

# Awns

Subjects: **Biology**

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Awns are extending structures from lemmas in grasses and are very active in photosynthesis, contributing directly to the filling of the developing grain. Barley (*Hordeum vulgare* L.) awns are highly diverse in shape and length and are known to be controlled by multiple awn-related genes. The genetic effects of these genes on awn diversity and development in barley are multiplexed and include complementary effect, cumulative effect, duplicate effect, recessive epistasis, dominant epistasis, and inhibiting effect, each giving a unique modified Mendelian ratio of segregation. The complexity of gene interactions contributes to the awn diversity in barley. Excessive gene interactions create a challenging task for genetic mapping and specific strategies have to be developed for mapping genes with specific interactive effects. Awn gene interactions can occur at different levels of gene expression, from the transcription factor-mediated gene transcription to the regulation of enzymes and metabolic pathways. A better understanding of gene interactions will greatly facilitate deciphering the genetic mechanisms underlying barley awn diversity and development.

barley

awn

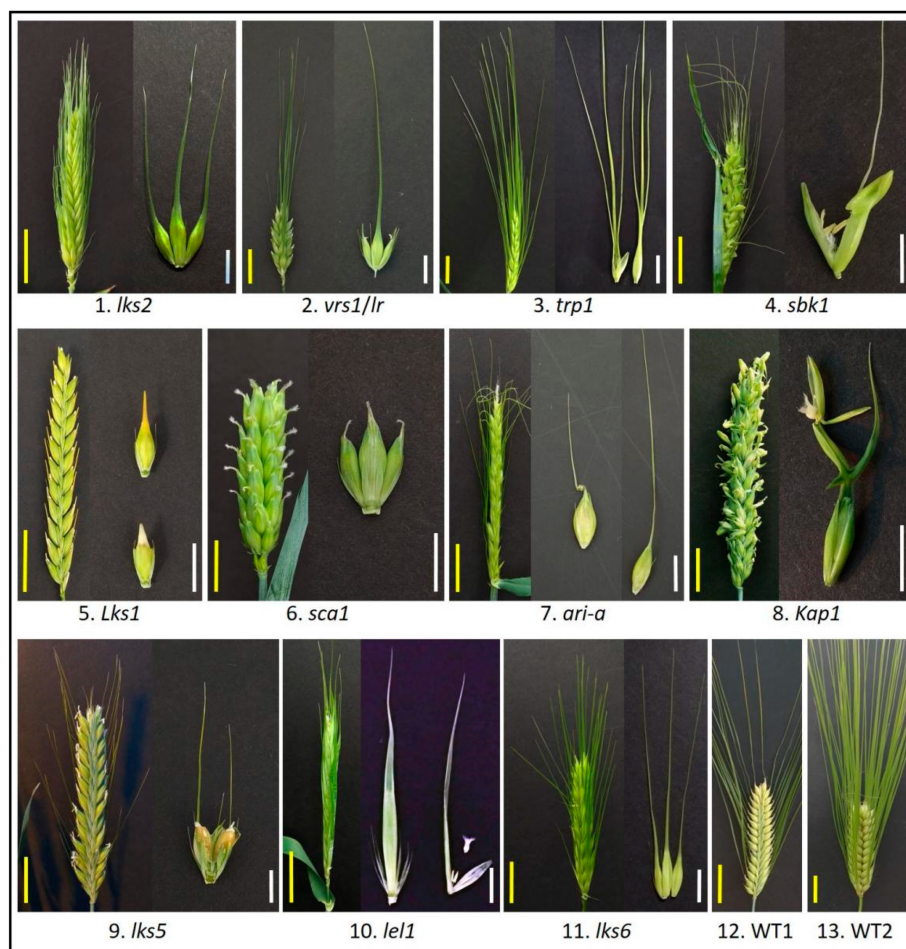
gene interaction

transcription factor

gene mapping

## 1. Introduction

The development of grass awns has become a topic of intense research largely owing to its important function in grain filling <sup>[1]</sup>. Awn in barley (*Hordeum vulgare* L.) is more diverse than in rice and wheat <sup>[2]</sup>. The awnness trait can be distinguished into different phenotypes, including awnless, straight (long, longer than the length of spike axis; short, shorter than the length of spike axis; and awnlet, shorter than 1 cm), hooded, leafy, and crooked at the end of a lemma (Figure 1). They are controlled by different awnness loci that interact with each other. Analysis of the interactions among these loci can potentially reveal the mechanisms by which awn development is regulated. This topic has not been systematically studied, although some historic and recent investigations may have provided interesting hints <sup>[3][4][5]</sup>.



**Figure 1.** Barley awn diversity. Barley awn mutants obtained from the National Small Grains Collection, USDA-ARS (Agricultural Research Service, United States Department of Agriculture), Aberdeen Idaho. **1-*lks2***, short awn; **2-*vrs1(lr)***, six-rowed with awnless lateral spikelet; **3-*trp1***, triple awned lemma; **4-*sbk1***, subjacent hooded lemma; **5-*Lks1***, awnless; **6-*sca1***, short crooked awn; **7-*ari-a***, short awn; **8-*Kap1***, hooded lemma; **9-*lks5***, short awn; **10-*lel1***, leafy lemma; **11-*lks6***, short awn; **12-WT1**, wild type, two-rowed with long awn; **13-WT2**, wild type, six-rowed with long awn. Yellow scale bar = 3 cm; White scale bar = 1 cm.

The genetic control of awn development in barley is very complicated, involving all sorts of gene interactions. Part of the genes and interactions for awn development found in barley are summarized in Table 1.

**Table 1.** Gene interactions for awn development in barley.

Interaction	Genes	Segregation in F <sub>2</sub> generation	Reference
Comp.	<i>N/n</i> and <i>H/h</i>	9 HA ( <i>N_H_</i> ): 7 NA ( <i>N_hh</i> + <i>nnH_</i> + <i>nnhh</i> )	[6]
Dup.	<i>Lel1/lel1</i> and <i>Lel2/lel2</i>	15 NA ( <i>Lel1_Lel2_</i> + <i>Lel1_lel2lel2</i> + <i>lel1lel1Lel2_</i> ): 1 LF ( <i>lel1lel1lel2lel2</i> )	[7]
Cum.	<i>Lks2/lks2</i> and <i>Lks5/lks5</i>	9 LA ( <i>Lks2_ Lks5_</i> ): 6 SA ( <i>Lks2_ lks5lks5</i> + <i>lks2lks2 Lks5_</i> ): 1 AL ( <i>lks2lks2 lks5lks5</i> )	[8]

Interaction	Genes	Segregation in F <sub>2</sub> generation	Reference
Rec. epi.	<i>Lks2</i> / <i>lks2</i> and <i>Kap1</i> / <i>kap1</i>	9 HA ( <i>Lls2_Kap1_</i> ): 3 LA ( <i>Lks2_kap1kap1</i> ): 4 SA ( <i>lks2lks2Kap1_</i> + <i>lks2lks2kap1kap1</i> )	[5]
Dom. epi.	<i>Lsa1</i> / <i>lsa1</i> and <i>Kap1</i> / <i>kap1</i>	12 AL ( <i>Lsa1_Kap1_</i> + <i>Lsa1_kap1kap1</i> ): 3 HA ( <i>lsa1_lsa1Kap1_</i> ): 1 ST ( <i>lsa1_lsa1kap1kap1</i> )	[3]
Inh.	<i>S/s</i> and <i>A/a</i>	13 AL ( <i>S_A_</i> + <i>S_aa</i> + <i>ssaa</i> ): 3 LA ( <i>ssA_</i> )	[9]

Note: Comp., complementary; Dup., duplicate; Cum., cumulative; Rec. epi., recessive epistasis; Dom. epi., dominant epistasis; Inh., inhibiting; HA, hooded awn; NA, normal awn; LF, leafy awn; LA, long awn; SA, short awn; AL, awnless; ST, straight awn.

## 2. Molecular Mechanisms of Awnness Gene Interactions in Barley

There has so far been a limited understanding of molecular mechanisms of awn gene interactions. Analysis of the expression patterns of awn genes *An-1* and *An-2* in rice suggests that *An-1* regulates the formation of awn primordia, while *An-2* promotes awn elongation [10]. The upstream genes often regulate the expression of downstream genes. In barley, the mutant gene *prbs* (poly-rowed-and-branched spike) is recessive epistatic over the row type gene *Vrs1/vrs1*, and *prbs* may function upstream of *vrs1* [11][12]. Two awnness-specific genes have so far been cloned in barley and they each encode a type of transcription factor. One is *Kap1* for hooded lemma 1, while the other is *lks2* for short awn 2. Barley *lks2* is recessive epistatic over the hooded-awn gene *Kap1*, and may function upstream of *Kap1* [13][14]. *Lks2* encodes a SHORT INTERNODES (SHI)-type transcription factor [14]. The SHI proteins contain two conserved regions, the RING-finger motif and the IGGH domain—the former being implicated in zinc-binding and the latter being required for dimerization and transcription activation [15]. *Kap1* encodes KNOX-type transcription factor. KNOX family is known to regulate the maintenance of the shoot apical meristem and the initiation of lateral organs in plants [16]. Awnless gene *B1* in wheat encodes C<sub>2</sub>H<sub>2</sub> zinc finger proteins [17], which may act as transcriptional repressors to regulate gene expression in developmental processes such as the formation of flower, seed, and rudimentary glume [18]. Barley *HvFT3*, as the counterpart of awnless gene *B1* in wheat, functions upstream of the row-type genes (*Vrs1*, *Vrs4*, and *Int-c*) [17][19].

Genomics studies could be helpful to reveal molecular mechanisms of gene interactions in the future. CRISPR (clustered regularly interspaced short palindromic repeats) knocking out could be a method to prove gene interaction at molecular level. By knocking out the upstream genes, the downstream genes will be expressed and produce corresponding phenotypes. Time-series transcriptomics data provided abundant proof of metabolic processes [20], then gene interactions at molecular and metabolic level could be proved. The yeast two-hybrid technique is also a good system to find the interactive protein, and then provides direct proof for gene interaction.

## 3. Concluding Remarks

Barley awns are highly diverse in morphology, varying from long, short, awnlet, to awnless in length, and from straight to hooded or crooked in shape. A set of genetic loci associated with the diversity of awns have been identified. Interactions among awn genes contribute to this diversity. Further research on awn gene interactions at the genetic, metabolic, and molecular levels will provide insights into the essence of the interactions and elucidate the mechanisms of awn initiation and development in barley.

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