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ORIGINAL RESEARCH

Asian corn borer damage is affected by rind penetration strength of corn stalks in a spatiotemporally dependent manner

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Abstract

Asian corn borer, *Ostrinia furnacalis* (Guenée), is an important insect pest of maize throughout most of Asia. The rind of a maize stalk is a key barrier against corn borer larvae boring into the plant. There is a need to better understand the relationship between stalk strength and *O. furnacalis* larval injury, particularly for elite maize genotypes. To determine whether stalk strength is involved in maize resistance to *O. furnacalis* larval injury, 39 maize lines were evaluated in 2012 and 2013. Rind penetration strength (RPS) was measured at tassel (VT) and milk (R3) stages as a possible stalk resistance trait for *O. furnacalis*. RPS of primary ear internode at VT and R3 accounted for 37 and 38% of the variance in *O. furnacalis* injury (measured as number of holes) for simulated (artificially infested) first and second generation *O. furnacalis*, respectively. Relationships between stalk RPS values and tunnel length were weak. Results suggest that harder stalks have enhanced resistance to stalk boring but not to pith feeding or tunneling of *O. furnacalis* larvae. The RPS measures could provide classical maize breeders an important tool for evaluating stalk strength and corn borer resistance in maize. The assessments should focus on the internodes primary ear or above/below primary ear during both VT stage for first generation and R3 stage for second generation *O. furnacalis* resistance.

KEYWORDS
Ostrinia furnacalis, rind puncture strength, stalk resistance, *Zea mays*

1 | INTRODUCTION

Asian corn borer (ACB), *Ostrinia furnacalis* (Guenée), is one of the most destructive insect pests of maize (*Zea mays* L.) across East Asia. *O. furnacalis* feeding occurs at economically damaging levels in China, the Philippines, Japan, Korea, Thailand, Indonesia, Malaysia, and other countries (Afidchao et al., 2013; All China Corn Borer Research Group, 1988).

The number of *O. furnacalis* generations per year is influenced by latitude and climate and ranges from one to seven, but two to three generations per year is normal in most major maize growing regions in China (All China Corn Borer Research Group, 1988). First generation adults typically deposit egg masses on leaves of vegetative maize. Newly eclosed neonates feed on whorl leaves, and later instars bore or tunnel into the stalk to feed on pith tissues. Second generation

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adults generally oviposit on maize leaves during the silk stage, allowing neonates to feed on reproductive tissues; later instars tunnel into the stalk or the cob (Zhou & He, 1996). Stalk feeding causes physical injury, disruption of nutrient and water transport, and increased stalk lodging (Martin et al., 2004), which complicates harvesting and reduces grain yields (Ma et al., 2014). In addition, larval tunnels weaken the plant and expose both stalk and cob tissues to bacterial and fungal infections, which ultimately affect grain quality (Gatch & Munkvold, 2002).

Insecticide applications are used to control *O. furnacalis* in maize, but it is very difficult to control larvae once they tunnel into the stalk (Gibson et al., 2009). Insecticides are often viewed unfavorably because of possible impacts to human health and the environment, and the potential for development of pest resistance and outbreaks of secondary pests (Bruce, 2010; Mitchell et al., 2016). Thus, host plant resistance through conventional plant breeding is a critical component of *O. furnacalis* integrated pest management (IPM). This method provides an economical and ecologically sound approach to minimize maize yield losses due to *O. furnacalis* (He et al., 2003).

Stalk strength is a physical barrier against larval boring (Butrón et al., 2002; Suby et al., 2020); however, previous studies on stalk strength in maize have often focused on its relationship with stalk lodging (Feng et al., 2010; Flint-Garcia et al., 2003; Gibson et al., 2009; Kamran et al., 2018; Kvedaras & Keeping, 2007; Liu et al., 2011; Ma et al., 2014; Robertson et al., 2017; Sekhon et al., 2020; Stubbs et al., 2020) or colonization of fungal pathogens, such as *Diplodia zeae* (Schweinitz) (Chambers, 1987) and *Gibberella zeae* (Schweinitz) (Pe et al., 1993). Stalk strength usually is measured by bending, puncturing or crushing the rind, or by measuring rind thickness (Thompson, 1963). Rind penetration strength (RPS, also known as rind puncture resistance [RPR]), the maximum force required to puncture the rind of stalks, is the measure often used to evaluate stalk strength (Guo et al., 2021; Liu et al., 2020), because puncturing the rind is similar to a larva boring into the rind (Gibson et al., 2009). The rind penetrometer, first used by Zuber and Grogan (1961), is an instrument used to measure RPS that often is used to correlate stalk strength with corn borer injury (Butrón et al., 2002; Gibson et al., 2009; Martin et al., 2004; Santiago et al., 2003).

Several breeding efficacy studies have focused on the relationship between maize stalk strength and borer resistance (Martin et al., 2004). Martin et al. (2004) selected Missouri Second Cycle Stiff Stalk Synthetic (MoSCSSS) for stalk strength by using a rind penetrometer to improve resistance to *Ostrinia nubilalis* (Hübner). Suby et al. (2020) showed that penetration resistance (PR) of seventh internode can be the characteristic trait for maize stalk resistance to *Chilo partellus* (Swinhoe) in maize. These two studies illustrated that high rind strength was effective at providing resistance to maize borer injury as well as resistance to stalk lodging. This was further demonstrated by López-Malvar et al. (2017), who reported that resistant inbred line EP39 showed higher rind and pith puncture resistance. However, a study on maize stalk resistance to Mediterranean corn borer, *Sesamia nonagrioides* (Lefèbvre), demonstrated that stalk strength and resistance to stem injury could be uncoupled (Santiago et al., 2003). In particular, inbred lines EP42 and EP47 have strong stalks that are not stem resistant to *S. nonagrioides* injury, while injury-resistant inbreds A509, CM151 and PB130 had some of the lowest RPS values (Santiago et al., 2003). These results were inconsistent from one corn borer species to another and one maize genotype to another, revealing the complexity of interactions between maize and its stalk pests. Butrón et al. (2002) reported that when maize varieties exhibited physical resistance to *S. nonagrioides* injury, RPS was only useful as an indicator of resistance if the main source was physical in nature. Similarly, an investigation by Gibson et al. (2009) indicated that other factors such as larval survival were more directly limiting damage by southwestern corn borer, *Diatraea grandiosella* (Dyar), compared to physical stalk strength. Overall, it is clear that the relationship between stalk strength and resistance to corn borer entry and tunneling is complex and influenced by corn borer species, maize genotype, and plant developmental stage at the time of infestation.

Although few studies have investigated the relationship between stalk strength and *O. furnacalis* injury, the relative timing of crop damage associated with the first and second generations of *O. furnacalis* is well documented in China. First generation *O. furnacalis* damage is typically highest during the vegetative tassel (VT) stage, meaning that oviposition occurs in late vegetative whorls (Lu et al., 2005). Second generation *O. furnacalis* damage is typically highest during the milk stage of kernel development (R3, Reproductive 3), following oviposition on mature tissues at the time of silk emergence (Li et al., 2002). Thus, it is especially important to determine the phenotypic correlation between stalk strength and *O. furnacalis* injury at the VT and R3 stages.

One goal of this study is to assess the relationships between RPS and *O. furnacalis* stalk resistance at VT for first generation damage, and at R3 for second generation damage for 26 maize doubled haploid lines and 13 inbred lines, almost all of which were developed in China.

A second goal is to identify the internode or node whose RPS value best correlates with first and second generation *O. furnacalis* injury. A critical ancillary goal is to refine and simplify procedures for identifying maize resistance to corn borers that breeders can incorporate into classical host plant resistance breeding programs (Sandoya et al., 2010).

2 | MATERIAL AND METHODS

2.1 | Plant materials and experimental design for field experiments

All trials were conducted at Langfang Experiment Station of Institute of Plant Protection, Chinese Academy Agricultural Sciences (IPP, CAAS), Hebei province (39°30′N, 116°36E). Thirteen maize inbred lines were evaluated: B73, By815, c8605, Mo17, Huang c, Chang7-2, Qi319, Tie7922, Xu178, Zheng58, Zi330, 1145, and 8112. These inbred lines represent a broad range of genetically diverse maize. The maternal inbred line Zheng58 (Z58) is dent corn of the Reid heterotic group, and the paternal inbred line Chang7-2 (C7-2) is flint corn. The single cross (ZD958) of these two parental lines is one of the most widely planted commercial varieties in China. Twenty-six maize doubled haploid lines derived from the Zheng58 and Chang7-2 cross were evaluated: D125, D126, D132, D142, D146, D147, D150, D154, D159, D172, D175, D179, D183, D186, D189, D195, D201, D212, D233, D246, D262, D271, D279, D280, D296, and D301. These lines were initially planted in June 2012, followed by two field trials in May 2013 (Trial 1) and June 2013 (Trial 2). Initial seed stocks for all 39 maize isolines were supplied by Professor Chen Shaojiang of China Agricultural University.

The first planting date primarily increased seed for subsequent experiments, therefore only one replicate with 40 plants for each genotype was conducted as a pilot study. The two field trials were arranged in a randomized complete block design with three replicates for each genotype. In each plot, 40 seeds were planted in each of four rows with .60 m between row spacing. Then each row was thinned to 20 plants spaced .30 m apart. The middle two rows were used for *O. furnacalis* infestations (rows 2 and 3 for first and second infestations, respectively), and row four, which was not infested, was used for the RPS measurements. Irrigation, weeding and fertilization during the study followed conventional practices for the region.

2.2 | Infestation of larvae and field resistance evaluation

Artificial infestations of *O. furnacalis* were used to simulate first and second generation natural infestations using methods described by He et al. (2000). Black-head stage egg masses were applied at both whorl (V8) and silk stages. The equivalent of two egg masses (≈40–60 eggs) was transferred into a 1.5-ml polypropylene tube and then placed in the maize V8 whorls or on the silks for each plant. Twenty plants were infested in each plot for each infestation in the middle two rows. Injury approximating natural first and second generation *O. furnacalis* larvae was generated by timed infestations of neonates at V8 whorl (row 2) and silk (row 3) stages, respectively (He et al., 2000). Stem injury caused by simulated first generation (subsequently called first generation) *O. furnacalis* was evaluated at silk stage and the injury caused by simulated second generation (subsequently called second generation) *O. furnacalis* was evaluated at harvest. Each experimental plant was dissected for evaluation, and measurements included tunnel lengths (cm) and larval hole counts. For recording purposes, each maize plant was divided into three sections: (1) upper: tassel to (but not including) internode above main ear, (2) middle: internode and node above primary ear, ear internode and node, and internode below primary ear, and (3) lower: sections remaining underneath the internode below the primary ear. *O. furnacalis* injury data collected per plant section included: cumulative length of tunnels (cm) and number of holes.

2.3 | Measurement of maize stalk strength

RPS was selected as an indicator of stalk strength. Five plants of similar height and stalk diameter were selected from row 4 from each plot at VT and R3. After sheath removal, a penetrometer (SY-S03, Shiya Technology Company, Shijiazhuang) was used to measure rind strength. Plants were divided into three sections (upper, middle, and lower), as described above. One RPS measurement was made for each of the upper and lower sections, and multiple measurements were taken for the middle section. Measures for maize rind strength were taken from the following plant locations: internode above primary ear (IAPE), node above primary ear (NAPE), internode of primary ear (IPE), node of primary ear (NPE), internode below primary ear (IBPE), and fourth internode above ground (I4AG) at both VT and R3 developmental stages. To measure stalk strength, a rind penetrometer was fastened to a testing jig and driven by a handle that was fabricated to facilitate measuring stalk strength by ensuring uniform acceleration of the needle (Peiffer et al., 2013). Each maize stalk was clamped down firmly to the base of the testing platform by two retention clips. The center of the flat side of the internode was held in line with the rind penetrometer needle. This allowed the penetrometer needle to be inserted perpendicularly into the flat side of the internode. RPS values were recorded when the stop bar first contacted the stalk. Each internode was punctured at two adjacent sites, and values were averaged.

2.4 | Statistical analysis

RPS measures at 12 section-by-stage combinations along the length of the stalks at VT and R3 stages were compared, and Tukey HSD post hoc tests were used to determine significant differences at a 95% confidence level. Similarly, *O. furnacalis* injury traits (holes and tunnels) at six section-by-stage combinations were compared, and Tukey HSD post hoc tests were used to determine significant differences at a 95% confidence level. Genetic effects on RPS measures and *O. furnacalis* injury traits were analyzed separately at VT and R3 stages using one-way ANOVAs to determine stalk section(s) that were influenced most by maize genotypes. To characterize effect of rind strength on *O. furnacalis* injury, correlation coefficients between stalk RPS measure and *O. furnacalis* injury traits were estimated using the multivariate platform in JMP®. One-way ANOVAs were performed to determine the effect of internode RPS measures on the number of holes in the middle stalk section. All analyses were performed using JMP® 16.1.0 (SAS Institute Inc., Cary, NC, 1989–2021).

3 | RESULTS

3.1 | RPS analyses of maize genotypes and stalk sections

RPS measures varied dramatically according to maize genotypes, stalk section, and stage at time of sampling (Table 1, Figure 1). RPS values increased from top to bottom of the plant for both VT and R3 maize (Figure 1). At VT, the nodes were much softer than the corresponding internodes. RPS of IAPE and IPE were 18.05 ± 0.32 and 22.28 ± 0.29 N/mm², but their node values were lower (NAPE; 10.08 ± 0.18 N/mm², NPE; 12.56 ± 0.61 N/mm²). However, at R3 the results were opposite. RPS of IAPE and IPE were 22.90 ± 0.31 and 27.23 ± 0.33 N/mm², respectively, but RPS of their corresponding nodes were higher, NAPE; 25.74 ± 0.28 and NPE; 31.43 ± 0.34 N/mm² (Figure 1). The R^2 values of maize isoline identity (genotypes) for all the RPS measures were highly significant (p < .001), but RPS of IPE and IBPE R^2 were the highest among all the comparisons (Table 1). These values were all higher than .5 during the VT stage and higher than .6 for the R3 stage. The most notable R^2 values of maize genotype for *O. furnacalis* stalk hole injury were in the middle section of the stalk for both VT and R3 stages. None of the corresponding R^2 values for *O. furnacalis* tunneling were significant (Table 1).

TABLE 1 Stalk strength and *O. furnacalis* injury traits, holes and tunneling, are influenced by maize isoline identity (genotype)

	Stage: VT		Stage: R3	
	R^2	*p* value	R^2	*p* value
RPS IAPE	.37	<.001	.56	<.001
RPS NAPE	.31	<.001	.46	<.001
RPS IPE	.51	<.001	.66	<.001
RPS NPE	.31	<.001	.55	<.001
RPS IBPE	.54	<.001	.63	<.001
RPS I4AG	.34	<.001	.57	<.001
Holes upper	.21	.092	.29	<.001
Holes middle	.51	<.001	.38	<.001
Holes lower	.26	<.05	.23	<.05
Tunneling upper	.21	.095	.19	.240
Tunneling middle	.23	.058	.20	.141
Tunneling lower	.22	.057	.15	.667

Note: *p* values calculated with false discovery rate (FDR) correction. Abbreviations: I4AG, the 4th internode above ground; IAPE, internode above the primary ear; IBPE, internode below primary ear; IPE, internode primary ear; NAPE, node above primary ear; NPE, node primary ear; RPS, rind penetration strength.

3.2 | Correlations of RPS values with stalk injury for first and second generation *O. furnacalis*

The number of holes and length of tunnels caused by *O. furnacalis* varied slightly according to stalk section and stage at time of sampling (Figure 2). For first and second generation *O. furnacalis* on maize, correlations were made between RPS and *O. furnacalis* injury traits in upper, middle and lower sections (Figure 3, Table S1). For first generation *O. furnacalis* (VT), many of the RPS values were highly correlated, strongest correlations with IPE and IAPE. RPS values, particularly RPS of internodes, had significant negative correlations with number of holes in the middle stalk section, and the correlation coefficients between number of holes and RPS of IPE were the strongest (Figure 3, Table 2 and S1). For second generation *O. furnacalis*, again all the RPS values were highly correlated; and RPS measures,

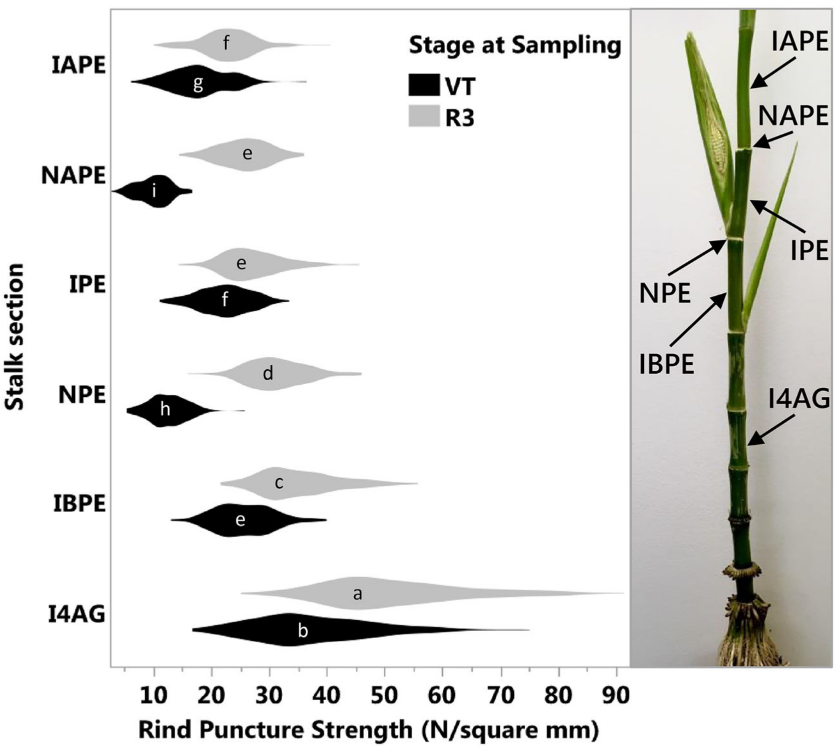

FIGURE 1 RPS varies dramatically according to stalk section and stage. Equal width violin plots are shown with Tukey HSD connecting letter reports to indicate statistically distinct RPS means among the 12 stalk section-by-stage combinations. Despite not having equal areas, each "violin" is based on data from all 234 plots, arising from two trials × three replicates × 39 genotypes. The position of each stalk section is also shown on a defoliated plant at the tassel (VT) stage, which occurs ∼24 days prior to R3, when kernel development has reached the R3. I4AG = 4th internode above ground; IBPE = internode below primary ear; NPE = node of primary ear; IPE = internode of primary ear; NAPE = node above primary ear; IAPE = internode above primary ear

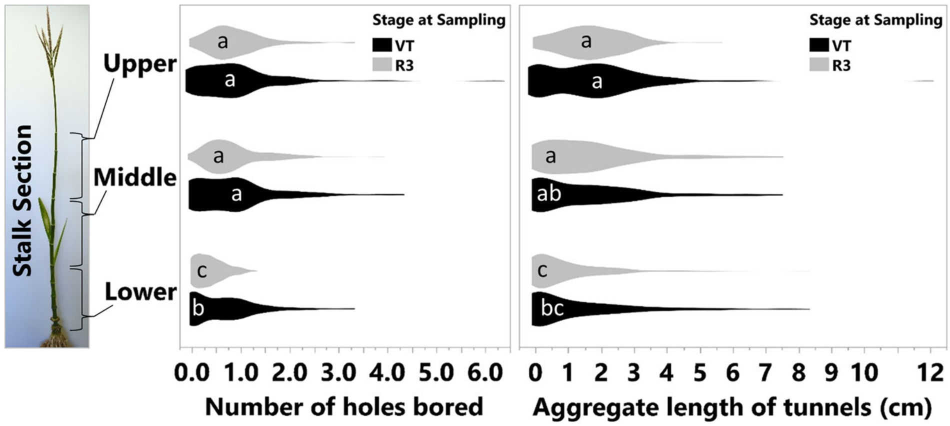

FIGURE 2 ACB damage varies slightly according to stalk section and stage. For both the holes and tunnels measures of ACB damage, equal width violin plots are shown with Tukey HSD connecting letter reports to indicate statistically distinct means among the six stalk section-by-stage combinations. Despite not having equal areas, each "violin" is based on data from all 234 plots, arising from two trials × three replicates × 39 genotypes. The position of each stalk section relative to the top ear is also shown on a defoliated plant at the tassel (VT) stage

FIGURE 3 Pairwise trait correlations among stalk strength and ACB injury traits at VT and R3 stages. Correlation (*r*) and statistical significance (*p*) values are shown in the lower and upper matrices for each stage, respectively. $N = 234$ for each of the 132 correlations. For each stage, the strongest positive and strongest negative correlations and their corresponding *p* values are marked with diamonds and stars, respectively. Boundary lines have been added to assist in visualizing relationships within and between the sets of stalk strength and ACB injury traits. (See Table S1 for correlation and probability matrices)

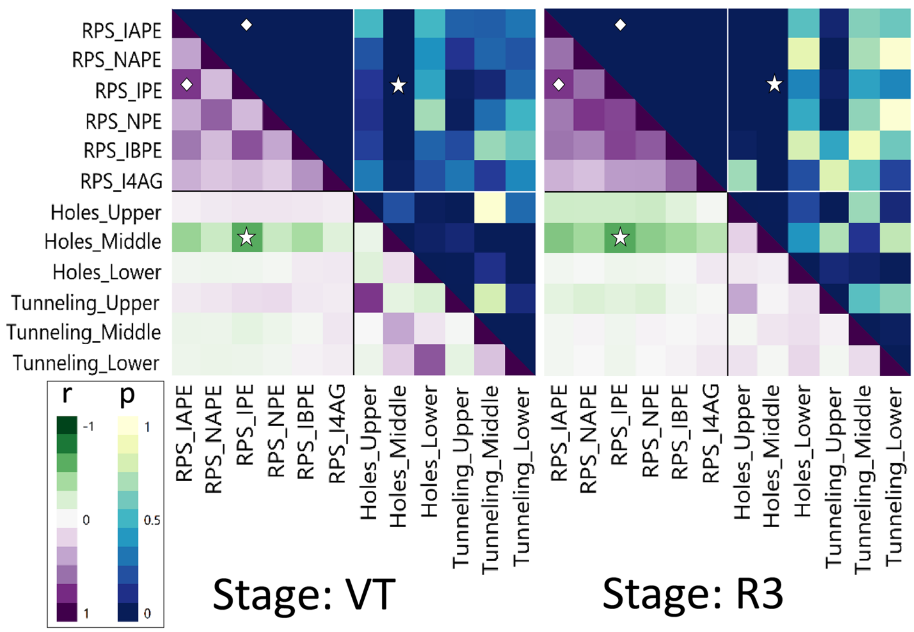

TABLE 2 Correlation analyses between rind penetration strength (RPS) for internode above primary ear (IAPE), internode of primary ear (IPE), and internode below primary ear (IBPE) and *O. furnacalis* injury (holes and tunnels) during VT and R3 maize stages

	IAPE		IPE		IBPE	
Stage	VT	R3	VT	R3	VT	R3
Holes upper	.04	−.24**	.10	−.24**	.09	−.15*
Holes middle	−.44***	−.5***	−.61***	−.62***	−.39***	−.41***
Holes lower	−.04	−.04	−.05	−.06	.08	−.02
Tunnels upper	.08	−.13*	.15*	−.14*	.09	−.05
Tunnels middle	−.08	−.03	−.12	−.05	−.03	.01
Tunnels lower	−.07	−.04	−.07	−.06	.04	.04

*$p < .05$.
**$p < .001$.
***$p < .0001$.

particularly RPS of IAPE, IPE and IBPE had significant negative correlations with number of holes in the middle section (Figure 3, Table 2 and S1). In most cases, *O. furnacalis* tunnel injury had no or minor correlations with RPS of IAPE, IPE and IBPE (Figure 3, Table 2 and S1). However, the *O. furnacalis* injury traits (number of holes and the aggregate length of tunnels) in the middle stalk section were significantly correlated ($r = .27$, $p < .0001$) (Figure 4, Table S1).

Individual one-way ANOVAs were performed to determine the degree to which RPS measures along the length of the stalk accounted for variance in number of holes in the middle stalk section. For first generation *O. furnacalis*, R^2 values ranged from .03 for RPS of I4AG to .37 for RPS of IPE, and for second generation *O. furnacalis*, R^2 values ranged from .11 for RPS of I4AG to .38 for RPS of IPE. For both first and second generation *O. furnacalis*, RPS of IPE at VT and R3 stages, respectively, accounted for more variance in the number of holes than did any other RPS measure (Table 3, Figure 4). Therefore, RPS of IPE at VT and R3 stages were consistently moderately good predictors of number of holes from first and second generation *O. furnacalis* injury.

3.3 | RPS analyses of maize genotypes

Stacked bar charts of RPS (N/mm^2) of IPE for 39 maize genotypes at VT and R3 stages suggest that inbred lines Huang c, Tie7922, Zheng58 and doubled haploid lines D126, D233 had the highest RPS values and were stable among development stages (Figure 5). In general, those accessions with high RPS values also had low numbers of holes in the stalks from *O. furnacalis* injury. Notably, RPS of IPE consistently had the highest correlations compared with RPS of other measured internodes or nodes (Figure 3, Table 2 and S1).

4 | DISCUSSION

Host plant resistance traits against insect pests are generally separated into those that lower plant attractiveness to insects

TABLE 3 Separate one-way ANOVAs at VT and R3 developmental stages for variance in number of holes in the middle stalk section attributed to RPS at internodes and nodes along the length of the stalk

	Stage: VT		Stage: R3	
	R^2	*p* value	R^2	*p* value
RPS IAPE	.19	<.0001	.25	<.0001
RPS NAPE	.07	<.0001	.17	<.0001
RPS IPE	.37	<.0001	.38	<.0001
RPS NPE	.07	<.0001	.22	<.0001
RPS IBPE	.15	<.0001	.17	<.0001
RPS I4AG	.03	.0147	.11	<.001

Abbreviations: I4AG, the 4th internode above ground; IAPE, internode above the primary ear; IBPE, internode below primary ear; IPE, internode primary ear; NAPE, node above primary ear; NPE, node primary ear; RPS, rind penetration strength.

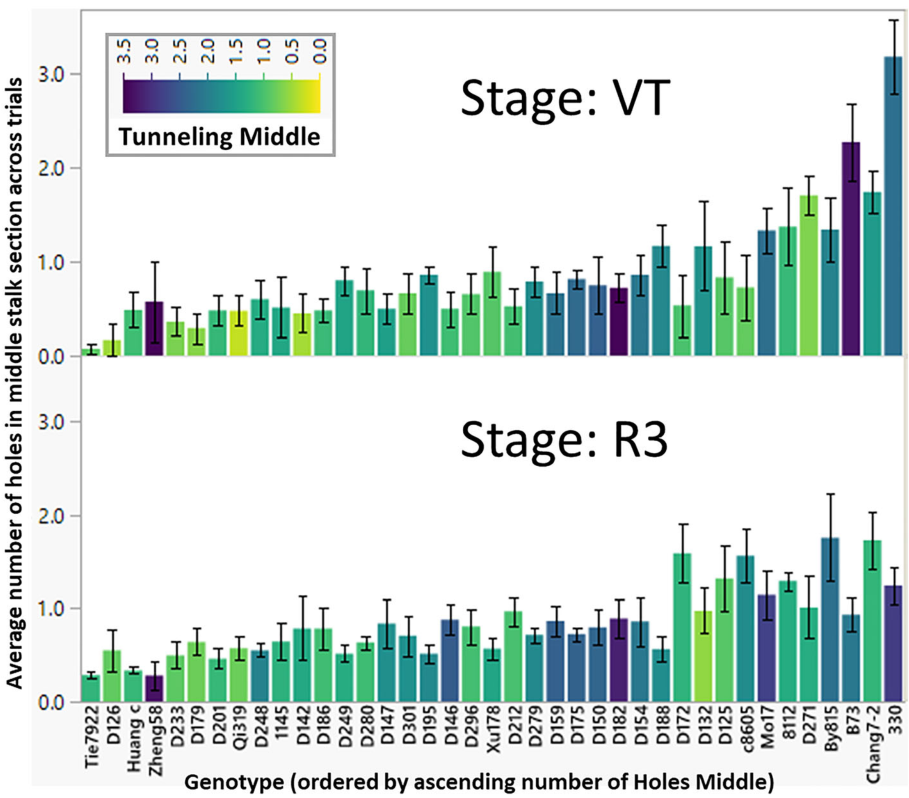

FIGURE 4 Relationship between holes and tunneling. Each bar (± standard error) depicts number of holes in the middle stalk section for each genotype. Ordering of genotypes according to ascending number of holes in the middle stalk section averaged across developmental stages facilitates visualization of relationships, with average tunneling in the middle stalk section (cm) shown by a color overlay. One-way ANOVAs revealed that experiment wide, genotype accounted for 33% of the variance for average number of holes middle, and 19% of the variance for average tunneling (cm) middle

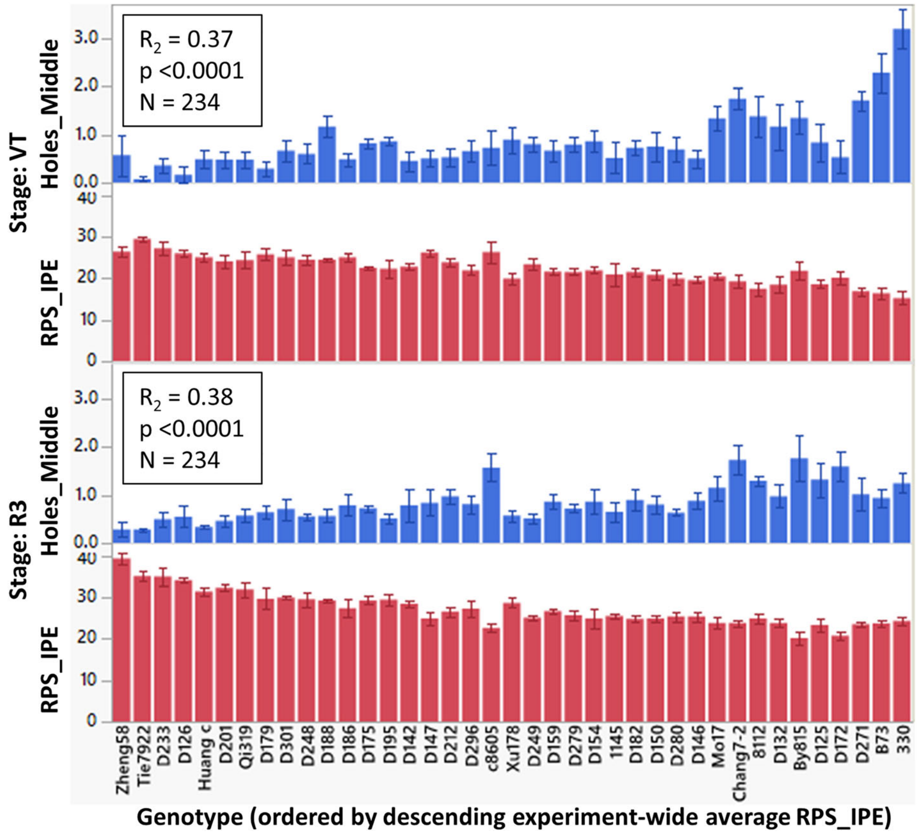

FIGURE 5 Bivariate relationship between Holes Middle and RPS IPE at VT and R3 stages. Averaged across 6 plots per genotype per stage, each red bar (± standard error) depicts RPS_IPE, and each blue bar (± standard error) depicts Holes Middle. Ordering of genotypes according to RPS-IPE values facilitates visualization of relationships. One-way ANOVAs reveal that 37% and 38% of the variance for Holes Middle can be accounted for by RPS IPE at the VT and R3 stages, respectively

(nonpreference or antixenosis), impair development (antibiosis) or allow a plant to compensate for injury by an insect (tolerance) (Barros-Rios et al., 2011; Hellmich et al., 2008; Painter, 1968; Santiago et al., 2013). This study focused on characterizing maize stalk strength as a component of resistance to injury by *O. furnacalis* using 13 inbred lines and 26 doubled haploid lines developed in China. Stalk strength could be considered a combination of host-plant-resistance traits: antixenosis, antibiosis, and tolerance; because corn borer larvae may prefer not to bore into stronger stalks, such stalks also could impair larval development, and rind strength could make plants more tolerant to insect injury.

In this study, multiple RPS measures were taken at nodes and internodes in the upper, middle and lower maize stalk. In total, strengths of six stalk tissues were evaluated to determine which would be the most reliable predictors, consequently facilitating the use of RPS in breeding for resistance. The upper, middle and lower stalk areas were selected because corn borer stalk injury (holes and tunnels) from *O. furnacalis* occurs in all three areas. Injury occurs primarily in the middle of the stalk (Wen et al., 1992). However, corn borer injury is also common for the internode below the tassel, and for first generation *O. furnacalis* there is a tendency for larvae to move from tassel to lower on the stalk. In the lower stalk, the RPS of the fourth internode above ground was measured for its importance for resistance to stalk lodging (Gou et al., 2010). Because of the comprehensive measurements, this study provided more RPS assessments than similar studies conducted on maize stalk strength and resistance to lepidopteran larvae (Gibson et al., 2009; Santiago et al., 2003).

The inbred lines Huang c, Zheng58, and Tie7922, and doubled haploid lines D233, and D126 had the highest RPS values, and were consistent across VT and R3 stages of maize development. These lines may be of interest for further development of stalk resistance to *O. furnacalis* with classical breeding methodologies. The results of this study also suggest that the RPS measures for the internodes of the primary ear and above/below primary ear at VT and R3 stages are the most informative traits that breeders could target for reducing number of corn borer holes by increasing stalk strength in maize plants. RPS measures of IPE at VT and R3 stages were correlated with the first and second generation *O. furnacalis* injury (hole) levels, respectively. This procedure provides maize breeders a key tool for evaluating stalk strength-based resistance to corn borers, as well as to stalk lodging. The RPS values of the three internodes (IAPE, IPE, and IBPE) were highly correlated, which is expected because all of these plant stalk tissues likely have similar physical and chemical attributes. However, when measurements are highly correlated, a point of diminishing returns is reached with multiple stalk measurements for identification of resistant *O. furnacalis* genotypes. Accordingly, focusing on RPS measures of one or more of the three internodes IAPE, IPE, or IBPE at VT and R3 stages should best aid breeders in evaluation of stalk strength-based resistance to *O. furnacalis* and stalk lodging.

The RPS measure, however, is not a good predictor of *O. furnacalis* tunnel lengths. RPS had significant but minor correlation with tunnel length in the upper stalk section by the first generation for IPE only and for tunnel length by the second generation for IPE and IAPE. The other RPS measures were not significantly correlated with *O. furnacalis* tunnel lengths. Perhaps this is because tunneling occurs after larvae penetrate the rind where pith characteristics are more important than rind strength.

Similar stalk strength and injury results were found by Butrón et al. (2002) and Gibson et al. (2009). Like this study, they found that both stalk strength and insect holes in the stalk were influenced by maize genotype and maize developmental stage. They also found stalk injury varied with corn borer species. The resistance originating from maize stalk strength to second generation corn borer injury was investigated by Flint-Garcia et al. (2003) and Martin et al. (2004), who observed RPS was effective in predicting resistance to second generation *O. nubilalis* injury.

Stalk resistance to corn borers is not due to stalk strength alone. For instance, antibiotic substances present in the pith are likely responsible for field resistance of inbred CM151 to the Mediterranean corn borer, *Sesamia nonagrioides* (Lefèbvre) (Ordás et al., 2002). Indeed, stalk resistance appears to be influenced by a variety of factors. Martin et al. (2004) found crude fiber, cellulose, lignin and silica were all important factors to consider when selecting for reduced *O. nubilalis* stalk injury.

Stalk resistance to corn borers is influenced by plant chemistry (Gesteiro et al., 2021). Thus, stalk resistance to *O. furnacalis* is likely not attributable to stalk strength alone. Instead, stalk resistance appears to be a result of the interaction of several structural and nonstructural factors, perhaps including some factors that have not yet been evaluated for any maize boring insect species. Future studies to improve conventional maize stalk resistance to stalk boring insects should include the RPS evaluations discussed in this paper in combination with other chemical, structural, and nonstructural components of the rind.

5 | CONCLUSIONS

In summary, RPS measures of three internodes (primary ear, above primary ear, and below primary ear) were the best predictors of stalk physical resistance to Asian corn borer, *O. furnacalis*, injury for both VT and R3 maize. This was determined by comparing the correlations of RPS values with *O. furnacalis* injury for stalk nodes and internodes in the upper, middle and lower parts of the stalk. In general, these measures were highly correlated with the number of holes in the stalk made by *O. furnacalis* but were not highly correlated with tunnel lengths, which suggests other factors than rind strength should be considered after *O. furnacalis* bore into the stalk. These measures provide an important tool for improving maize stalk physical resistance to *O. furnacalis*.

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

AUTHOR CONTRIBUTION

Jingfei Guo, Kanglai He, and Zhenying Wang designed the experiments. Jingfei Guo performed the experiments and wrote the paper. Jingfei Guo, Richard L. Hellmich, Miriam Lopez, and Nick Lauter analyzed the data and revised the manuscript. Yujie Meng and Shaojiang Chen contributed materials. All authors read and approved the manuscript.

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