

( 続紙 1 )

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論文題目	Genetic studies on spike and grain morphologies and on recombination frequency in common wheat by whole genome genotyping (普通系コムギの全ゲノムジェノタイピングによる穂と穀粒の形態および組換え頻度の遺伝学的研究)		
(論文内容の要旨)			
<p>Common wheat (<i>Triticum aestivum</i> L.) is the most widely cultivated crop in the world. To tackle a growing population and changing climate, wheat genetics and genomics leading to identification of genes that control valuable agricultural characters, such as stress tolerance and high yield, are in great demand. The genome of common wheat (genome constitution AABBDD, <math>2n = 6x = 42</math>) is characterized by its large size, sequence homology among the A, B and D genomes, and an abundance of transposable elements, all of which have hampered genetic analysis of traits of interests, especially of complex traits. During the last decade, the emergence of second-generation sequencing technology has enabled genome-wide genotyping for each individual in a segregation population or in a genetically diverse stock.</p> <p>In this dissertation, I applied RAD-seq, a genotyping method based on second-generation sequencing of a representative portion of genomic sequence defined by restriction sites, to common wheat for the purpose of studying the following three themes. In Chapter 2, I examined the spike morphology with an emphasis on awn morphology that is related to drought tolerance. Although three awn inhibitor genes, <i>Hd</i>, <i>B1</i>, and <i>B2</i>, have been identified by classical genetics, we still do not know how much of the variation in awn length observed in common wheat cultivars can be explained by them. Moreover, the possibility that other loci could influence awn lengths had not yet been extensively studied. I performed a genome-wide association study (GWAS) on 185 accessions of common wheat for awn lengths measured at the top and the middle of the spikes. I found that a single-nucleotide polymorphism (SNP) that affects awn length at the middle of the spike resides in the promoter region of the <i>B1</i> gene, recently cloned awn inhibiting gene, which accounted for as much as 25% of the variation within the core collection. In contrast, no significant marker-trait association (MTA) with awn length was detected in the vicinity of the <i>Hd</i> and <i>B2</i> loci, suggesting that these loci only contribute to a fraction of the overall variation of awn length observed in common wheat varieties. I did not detect any increase in linkage disequilibrium around the <i>B1</i> locus within accessions carrying the awn-inhibiting <i>B1</i> allele. This result suggests that the <i>B1</i> locus has not been under intense selection pressure. I detected four QTLs other than <i>Hd</i>, <i>B1</i> and <i>B2</i>. To my knowledge, none of these regions contained genes homologous to any known genes identified in relation to awn morphogenesis in rice and barley, nor corresponded to the region of previously reported QTL for awn elongation in wheat.</p>			

In Chapter 3, I searched for genomic regions associated with grain size and shape, which can affect total yield and milling yield. I investigated the genetic diversity in terms of grain morphology within the core collection of hexaploid wheat accessions of NBRP-Wheat, which consists of 190 accessions. I scanned images of grains of each accession and recorded six metric characters: area size, perimeter length, grain length, grain width, length-to-width ratio, and circularity. Additionally, I measured hundred-grain weight. Principal component analysis of these seven characters demonstrated that two principal components (PC<sub>core1</sub> and PC<sub>core2</sub>) explain more than 96% of the variation in the core collection. The correlation coefficients between the principal components and characters indicate that PC<sub>core1</sub> is related to grain size and PC<sub>core2</sub> to grain shape. From a GWAS, I detected a total of 17 significant MTAs for five traits: two for area size, three for perimeter length, four for grain length, six for grain width, and one for hundred-grain weight, as well as one MTA for PC<sub>core2</sub>. No predominant peaks of MTAs were found for any characters of grain morphology, and the number of significant MTAs was fewer than those found for awn morphology, an indication that grain morphology in common wheat is not regulated by a few genes with a strong effect but by the cumulative effects of many genes.

In Chapter 4, the effect of an alien chromosome segment on recombination frequency was evaluated to confirm if the introduction of alien chromatin increases the recombination frequency of an innate genome as reported in other plants. The low recombination frequency in the common wheat genome presents a challenge when attempting to breed new varieties and genetically map genes of interests. While an alien chromosome addition in the *Brassica* species leads to a genome-wide elevation in recombination frequency, the general effect of alien chromosomes on meiotic recombination remains poorly understood in other crop species. I investigated whether an alien chromosome segment translocated from *Aegilops sharonensis* Eig would affect the recombination frequency in the A and B genomes of common wheat. I detected a 5% increase in total map length of the A and B genomes in the cross with the alien segment compared to the control. On the chromosome base, chromosomes 7A had a significantly larger number of crossovers. The recombination landscape was similar between the populations, indicating that the differences in the chromosome-scale recombination rate should be attributed to accumulations of slight differences in the recombination rate between markers.

In this dissertation, I successfully applied whole genome genotyping with RAD markers for a wide range of genetic analyses of complex characters in common wheat. I would like to conclude that my dissertation demonstrates feasibility to identify genes of interest in wheat.

注) 論文内容の要旨と論文審査の結果の要旨は1頁を38字×36行で作成し、合わせて、3,000字を標準とすること。  
論文内容の要旨を英語で記入する場合は、400～1,100 wordsで作成し  
審査結果の要旨は日本語500～2,000字程度で作成すること。

(続紙 2)

(論文審査の結果の要旨)

普通系コムギ (*Triticum aestivum* L.) は世界で最も広く栽培されている作物である。約16 Gbという巨大なゲノムサイズや倍数性、そして反復配列によるゲノムの複雑性のため、詳細な遺伝学的解析は困難だとされてきた。2018年に参照ゲノム配列がようやく解読され、コムギ遺伝学は新しい時代を迎えつつある。本研究では、コムギの芒の長さや粒形、そして遺伝的組換え頻度という、複雑な要因に支配されている形質について、RAD-seq法という次世代シーケンサー技術を用いた全ゲノムジェノタイプング手法と参照ゲノム配列、そして普通系コムギの多様性をカバーするコアコレクションを駆使して、形質を支配する遺伝子座の特定を行った。本研究の評価できる点は、以下の通りである。

1. 普通系コムギの芒の長さに関わる遺伝因子についてゲノムワイド関連解析を行い、穂の中央部の小穂につく芒の長さの多様性の25%がBI遺伝子座によって説明できることを示した。芒の長さを支配していることが報告されている別の2遺伝子座の近傍にはマーカーと形質間に相関がないことを明らかにした。普通系コムギの芒の長さの多様性を説明する新規の4ゲノム領域を発見した。
2. 普通系コムギの粒形が、粒の大きさと形を規定している2つの主成分で96%以上説明されることを示した。ゲノムワイド関連解析により、粒形の多様性と関連する17の新規なゲノム領域を発見した。この解析により、粒形が複数の遺伝子座によって支配されていることを示した。
3. 外来の染色体断片を持つコムギの組換え頻度と乗換え数を正常系統と比較することにより、外来染色体断片を有する分離集団では組換え頻度が上昇していることをイネ科植物で初めて明らかにした。

以上のように、本論文はコムギの量的形質の遺伝解析に参照ゲノム配列情報に紐付けされたゲノムワイドマーカーを用いることの有効性を明確に示し、また、コアコレクションを用いた相関解析が有用形質を支配する遺伝子の解析に適していることを明らかにしたものであり、植物遺伝学、育種学、ゲノム科学の発展に寄与するところが大きい。

よって、本論文は博士(農学)の学位論文として価値あるものと認める。

なお、令和2年10月8日、論文並びにそれに関連した分野にわたり試問した結果、博士(農学)の学位を授与される学力が十分あるものと認めた。

また、本論文は、京都大学学位規程第14条第2項に該当するものと判断し、公表に際しては、当該論文の全文に代えてその内容を要約したものとすることを認める。

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ただし、特許申請、雑誌掲載等の関係により、要旨を学位授与後即日公表することに支障がある場合は、以下に公表可能とする日付を記入すること。

要旨公開可能日： 年 月 日以降 (学位授与日から3ヶ月以内)