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PLANT BREEDING REVIEW

A "solid" solution for wheat stem sawfly (Hymenoptera: Cephidae) resistance: Genetics, breeding and development of solid stem wheat

Akshara Bathini[1] | **Lavanya Mendu**[1] | **Nagendra Pratap Singh**[1] | **Jason Cook**[1] | **David Weaver**[2] | **Jamie Sherman**[1] | **Megan Hager**[2] | **Suchismita Mondal**[1] | **Venugopal Mendu**[1]

[1]Department of Plant Sciences and Plant Pathology, Montana State University, Bozeman, Montana, USA

[2]Department of Land Resources and Environmental Sciences, Montana State University, Bozeman, Montana, USA

Correspondence
Venugopal Mendu, Department of Plant Sciences and Plant Pathology, Montana State University, Bozeman, MT, 59717, USA.
Email: venugopal.mendu@montana.edu

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Abstract

Wheat (*Triticum* spp. L) production needs to be improved to meet the needs of a global population of >9 billion people by 2050. Increasing the productivity of the crop under conditions of abiotic and biotic stress to achieve food security continues to be a challenging proposition. Wheat stem sawfly (WSS) (*Cephus cinctus* Norton) has been considered as a serious pest of wheat since the late 19th century, causing devastating losses of wheat productivity in the Northern Great Plains of United States and regions of Canada. Developing resistant varieties of wheat that show consistent agronomic performances in varying environments is an effective strategy to manage WSS infestations. To achieve this goal, it is necessary to understand the underlying mechanisms of WSS infestation, damage, subsequent response of the host plant, and resulting yield losses. The review focuses on genetics, breeding, and development of solid stem (SS)-mediated WSS resistance in wheat since it has been the most effective method of genetic resistance in reducing wheat yield losses. Furthermore, the knowledge gaps that need to be addressed to develop an effective resistant cultivar against WSS are also discussed.

1 | BACKGROUND

With the exponential increase in global population and reduction in cultivable land, there is a need to increase food production per unit area of land. Cereal crops are a staple food source worldwide and wheat (*Triticum* spp. L) is one of the most consumed and cultivated among cereal crops, providing approximately 18% of daily calorie intake (Erenstein et al., 2022). The global production of wheat is 779.6 million metric tons (USDA, 2022) and to meet the wheat consumption needs of the burgeoning population, a supplemental 132 million metric tons of wheat need to be produced annually through 2050 (Erenstein et al., 2022). After corn (*Zea mays* L.) and soybean (*Glycine max* L.), wheat stands third in terms of US acreage. The annual production of wheat in the United States is 6.22% of world's wheat production, that is, 48.2 million metric tons (USDA, 2022–2023) and Canada accounts for 4% of global wheat

Abbreviations: HPR, host plant resistance; MAS, marker-assisted selection; PCD, programmed cell death; QTL, quantitative trait loci; SS, solid stem; WSS, wheat stem sawfly.

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production, that is, 30.9 million metric tons (USDA FAS, 2022). Wheat was first cultivated 8000–10,000 years ago during the Neolithic revolution in the Fertile Crescent (Shewry, 2009). While diploid einkorn wheat (*Triticum monococcum* L.) and tetraploid emmer (*Triticum dicoccum* L.) were first cultivated in the Fertile Crescent and the Near East (Harlan & Zohary, 1966), natural hybridization and anthropogenic selection led to development of tetraploid/durum wheat (*Triticum turgidum* L. subsp. *durum*) in the Near East and hexaploid/bread wheat (*Triticum aestivum* L.) nearby Western Asia (Velimirovic et al., 2021). Currently, bread wheat and durum (pasta) wheat are the most commonly cultivated wheat species, with 95% of the wheat grown globally being bread wheat and 5%–8% durum wheat (Shewry, 2009). Durum wheat contributes to 2%–5% of US wheat production, with North Dakota and Montana being the major producers (USDA, 2022), whereas the majority of Canada's wheat is grown on the Prairies (USDA FAS, 2022).

There are several constraints that affect the productivity of wheat, which include heat, drought, and biotic factors such as rust diseases and insect damage. Biotic stresses, to which insect damage contributes the most, account for about 20%–37% of yield losses worldwide in wheat (Qayyum, 2021). Among the biotic factors, overall harvest losses caused by wheat stem sawfly (WSS) (Hymenoptera: Cephidae: *Cephus cinctus* Norton) (Ainslie, 1920) infestation account for more than 350 million dollars per year in Western Northern Great Plains of United States and regions of Canada (Beres et al., 2011b). Recent reports suggest that the WSS is spreading further into other states such as Colorado, Nebraska, and Kansas, and historical infestations are increasing in the Dakotas and Canadian Prairies (Olfert et al., 2019; Peairs & Irell, 2014). The continuous adaptation of the WSS within historic, and into new wheat growing areas is the major reason for a rapid rise in losses due to WSS in Western North America. WSS injury manifests in several ways. First, the feeding of WSS larvae on the inner tissues of the stem not only reduces the photosynthetic capacity of flag leaf, but also reduces vascular transport of nutrients and water, reducing head weight and protein content of the grains thus resulting in both yield and quality loss (Delaney et al., 2010; Holmes, 1977). Second, yield is also severely reduced due to the lodging (Figure 1) of girdled stems particularly when high winds occur (McCullough et al., 2020) resulting in reduced harvesting efficiency (due to loss of grain from fallen heads). Infestation occurs during the next season from overwintering survivors in wheat stubble (Ainslie, 1920; Beres et al., 2007). The signs of WSS infestation include a dark visible region below the nodes on the outer surface of the ripening stem at soft dough stage, distorted, wilted kernels, and very diagnostic cut stems at maturity (Morrill, Gabor, & Kushnak, 1992). Susceptible varieties show severe lodging at maturity as a manifestation of stem cutting by WSS larvae

Core Ideas

- Wheat stem sawfly is a major problem with no insecticide control mechanism.
- Solid stem varieties have been employed for wheat stem sawfly resistance.
- The review focused on providing comprehensive information on solid stem genetics, breeding, and development.

(Figure 1). A recent review on sawfly resistance has focused on the integrated approach of host plant resistance (HPR), that is, solid stem (SS), biological control to manage WSS, and a non-preference trait that affects oviposition behavior of WSS (Peirce et al., 2022). The review covered genetic mechanisms of SS in durum and bread wheat and also discussed possibilities of identifying new sources of HPR from wild relatives, land races of wheat, and other grass species that host WSS such as barley (*Hordeum vulgare* L.), oats (*Avena sativa* L.), and triticale (× *Triticosecale* Wittmack). In the current review, we briefly discuss WSS biology, management of WSS, and its interaction with the host plant (wheat). Furthermore, a detailed overview of developmental biology, anatomy, genetic, molecular, and physiological aspects of SS trait is provided since this trait is the best available management strategy to date that minimizes the losses caused by WSS.

2 | DISTRIBUTION, BIOLOGY, AND LIFE CYCLE OF WHEAT STEM SAWFLY *(Cephus cinctus)*

WSS is endemic to North American native grasslands and adapted to wheat during the late 19th and early 20th century (Criddle, 1923). When the area of cultivated wheat expanded into the Western dryland habitat in North America, the WSS rapidly became a serious pest affecting wheat yields (Cockrell et al., 2021; Olfert et al., 2019). Historically, regions that were prone to heavy damage due to WSS were Montana, North Dakota, Alberta, Saskatchewan, and Manitoba (Beres et al., 2011). It was first reported as a wheat pest in Canada in 1895 (Ainslie, 1920); later, large WSS infestations occurred in parts of Eastern South Dakota, Wyoming, Idaho, Eastern Colorado, Northwest Kansas, Western Nebraska, and the Columbia Basin, Palouse regions of Washington State (Fulbright et al., 2017). Populations of native *C. cinctus* are distributed in Western United States and Canada (Criddle, 1923), while the introduced species *C. pygmaeus* (L.) is only found in the Eastern United States and Canada (Streams & Coles, 1965). A detailed overview of WSS biology and

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FIGURE 1 Images showing wheat crop not infested with wheat stem sawfly (WSS) (left panel), infested with WSS (middle panel) and wheat stems cut by WSS larvae (right panel).

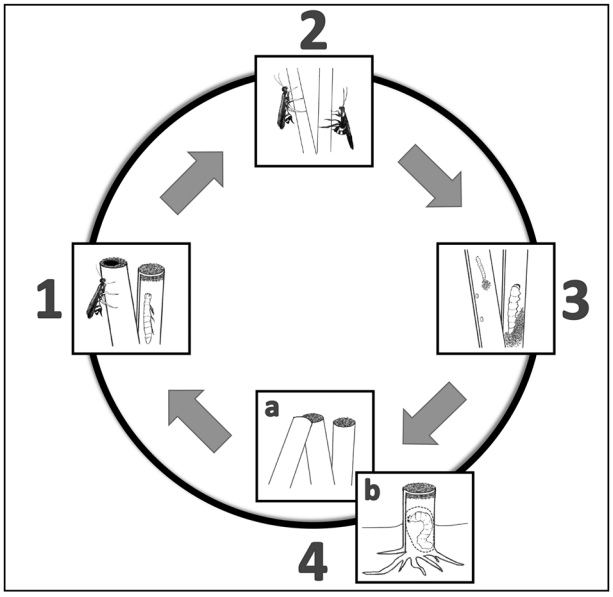


FIGURE 2 Life cycle of the wheat stem sawfly, *Cephus cinctus* Norton. (1) Larvae enter the pupal stage inside the stubs of cut stems in the spring (right image) and adults emerge (left image). (2) Adult sawflies emerge from the stems and mate shortly after emergence and live for 7–10 days. (3) Eggs are laid in the lumen of stems and hatch in 5–10 days (left image). Neonate larvae feed on parenchyma tissue throughout the stem for up to 8 weeks. (4a) At the end of the growing season, the larva travels to the base of the plant then cuts a groove encircling the inside of the stem. (4b) The larva produces a thin, transparent hibernaculum at the apex before entering obligate diapause. It remains protected inside the stub just below soil level throughout this period which can last 8–10 months.

management can be found in dedicated review papers (Beres et al., 2011; Fulbright et al., 2017). The life cycle of the WSS cannot be successfully completed without infesting a grass or cereal stem (Figure 2) and it coincides with the phenological development of host plants (Ainslie, 1920). Females choose newly formed internodes to oviposit and puncture the stem with a curved saw-like ovipositor (Beres et al., 2011). The WSS larvae feed inside the stem on thin walls of parenchymal cells and vascular tissues that are readily available in wheat. The larvae then prepare for overwintering when the plant approaches physiological maturity (Beres et al., 2012), and are influenced in this process by environmental signals, reduced moisture, and increased light penetration through the ripened stem (Holmes, 1975).

The larvae soon move to the stem's base, girdle its interior circumference by cutting a V-shaped notch, fill it with frass so that the stem severs and lodges which leaves the remaining ''stub'' with a waterproof frass plug at the apex (Ainslie, 1920), and finally overwinters by residing within a diaphanous hibernaculum. When the spring temperatures rise, the larvae begin the pupal stage during which wings develop and characteristic pigmentation occurs in the formation of an adult (Fulbright et al., 2017). The adult wheat stem sawflies emerge from their hibernaculum by chewing through the frass plug that seals them within the stem. WSS can emerge and oviposit from mid-May to mid-July and winter wheat are prone to high infestation rates when compared to spring wheat. WSS biotypes that infest winter wheat emerge earlier to coincide with the life cycle of winter varieties (Morrill & Kushnak, 1996).

2.1 | Management of WSS

The nature of the WSS lifecycle makes measures aimed at control of larvae particularly challenging. Application of insecticides has been largely ineffective against WSS since the larvae develop while protected inside the stem and adults live only a short time. The grain quality might be compromised

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even though the insecticide targets the larvae (Beres et al., 2011). Delayed sowing to avoid WSS damage (Morrill et al., 1998) can expose wheat to various abiotic stresses during grain fill stage that compromises yield and quality (Jatoi et al., 2021). Female WSS oviposits in oats, and because larvae do not thrive in this crop it can be used as a trap crop (Beres et al., 2011; Criddle, 2014). The oat-infested WSS larvae die right after hatching, potentially from an excess production of sap by the oat plants (Beres et al., 2011; Criddle, 1923); however, there has been no definitive explanation for this (O'Keeffe et al., 1960; Weaver et al., 2004). Practicing shallow tillage in infested fields can unearth the overwintering larvae and expose them to desiccation or cause them to freeze (Holmes & Farstad, 1956), however this practice is also detrimental to beneficial parasitoids and does not conserve soil moisture. In contrast, no-till cultivation is a soil moisture conservation practice favored by many growers (Beres et al., 2011; Weaver et al., 2004) that prevents the aforementioned detrimental effects. *Bracon cephi* (Gahan) and *Bracon lissogaster* (Muesebeck) (*Hymenopetra*: Braconidae) are ectoparasitoids that paralyze the late instar larvae of WSS by inserting their ovipositor through the wheat stem (Runyon et al., 2001). Because these parasitoids overwinter in the stems above the ground, ploughing the wheat stubble to reduce WSS damage will increase their death rate that results in reduction of their parasitism on WSS (Runyon et al., 2002). Their population is also affected by the height at which the wheat stems are harvested and application of insecticides (Beres et al., 2011; Nelson & Farstad, 1953). Mono culturing of SS lines can sometimes impact the host availability for the parasitoids, so blending of SS and hollow stemmed cultivars may relatively increase the parasitoid population (Cárcamo et al., 2016; Rand et al., 2012).

2.2 | Host plant-mediated genetic resistance against WSS

Since chemical and cultural pest management approaches cannot be relied on completely to control the WSS, host plant-mediated genetic resistance is critical to control/manage the pest. HPR integrated with beneficial parasitism may be an effective way to enhance the mortality rate of WSS (Buteler et al., 2015). HPR can take the form of antibiosis and antixenosis. Antibiosis means plants are less suitable for pest survival, for example, increased mortality due to SS. When the insect does not prefer to infest the crop, it is called antixenosis or non-preference trait. The female WSS chooses its host to oviposit by sensing a characteristic ''green'' odor (Hatanaka, 1993) that occurs due to eight volatile compounds secreted by wheat foliage and stems among which (Z)−3-hexenyl acetate and (Z)- 3-hexen-1-ol serve as attractive signals (Piesik et al., 2008; Weaver et al., 2009). Greater knowledge of volatiles could perhaps be deployed to attract WSS away from cash crops into trap crops (Sherman et al., 2010). Although female wheat stem sawflies are selective in when and where they oviposit, depending on stem height, stem diameter, growth stage, and volatile production (Buteler & Weaver, 2012), antixenosis has not been commonly deployed in wheat production as a control measure thus far. The growers do not efficiently deploy this strategy perhaps due to lack of adequate experimental replications and stable yield data (Weaver, 2012). Studies on volatile compounds indicate that ovipositing females prefer certain genotypes, for example, the hollow spring wheat cultivar, Reeder (PI 613586) that has poor levels of pith expression over semi-solid spring wheat cultivar, Conan (PI 607549) (Sherman et al., 2010; Weaver et al., 2009). Additionally, the sex ratio of WSS may depend on the quality of the host plant. Within the same cultivar, female WSS prefer stems with wider diameter like main stems and males prefer stems with narrower diameter such as later formed tillers (Cárcamo et al., 2005; Morrill & Weaver, 2000). Though the death rate of WSS was found to be higher due to the pith expressed in solid stems (Buteler et al., 2015), the sex ratio was not shown to be affected by the SS trait. It cannot be ruled out that past studies observed SS cultivars with narrower diameter when compared to hollow stemmed varieties (Ford et al., 1979). However, there is still a need for extensive studies on interactions between non-preference of WSS and SS phenotypes.

The major emphasis of HPR has been on SS varieties that suffer less damage and do not lodge readily due to the solid internodes (Figure 3). In the 1920s, initial research studies exploring WSS damage were conducted on *C. pygmaeus*, also referred to as the European stem sawfly, and it was discovered that plants with pith filled stems, called "solid stems", suffered less damage (Schegolev, 1926). Since the late 1950s, breeding for WSS resistance has been expanded by deploying the SS trait in wheat cultivars (Houshmand et al., 2007), that is able to impede and kill larvae through pith filled stems. Selecting SS can be done by scoring for solidness from cut stems in the field. Wheat germplasm from across the world has been screened to identify genotypes that are resistant to WSS, including S-615 (Cltr 12157) (Portugal landrace) (Platt, 1964) which provides the SS trait for a majority of North America's bread wheat cultivars (Cook et al., 2017; Larson & Macdonald, 2011b), Conan (hard red spring wheat that possess *Qss.msub*-3BL.*c* allele) (Weaver et al., 2009), and Janz (white spring wheat that gained its trait of SS from *Agropyron elongatum*) (Beres et al., 2013) (Table 1).

Rescue, Chinook, and Cypress are the cultivars that are derived from S-615 (Larson & MacDonald, 1966) with Rescue being the first SS bread wheat cultivar that was developed and grown widely over the Northern great plains of North America in early 1950s (Larson & Macdonald, 1962). Golden

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FIGURE 3 Images showing comparative performance of solid stem (SS) and hollow stem lines. The hollow stem lines (left side of the picture) showed higher lodging compared to SS lines (right side of the picture).

TABLE 1 List of solid stem sources and derived cultivars.

Source of solid stem	Origin	Wheat species	Derived solid stem cultivars
S-615 (Platt, 1964)	Portugal landrace	*Triticum aestivum* L.	Rescue, Chinook, Cypress (Larson & MacDonald, 1966), AAC Bailey, Unity, Fortuna, Choteau, Leader, Lancer, Mckenzie, Mott (Nilsen et al., 2017), Majority of spring and winter wheat varieties grown in NORTH America (Larson & Macdonald, 1962), AC Eatonia (DePauw et al., 1994) , AC Abbey (DePauw et al., 2000), Lillian (DePauw et al., 2005) (Canadian Western Red Spring cultivars)
Conan (semi-solid hard red spring wheat) (Weaver et al., 2009)	Developed by Westbred, LLC, USA (1997)	*Triticum aestivum* L.	–
Janz (white spring wheat) (Beres et al., 2013)	Alternative source: *Agropyron elongatum*	*Triticum turgidum* L. ssp. *durum*	–
Golden ball (Clark et al., 1922)	South Africa	*Triticum turgidum* L. ssp. *durum*	G-9608B1-L12J11BF02, G9608B1-L12J13AU01 (Clarke et al., 2005)
Biodur (Kemp, 1934)	Germany	*Triticum turgidum* L. ssp. *durum*	W9262-260D3 (Clarke et al., 2002; Nilsen et al., 2017), CDC Fortitude (Pozniak et al., 2015) , AAC Raymore (Singh et al., 2014) , AAC Cabri (Singh et al., 2017) (Western canada)
Trinakria (Ballatore et al., 1973; Clarke et al., 2002)	Italy	*Triticum turgidum* L. ssp. *durum*	–

Ball (Clark et al., 1922) and Biodur (Kemp, 1934) are the main sources of SS in durum wheat among many SS cultivars and landraces (Damania et al., 1997; Liang et al., 2022) with Biodur being the source of SS for the existing SS durum wheat varieties in Western Canada such as CDC Fortitude, AAC Raymore, AAC Cabri (Lanning et al., 2006; Liang et al., 2022; Pozniak et al., 2015; Singh et al., 2014, 2017). Among the members of Canadian Western Extra Strong cultivars, a haplotype was discovered that has alleles for hollow and solid stems in the same quantitative trait loci (QTL) (Nilsen et al., 2017). The SS lines that are currently used in Canada Red Western Spring class include AC Eatonia (DePauw et al., 1994), AC Abbey (DePauw et al., 2000), and AC Lillian (Beres et al., 2012; DePauw et al., 2005). Dagmar, Duclair,

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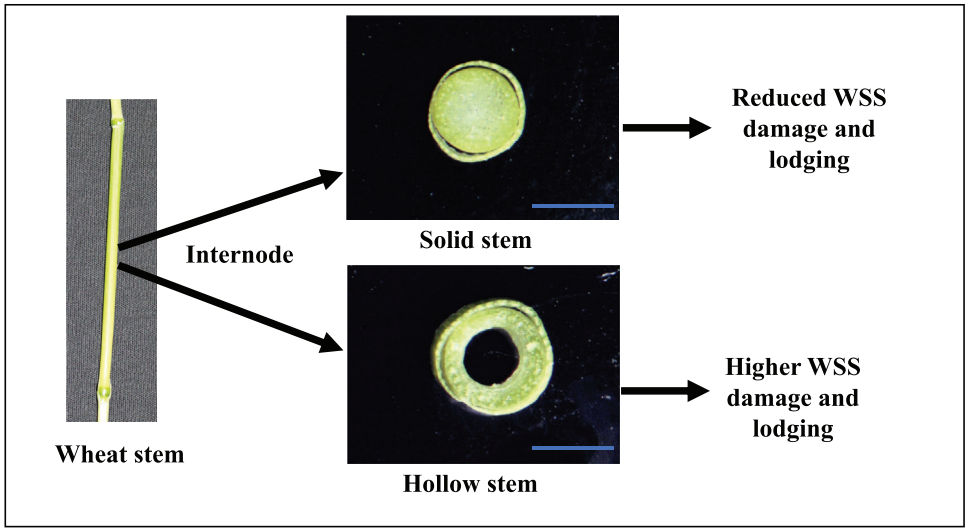


FIGURE 4 Images showing solid stem (SS) and hollow stem phenotypes. Wheat plants from hollow and SS lines were sectioned to depict phenotypes. Scale bar: 5 mm.

Corbin, Gunnison, and SY Longmire are available SS spring cultivars adapted to Montana and Western North Dakota (Montana 2021 Wheat Varieties, 2021). The WSS biotype reportedly evolved to emerge 10–20 days earlier than normal to run parallel with the phenological growth in winter wheat (Beres et al., 2012; Morrill & Kushnak, 1996). This adaptation could have taken place in part as a response to switching large areas of wheat cultivation from spring to winter wheat (Beres et al., 2012; Morrill, Gabor, & Kushnak., 1992) and may also be driving the emergence of new damaging populations in winter wheat grown south of Montana (Cockrell et al., 2021; Lesieur et al., 2016; McCullough et al., 2020).

2.3 | Developmental biology and anatomy of SS phenotypes

A typical angiosperm stem is comprised of three kinds of tissues: dermal tissue (epidermis, periderm), ground tissue (parenchyma, collenchyma, sclerenchyma), and vascular tissue (xylem and phloem) (Esau, 1960). In dicots, the peripheral arrangement of vascular bundles defines a central pith/medulla of parenchymatous cells with the presence of a cortex that contains both parenchymatous and sclerenchymal cells between dermal and vascular tissues. However, the vascular bundles in some monocots such as wheat, oats, barley, and rice (*Oryza sativa* L.) are arranged in two circles and may be scattered throughout the ground tissue in other monocots like maize and sorghum (*Sorghum bicolor* L.), which makes no clear distinction of cortex and pith in monocots (Esau, 1960). A range of two to five internodes with three to six nodes occur in a typical wheat stem (hollow or solid or semi-solid) (Clark et al., 1922) (Figure 4). While stems of wheat are solid at the nodal regions, internodal lacunae often form hollow spaces during internodal elongation, resulting in the hollow stem and providing spaces for WSS larvae to grow (Kebrom et al., 2012; Weatherwax, 1969). However, in SS wheat this hollow area remains filled with pith. In general, cells present in the pith lack elongation (undifferentiated) and may contain a combination of parenchymatous and non-parenchymatous cells such as sclereids (Evert, 2006). The anatomical study of wheat stems may disclose how the internal structure of SS cultivars confers non-preference by ovipositing WSS. The stem diameter and thickness of cell walls also determines the SS trait in wheat (Engledow & Hutchinson, 1925).

Breeding for cultivars containing the SS phenotype will provide both resistance to WSS infestation and tolerance to lodging. SS varieties, due to their thicker cell walls, contain higher cellulose and lignin per unit length of the stem compared to hollow stemmed lines. Thus, the susceptibility of hollow stemmed lines to WSS infestation (Lavergne et al., 2020) may be explained by the composition and mechanical differences of the stem (Kong et al., 2013). The growth and migration of WSS are hindered by the presence of pith in SS in several ways. First, it causes mortality of eggs through mechanical interference and antibiosis (Beres et al., 2012; Holmes & Peterson, 1960, 1961). Second, increased moisture present in pith may decrease hatch of WSS eggs and increase the mortality of neonates shortly after hatch (Holmes & Peterson, 1964). Third, it provides a mechanical barrier to larvae feeding (Kemp, 1934) and movement because the small larvae may find it difficult to chew through dense tissues of pith in SS, particularly as the pith dries during the maturation process (Biyiklioglu et al., 2018; Morrill et al., 1994). SS cultivars will thus affect survivorship, fitness, health of the larvae, and

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reduce negative impacts of WSS on grain yield (Beres et al., 2017; Subedi et al., 2020). However, SS phenotype does not affect the ability of the larvae to survive overwintering (Cárcamo et al., 2011). During times of heavy WSS pressure, cultivars with SS trait may have reduced losses by 7% due to stem cutting and increased yields by an average of 16% (Beres et al., 2009, 2007).

SS cultivars may have narrow diameter and placement of vascular bundles with minimal space in between them causing the stems to be rigid which prevents lodging (Ford et al., 1979). Additionally, they also have larger sclerenchyma girders and higher elasticity when compared to hollow varieties (Bainsla et al., 2018; Biffen, 1905; Engledow & Hutchinson, 1925; Karim & Jahan, 2013). Higher stem wall thickness also confers increased stalk strength and lodging resistance by avoiding ovalization and collapse of the stem in SS varieties (Kong et al., 2013; Liang et al., 2022). Therefore, solid pith parenchyma and the thicker walls of mechanical tissue of the stem are crucial factors for lodging resistance as well (Kong et al., 2013). The SS cultivars are able to produce more callus tissues and regenerate more easily compared to hollow stemmed varieties (Weigt et al., 2016). This could be due to the active cell divisions occurring in the pith parenchyma of SS cultivars. These starch-storing parenchymatous cells contribute to 11% dry weight and account for up to 13% of carbohydrates of such stems (Evert, 2006; Saint Pierre et al., 2010). The weight per unit length of stem is higher in SS varieties which explains the higher content of carbohydrates per unit length of stem (Ford et al., 1979). The amount of pith filled at the upper stem internode is highly correlated with the water-soluble carbohydrate (WSC) content in the stem, and in the pith parenchyma of SS varieties sugars are accumulated during stress conditions (Saint Pierre et al., 2010). The reserved carbohydrates could possibly contribute to grain yield during stress through remobilization (Lavergne et al., 2020; Saint Pierre et al., 2010).

Historically, stem solidness was measured at maturity. In Montana, the SS characteristic of spring wheat can be assessed as soon as two internodes are detectable, at Zadok stage 32 which is typically 37 days after planting and is also assessed approximately 44 days after planting, at heading which is Zadok stage 49 (Varella et al., 2016). By analyzing the SS trait at elongation and maturation stages, the temporal patterns of pith expression can be explored (Varella et al., 2016). The level of pith is given a score ranging between 1 and 5 for each of the five internodes: 1 being hollow and 5 being completely solid. The scores are summed to obtain a total stem solidness score range of 5–25 with 5 being hollow and 25 being completely solid (Wallace et al., 1973). Variation in temporal expression of solid stemmed phenotype influences the breeding procedure. For instance, Conan (spring wheat variety) shows resistance to WSS despite having low levels of stem solidness at maturity (Sherman et al., 2010). In addition to having greater stem solidness during the critical early developmental stage, there is increased pith moisture and greater stem tissue density in Conan when oviposition of WSS occurs (Varella et al., 2016). The moisture present in the tissues may impede the hatch of WSS eggs (Holmes & Peterson, 1964). Pith moisture is reduced later at wheat maturity when the WSS larvae start tunneling and mining the stem which could result in loss of weight, desiccation, and subsequent mortality of the larvae (Holmes & Peterson, 1960; Talbert et al., 2014). The reduction in pith in Conan could be due to pith autolysis where the parenchymatous cells of SS are destroyed resulting in a hollow space inside the stem (Farage-Barhom et al., 2008; Varella et al., 2016). This characteristic of Conan might enhance its agronomic performance (Cook et al., 2019) when compared to other cultivars since fewer carbon resources would be needed for grain filling due to the hollowing of the stem during maturity stage. Similar to Conan, Rambo was widely grown in WSS highly infested wheat cultivating areas of Montana for the same reason (ruckman, 2007). However, cross-sectioning of early semi-solid varieties such as Conan must be performed at its early development (since it is an early SS variety), which is more challenging when compared to the sampling done at maturity for other SS varieties with S-615 type pith. Because the solidness at the early plant developmental stage exists for a shorter time in Conan, it requires additional efforts for longitudinal sectioning while phenotyping when the stems are tender (Cook et al., 2019). Overall, most SS varieties can help to decrease WSS damage and crop yield loss.

2.4 | Genetics, heritability, and mapping of SS phenotypes

Breeding for the SS trait offers advantages for developing wheat that suffers less damage as there is a strong association between SS phenotype and resistance to WSS (Bainsla et al., 2020). Further, the trait is heritable (Bainsla et al., 2020) and can be phenotyped at the stem elongation stage of wheat prior to the grain-filling stage itself. Although SS is under genetic control, the phenotype is highly influenced by non-genetic components like environmental conditions, nitrogen (N) application, and sowing density (Beres et al., 2012). However, the impact of non-genetic factors is stronger in bread wheat than in durum wheat (Liang et al., 2022; Platt & Farstad, 1949). Environmental factors such as cold temperatures, low light intensity, moisture, and precipitation reduce SS (Holmes, 1984; Platt & Farstad, 1949). High light intensity causes increased cell divisions necessary for the full development of pith parenchyma (Beres et al., 2017). Longer photoperiod durations are also shown to reduce the percentage cutting by WSS (Platt & Farstad, 1946). SS was also reported to be enhanced when plants were exposed to

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higher temperatures or drought during stem elongation (Hayat et al., 1995) because, when moisture limits the environment, the water holding capacity of pith parenchyma may provide drought (Saint Pierre et al., 2010) and heat tolerance. Precipitation interferes with photoperiodic intensity and reduces pith expression in SS cultivars (Holmes, 1984). Increased N levels induce the development of canopy and associated shading which reduces the intensity of sunlight and pith expression (Holmes, 1984). The SS of S-615 was reduced when artificial shading was provided (McNeal, 1956) and pith expression was shown to increase at a sowing density of 300 seed m^{-2}, but decrease at higher plant densities (Beres et al., 2011, 2012). In addition, SS shows spatial inconsistency while varying with environmental conditions (Bainsla et al., 2020). Analysis of the amount of solidness expressed in F_1 plants from different cross combinations showed that it was reduced from first (basal) through third internode (PAUW & Read, 1982; Pluta et al., 2021), with second internode best expressing semi-solidness (Bainsla et al., 2020). The later formed and upper internodes showed slower production of pith compared to the growth of the cell wall (McNeal, 1956; Putnam, 1942). Complementary additive factors that are dispersed among parents and environmental influences may be the reasons for variation of pith expression within a tiller and also among tillers belonging to the same plant in F_1 combinations (Bainsla et al., 2020). SS interacts with other characteristics like stem elongation and tillering capacity (Bainsla et al., 2020) making it quite complex to study in detail. A tiller inhibition gene (*tin*) associated with chromosome 1AS was identified that reduces the number of tillers in wheat, causes thicker cell walls with high lignin content as well as allows early elongation of basal internodes (Kebrom et al., 2012). Interestingly, all these parameters are also associated with SS at the basal internodes (Hyles et al., 2017).

Screening tests used for the SS trait are not only laborious and tedious (Houshmand et al., 2007) but representative scoring of SS is also difficult due to environmental influences on pith expression (Cook et al., 2004; Weiss & Morrill, 1992). Hence, the development and use of marker-assisted selection (MAS) has been effective in introgressing alleles for SS trait into locally adapted wheat cultivars (Houshmand et al., 2007). The SS phenotype of wheat is used as a ''perfect'' marker for resistance to WSS. It is considered a perfect marker when the characters of the trait are producing the phenotype of interest. There are five chromosomes of homologous groups 3 and 5 reported to carry genes for pith production (Houshmand et al., 2007; Larson & MacDonald, 2011a) and three chromosomes that carry genes which inhibit pith production (Larson & MacDonald, 2011a). Chromosome 3B is associated with the SS trait with one locus being on short arm and five loci on the long arm (Biyiklioglu et al., 2018). In a cross between solid and hollow stemmed lines, a locus called *Qss.msub*-3BL (identified at same position in bread and durum wheat), located on the long arm of chromosome 3BL was reported (Cook et al., 2004) that contributes around 76% of total variation for SS in the recombinant inbred population produced and is not associated with low yield (Cook et al., 2004; Houshmand et al., 2007). When double haploid lines (with the parental SS allele associated with *Qss.msub*-3BL) were grown in Bozeman, MT, Moccasin, MT, and Williston, ND, they showed an average stem solidness score of 14.4 (Cook et al., 2004). Additionally, a smaller amount of variation (31%) is contributed by a secondary locus *Qssmsub*-3DL which increased the average stem solidness score (Lanning et al., 2006). The presence of QTL on 3DL in line with the 3BL not only provides additional resistance to WSS but also shows no additional reduction in the yield beyond the 3BL locus (Lanning et al., 2006). In addition to providing resistance to WSS larvae through the SS trait, the genes at the *Qss.msub*-3BL loci modulate the amount of wheat stem cutting by sawflies (Sherman et al., 2010; Talbert et al., 2014). The SS genes are located between *Xgwm247* and *Xgwm114* microsatellite markers (Houshmand et al., 2007; Somers et al., 2004). *Xgwm340*, when compared to *Xgwm247*and *Xgwm547* markers, was identified to be closest to the *Sst1* locus, indicating that it could be the best marker to select for SS cultivars (Cook et al., 2004; Kong et al., 2013). The relationship between the two traits of SS and sawfly resistance supports the concept of pleiotropy but there seems to be some close linkage between the genes (Houshmand et al., 2007). There are several markers located on the 3A, 3B, 1B, and 5D chromosomes that are associated with early stem solidness (ESS) (Varella et al., 2015). *Qss.msub*-3BL controls both the ESS and late stem solidness traits expressed during jointing, booting, and anthesis stages, respectively. Additionally, *Qss.msub*-3AL was also detected for SS scored at early plant development in durum wheat (Varella et al., 2019). The hexaploidy QTL, *Qss.msub*-3BL.c (Conan-derived allele), showed similarities with the durum wheat QTL, *Qss.msub*-3AL associated with ESS in expressing SS and WSS resistance (Houshmand et al., 2007). Reportedly, ESS plays a major role in resistance to WSS as it aligns with the time of oviposition of WSS females and reduces rates of oviposition (Varella et al., 2016). The ESS phenotype is highly useful for spring wheat compared to winter wheat as ESS better coincides with WSS infestation in spring wheat development. In winter wheat, the WSS emergence not only coincides with duration between stem elongation and anthesis but also the post-anthesis period. High WSS infestation was observed in winter wheat after the degradation of pith produced by Conan-derived allele (Wong et al., 2023). It will be interesting to fine map and identify the genes associated with ESS and SS phenotypes. This will help in understanding the mechanism behind SS development and specifically, the differences in genetics behind ESS and SS phenotypic development.

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There are markers on the chromosomes 2D, 3B, and 4A, which are associated with reduced susceptibility of the host plant to WSS infestation. For instance, a QTL on chromosome 2D has been identified that is associated with late heading date (Sherman et al., 2010). Heading date is a potential factor to consider when breeding for WSS resistance because the varieties that delay their heading date may escape WSS infestation as the development of their stems will not be sufficient for oviposition by female WSS. QTLs on chromosomes 2D (*Qwss.msub*-2D.*b*) and 3B (*Qss.msub*-3BL.*c*) are associated with reduced oviposition by WSS and a QTL on chromosome 4A (*Qwss.msub*-4A.*1b*) is associated with decreased host attractiveness, thus lessening stem cutting (Sherman et al., 2010; Varella et al., 2017). Susceptibility to WSS is affected by QTLs on other chromosomes. These include QTLs on 1B and 5B that are associated with early heading date, leading to more stem cutting (Sherman et al., 2010); QTL on chromosome 1D which controls cell defense responses and cell death because they take place often in hollow stemmed phenotypes. Also, QTLs on chromosomes 4DS and 4BS, where genes *Rht-B1* and *Rht-D1* controlling plant height are located (Varella et al., 2016), may affect susceptibility to WSS since stem sawflies prefer taller plants for their oviposition (Buteler et al., 2009) and a relation seems to occur of height with SS and susceptibility to WSS (McKenzie, 1965). The SS trait is a complex one which is controlled by a major gene along with minor genes (Clarke et al., 2002; Larson & MacDonald, 2011a). The expression of SS could be due to additive, dominant, or recessive gene action. The role of digenic epistasis in controlling pith production cannot be ruled out since epistatic interactions between minor loci were observed (Dhariwal et al., 2022; McNeal, 1956). In durum wheat, the association of *Sst 1* locus, *Qss.msub*-3BL (Houshmand et al., 2007) and the secondary QTLs on chromosomes 2A and 2D caused a greater increase in stem solidness when compared to *Sst1* acting alone (Cook et al., 2004; Nilsen et al., 2017). Durum cultivars have a consistent expression of SS, are genetically more stable, and less affected by non-genetic factors compared to the SS bread wheat (Liang et al., 2022; Platt & Farstad, 1949). Additionally, the yield losses due to WSS damage in durum cultivars were comparatively lesser than bread wheat varieties (Özberk et al., 2005). The intermediate stem solidness of bread wheat may be due to the recessive action of a single SS gene from S-615 that most bread wheat genotypes carry, but is not completely expressed due to some epistatic interactions and inhibitors (Dhariwal et al., 2022; Hayat et al., 1995). In contrast, studies using crosses between the durum SS line Golden ball (C.A.N. 1324) (Clark et al., 1922) and the hollow stemmed line Alaska (Clark et al., 1922) showed that a single partially dominant gene controls the stem solidness trait (Clarke et al., 2002; Putnam, 1942; Wang et al., 2006). Furthermore, a preponderance of evidence for single dominant gene action for SS is reported in backcross populations of durum wheat (Clarke et al., 2002).

2.5 | Mapping and characterization of *TdDof* locus

The copy number variation of the *TdDof* gene is present within a physical interval of 2.5 Mb inside the *Sst1* locus on Chromosome 3B, which was reported to control the SS trait. Increased expression of *TdDof* caused the SS phenotype in bread wheat (Appels et al., 2018) and durum wheat. Three copies of *TdDof* arranged in tandem orientation are reported to be present in SS cultivars. Between *TdDof1* and *TdDof2* and in between *TdDof2* and *TdDof3*, a 25-bp insertion sequence (AGATGTCTTAGAACGTCGTCTTAGA) has been identified in CDC Fortitude durum wheat (SS) (Pozniak et al., 2015); this pattern was not observed in Kofa (PI584336) (hollow stemmed), which instead contains a single copy of *TdDof* (Nilsen et al., 2020). Transgenic overexpression of *TdDof* induced solidness in a hollow cultivar and its deletion resulted in loss of solidness in SS cultivar. It was shown that in Pithless1 (*TdDof* deletion mutant), at Zadoks stage 32, the pith first starts breaking down and undergoes programmed cell death (PCD) before collapsing into culm lumen (Nilsen et al., 2020). The central parenchymal cell walls of Pithless1 were distorted, irregular, and broken as observed under light and electron microscopy (Nilsen et al., 2020), but were intact in SS lines. The differences observed between solid and hollow stemmed cultivars could be due to *TdDof*'s spatial pattern of expression in the stem (Nilsen et al., 2020). At Zadoks stage 32, transcripts of *TdDof* were most expressed in pith parenchymal cells in both the solid and hollow stemmed cultivars (Nilsen et al., 2020). During Zadoks stage 34, *TdDof* was expressed only in the unimpaired parenchyma cells of hollow stem varieties. Conversely, in SS cultivars, the expression level remained the same (Nilsen et al., 2020). Chromosomes 2A and 2B have two NAC transcription factor genes (no apical meristem, *Arabidopsis* transcription activation factor, Cup-shaped cotyledon superfamily), and chromosomes 3A and 3B have three CEP (Cysteine proteinase) genes that were identified to be upregulated in hollow stem cultivars where there is low expression of *TdDof* (Nilsen et al., 2020). These results indicate that there may be a correlation between overexpression of *TdDof* and suppression of NAC and CEP genes, which are involved in cell wall degradation in SS cultivars (Nilsen et al., 2020).

2.6 | Biochemistry and physiology of SS phenotypes

There are other possible explanations too for the difference in the pith expression in the stems. The differences in biochemical activity between the Pithless1 and CDC Fortitude were also observed at Zadoks stage 32, 33, and 34 (Nilsen et al., 2020). The osmolality of compounds like glutamate, gamma-glutamyl acid, and associated amino acids

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is increased in Pithless1 during controlled desiccation (Nilsen et al., 2020). These substances are also discovered to be responsible for PCD in hollow stemmed cultivars (Nilsen et al., 2020). In relation to SS, around 43 putative high confidence genes were discovered within the wild emmer wheat (WEW) reference sequence common interval (Nilsen et al., 2017). These genes encode ribosomal proteins like RPS17, RPS19, RPS28, T*dDof*2, and protein kinase superfamily protein (Nilsen et al., 2017). Interference of function of these ribosomal proteins may also result in the hollow stem phenotype as enhanced expression of ribosomal proteins results in higher tissue production due to rapid cell division (Nilsen et al., 2017). The potential defense of the host plant against WSS infestation may also be achieved through the action of DIMBOA glucoside beta-D-glucosidase and triacetin 3′,4′,5′-O-trimethyltransferase, which are involved in the phenylpropanoid pathway (Biyiklioglu et al., 2018). Second, the energy and sugar compounds required for the survival of plants under stress conditions are provided by the pentose sugar pathway. Thus, at the metabolic level, these two pathways have been reported to be reactive to WSS infestation (Biyiklioglu et al., 2018) and the differences in the SS in various cultivars may also be attributed to interference within both these pathways (Biyiklioglu et al., 2018).

Yet, the ultimate adoption of SS cultivars for crop production depends on whether they can provide good grain yield and quality. Traditionally, concerns regarding SS cultivars were derived from the lower yields and unclear harvest indices. In the absence of severe WSS infestation, hollow stemmed cultivars show better agronomic performances compared to SS cultivars (Cook et al., 2004; Weiss & Morrill, 1992) because the energy and carbon resources required to develop pith in a SS cultivar can instead be used for grain development (Ford et al., 1979). It is also believed that the poor yield of SS cultivars could be due to the transfer of undesirable genes from S-615 (Cook et al., 2004; Hayat et al., 1995). However, there is no strong evidence of association between the chromosomal region that controls the SS trait and the chromosomal region that controls grain yield (Lanning et al., 2006). The development of hollow stemmed WSS-resistant cultivars would likely increase grain yields in the presence of moderate WSS infestation. Since the occurrence of heavy stem sawfly pressure is unpredictable across regions, when there is a serious infestation of WSS, SS cultivars perform better agronomically compared to hollow-stemmed ones (Beres et al., 2011, 2009; Weiss & Morrill, 1992). SS can also increase yield by storing reserves of water-soluble carbohydrates during drought conditions (Blum, 1998; Nilsen et al., 2020; Pollock, 1986; Saint Pierre et al., 2010). During wet conditions at the grain filling stage, the soil N content is reduced either through leaching or denitrification which leads to low protein accumulation, whereas during drought conditions, proteins may accumulate and reduce the yield (Liu et al., 2022). Marker-assisted backcross approaches have been used to introgress the early SS allele, *Qss.msub*-3BL.*c* from the cultivar Conan into hollow and SS lines containing *Qss.msub*-3BL.*a* or *Qss.msub*-3BL.*b* alleles (Cook et al., 2019; Varella et al., 2017). This is an excellent idea for integrating ESS and higher grain yields.

2.7 | Future approaches

Many factors have not been adequately addressed in breeding for SS wheat cultivars to properly achieve effective management of WSS infestation. (1) In SS cultivars, not all wheat plant tillers exhibit uniform solidness. Additionally, the main stem and tillers differ in expressing SS phenotype resulting in non-uniform resistance expression and thus, continuance in serving as a host for WSS that leads to ongoing propagation of WSS. Hence, developing uniform SS varieties is highly desirable for stable yields and reducing the WSS populations. (2) The response of the host plant to WSS is much more complex than mere restriction of the larval growth. Therefore, unraveling the response mechanisms of both wheat plants and WSS, such as antibiosis, could provide a gateway for the effective management of WSS. (3) The advantage of SS phenotypes in minimizing WSS damage preponderates the variational impacts it may have on parasitoid population. Hence, there is still potential to enhance performance of these parasitoids in SS cultivars (Rand et al., 2020), and integrating HPR with biological control may yield better results. The populations of the parasitoids can also be conserved by minimizing postharvest tillage. (4) The resources required for the development of pith parenchyma present in SS cultivars could be useful for grain development. Hollow stemmed varieties with thinner diameters that tend to have a beneficial aspect of nonpreference by the female WSS can be developed by increasing the seed rates (Cárcamo et al., 2016). Wheat growers could then cultivate these cultivars without being concerned about WSS damage and unstable yields. (5) Since there is no significant association observed between chromosomal regions that control the SS and the regions that control yield, there is still potential to develop SS cultivars that provide better yields.

AUTHOR CONTRIBUTIONS

Akshara Bathini: Writing – original draft; writing – review & editing. **Lavanya Mendu**: Conceptualization; writing – original draft; writing – review & editing. **Nagendra Pratap Singh**: Writing – review & editing. **Jason Cook**: Writing – review & editing. **David K. Weaver**: Writing – review & editing. **Jamie D. Sherman**: Writing – review & editing. **Megan Hager**: Writing – review & editing. **Suchismita Mondal**: Writing – review & editing. **Venugopal Mendu**: Conceptualization; Funding acquisition; Investigation; Writing – original draft; Writing – review & editing.

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CONFLICT OF INTEREST STATEMENT

Lavanya Mendu (research assistant professor) is spouse of Venugopal Mendu (associate professor). Both are faculty in the Plant Sciences and Plant Pathology Department at Montana State University.

ORCID

Jason Cook https://orcid.org/0000-0002-7753-6191

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