repeated sampling over time. Although counts were discreet, the data approximated a normal distribution. We also analyzed each set of paired genotypes separately with mixed linear models.

We tested for aphid host-plant preference with matched pair analyses. We calculated the difference in the number of aphids between plants paired within the same pot and compared the difference to zero with a t test. To account for any time required to choose a preferred genotype, we only analyzed preference at 48 h as a "final" choice. We examined how quickly aphids chose plants by comparing aphid preference (the difference between paired plants) among time points with a mixed model with individual plant as a random effect, and we tested for significant differences among time points with Tukey–Kramer multiple contrasts.

We restricted most analyses of terpenoids to compounds that were > 25 µg per g of leaf tissue. The effects of terpenoids on herbivores are typically dose dependent (Langeheim 1994), so these most abundant compounds are most likely to explain herbivore performance. In addition, compounds at lower concentrations also tended to be more variable (with standard deviations larger than means, Table S1). We compared these compounds among clones using MANOVA, followed by ANOVAs and all pairwise multiple Tukey–Kramer comparison for each individual compound. We also analyzed limonene, which was only present in one clone but at high concentrations (see Results), by comparing its abundance in the only clone in which it was detected to zero with a *t* test. Limonene was not included in our MANOVA because its inclusion violated the assumption of multivariate normality. We compared the total amount of identified terpenoids (including both low and high concentration compounds) among clones with an ANOVA. Concentrations were square root or natural log transformed to normalize residuals, as required by our statistical tests. To further visualize differences in the most abundant terpenoids, we used a principal component analysis (PCA) and grouped components by clone and by ducking or erect genotypes. We rescaled and centered variables (terpenoid concentrations) before calculating components using the "prcomp" command in R.

Results

Aphids had significantly higher survivorship on ducking clones than on erect (Mixed linear model: time*ducking $t = 7.1$, $p < 0.0001$). This was true for each of three pairs of clone (Fig. 1; Table S1): CCH and Bell0 (Mixed linear model: time * ducking $t = 2.9$, $p = 0.005$), CC17 and REI (Mixed linear model: time*ducking $t = 4.3$, $p < 0.0001$), CC25 and S110 (Mixed linear model: time*ducking $t = 2.0$, $p = 0.047$).

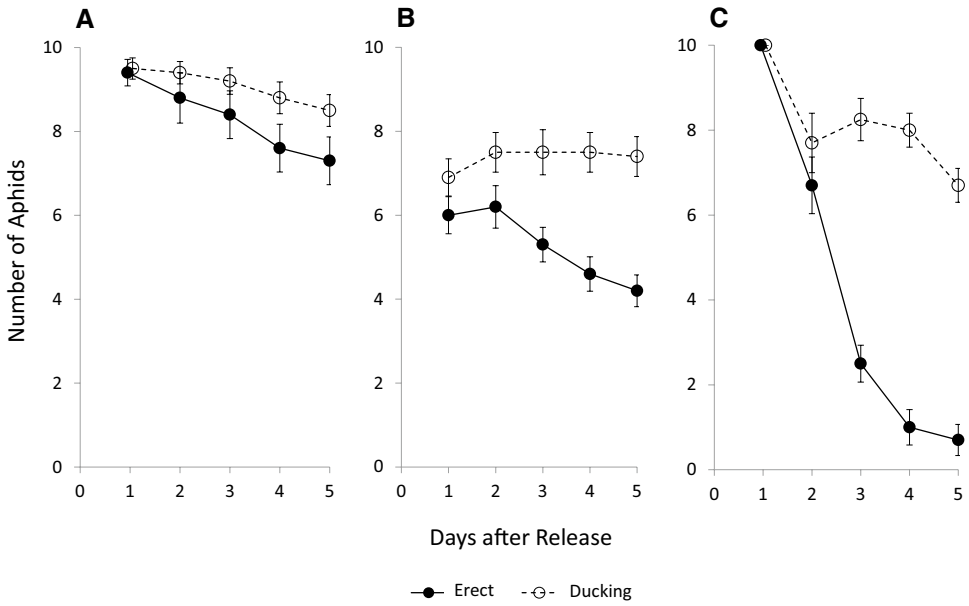

Fig. 1 Survivorship of first instar *Uroleucon nigrotuberculatum* aphids on ducking (open markers) and erect goldenrod clones (closed markers) by pairs Bell0 and CCH (**a**), REI and CC17 (**b**), and S110 and CC25 (**c**). Bars represent standard error. Aphid survivorship was significantly higher on all ducking clones compared to their erect clone counterparts

Aphids preferred ducking plants in two of our choice combinations, but not the third (Fig. 2). Aphids preferred both CC25 and CC17 over S110 (matched pairs *t* test: CC17 $t = 2.5$, $p = 0.032$; CC25 $t = 7.7$, $p < 0.0001$), but showed no preference for either CCH or Bell0 (Matched pairs *t* test: $t = 1.2$, $p = 0.28$). When aphids did choose between clones, there was no immediate preference, but rather aphids required 90 min to 18 h before settling on the preferred plant (mixed model: CC17/S110 $F_{3,25} = 3.3$, $p = 0.04$; CC25/S110 $F_{3,24} = 6.9$, $p = 0.002$; Fig. 2).

We identified 20 terpenoids from our leaf samples (Table S2). Of these, 6 had concentrations of at least 25 $\mu g*g^{-1}$ of leaf tissue: α-pinene, β-pinene, myrcene, bornyl acetate, caryophyllene, and germacrene D. In addition, limonene was abundant in one clone (REI), but absent from all other clones (Fig. 3, Table S2). The six most abundant compounds varied significantly among clones (MANOVA: $F_{5,51} = 8.9$, $p < 0.0001$), but PCA revealed that most clones overlapped significantly in their terpenoid profiles, except those of CC25 (Fig. 4a). The multivariate difference among clones was driven by α-pinene (ANOVA: $F_{5,51} = 10.1$, $p < 0.0001$), β-pinene (ANOVA: $F_{5,51} = 11.9$, $p < 0.0001$), myrcene (ANOVA: $F_{5,51} = 18.8$, $p < 0.0001$), and bornyl acetate (ANOVA: $F_{5,51} = 10.5$, $p < 0.0001$), while caryophyllene and germacrene D did not differ among clones (ANOVA: caryophyllene $F_{5,51} = 1.1$, $p = 0.39$; germacrene D $F_{5,51} = 2.2$, $p = 0.07$; Fig. 3). REI had concentrations of limonene significantly greater than zero (*t* test: $t = 5.1$, $p = 0.0007$). The sum of all identified terpenoids also varied by clone (ANOVA: $F_{5,51} = 3.0$, $p = 0.02$); however, despite this significant result, Tukey–Kramer comparisons revealed no pair-wise differences. (Terpenoid concentrations in S110 were greater than Bell0 and CCH, but the differences only approached significance with *p*-values = 0.06 and $p = 0.08$, respectively.)

Despite differences in terpenoid content among clones, there was no clear relationship between terpenoids and ducking or aphid performance (Fig. 3). While the less suitable host for aphids (S110; Figs. 1, 2) tended to have the most terpenoids (Fig. 3), the ducking clone CC17 also had high terpenoid content (Fig. 3), but was a much more suitable aphid host (Fig. 1). Ducking plants did not consistently have greater or lesser terpenoid concentrations (Fig. 3), and PCA revealed substantial overlap in ducking and erect terpenoid profiles (Fig. 4b). Total terpenoid concentration was similar between ducking and erect clones (ducking mean = 864 ± 376 $\mu g * g^{-1}$; erect mean = 918 ± 490 $\mu g * g^{-1}$; mean ± S.D.; ANOVA: $F_{1,55} = 0.07$, $p = 0.79$).

Discussion

Aphids survived better on ducking than erect clones for all three pairs of goldenrod genotypes (Fig. 1), suggesting that, indeed, a cernuous growth form increases vulnerability to aphid attack. The mechanism behind this trade-off, however, remains unclear. Terpenoid concentrations failed to reveal any clear patterns between ducking and erect clones or with aphid performance (Figs. 3, 4). This contrasts with a previous study on *U. nigrotuberculatum* and *S. altissima* that found a nearly significant correlation between high concentrations of β-pinene and reduced aphid abundance

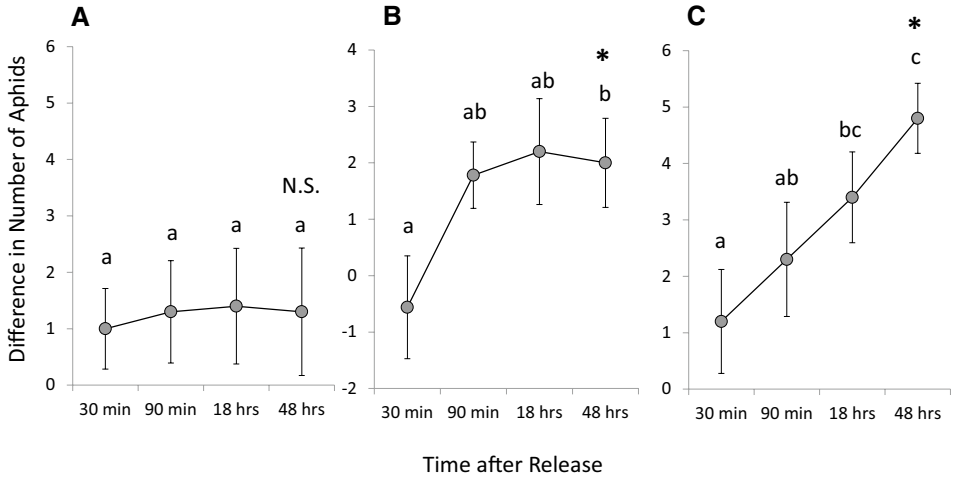

Fig. 2 Preference of adult *Uroleucon nigrotuberculatum* aphids for ducking over erect goldenrod clones over time. Aphid preference is the difference in the number of aphids between paired ducking and erect plants, with positive values indicating preference for the ducking plant. Bell0 and CCH are shown in A, with CC17 and S110 shown in B, and CC25 and S110 shown in C. Bars represent standard error. Times of observation that share letters were not significantly different at $\alpha = 0.05$, and * indicates that aphids significantly preferred one clone after 48 h

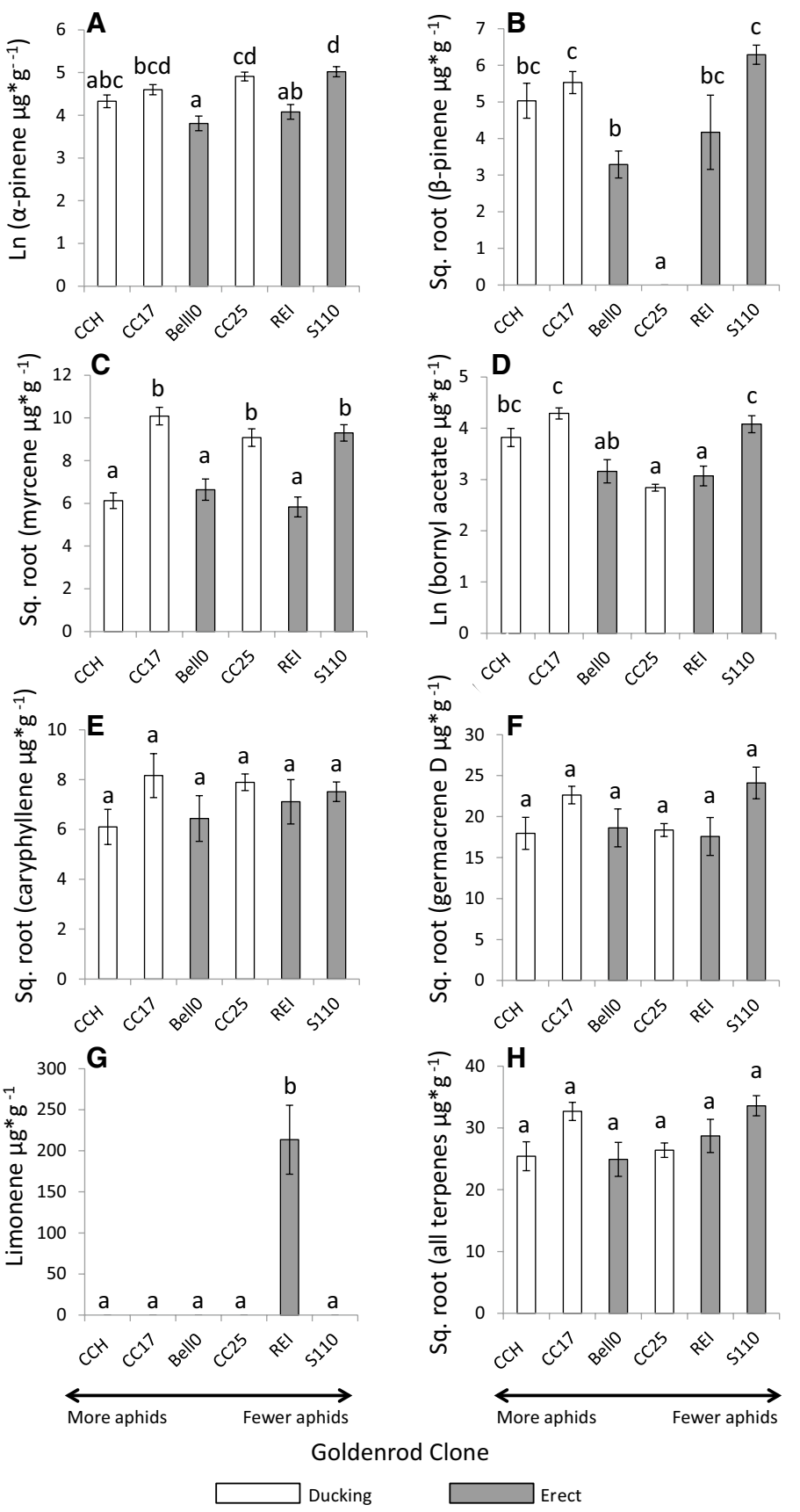

Fig. 3 Terpenoid concentrations in six goldenrod clones (terpenoid mass in µg per fresh leaf tissue mass in g), ordered from most suitable host for aphids on the left to less suitable host for aphids on the right, based on aphid survival data. White bars show data for ducking clones, and grey bars show erect clones. **a** Shows α-pinene, **b** β-pinene, **c** myrcene, **d** bornyl acetate, **e** caryophyllene, **f** limonene; and **h** shows the sum of all 20 identified terpenoids. Any transformations, which helped satisfy assumptions of normality, are indicated on the *y*-axes. Bars represent standard error, and bars that do not share a letter are significantly different at $\alpha = 0.05$

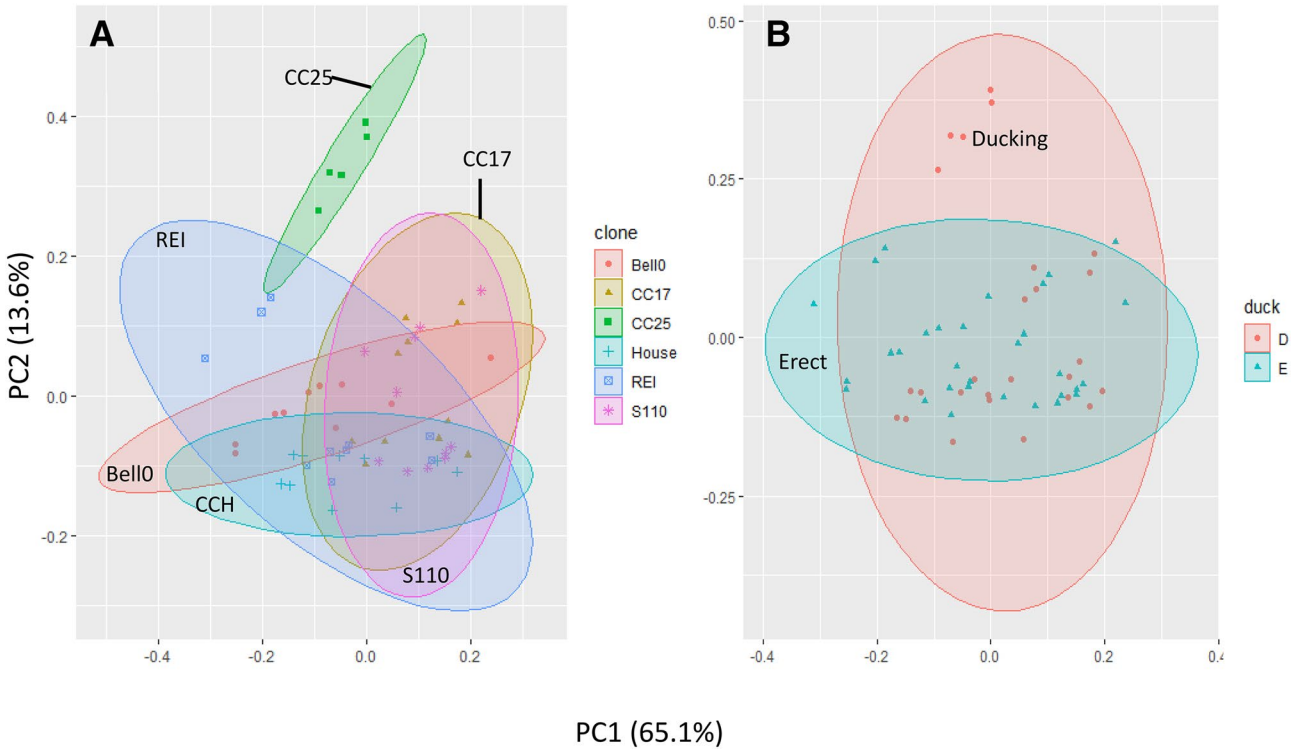

Fig. 4 Plots of a principle components analysis that groups principal component values by goldenrod clone (**a**) or by ducking and erect goldenrod genotype (**b**). The amount of variance explained by each component is given in parentheses on the axes. PC1 largely represents total abundance, while positive values of PC2 represent α-pinene, myrcene, and caryophyllene and negative values represent β-pinene, bornyl acetate, and germacrene D

(Williams and Avakian 2015). Our data show that high levels of β-pinene coincided with low aphid survival in erect clones; this was not true for ducking clones (Fig. 3b), so β-pinene concentrations alone cannot explain differences in aphid performance between ducking and erect defensive strategies. However, ducking might interfere with β-pinene as a defense against aphids and thereby increase susceptibility in ducking genotypes, but such a mechanism requires additional investigation. After failing to detect terpenoid patterns to explain aphid performance, we also examined whether the number of trichomes per unit area or the length of trichomes might explain aphid survival (Levin 1973); however, trichome density and length also failed to correspond to aphid performance (See Supplementary Material; Fig. S1).

While they can reduce aphid performance (Manninen et al. 1998; Wang et al. 2008; Hagenbucher et al. 2013), terpenoids are not generally believed to be strongly induced by aphid feeding (Walling 2008; Hagenbucher et al. 2013). Instead, plants more often respond to aphid attack by producing phenols and proteinase inhibitors (Smith and Boyko 2007), although evidence for the definitive function of these compounds on aphids is usually lacking (Smith and Chuang 2014). Additionally, plants may also induce antimicrobial defenses that might disrupt aphid gut symbionts (Smith and Boyko 2007). Links between ducking and these compounds or their associated regulatory pathways might yield further insight into how ducking might trade off with other defenses.

In addition to toxic effects, terpenoids can also act as airborne signals and cues that might attract the natural enemies of herbivores or deter herbivore feeding (Langenheim 1994). The sesquiterpene β-farnesene is an alarm pheromone in many, but not all, aphids that causes them to stop feeding and flee the area (Francis et al. 2005; Unsicker et al. 2009). β-farnesene might act as aphid repellent, although its effectiveness as part of a volatile blend remains uncertain (Unsicker et al. 2009). *Solidago altissima* emits β-farnesene from both damaged and undamaged tissues (Helms et al. 2014), and we detected β-farnesene within leaf tissue from all 6 clones (Table S1). However, all clones emitted similar amounts of β-farnesene (Table S1), so it is unlikely to explain differences in aphid host-plant preference. In addition, aphids did not immediately choose their ultimately preferred clone (Fig. 2), suggesting that aphids predominantly used tactile or gustatorial cues, perhaps in combination with airborne cues, to assess host suitability. It should also be noted that we tested the response to ducking and erect stems of individuals from only one population of aphids. Given

that aphid responses to plant genotypes can vary significantly across regions (e.g., Kim et al. 2008), it is possible that aphids from other regions may have responded differently to the genotypes included in our experiment, though ducking plants are consistently in the minority (Wise and Abrahamson 2008).

Despite apparent advantages in defense, ducking genotypes have not spread in field populations (or gone to extinction), suggesting that the polymorphism is maintained by counterbalancing selection pressures. Our data suggest that variation in aphid abundance (Cappuccino 1988) could explain variation in the fitness in ducking genotypes, but there are other non-mutually exclusive mechanisms and trade-offs that might explain the observed distribution of defense strategies. One possibility is that the frequency of ducking genotypes in the field only appears stable over short periods of time and that ducking is actually a recent mutation that has not yet spread through *S. altissima* populations (Wise and Abrahamson 2008). Ducking genotypes, however, are widely distributed and found in both eastern hexaploid and Midwestern diploid populations (ECY pers. obs.), suggesting that there has been more than adequate time for the trait to spread in local populations. The fitness of ducking plants in an area likely depends on the abundance of ducking genotypes and *E. solidaginis* (Wise and Abrahamson 2008). Because ducking influenced oviposition choice, but not larval performance of at least one herbivore (the goldenrod gall fly *E. solidaginis*), the benefits of ducking may only manifest if herbivores can choose erect stems, rendering the defense ineffective if ducking is the dominant strategy. Finally, ducking plants straighten under low-light conditions (Wise and Abrahamson 2008), suggesting that ducking plants might be poor competitors for light. On the other hand, plasticity in the ducking phenotype also indicates that ducking genotypes can change their growing strategy to increase access to light and maintain their fitness in light-limited environments. Light competition can impair plant defense mechanisms (Ballaré 2014); however, plants in our aphid survival experiment were sufficiently separated that every plant had approximately equal light exposure.

Costs of ducking in *S. altissima*, both ecological and intrinsic, have thus far been difficult to detect (Wise 2009; Wise et al. 2010a); however, the effect of ducking on attack by *U. nigrotuberculatum* or any other aphid had not been previously investigated. Our laboratory experiments allowed us to control exposure to herbivores and avoid the noisy variance of field studies, but removed any possibility of detecting ecological costs or interactive effects that might promote or mask trade-offs between ducking and other forms of defense (e.g., Wise 2009; Wise et al. 2010b). Importantly, the plants we used for our experiments were of an age that can be colonized by *U. nigrotuberculatum* aphids in the field (Cappuccino 1988; Williams and Avakian 2015), suggesting that our results should have relevance to natural communities, but it will be important to perform similar research in field settings to confirm their relevance. Nevertheless, our data suggest that aphids are a promising focal species to study trade-offs between ducking and erect genotypes under more natural, field conditions and how these trade-offs might interact with other selective agents.

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