



Architecture of paleas and lemmas dominates seed shattering trait in naked oat (*Avena nuda*)

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Abstract

Seed shattering in naked oat (*Avena nuda*) is a severe problem, resulting in significant yield losses. In the present study, the seed-shattering rates were characterized in a set of 177 naked oat cultivars and lines. Eight cultivars with different seed-shattering rates were studied in several morphological and physiological traits that may be related to seed shattering at different developmental stages. Three types of paleas, viz. boat type, defect type and flaky type, were identified at the dough stage, and the proportion of the boat-type paleas were found to positively correlate with seed shattering. In a following scaling-up morphological study on paleas and lemmas in 32 cultivars with different seed-shattering rates, the length, width and the thickness of paleas and lemmas were investigated, and the ratio of the bottom/medium thickness of both paleas and lemmas showed high association with seed shattering tolerance in naked oat. These indicate that the architecture of paleas and lemmas has a particularly obvious correlation with seed shattering in naked oat. More intriguingly, a unique zigzag pattern of the cell wall was found in lemma tissues of naked oat, which may increase the toughness and strength of lemmas and help with seed retention.

Keywords Abscission zone · Lemma · Palea · Seed shattering · Zigzag pattern of cell walls · *Avena nuda*

Introduction

Oat is the seventh most economically important cereal crop for its high nutritional value with a distinct nutrient profile among cereals (Sadiq et al. 2008). Studies have found that oat is rich in β -glucan, dietary fiber and minerals, which makes oat a potential therapy against diabetes mellitus and cardiovascular diseases (Sadiq et al. 2008). Oat starch is

also found to be with unique physical and chemical characteristics due to its composition proportion, and this gives oat starch its unique pasting properties (Punia et al. 2020). Recent studies have also shown that oat proteins can help treating sports injuries and enhance the body's athletic abilities significantly (Xia et al. 2018). As a promising candidate of “healthy food,” oat has drawn a lot of attention during the last few years for its healthcare-beneficial nature.

The earliest recorded cultivation of oat was dated back to the twentieth century B.C. in Egypt, much later than rice and wheat (Moore-Colyer 1995). This gives oat comparatively more de-domesticated traits, including the tendency for seed shattering, which makes a major cause of yield loss in oat production. Seed shattering refers to a natural shedding of seeds when they ripe (Maity et al. 2021). It is an essential trait for wild plants to reproduce normally. However, for most domesticated crops, it is a major limiting factor that causes yield loss. Many studies have focused on seed shattering for understanding its molecular mechanisms, and alleviating seed shattering in crops.

Most studies on cereal seed shattering were conducted at genetic level and inevitably focused on the development of the abscission zone (AZ), which is the developmentally

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defined region for ordinary organ dispersal in plants, and a major factor affecting seed shattering in cereals such as rice and wheat (Di Vittori et al. 2019; Dong and Wang 2015; Li and Olsen 2016; Maity et al. 2021).

The development of AZ and the lignin deposition at this section was known to be decisive on seed shattering (He et al. 2021; Jiang et al. 2019a; Yoon et al. 2015; Yoon et al. 2017). The genetic control of seed shattering was well studied in rice, and at least two major genes, *qSH1* and *SH4*, have been found to condition rice seed shattering through regulating AZ development (Di Vittori et al. 2019; Dong and Wang 2015; Li and Olsen 2016; Maity et al. 2021; Zhang et al. 2019). Other genes such as *SH5* and *SSH1/SNB* are also believed to have large influences on seed shattering by interacting with *qSH1* (Jiang et al. 2019a; Yoon et al. 2014). Mutagenesis and transgenic methods have been frequently used to illustrate the function and mechanisms of these genes, which affected seed shattering through modifications on AZ formation or lignin deposition in the AZ regions (Jiang et al. 2019a; Lv et al. 2018; Tsujimura et al. 2019).

The gene *Q*, a homolog of the rice gene *SNB*, has been extensively studied on wheat domestication, including seed shattering (Dong and Wang 2015; Li and Olsen 2016; Maity et al. 2021; Simons et al. 2006). The results showed that gene *Q* governed the rachis brittleness and glume structure and affected seed shattering in wheat (Jiang et al. 2019b; Madsen and Brinch-Pedersen 2020; Zhang et al. 2020). The functions of the alleles of the gene *Q* have also been analyzed in modulating multiple domestication characters of wheat (Xie et al. 2018; Zhang et al. 2011). Interestingly, both the homologous genes *SNB* in rice and gene *Q* in wheat were reported to be regulated by *miR172*, a micro-RNA that regulates the transcript level of rice *SNB* and wheat gene *Q* by altering the mRNA splicing (Debernardi et al. 2017; Greenwood et al. 2017; Jiang et al. 2019a; Liu et al. 2018; Wolde et al. 2019; Xu et al. 2018). These supported the idea of the existence of shared regulation pathway among cereals in seed shattering. Similarly, seed shattering studies in sorghum also focused on the genetic mechanisms based on non-shattering mutants. *Sh1* and *SpWRKY* in sorghum were both found to control spikelet dispersal via regulation on AZ development (Lin et al. 2012; Tang et al. 2013).

The dispersal unit (DU) is the combination of plant organs that separate from the mother plant. In cereals, DU comprises the embryo and accessory organs such as paleas, lemmas and florets. The accessories of cereal DU were found not only to provide physical shields for embryos, but also affect germination (Graf 2020). The composition of the DU is determined by the location of the AZ that has the function of disarticulation, and consequently, seed DU composition can vary from the embryo itself to the whole inflorescence (Di Vittori et al. 2019; Doust et al. 2014; Li and Olsen 2016). Based on years of observation, for most cereal and grass species, we have found that DUs consist of seeds and appurtenance originated from floral structures, except for few cases such as naked oat, whose disarticulation occurs in the AZ between the seed and the hulls (Fig. 1), which causes seed shattering in naked oat. This type of disarticulation gives its own characteristics of processing and usage, as no shelling is necessary for naked oat; it is different from *Avena sativa* that is also widely cultivated in China.

Seed shattering in naked oat considerably affects the production, but the morphological and physiological florets characteristics have not been investigated yet. In this study, the seed-shattering rates were identified in a set of 177 naked oat cultivars and lines, and florets characteristics affecting seed shattering tested and analyzed in naked oat cultivars with different seed shattering tolerance. This will lay a foundation for improvement of naked oat cultivars.

Materials and methods

Plant materials

A diverse panel of 177 naked oat cultivars and lines randomly selected from the core oat collections, including 80 landrace cultivars, 25 cultivars from foreign countries, 69 Chinese cultivars and 3 advanced breeding lines (Supplementary Table 1), were used in this study; these cultivars can well represent the distribution of seed shattering traits in naked oat. The cultivars are stable in agronomic traits such as growth period, plant height, and yield. The seed shattering trait of the 177 cultivars was identified (see below).

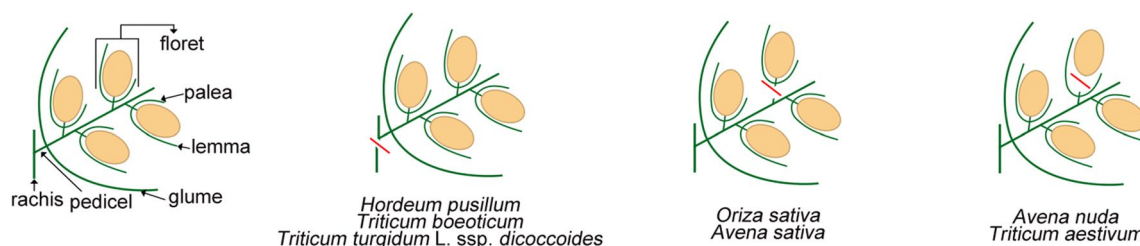


Fig. 1 Composition patterns of general cereal dispersal units. The red dash represents the position where the abscission usually occurs

Field trials

The field trials were conducted at Zhangbei County, Zhangjiakou, Hebei province, and Jining District, Ulanqab, Inner Mongolia Autonomous Region, China, in 2019, 2020 and 2021 under normal field managements. The cultivars were sown in single 1.5-m rows with 20 cm spacing between rows in late April of each year. The 5 g of seeds was sown evenly in each row with a depth of 2 cm. The field management was following normal local field practice. The trials were kept free of weeds with broad-range herbicides.

Identification of seed-shattering rates

Three spikes in each cultivar were selected and bagged with transparent mesh bag at the milking stage and were collected at the dough stage. The samples were then placed at room temperature for 48 h and processed for seed shattering statistics. The treatment of the materials is as follows: Bags were lifted to a plane of two meters high and dropped freely onto a cement pavement for three times. The seeds fell freely into the mesh bag, and the fallen seeds and the remaining seeds of the whole spike in the mesh bag were counted. The seed shattering rate was calculated as follows:

$$\text{Seed shattering rate} = \frac{\text{Seeds fallen in the bag}}{\text{Seeds of the whole spike}} \times 100\%$$

Phenotypic identification of the florets in the cultivars with different seed shattering tolerance

Eight out of 177 naked oat cultivars were chosen for this study, including Large Naked Oat-2 (seed shattering rate 9.28%), 1-6-800 (7.80%), Xia Naked Oat-1 (8.21%) and Heizhuzi Naked Oat (13.42%), representing the cultivars with weak seed shattering tolerance, and Yanke-1 (2.17%), Baxuan-4 (2.39%), 83,113-6 (1.66%) and Yuan Naked Oat (0.91%) representing those with strong seed shattering tolerance. The seeds were sown in field located in Inner Mongolia Agricultural University in 2021 following the method mentioned above. These eight cultivars shared comparatively good consistency of seed-shattering rates and were suitable for preliminary screening of phenotypes that might correlate to seed shattering, including the breaking tensile strength (BTS) of seeds, paleas and lemmas, and the length, width and thickness of paleas and lemmas. All phenotypes were identified at grain filling, milking and dough stages, respectively. Three plants were randomly chosen at each of grain filling, milking and dough stages for each cultivar. And for each plant, the first spikelet on apical side was picked

from a spike randomly. The spikelets were then removed of glumes, and then, the first floret at the bottom of each spikelet was collected and proceeded for measurements.

The BTS of seeds, paleas and lemmas was measured using tweezers and a dynamometer; the hook of the dynamometer was attached to the nodes of the receptacles using fine cotton threads, and then, the BTS was scored, with seeds, paleas or lemmas being clamped with tweezers and pulled toward the opposite direction until the junction between the target tissues and the rest of the spikelet were broken. The length and width of paleas and lemmas were measured using a ruler, and the thickness was measured using a micrometer. The paleas were flattened in a way as shown in Fig. 5b, with the paleas being stripped apart from the bottom into three pieces, including middle part and two flanks. The most maximum width of these three pieces was measured separately and added together as the index of the width of the paleas. Three repeats were taken for each trial.

Among the 177 cultivars, 11 cultivars with weak seed shattering tolerance and 21 with strong seed shattering tolerance were chosen for the characterization of length, width and thickness of palea and lemma at the dough stage to identify the potential correlation between these phenotypes and seed-shattering rates. All the 32 cultivars chosen shared comparatively good consistency of seed-shattering rates over three years and two locations for a reliable study. The spikelets of the 32 cultivars used for the identification of the length, width and thickness of the hulls were collected at the dough stage in Jining and Zhangbei in 2021, and three spikelets were chosen for each cultivar in each location. Samples were collected using the same method as the sampling of the eight cultivars. The cultivars were selected based on their distribution of seed shattering rate and relatively good consistency of the seed shattering rate to add to the accuracy of this research. The measurements of the length, width and thickness of the hulls were in the same way as mentioned above.

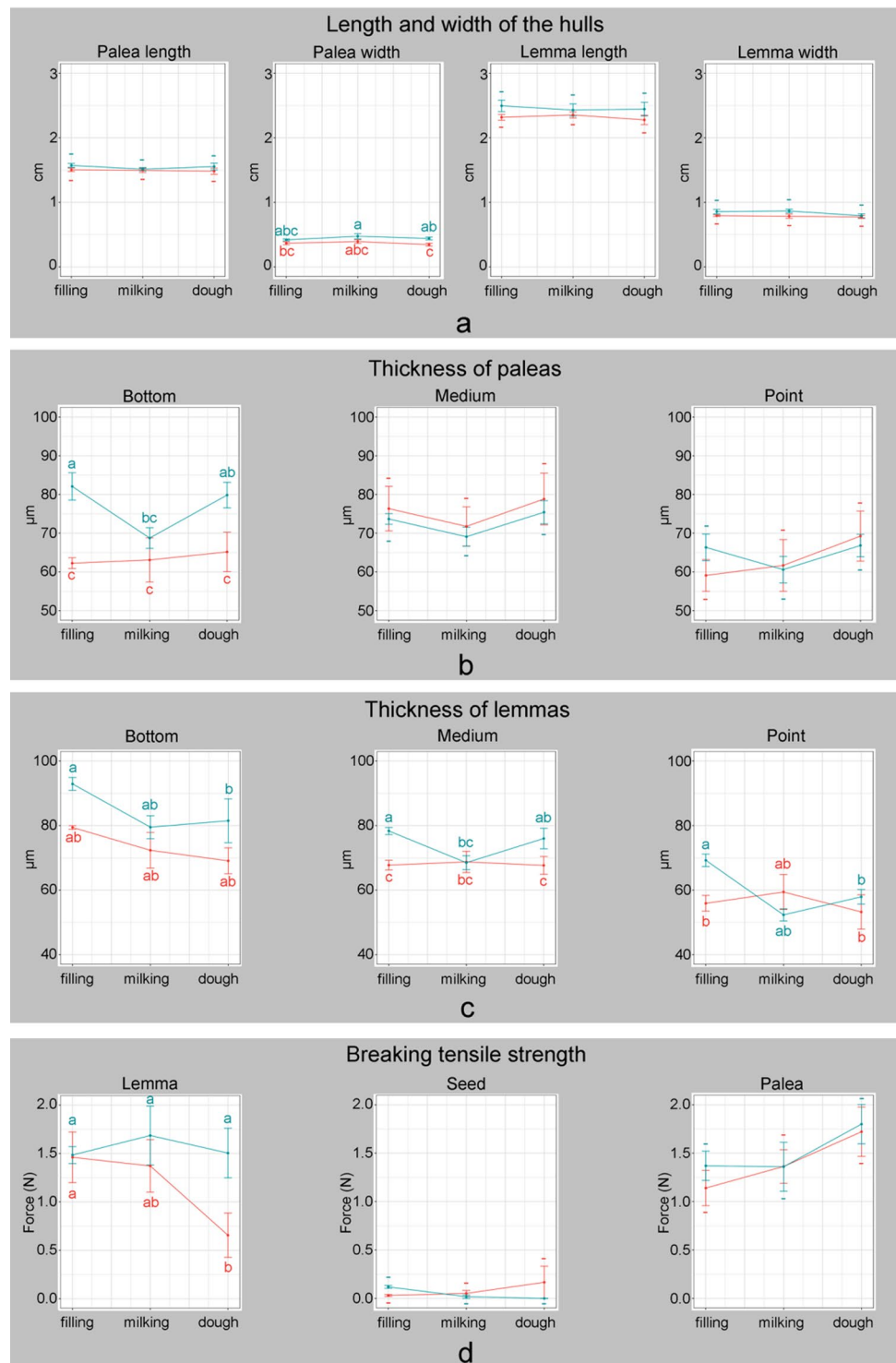
Microscopic observations

The paleas and lemmas used for microscopic observation was collected in the same way as phenotypic identification. The materials were sectioned into squared pieces of 3 mm wide and unfolded evenly onto the slides (CITOTEST®). The materials were then dyed using the Safranin-quick green staining kit (Solarbio®), following the protocols of the manufacture. The slides were observed using Nikon ECLIPSE Ti microscope systems.

Statistical methods

One-factor ANOVA and Duncan multiple comparison was performed for the statistics of the data presented in Fig. 2

Fig. 2 Phenotypes of the strong and weak shattering tolerance groups at different stages in the eight oat cultivars. The red and green lines represent the weak and strong shattering tolerance groups, respectively. The “bottom,” “medium” and “point” represent the relative positions of the paleas or lemmas where the thickness was measured. The results of one-factor ANOVA and Duncan multiple comparison are given in the longitudinal position with letters ($n=4$), while the groups that showed no significant differences at all were labeled with “-” mark. The significance threshold was set at 0.05



using SPSS 19, the significance threshold being set at 0.05. Independent sample t test was used for the statistics in Fig. 3 using SPSS19. Z-score was used for the standardization of the seed shattering rate using *R* 4.1.3, to eliminate the group differences of the data from different location and year, so that the seed shattering rate of different cultivars and lines could be compared to each other with confidence.

Results

Identification of seed shattering tolerance in naked oat

A diverse panel of 177 naked oat cultivars and lines were selected, representing the major germplasm of naked oat in

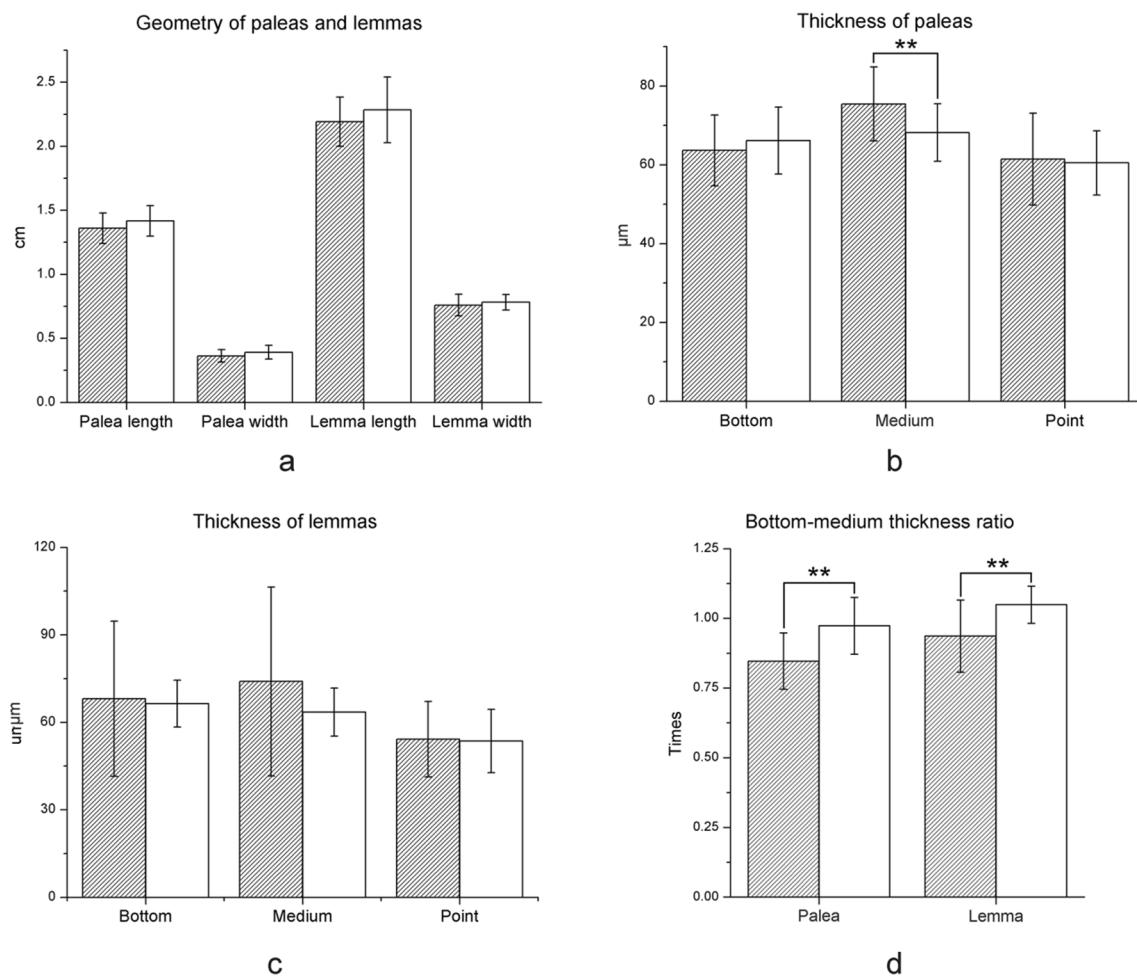


Fig. 3 Characteristics of the strong and weak seed shattering tolerance groups in 32 naked oat cultivars (11 in weak seed shattering tolerance group and 21 in strong seed shattering tolerance group). Squared bars: weak seed shattering tolerance group; white bars:

strong seed shattering tolerance group. Independent sample t test was used for statistical analysis, and ** represents significant differences at $P < 0.01$ between the strong and weak seed shattering tolerance groups

China, for identification of the seed shattering tolerance. The experiment was performed in three successive years (2019, 2020 and 2021) and two different ecological sites (Zhangbei County and Jining District). The seed-shattering rates in different years and locations were recorded accordingly. (Supplementary Table 1). Among 177 naked oat cultivars, ten had a seed shattering rate of less than 2%, 145 had seed-shattering rates between 2 and 9%, and 22 had a seed shattering rate of more than 9%, accounting for 5.65%, 81.92% and 12.43%, respectively (Supplementary Fig. 1). The seed-shattering rates of the 177 cultivars showed high consistency among years and locations, with correlation coefficients of 0.92–0.99 between environments, and mean values and standard deviation of $10.94 \pm 7.68\%$, $3.09 \pm 3.25\%$ and $6.15 \pm 5.60\%$ in 2019, 2020 and 2021, respectively (Supplementary Table 2).

The variation of seed-shattering rates is comparatively high for the 177 cultivars, ranging from 0.63–14.71%

(0.09 to 2.86 for standardized data). This might be caused by the undergoing segregation of seed shattering trait of the oat population, as well as the climatic differences of the diverse geography and particular years. Seed shattering trait of most of the cultivars was not consistent enough for precise analysis, and taking all 177 cultivars into account would introduce this high deviation to the analysis, thus bringing about more uncertainty and interference. As a result, cultivars with minimum and maximum values of seed-shattering rates, i.e., the strong and weak seed shattering tolerance groups, were used to compensate for the low consistency of the overall data. The strong and weak shattering tolerance groups were restricted to cultivars that held a comparatively low deviation of seed-shattering rates, which would ensure the reliability of the study.

Phenotypes of paleas and lemmas of naked oat at different developmental stages

Eight cultivars were selected to clarify the phenotypes of paleas and lemmas at different developmental stages, including Large Naked Oat-2 (seed shattering rate 9.28%), 1–6-800 (7.80%), Xia Naked Oat-1 (8.21%) and Heizhuzi Naked Oat (13.42%), representing the group with weak seed shattering tolerance, whereas four other cultivars, Yanke-1 (2.70%), Baxuan-4 (2.39%), 83,113–6 (1.66%) and Yuan Naked Oat (0.91%), representing the group with strong seed shattering tolerance.

Data were analyzed to identify the differences between the two groups at different developmental stages ($n=4$). At the grain-filling, milking and dough stages, the average length of paleas was 1.51 ± 0.05 cm, 1.50 ± 0.06 cm and 1.48 ± 0.09 cm, respectively, in the cultivars with weak seed shattering tolerance, and 1.57 ± 0.06 cm, 1.51 ± 0.05 cm and 1.55 ± 0.10 cm, respectively, in those with strong seed shattering tolerance. The average width of paleas was 0.37 ± 0.04 cm, 0.39 ± 0.06 cm and 0.35 ± 0.05 cm, respectively, in the cultivars with weak seed shattering tolerance, and 0.42 ± 0.03 cm, 0.47 ± 0.08 cm and 0.44 ± 0.04 cm, respectively, in the strong ones. The average length of lemmas was 2.32 ± 0.09 cm, 2.35 ± 0.09 cm and 2.28 ± 0.14 cm, respectively, in the cultivars with weak seed shattering tolerance, and 2.50 ± 0.18 cm, 2.43 ± 0.19 cm and 2.44 ± 0.21 cm, respectively, in the strong ones. No significant differences of length or width among the three developmental stages were detected in either groups, indicating that the growth of hulls had stopped by the grain-filling stage (Fig. 2a, Supplementary Table 3). The average length and width of paleas and lemmas at all three stages of the strong seed shattering tolerance group were all bigger than the weak tolerance group; however, no significant differences were found except for the width of paleas at the dough stage ($P < 0.05$). The average BTS values of lemmas in the cultivars with weak seed shattering tolerance at the filling, milking and dough stages were 1.46 ± 0.52 N, 1.37 ± 0.54 N, and 0.66 ± 0.46 N, respectively, showing a declining trend along with the progress of developmental stages, whereas this trend was not observed in the cultivars with strong seed shattering tolerance. Apart from this, no significant differences were found among the BTS data of the three developmental stages in the strong or weak tolerance groups. No significant differences between the two tolerance groups were found either. The BTS of seeds showed no significant differences among developmental stages for the cultivars both with strong and weak seed shattering tolerance, indicating the AZ where the disarticulation occurs had fully developed at the grain-filling stage (Fig. 2d). The BTS of seeds was consistently low between the two groups regardless of the three developmental stages and seed-shattering rates, suggesting that

the AZ at the disarticulation site had no contribution to the segregation of the seed shattering phenotype in naked oat.

The length and width of paleas and lemmas in naked oat with different seed shattering tolerance

In total, 32 cultivars were selected for phenotyping the length and width of paleas and lemmas, including 11 cultivars with an average seed shattering rate of $9.77 \pm 2.49\%$ and 21 with an average seed shattering rate of $2.68 \pm 0.89\%$ (Supplementary Table 4). These two groups represented cultivars with weak and strong seed shattering tolerance, respectively. Data were analyzed between the two groups, with the number of observations of the weak tolerance group being 11 and 21 for the strong tolerance group. The average length and width of paleas were 1.36 ± 0.12 cm and 0.36 ± 0.05 cm in the cultivars with weak seed shattering tolerance, and 1.41 ± 0.12 cm and 0.39 ± 0.05 cm in the strong ones (Fig. 3a). The length and width of lemmas were 2.19 ± 0.19 cm and 0.76 ± 0.08 cm, respectively, in the cultivars with weak seed shattering tolerance, and 2.28 ± 0.26 cm and 0.78 ± 0.06 cm, respectively, in the strong ones (Fig. 3a). The average length and width of paleas and lemmas were both slightly smaller in the cultivars with weak seed shattering tolerance than those in the strong ones, although no significant differences were present between the indexes of two groups for these phenotypes.

The thickness of paleas and lemmas at different positions in naked oat with different seed shattering tolerance

The average thickness at the bottom, middle and point positions of paleas in the above-mentioned 11 cultivars with weak seed shattering tolerance were 64 ± 9 μ m, 75 ± 9 μ m and 61 ± 12 μ m, respectively, whereas those were 66 ± 9 μ m, 68 ± 7 μ m and 60 ± 8 μ m, respectively, in the above-mentioned 21 cultivars with strong seed shattering tolerance (Fig. 3b). The lemma thickness at these three positions was 68 ± 27 μ m, 74 ± 32 μ m and 54 ± 13 μ m, respectively, in the cultivars with weak seed shattering tolerance, and 66 ± 8 μ m, 64 ± 8 μ m and 54 ± 11 μ m, respectively, in those with strong ones (Fig. 3c). The thickness of paleas in naked oat showed the same trend for both groups in general, in the order of middle > bottom > point. The thickness of paleas in the middle part showed significant differences between the strong and the weak seed shattering tolerance groups ($P < 0.01$, Fig. 3b). There were no significant differences between the thickness of lemmas of the two groups; however, the bottom-medium thickness ratio of both paleas and lemmas was significantly different between the groups with different seed shattering tolerance ($P < 0.01$, Fig. 3d).

Correlation between phenotypes and seed shattering tolerance

Analysis of the data above showed that: 1) the values of length and width of paleas and lemmas in cultivars with weak seed shattering tolerance were all a bit smaller than those in the strong ones, with the values of the weak tolerance group being 95.45% of the strong tolerance group in average (Fig. 3); 2) The bottom-medium thickness ratio of paleas and lemmas represented the shape of the plant tissue and were significantly correlated with seed shattering rate (Fig. 3). In summary, the architecture of paleas and lemmas significantly contributed to seed shattering trait in naked oat.

The shapes of paleas in the cultivars with different seed shattering tolerance

A morphological polymorphism in paleas was observed in above-mentioned eight cultivars with different seed shattering tolerance. The palea shapes of different cultivars at dough stage comprised three types: boat type, defect type and flaky type. The seeds were wrapped tightly in the boat-type paleas, which could provide more protection and prevent seeds from shattering. The defect-type paleas basically held the shape similar to the boat-type paleas, but curls or deformations were found within; thus, the seeds were held loosely within paleas. The flaky-type paleas had very little flank area and could barely hold the seeds from shattering. By comparison of their sides, the flank space of these three types of paleas was in an order of boat > defect > flaky. A larger flank space led to a strong holding capacity of the paleas. The frequencies of three types of paleas were investigated in the cultivars with strong and weak seed shattering tolerance, and the results showed that: 1) all the three types of paleas (boat, defect and flaky) were present in the cultivars with weak seed shattering tolerance, while only the boat and defeat types of paleas were observed in the cultivars with strong seed shattering tolerance; 2) the cultivars with strong seed shattering tolerance had a percentage of boat-type paleas of 88.89%, while the boat type in the cultivars with weak seed shattering tolerance was 30.56% (Fig. 4). These findings indicated that the more proportion of the boat-type paleas in naked oat population was, the stronger seed shattering tolerance would there be in the cultivars. (Fig. 5a)

Microscopic observation of paleas and lemmas

The microscopic observation was performed to further investigate the differences of tissue section for the hulls in above-mentioned eight cultivars with different seed shattering tolerance. The result showed that there were no obvious differences of microstructure in the paleas or lemmas of the

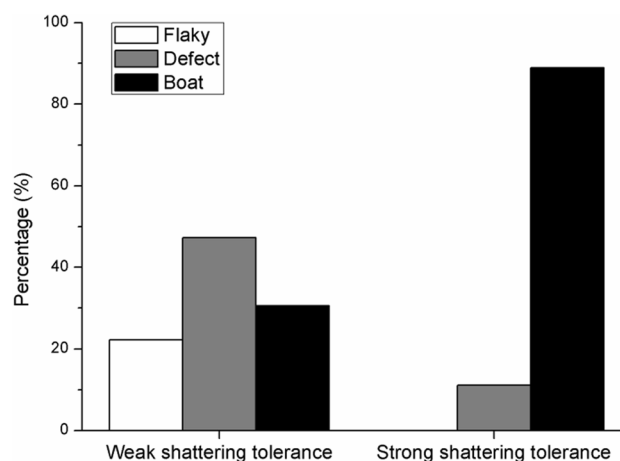


Fig. 4 Stacked bars of three types of paleas in the groups of strong and weak seed shattering tolerance, respectively, in the eight oat cultivars

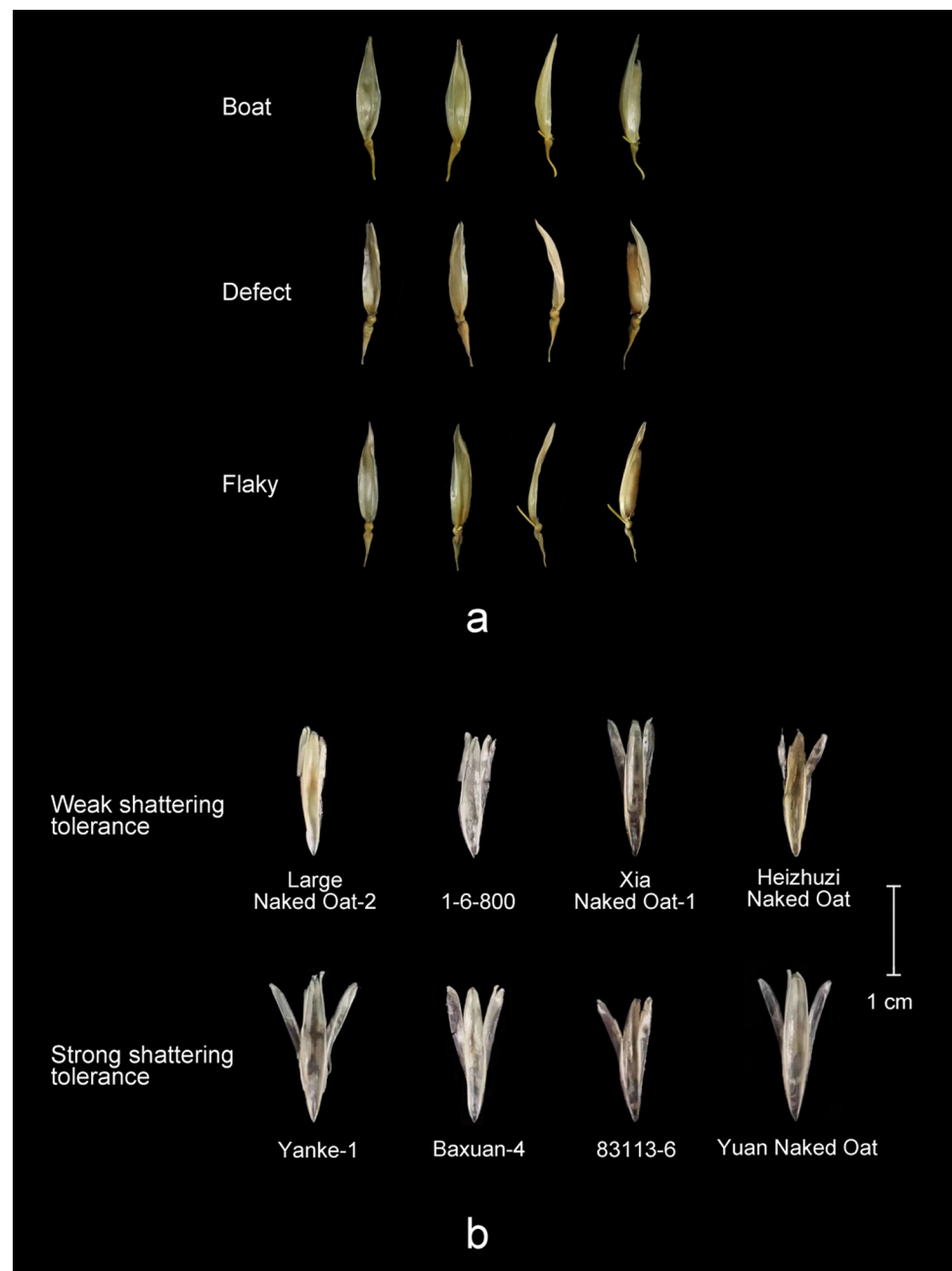
cultivars with different seed shattering tolerance (Fig. 6). However, an intriguing way of the arrangement of cell wall in oat lemmas and a zigzag pattern was found, which showed no obvious differences between two groups. This zigzag pattern of the cell wall enlarged the contact area of the cells to each other and may provide stronger adhesion to lemmas cells, adding to the strength and toughness for the lemmas in naked oat (Fig. 6).

Discussion

In this study, we identified a significant correlation between the seed shattering rate and the architecture of lemmas and paleas and found that the BTS of the disarticulation site was not associated with seed shattering tolerance in naked oat. This is likely due to the reason that seed shattering from the mother plant is not determined completely by the development of the AZ, although the AZ development is an important determinant for seed shattering in other cereals (Yoon et al. 2015; Jiang et al. 2019a; Yoon et al. 2017). The cultivars with strong seed shattering tolerance had much thicker and bigger hulls than those with weak seed shattering tolerance in naked oat, which could be attributed to the fact that thicker and bigger hulls can hold seeds more firmly and add the mechanical support to seeds. Further observation suggested that the thicker bottom area and larger flanks of paleas could bring more rigidity, making the seeds less shattering due to better protection from paleas.

The significant correlations between the shape of hulls and seed shattering tolerance identified in our study are in agreement with previous reports, as was found out in wheat that gene *Q* conferred seed shattering through modulating glume development (Zhang et al. 2020). The

Fig. 5 The morphology of the paleas of cultivars in different shattering groups. **a**: boat-, defect-, and flaky-type paleas; **b**: Comparison of the typical flattened paleas of two groups. The samples were collected at dough stage



increasing thickness at the bottom of the glume where the spikelet is connected to the rachis created a robust support for the spikelet, resulting in a low seed shattering in wheat (Zhang et al. 2020). The present study supported the conclusion of previous studies that the gene *Q* modulated the glume structure, conditioning seed shattering in wheat (Madsen and Brinch-Pedersen 2020; Xu et al. 2018; Liu et al. 2018). Taken together, these studies expended the understanding of seed shattering, that the architecture of inflorescence structure could be a key regulator of seed shattering in the natural shedding of cereals beside the development of AZ.

In this study, no obvious relationships between the BTS of seeds and seed-shattering rates were identified, indicating that the development of the AZ at the position of DU was not a determinant of the seed shattering rate in naked oat. However, there is no doubt that the AZ between seeds and hulls is a physical link related to seed shattering events in naked oat, giving significance to potential future studies into the genetic background of the AZ development in naked oat. This is going to be a challenging task, as different genetic basis of seed shattering was observed in different cereal species. There are evidences indicating diverse seed shattering locations governed by different orthologous loci:

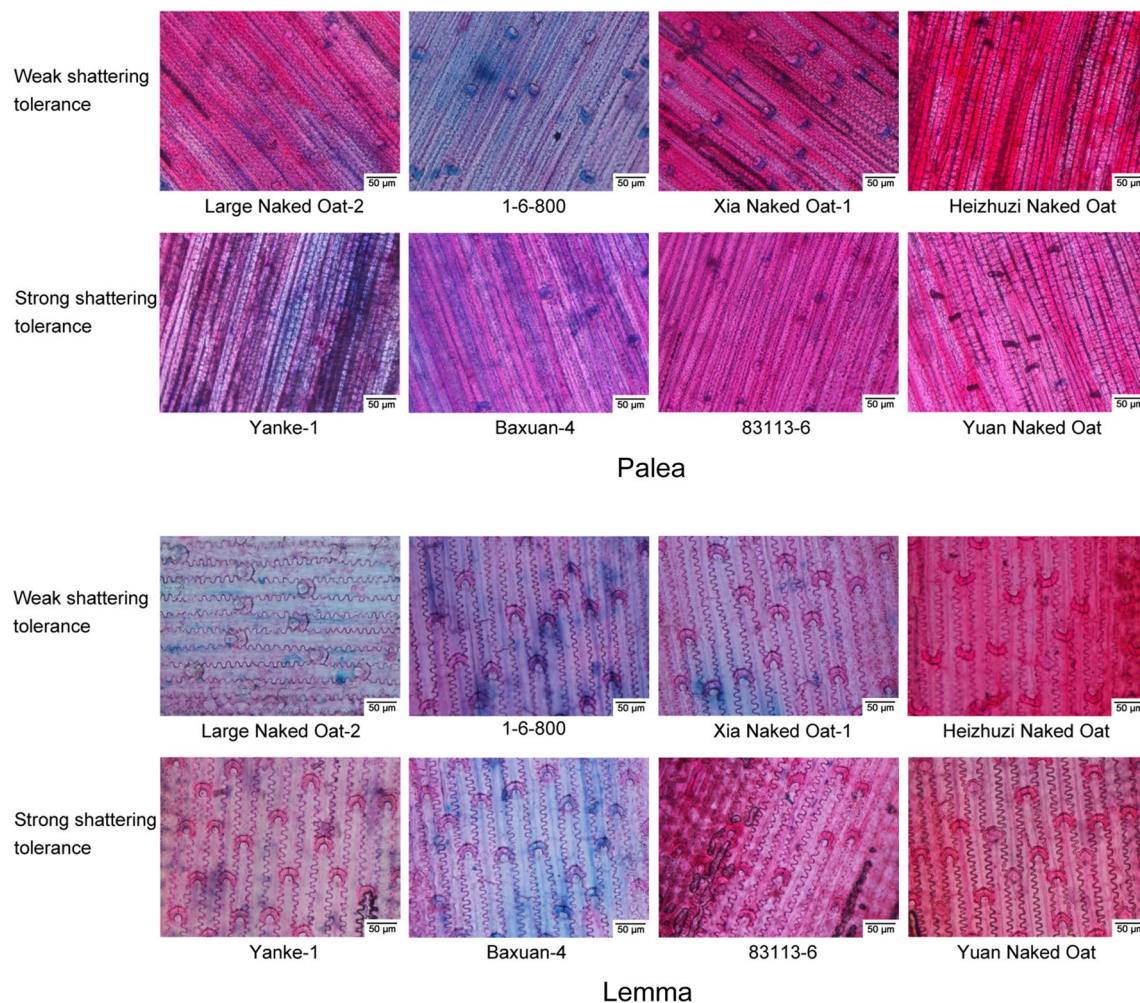


Fig. 6 Microscopic observation of paleas and lemmas of cultivars in different shattering groups. Samples were taken at the sections of 5 mm's to the apical side from the point of the junction between the hull and the rachilla

Br1 controlled barrel-type spikelet dispersal in *Triticum timopheevii*, while *Br2* conferred wedge-shaped spikelet dispersal in *Aegilops tauschii* (Li and Gill 2006). However, no orthologs of *Br1* or *Br2* were detected in rice, which further confirmed this thesis, as the disarticulation events occurred at the AZ below the florets, governed by *qSH1*, *sh4*, *SNB*, *SH5* and other related genes in rice (Di Vittori et al. 2019; Maity et al. 2021; Dong and Wang 2015; Li and Olsen 2016; Jiang et al. 2019a; Zhang et al. 2019; Yoon et al. 2014). In naked oat, seed shattering relies on the disarticulation of the AZ between seeds and hulls, which is different from all the cases in other reports. Studies in this mechanism of seed shattering may bring new insights into the understandings of the field.

An increasing number of studies have focused on oat nutrients during the last few years, as oat has been proven to be of great nutritious and healthcare value (Punia et al. 2020; Singh et al. 2013; Valido et al. 2021). However, as a

critical cause of yield loss in modern oat production, seed shattering in oat had not been studied systematically yet. Our study aimed to reveal the physiological mechanism of seed shattering in naked oat, and to lay the foundation for further studies as well as breed improvement. Additionally, the results of our study showed that the architecture of hulls was a key factor for regulation of seed shattering in naked oat, which broadened the research ideas of studies into seed shattering of cereals.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s42976-022-00347-1>.

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Author contributions XL performed the experiments and wrote the manuscript. KZ participated in the experiments, field works and data collections. YY and BH provided plant materials and funding resources, supervised the research, and assisted in writing the manuscript.

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Declarations

Conflict interest The authors have no competing interests to declare that are relevant to the content of this article.

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