Genetic variation for susceptibility to storm-induced stem breakage in Solidago altissima: the role of stem height and morphology

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**A B S T R A C T**

While storms can have obvious ecological impacts on plants, plants’ potential to respond evolutionarily to selection for increased resistance to storm damage has received little study. We took advantage of a thunderstorm with strong wind and hail to examine genetic variation for resistance to stem breakage in the herbaceous perennial *Solidago altissima*. The storm broke the apex of nearly 10% of 1883 marked ramets in a common-garden plot containing 26 genets of *S. altissima*. Plant genets varied 20-fold in resistance to breakage. Stem height was strongly correlated with resistance to breakage, with taller stems being significantly more susceptible. A stem’s growth form (erect versus nodding) had no detectable effect on its resistance to breakage. Therefore, we rejected the hypothesis that a function of the nodding, or “candy-cane,” morphology is protection of the apex from storm damage. The significant genetic variation in *S. altissima* for stem breakage suggests that this plant has the capacity to respond to selection imposed by storms — particularly through changes in mean stem height. Tradeoffs between breakage resistance and competition for light and pollinators may act to maintain a large amount of genetic variation in stem height.

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1. Introduction

As sedentary organisms, plants are subjected to damage from a large variety of sources — both biotic, such as pathogens and herbivores, and abiotic, such as fire, frost, and storms (White, 1979; Belsky et al., 1993; McPherson and Williams, 1998; Kopfer et al., 2002; Peltzer and Wilson, 2006). Although both biotic and abiotic interactions can have substantial impacts on plant fitness, there has been relatively little emphasis on the evolutionary potential of plant populations to resist abiotic factors, such as storm damage (Agrawal et al., 2004). Perhaps this is because plant damage from storms tends to be more stochastic and less predictable than damage from biotic sources. Nevertheless, plant populations have the ability to evolve in response to the potentially strong selection imposed by storms if the populations possess genetic variation for resistance to the damage.

Several morphological traits are involved in determining a plant’s susceptibility to breakage, including stem height, thickness, bulk-tissue density, and elasticity (Niklas, 1995). Stem height is particularly interesting, as it is constrained allometrically by other stem traits (Nagashima and Terashima, 1995; Niklas, 1995), and it has such a strong influence on the plant’s interactions with abiotic and biotic factors in its environment. Greater height should be selectively advantageous because tallness would increase a plant’s ability to compete for light and pollinators. However, the height of plants may not only be limited by physical constraints but by selective disadvantages that accompany greater tallness, such as increased exposure of the apex to winds and hail. Thus, variation in stem height in plant populations may be maintained by balancing selection.

Stems may vary not only in height, but also in architectural (or growth form) features that can affect exposure to wind and storms. For instance, Rudgers and Whitney (2006) described ecological implications of an architectural dimorphism in the shrub *Baccharis pilularis* (Asteraceae), which exists as both erect and prostrate morphs. Likewise, we recently described a stem dimorphism in *Solidago altissima* (Asteraceae) in which the majority of plant genets produce erect stems (with the apex pointing upward), while a substantial minority (~25% or less) produce temporarily nodding stems (Wise and Abrahamson, 2008b). These nodding stems, which we dubbed “candy-cane” stems, emerge from the ground erect, but after 3–4 weeks, each stem’s apex begins to nod until the apical-leaf bud is pointing directly downward. The apex may remain in a nodding position for over a month, but the stem straightens by
mid-to-late summer so that candy-cane and erect stems do not differ in height by the time flower buds are formed (Wise and Abrahamson, 2008b).

The nodding morphology of S. altissima has long been recognized (Croat, 1972; Weber, 1997), but no function had been proposed for nodding until recently. Because we have found nodding genets in all sizable S. altissima populations (as well as populations of Solidago gigantea and Solidago junccea), we believed nodding likely serves a widespread ecological function. Specifically, we proposed that nodding serves as a defensive trait against apex-attacking herbivores (Wise and Abrahamson, 2008b). Since then, we have found that candy-cane genets are roughly twice as resistant to three apex-attacking herbivores: two apical rosette-gall inducing Cecidomyiids (Rhopalomyia solidaginis and Asphondylia solidaginis) and the ball-gall inducing tephritid fly Eurosta solidaginis (Wise and Abrahamson, 2008b; Wise, 2009; Wise et al., 2009). Because the nodding occurs during the period that these herbivores are searching for apices to oviposit into, we called this defense tactic “resistance by ducking” (Wise and Abrahamson, 2008b).

Although the resistance value of ducking has been established, herbivory defense is not necessarily the raison d’être for the nodding stems. A particularly likely candidate for a function of nodding is protection of the apical meristem from storm damage. In addition to reducing a stem’s effective height, nodding may help hide the tender shoot apex from hail or wind shears during the time of year (late spring and early summer) when strong storms are common.

Here, we report on the results of a semi-natural experiment in a common-garden plot that contained numerous clonal replicates of 26 different S. altissima genets (21 erect and 5 candy-cane genets). On 25 May 2004, a strong thunderstorm with hail broke the apex of nearly 10% of the S. altissima ramets in the garden. We used data on stem breakage to address three main questions: (1) Do plant genets differ in susceptibility to storm damage (i.e., is there genetic variation for susceptibility)? (2) How does stem height affect susceptibility to damage? and (3) Are candy-cane genets less susceptible to damage from storms than erect-stemmed genets?

2. Materials and methods

2.1. Study species

S. altissima is a common herbaceous perennial native to eastern and central North America (Barlyk et al., 2006). It is known for its prodigious display of yellow flowers, visible along roadsides and in old fields in the late summer and early fall. Once established in a disturbed area, S. altissima spreads clonally by sending up ramets from rapidly growing rhizomes (Hartnett and Bazzaz, 1985; Abrahamson and Weis, 1997; Meyer and Schmid, 1999). Previous studies have shown that stem height is extremely variable, and that much of this variation is genetically controlled (Horner and Abrahamson, 1992, 1999; Wise and Abrahamson, 2008a).

In central Pennsylvania, the area of this study, S. altissima ramets begin emerging in late April. In the majority of genets (~75% or more), all ramets remain erect from emergence through flowering and senescence. In candy-cane genets, all ramets begin to nod within a month after emergence, and the stems remain nodding throughout the vegetative growth phase (Wise and Abrahamson, 2008b). In the disturbed habitats in which S. altissima dominates, goldenrods tend to be among the tallest plants, such that the tops of the plants are potentially exposed to wind and hail. Previous work has shown that damage to apical meristems puts goldenrod ramets at a substantial growth and reproductive disadvantage (Hartnett and Abrahamson, 1979; Wise et al., 2006a; Wise and Abrahamson, 2008a; Wise, 2009).

2.2. Experimental design

This common-garden experiment was originally designed to study goldenrod’s defense against herbivores. More details on the design can be found in Wise et al. (2008). As a source of plants for the garden, S. altissima rhizomes were excavated from a 3-ha field population in Union County, Pennsylvania, USA (N40° 57.9’ W76° 57.3’) in the early spring of 2003. The rhizomes came from 26 widely separated genets, five of which produced candy-cane stems and 21 of which produced erect stems. The rhizomes were cut into segments and placed into flats in commercial growing medium (ProMix BX™, Premier Horticulture Ltd., Dorval, Quebec, Canada) in a greenhouse at Bucknell University. After shoot emergence, ramets were transplanted individually into 16.5-cm plastic azalea pots prior to transplanting into a garden plot adjacent to the greenhouse.

The garden plot was prepared by herbiciding, clearing, and tilling. The plot was separated into rows 90-cm apart, and positions within rows were flagged at 90-cm increments. The rows were assigned to 15 statistical blocks, with 26 consecutive positions per block. Within each block, one randomly selected ramet from each of the 26 goldenrod genets was randomly assigned a position. The ramets were removed from their pots and transplanted into the garden on 15–19 June 2003. All 390 ramets survived transplanting and produced new ramets the next spring.

We planted additional goldenrod ramets along each border of the plot to lessen potential “edge effects” on the experimental ramets. The west side of the garden plot was bordered by the greenhouse, and the other three sides were bordered by large open areas of mowed grass. The experimental blocks ran parallel to the greenhouse, with the first block being closest to the greenhouse. Thus, each successive block was less likely to receive any protection from strong winds coming from the west.

In spring of 2004, we flagged the five closest ramets to each of the 390 original positions that clearly arose from the ramet planted the previous June. For some planting positions, five new ramets were not available, but there were always at least two clearly identifiable new ramets, and the mean number of ramets tagged per planting position was 4.83 (std = 0.53). On 25 May 2004, a thunderstorm with strong wind gusts and hail hit the garden plot. The storm broke the apices off of nearly 10% of the ramets.

2.3. Data analysis

To determine whether there was broad-sense genetic variation (i.e., variation among genets) for susceptibility to stem breakage, we analyzed the garden data in two ways. First we ran a nominal-logistic model where we considered each marked ramet as an independent sampling unit. The model included genet and block as explanatory variables, and the response was either “broken” or “intact.” The nominal-logistic model assumes no autocorrelation in breakage response among the five marked ramets within a planting position. This assumption is not unreasonable, given the uniformity of the garden plot and the large spatial scale of the treatment (i.e., the storm) relative to the spatial scale of the garden plot.

Second, to account for potential spatial autocorrelation, we ran an ANOVA with the 390 planting positions considered the independent sampling units. The response variable was the proportion of the five marked ramets that were broken at each planting position, and the explanatory variables were genet and block, which were both considered random effects. The proportions (±0.01) were natural-log transformed prior to analysis to homogenize the variance among genets. While the ANOVA eliminated the potential problem of auto-correlation, it had the shortcoming that the response variables could only take a discrete set of values (0/5, 1/5, 2/5, etc.). Therefore, we present the results of both the nominal-logistic model and the
ANOVA to compare the results when the responses were considered discrete versus continuous. (The inferences of the two models turned out to be the same).

To determine whether stem morphology affected susceptibility to breakage, we ran analogous analyses to the two in the previous paragraph, but instead of plant genet, we included stem morphology (candy-cane or erect) as an explanatory variable. In the ANOVA, stem morphology was considered a fixed-effects factor, and we included genet nested with stem morphology to separate the effects of stem type from other influences of plant genet. All analyses in this paper were run with JMP-IN 4.0.4 (SAS Institute, Cary, North Carolina).

2.4. Plant height

Ideally, we would have measured stem heights just prior to the storm. Then we would be able to calculate a relationship between stem height and probability of breakage on both a phenotypic (individual-ramet heights) and genotypic (genet-mean heights) basis. Fortunately, we retained clonal progeny from each of the 26 genets used in the garden experiment to grow rhizomes for future experiments. In late April of 2005, we cut rhizomes of each of the genets into 2-ml segments, which we measured by water displacement in a 100-ml graduated cylinder, and planted the segments in plastic flats (Wise et al., 2006b). In mid-May, we transplanted 18 ramets of each genet from the flats into separate 16.5-cm diameter pots, again using ProMix BX™ growing media. The experiment was split into two randomized blocks, representing the east and west sides of the greenhouse, with half of the ramets from each genet being placed in each block. The final height of the ramets was measured at the onset of senescence.

As a surrogate for ramet height in the garden experiment, we used the least-squares means for the plant genets from the greenhouse experiment from an ANOVA that included genet, block, and the interaction of genet-by-block as random effects. The absolute stem heights under greenhouse conditions will differ from the absolute heights of the stems in the garden for two reasons. First, the heights from the greenhouse were taken at the end of the growing season, when the ramets would be taller than the point in the season when the storm occurred. Second, because greenhouse conditions were more uniform, there was likely to be more variation in stem height among the garden plants. Nevertheless, because stem height is under strong genetic control, with a broad-sense heritability, or “clonal repeatability” (Falconer, 1989), of 0.63 (see Results below), we expect the relative heights of clonal replicates of the same genets in the garden plot. Therefore, to estimate the effects of stem height on susceptibility to breakage, we calculated the product–moment correlation between least-squares genet-mean stem heights in the greenhouse and the proportion of ramets per genet broken by the storm in the garden.

3. Results

The storm on 25 May 2004 broke the apex of 179 (9.5%) of the 1883 marked S. altissima ramets in the garden experiment. The most damage-susceptible genet had 23% of its stems broken, and the most damage-resistant genet had only 1% of its stems broken (Fig. 1). Both the nominal-logistic analysis (likelihood-ratio \( X^2 \) for genet = 66.005, \( P < 0.0001 \)) and the ANOVAs (Table 1) found the inter-genet differences to be significant, indicating broad-sense genetic variation for susceptibility to breakage.

There was also significant broad-sense genetic variation for stem height in the greenhouse experiment (Table 2). Genet means ranged from 98 to 208 cm, and the genet factor alone accounted for 63% of the variation in stem height (i.e., the broad-sense heritability was 0.63). The genet-by-block interaction accounted for 3% of the variation. The genet-mean heights in the greenhouse were strongly and positively correlated with the genets’ susceptibility to breakage in the garden experiment (\( r = 0.59, P = 0.003; \) Fig. 2).

Despite the presence of inter-genet differences in susceptibility to breakage, the susceptibility was nearly identical for the two stem morphs: 9.8% of the 358 candy-cane ramets were broken, and 9.4% of the 1525 erect-stemmed ramets were broken by the storm. Neither the nominal-logistic analysis (likelihood-ratio \( X^2 \) for stem morph = 0.0505, \( P = 0.82 \)) nor the ANOVA (Table 1b) found the stem morphs to differ in susceptibility to damage.

4. Discussion

4.1. Stem breakage

The kind of apex damage caused by the storm in this study has been shown to curtail the growth of goldenrod’s stem, lessen the likelihood that a ramet will flower, and substantially decrease seed production (Hartnett and Abrahamson, 1979; Wise et al., 2006a; Wise and Abrahamson, 2008a; Wise, 2009). For example, in a recent greenhouse study, manual clipping of goldenrod apices in

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late spring reduced mean seed production by 58% (Wise and Abrahamson, 2008a). Because apical damage can have such a high fitness cost, goldenrod may experience strong selection pressure to decrease susceptibility to stem breakage where storms are frequent.

Regardless of the strength of such selection, a plant population can only respond evolutionarily if it possesses genetic variation for the selected trait. The goldenrod population in this study did possess a significant amount of genetic variation for resistance to stem breakage. Across the 26 genets sampled from the field population, the proportion of ramets broken in the storm ranged from 1% for the most damage-resistant genet to 23% for the most damage-susceptible genet.

It is important to note that this variation among genets is “broad-sense” genetic variation, which is composed of additive genetic variation plus genetic variation due to dominance and epistasis (i.e., interactions among genes) (Falconer, 1989). In addition, differences among genets in the garden plot may be influenced by differences in the microhabitat of the source field, although two generations of growth in a common garden should minimize such carryover effects (Roach and Wulff, 1987). Heritability in the “narrow” sense is the ratio of additive genetic variation to phenotypic variation. Because broad-sense genetic variation has more components, broad-sense heritability is generally seen as an upper-limit estimate to narrow-sense heritability (Falconer, 1989). Broad-sense heritability is applicable in the context differential persistence and spread of existing genotypes in the population (i.e., “genotype sorting” among clones), while narrow-sense heritability is more relevant in the context of allele-frequency changes in the next generation (resulting from natural selection on individuals rather than sorting among clones) (Hartl and Clark, 1989).

Physical damage from abiotic stresses like storms is common throughout the plant kingdom (White, 1979). Stem breakage of the type observed in this study is certainly more obvious and dramatic in its ecological and economic effects when it occurs in trees. Therefore, much more research on storm damage has justifiably focused on tree species (e.g., Cooper-Ellis et al., 1999; Peltzer and Wilson, 2006). Similarly, much research has gone into factors involved in storm damage and stem breakage in crop plants (e.g., Wilhelm et al., 1999; Sił et al., 2005). By contrast, storm damage to herbaceous plants in nature is less likely to be noticed. Nevertheless, we suspect that the kind of damage we observed in goldenrod is not uncommon across herbaceous plant species, particularly those growing in exposed areas such as open fields. In addition, there is no reason to suspect that the wide range of variation in susceptibility to breakage is unique to goldenrod. Therefore, storm damage may be a more pervasive factor in the evolutionary ecology of herbaceous plants than is generally appreciated.

### 4.2. Stem height

The height of a plant’s stem is a fundamental aspect of the plant’s overall architecture (Lawton, 1983; Haysom and Coulson, 1998). In general, greater height will help a plant compete for light and pollinators with its neighbors. The height that a plant attains is remarkably plastic and depends on numerous ecological factors, including light level, density of neighbors, and availability of inorganic nutrients (Nagashima and Terashima, 1995; Wise and Abrahamson, 2008a). If being tall were always an advantage, then one would expect natural selection to consistently favor tallness, such that genetic variation for height within plant populations would tend to be exhausted. The presence of substantial genetic variation in height would thus suggest that being tall may carry disadvantages as well as advantages, and thus that the plant population may experience conflicting selection pressures on height.

In our greenhouse study, we found more than a twofold range in genet-mean heights at maturity among 26 S. altissima genets, and the broad-sense heritability for stem height was 0.63. The plants had been grown from rhizomes that had been propagated for three growing seasons since being collected from a field population. Thus, the measurement of genetic variation is not likely to be much influenced by carryover effects from potential microenvironment differences in the source population (Roach and Wulff, 1987). Such a large amount of genetic variation suggests that disadvantages of tallness may counteract the advantages that tall goldenrod plants have in terms of competition of light and pollinators. The positive relationship that we found between genet-mean height and the probability of stem breakage strongly suggests that storms may select against tall plants. While directional selection for competitive ability may place relatively constant pressure to increase plant height, the selection that storms impose to decrease plant height is likely to be more spatially and temporally variable. Thus, the stochastic nature of storm occurrence might act to maintain genetic variation for stem height within and among plant populations.

### 4.3. Ducking stems

The ducking trait exhibited by some goldenrod genets (Wise and Abrahamson, 2008b; Wise, 2008; Wise et al., 2010) would seem to be an excellent solution for coping with potential storm damage. Ducking allows candy-cane stems to be shorter than they otherwise would be during the late spring and early summer, when storms are most prevalent (PEMA, 2009). These ducking plants do not have to pay the cost of short stature in early spring (prior to ducking) or late...
summer (after straightening), when they could be competing with other plants for light and pollinators, respectively. The physical conformation of the nodding apex — tucked beneath the highest point top of the stem — might also be expected to offer some protection from breakage.

Despite this potential advantage, there was no evidence in this study that candy-cane genets were any more resistant than erect genets to storm damage. Specifically, 9.8% of the candy-cane ramets and 9.4% of the erect-stemmed ramets were broken. Importantly, the storm occurred when the candy-cane ramets were nodding. Whatever the reduction in stem height that ducking allowed, it was apparently not sufficient to reduce the probability of breakage. The nearly identical probability of breakage of the two stem morphs also suggests that the physical conformation of the nodding apex does not offer protection from breakage.

In previous studies, we have shown that ducking plants enjoy a resistance advantage against several apex-attacking herbivores (Wise and Abrahamson, 2008b; Wise, 2009; Wise et al., 2010). However, before concluding that resistance to herbivory is the raison d’être for ducking, other potential functions (or non-adaptive side-effects) would need to be eliminated. Protection from apex damage caused by storms was a promising alternative hypothesis. The storm that endangered our original field experiment fortuitously provided a powerful test that rejected the storm hypothesis. While the herbivore-resistance hypothesis thus seems even more likely, it is still possible that nodding serves additional, yet-to-be-identified functions.

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