DNA double-strand breaks alter the spatial arrangement of homologous loci in plant cells

Takeshi Hirakawa1, Yohei Katagiri1, Tadashi Ando2 & Sachihiro Matsunaga1

Chromatin dynamics and arrangement are involved in many biological processes in nuclei of eukaryotes including plants. Plants have to respond rapidly to various environmental stimuli to achieve growth and development because they cannot move. It is assumed that the alteration of chromatin dynamics and arrangement support the response to these stimuli; however, there is little information in plants. In this study, we investigated the chromatin dynamics and arrangement with DNA damage in Arabidopsis thaliana by live-cell imaging with the lacO/LacI-EGFP system and simulation analysis. It was revealed that homologous loci kept a constant distance in nuclei of A. thaliana roots in general growth. We also found that DNA double-strand breaks (DSBs) induce the approach of the homologous loci with γ-irradiation. Furthermore, AtRAD54, which performs an important role in the homologous recombination repair pathway, was involved in the pairing of homologous loci with γ-irradiation. These results suggest that homologous loci approach each other to repair DSBs, and AtRAD54 mediates these phenomena.

Chromatin structure, dynamics, and arrangement in the nucleus are closely related to many biological processes such as DNA replication, transcription, and repair in eukaryotes including plants1–3. In nuclei of Arabidopsis thaliana, several chromatins form territories called chromosome territories (CTs)4. CT arrangement is regulated by nuclear proteins, and it appears to be important for growth and fertility in A. thaliana5. In recent years, three-dimensional chromatin structure in A. thaliana was revealed by the Hi-C method, and it is different from that of humans and Drosophila melanogaster6,7. Chromatin structure was related to epigenetic modification in those studies; therefore, it is also important for gene regulation and DNA replication in A. thaliana as well as other organisms. There are similar findings about chromatin arrangement and structure as above; however, little is known about chromatin dynamics in nuclei of A. thaliana. Fluorescence in situ hybridisation (FISH) and immunofluorescence staining has been mainly used to analyse the gene localization and chromatin distribution in nuclei of A. thaliana. These attractive methods allow the observation of chromatin arrangement in various tissues without requiring the production of transgenic lines; however, they require fixation of cells and high-temperature treatment for hybridisation. Therefore, they cannot be adapted to in vivo detection of chromatin dynamics and arrangement. Moreover, it is difficult to perform these methods in tissues and organs while maintaining their morphology. Recent advances in live-cell imaging techniques reveal the movement of genomic loci in vivo in DNA replication8, transcription9, and repair10. One live-cell imaging technique, a chromatin-tagging system that is based on the bacterial operator/repressor system, has been a powerful technique for analysing chromatin dynamics and arrangement in real time11,12. Plants have to respond rapidly to DNA damage, which threatens the genome stability that is required for correct growth and development, because they cannot move13,14. It is assumed that alterations of chromatin...
Chromatin dynamics support the response to DNA damage; however, little is known in plants. Here, we examined chromatin dynamics and arrangement in living roots of *Arabidopsis thaliana* with DNA damage, focusing our attention on the distance between homologous loci using the lacO/LacI-EGFP system. We revealed that the homologous loci kept a constant three-dimensional distance in the nucleus using live-cell imaging with a bacterial operator/repressor system. Moreover, the distance between two homologous loci in the interphase nucleus was shortened by γ-irradiation, which induces DNA double-strand breaks (DSBs).

We found that AtRAD54, which performs an important role in the homologous recombination (HR) repair pathway, was involved in the approach of two homologous loci under γ-irradiation. Our results suggest that the transient reduction in inter-allelic distance and increase in pairing frequency of homologous loci after DSB result in partial chromatin reorganisation of interphase nuclei and that AtRAD54 contributes to the subcellular movement of homologous loci in the HR repair pathway.

**Results**

**Distance of homologous loci is constant in nuclei of *A. thaliana***. In root tips of *A. thaliana* expressing lacO/LacI-EGFP, two dots of EGFP signal derived from homologous loci were detected in each nucleus (Fig. 1a). To observe the dynamics and arrangement of lacO/LacI-EGFP signals during mitosis, we generated a transgenic line of *A. thaliana* stably expressing both lacO/LacI-EGFP and H2B-tdTomato. In the meristematic zone of roots, the alignment of lacO/LacI-EGFP signals was observed on mitotic...
chromosomes at the metaphase plate (Fig. 1b, Supplementary Video 1). We focused on the distance between homologous loci, which is called the inter-allelic distance. To analyse the spatiotemporal dynamics of the inter-allelic distance, we performed time-lapse imaging of root nuclei in A. thaliana expressing lacO/LacI-EGFP. When the three-dimensional distance was measured, it was nearly constant in nuclei of both meristematic and elongation zones, although the nuclear morphology drastically changed. The inter-allelic distance in nuclei of the elongation zone was longer than that in nuclei of the meristematic zone (Fig. 1c,d, Supplementary Video 2, 3). In the elongation zone of A. thaliana, multiple DNA replications, which are known as endoreplications and endocycles, result in the formation of larger nuclei than those in the meristematic zone15. Then, to examine whether the inter-allelic distance depends on the size of the nucleus, we measured the inter-allelic distance and the volume of the same nuclei in roots of A. thaliana expressing lacO/LacI-EGFP and H2B-tdTomato. A correlation between the inter-allelic distance and the size of nucleus was found in roots (Fig. 1e,f). These results indicate that the inter-allelic distance depends on the size of the nucleus in A. thaliana roots. To investigate whether the inter-allelic distance is stochastically determined, we developed a mathematical model that mimics the nucleus in the meristematic zone (Fig. 2a). In this model, we calculated distances between two randomly generated points in a nucleoplasm in a Monte Carlo procedure16. The average value of inter-allelic distances measured in nuclei of the meristematic zone was significantly longer than the value obtained by the mathematical model (Fig. 2b). This result also suggests that the inter-allelic distance is constant in nuclei of A. thaliana roots.

DSBs induce the approach of homologous loci. DNA damage induces chromatin rearrangement in nuclei of human cells17. Therefore, we anticipated that the inter-allelic distance would be changed by DNA damage, and we focused on the inter-allelic distance with γ-irradiation and the radiomimetic reagent zeocin, which induce DSBs18. We measured inter-allelic distances in interphase nuclei after γ-irradiation and zeocin treatment. When the plant was irradiated with more than 100 Gy γ-irradiation or treated with 10μM zeocin, the inter-allelic distance was significantly shortened (Fig. 3a,b). The distance became shorter as the dose of γ-irradiation was increased. This reduction of the inter-allelic distance in a dose-dependent manner should reflect the amount of DSBs after γ-irradiation. To investigate whether the alteration of the inter-allelic distance by γ-irradiation depends on the secondary effect of the increase in the size of the nucleus, we measured the nucleus size after γ-irradiation. In the meristematic zone, the nucleus volume after γ-irradiation was not significantly different from that before γ-irradiation (Fig. 3c). These results demonstrate that the reduction in inter-allelic distance is directly caused by γ-irradiation and is not accompanied with DNA replication. Next, because we anticipated that the close approach of homologous loci was important for DNA repair, we examined the recovery of the inter-allelic distance in a time-course experiment after γ-irradiation. The shortened inter-allelic distance at 0 h after γ-irradiation was recovered to the original distance at 24 h after γ-irradiation (Fig. 3d). We also investigated the level of DSBs using a comet assay19. The level of DSBs was recovered at 24 h after γ-irradiation (Fig. 3e,f). In nuclei of human cells, chromatin arrangement, which is altered by DNA damage, returns after DNA repair17. These results suggest that homologous loci approach each other for DNA repair with γ-irradiation.
Figure 3. Effect of DNA double-strand breaks (DSBs) on the inter-allelic distance. 

a, b, Relationship between the inter-allelic distance and dose of γ-irradiation (n > 90, *P < 0.05, a) or 10μM zeocin (n > 90, *P < 0.05, b) in the meristematic zone of A. thaliana roots. 

c, Size of nuclei in the meristematic zone of A. thaliana roots irradiated with 150 Gy γ-irradiation (n = 122, P = 0.35). 

d, Inter-allelic distance in the meristematic zone nuclei of A. thaliana irradiated with 150 Gy γ-irradiation (n ≥ 90, **P < 0.01). 

e, Images of comets representing the control nucleus and the nucleus irradiated with 150 Gy γ-irradiation (top, Control; middle, 0h; bottom, 24h). Scale bar = 10μm. 

f, Levels of DSBs that were detected by a comet assay in A. thaliana roots irradiated with 100 Gy γ-irradiation (n ≥ 70, **P < 0.01).
AtRAD54 mediates the pairing of homologous loci with DSBs. When DNA damage including DSBs occurs in cells, DNA repair factors are expressed and repair damage in nuclei of *A. thaliana* [13,14]. Therefore, we expected that DNA repair factors were involved in the event that the inter-allelic distance was shortened by DSBs. There are at least four DSB repair pathways including the canonical-non homologous end joining (C-NHEJ), alternative-NHEJ (A-NHEJ), microhomology-mediated EJ (MMEJ), and HR repair pathway in *A. thaliana* [20]. We generated *atlig4-4* and *atrad54-1* plants expressing lacO/LacI-EGFP. AtLIG4 has ATP-dependent DNA ligase activity and catalyses the final step in the C-NHEJ pathway [21]. In contrast, AtRAD54, which is a chromatin re-modelling factor belonging to the SWI2/SNF2 family, has an important role in the HR repair pathway [22]. Although the inter-allelic distance shortened after γ-irradiation in the wild-type (Col-0) and *atlig4-4* cells, it was not significantly shortened in *atrad54-1* cells (Fig. 4a, Supplementary Fig. 1a). We observed the overlapped foci of two lacO/LacI-EGFP signals at low frequency (<7%), suggesting that these homologous loci were paired (Fig. 4b). When we measured the inter-allelic distance, the overlapped loci were excluded from the calculation. Although the frequency was not changed between wild-type and mutant cells before γ-irradiation, the frequency after γ-irradiation in *atrad54-1* was lower than that of wild-type and *atlig4-4* cells (Fig. 4b,c, Supplementary Fig. 1b). These results suggest that homologous loci might approach each other to repair DSBs through HR.

**Discussion**

We used the lacO/LacI-EGFP system, which allowed us to visualise specific loci where the tandem operator array was inserted in this study. Chromatin regions tagged with repetitive lacO sequences tend to form pairs with each other more frequently than regions without the sequences [23,24]. However, we could measure the constant values of inter-allelic distance in interphase nuclei of both meristematic and elongation regions using line 25:26, in which the pairing of lacO arrays was not higher than that of control loci [23,24]. Live-cell imaging and simulation analysis revealed that the inter-allelic distance is constant in interphase nuclei of *A. thaliana* roots. The inter-allelic distance of nuclei in the meristematic region of

---

**Figure 4. Regulation of the inter-allelic distance by AtRAD54 with DSBs.**

*a,* Inter-allelic distance in meristematic zone nuclei of wild-type and *atrad54-1* roots irradiated with 150 Gy γ-irradiation (n > 90, **P < 0.01). b,* Images of nuclei with paired loci and non-paired loci in the meristematic zone. Scale bar = 5 μm. c,* Frequency of meristematic zone nuclei with paired homologous loci in wild-type and *atrad54-1* roots irradiated with 150 Gy γ-irradiation. Five roots containing at least 30 nuclei were counted for each group (**P < 0.01). d,* Diagram of this research showing that the distance between homologous loci was constant and that DSBs induced the frequency of homologous loci pairing.
A. thaliana is approximately 3.5 μm, whereas that of Saccharomyces cerevisiae and SG4 cultured cells of D. melanogaster is about 1.2 μm and 2 μm, respectively. In plants and other organisms, the arrangement of homologous loci is regulated by various factors in interphase nuclei. Homologous loci are dispersed by condensin II, which is a protein complex that contributes to chromosome condensation and segregation during mitosis, in D. melanogaster. Condensin II also separates sister chromatids during S phase in human cells. Sister chromatids are separated in nuclei of A. thaliana leaves by the SMCS/6 complex, which is required for chromosome segregation during mitosis. In S. cerevisiae, the inter-allelic distance is constant; however, the mechanism that regulates the inter-allelic distance is unknown. Our results suggest that there are sub-nuclear mechanisms that separate homologous chromosomes during interphase in A. thaliana. When DSBs occur in nuclei of A. thaliana roots, the inter-allelic distance shortened. These results might suggest that homologous loci approached each other to repair DSB loci through HR. In S. cerevisiae, RAD54, which is a multifunctional factor for RAD51-mediated HR, catalyzes nucleosome redistribution to permit the pairing of homologous loci in synopsis and contributes to the long-range search for homologous loci after a DSB occurs. Furthermore, RAD54 belongs to the epistasis protein family of RAD52, which has several activities in HR. ATRAD54 interacts with ATRAD51, and atrad54 reduces the frequency of HR in A. thaliana. In atrad54-1 cells expressing lacO/LacI-EGFP, the distance between homologous loci was not shortened, and the frequency of nuclei with paired loci did not increase after γ-irradiation. These results might suggest that the approach of homologous loci is mediated by RAD54 after γ-irradiation (Fig. 4c,d). Pairing of homologous loci for DNA repair started 90 min and peaked 2 h after a DSB event in S. cerevisiae. Because γ-irradiation to A. thaliana took 3 h, our observed reduction in inter-allelic distance after DSB could exhibit the following situation after pairing with homologous loci. In this study, we cannot exclude the possibility that the approach of homologous loci occurs because of the collapse of all chromosomes with DSBs. To resolve this problem, it would be effective to investigate the distance between non-homologous loci with DSBs. However, measurements of the distance between non-homologous loci based on the bacterial operatoressor system are difficult because the simultaneous expression of different fluorescent proteins frequently induces silencing. Visualisation of specific loci with genome editing in cultured animal cells might be applicable to investigate the behaviour of non-homologous loci in nuclei. DNA damage induces not only the pairing of homologous loci but also chromatin rearrangements in S. cerevisiae and humans. Our results suggest that the transient reduction in inter-allelic distance and increase in pairing of homologous loci after DSBs might be accompanied by a partial modification of chromatin organisation through the local CT perturbation. Further studies to reveal the relationship between the movement of damaged loci and spatial alteration of the CT would lead us to a more detailed understanding of the mechanism of chromatin organisation during the DNA repair process.

Methods

Plant materials and growth conditions. A. thaliana (Col-0 accession) expressing lacO/LacI-EGFP was kindly provided by Antonius J. M. Matzke (Institute of Plant and Microbial Biology), atlg4-4 (Col-0 accession) was kindly provided by Toru Fujiwara (The University of Tokyo), and atrad54-1 (Col-0 accession) was kindly provided by Keishi Osakabe (The University of Tokushima). Seeds of A. thaliana were germinated on Murashige and Skoog (MS) medium plates (1/2 MS salts, 1% [w/v] sucrose, 1.5% [w/v] gellan gum). Plates were placed at 4°C for 1 day and then moved to an incubator and grown at 22°C in a 16-h light/8-h dark cycle.

Time-lapse imaging and three-dimensional analysis. Seeds of A. thaliana expressing lacO/LacI-EGFP were germinated on MS medium in a glass-bottomed dish. The dish was placed at 4°C for 1 day and then moved to an incubator and grown at 22°C in a 16-h light/8-h dark cycle. Seedling roots were observed 5 days after germination under an inverted fluorescent microscope (IX-81, Olympus) equipped with a confocal scanning unit (CSU-X1, Yokogawa) and a sCMOS camera (Neo 5.5 sCMOS, ANDOR). One stack of 0.5-μm z-axis steps was collected for 60 min (time interval: 10 min). Images were analysed with an ImageJ software plugin LP StackLine from LPixel (http://lpixel.net/). The meristematic zone and elongation zone were distinguished by the distance of adjacent nuclei as previously described. The meristematic zone was analysed with an ImageJ software plugin LP StackLine from LPixel (http://lpixel.net/). The meristematic zone and elongation zone were distinguished by the distance of adjacent nuclei as previously described.

γ-irradiation and chemical treatment. Five days after germination, seedlings were γ-irradiated using 32P Cs source (Research Institute for Biomedical Sciences, Tokyo University of Science) at a dose rate of 0.83 Gy/min. Five days after germination, seedlings were transferred to MS medium containing zeocin (Invitrogen). They were incubated for 1 day at 22°C in a 16-h light/8-h dark cycle.

Comet assay. A comet assay was performed with a neutral electrophoresis without alkaline denaturation protocol as previously described. Comet slides were not stained with ethidium bromide but with SYBR Green I (Invitrogen). Images of comets stained with SYBR Green I were acquired under an upright microscope equipped with a CCD camera (Gool Snap HQ2, Nippon Roper). Images were analysed with an ImageJ software plugin Comet Assay from Microscopy Services Laboratory (http://www.med.unc.edu/microscopy).
Monte Carlo simulation. We calculated distances between two randomly generated points in a spherical shell that satisfy $r' < r_n \leq r$ where $r'$ is the radius of the nucleolus (2.3 $\mu$m), $r$ is the radius of the nucleus (1.17 $\mu$m), and $r_n$ is the distance of point $x$ ($x = 1$ and 2) from the origin.

References

1. Misteli, T. Beyond the sequence: Cellular organization of genome function. Cell 128, 787–800, doi:10.1016/j.cell.2007.01.028 (2007).
2. Schubert, I. & Shaw, P. Organization and dynamics of plant interphase chromosomes. Trends Plant Sci 16, 273–281, doi:10.1016/j.tplants.2011.02.002 (2011).
3. Matsunaga, S. et al. New insights into the dynamics of plant cell nuclei and chromosomes. Int Rev Cell Mol Biol, 305, 253–301, doi:10.1016/b978-0-12-07695-2.00006-8 (2013).
4. Pecinka, A. et al. Chromosome territory arrangement and homologous pairing in nuclei of Arabidopsis thaliana are predominantly random except for NOR-bearing chromosomes. Chromosoma 113, 258–269, doi:10.1007/s00412-004-0316-2 (2004).
5. Schubert, V., Lermontova, I. & Schubert, I. The Arabidopsis CAP-D proteins are required for correct chromatin organisation, growth and fertility. Chromosoma 122, 517–533, doi:10.1007/s00412-013-0424-y (2013).
6. Feng, S. et al. Genome-wide Hi-C analyses in wild-type and mutants reveal high-resolution chromatin interactions in Arabidopsis. Mol Cell 55, 694–707, doi:10.1016/j.molcel.2014.07.008 (2014).
7. Grob, S., Schmid, M. W. & Grossniklaus, U. Hi-C analysis in Arabidopsis identifies the KNOT, a structure with similarities to the flancello locus of Drosophila. Mol Cell 55, 678–693, doi:10.1016/j.molcel.2014.07.009 (2014).
8. Kitanura, E., Blow, J. J. & Tanaka, T. U. Live-cell imaging reveals replication of individual replicons in eukaryotic replication factories. Cell 125, 1297–1308, doi:10.1016/j.cell.2006.04.041 (2006).
9. Chuang, C. H. et al. Long-range directional movement of an interphase chromosome site. Curr Biol 16, 825–831, doi:10.1016/j.cub.2006.03.059 (2006).
10. Mine-Hattab, J. & Rothstein, R. Increased chromosome mobility facilitates homology search during recombination. Nat Cell Biol 14, 510–517, doi:10.1038/nch2472 (2012).
11. Belmont, A. S. & Straight, A. F. In vivo visualization of chromosomes using lac operator-repressor binding. Trends Cell Biol 8, 121–124 (1998).
12. Robinett, C. C. et al. In vivo localization of DNA sequences and visualization of large-scale chromatin organization using lac operator/repressor recognition. J Cell Biol 135, 1685–1700 (1996).
13. Waterworth, W. M., Drury, G. E., Bray, C. M. & West, C. E. Repairing breaks in the plant genome: the importance of keeping it together. New Phytol 192, 805–822, doi:10.1111/nph.1469-8137.2011.03926.x (2011).
14. Yoshiyama, K. O., Sakaguchi, K. & Kimura, S. DNA damage response in plants: conserved and variable response compared to animals. Biology (Basel) 2, 1338–1356, doi:10.3390/biology2014338 (2013).
15. Hayashi, K., Hasegawa, J. & Matsunaga, S. The boundary of the meristematic and elongation zones in roots: endoreduplication together. Plant J 48, 827–842, doi:10.1111/j.1365-313X.2006.09297.x (2006).
16. Jovtchev, G. et al. Isolation and characterization of the RAD54 gene from Arabidopsis thaliana. Plant J 121–124 (1998).
17. Zhang, Z., Fan, H.-Y., Goldman, J. A. & Kingston, R. E. Homology-driven chromatin remodeling by human RAD54. Mol Cell 48, 67–78, doi:10.1016/j.molcel.2014.07.008 (2014).
18. Adachi, S. et al. Programmed induction of endoreduplication by DNA double-strand breaks in Arabidopsis. Proc Natl Acad Sci USA 108, 10004–10009, doi:10.1073/pnas.1103584108 (2011).
19. Menke, M., Chen, I., Angelis, K. J. & Schubert, I. DNA damage and repair in Arabidopsis thaliana as measured by the comet assay after treatment with different classes of genotoxins. Mutat Res, 87–93 (2001).
20. Charbonneau, C., Allain, E., Gallego, M. E. & White, C. I. Kinetic analysis of DNA double-strand break repair pathways in Arabidopsis. DNA Repair (Amst) 10, 611–619, doi:10.1016/j.dnarep.2011.04.002 (2011).
21. West, C. E., Waterworth, W. M., Jiang, Q. & Bray, C. M. Arabidopsis DNA ligase IV is induced by gamma-irradiation and interacts with an Arabidopsis homologue of the double strand break repair protein XRCC4. Plant J 24, 67–78, doi:10.1046/j.1365-313x.2000.00856.x (2000).
22. Osakabe, K. et al. Isolation and characterization of the RAD54 gene from Arabidopsis thaliana. J Plant Physiol 1685–1700 (1996).
23. Schubert, V. et al. Dynamic imaging of genomic loci in living human cells by an optimized CRISPR/Cas system. Nat Methods 12, 787–800, doi:10.1038/nmeth.201208008 (2013).
24. Schubert, V. et al. Cohesin gene defects may impair sister chromatid alignment and genome stability in Arabidopsis thaliana. Chromosoma 118, 591–605, doi:10.1007/s00412-009-0220-x (2009).
25. Heyer, W. D., Li, X., Rolfsmeyer, M. & Zhang, X. P. Rad54: the Swiss Army knife of homologous recombination? Nucleic Acids Res 34, 4115–4125, doi:10.1093/nar/gkl481 (2006).
26. Zhang, Z., Fan, H.-Y., Goldman, J. A. & Kingston, R. E. Homology-driven chromatin remodeling by human RAD54. Nat Struct Mol Biol 14, 397–405, doi:10.1038/nstmbial2223 (2007).
27. Forget, A. L. & Kowalczykowski, S. C. Single-molecule imaging brings Rad51 nucleoprotein filaments into focus. Trends Cell Biol 20, 269–276, doi:10.1016/j.tcb.2010.02.004 (2010).
28. Dion, V., Kalck, V., Horigome, C., Towbin, B. D. & Gasser, S. M. Increased mobility of double-strand breaks requires Mec1,Rad9 and the homologous recombination machinery. Nat Cell Biol 14, 502–509, doi:10.1038/nctb2465 (2012).
29. Paques, F. & Haber, J. E. Multiple pathways of recombination induced by double-strand breaks in Saccharomyces cerevisiae. Microbiol Mol Biol Rev 63, 349–404 (1999).
30. Miyanari, Y., Ziegler-Birling, C. & Torres-Padilla, M.-E. Live visualization of chromatin dynamics with fluorescent TALENs. Nat Struct Mol Biol 20, 1321–1324, doi:10.1038/nsmb.2680 (2013).
31. Chen, B. et al. Dynamic imaging of genomic loci in living human cells by an optimized CRISPR/Cas system. Cell 155, 1479–1491, doi:10.1016/j.cell.2013.12.001 (2013).
Acknowledgements
We thank Antonius J. M. Matzke for providing seeds of A. thaliana expressing lacO/LacI-EGFP, Toru Fujiwara for providing the atlig4-4 mutant, and Keishi Osakabe for providing the atrad54-1 mutant. This research was supported by CREST grants from the Japan Science and Technology Agency to S.M., a Grant-in-Aid for X-ray Free Electron Laser Priority Strategy Program (MEXT) to S.M., and MEXT/JSPS KAKENHI to S.M.

Author Contributions
T.H. and S.M. designed experiments and wrote the paper. T.H. performed experiments and analysed imaging data. Y.K. analysed imaging data of ploidy. T.A. constructed the mathematical model. S.M. supervised the project. All authors contributed to the discussion and reviewed the manuscript.

Additional Information
Supplementary information accompanies this paper at http://www.nature.com/srep

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Hirakawa, T. et al. DNA double-strand breaks alter the spatial arrangement of homologous loci in plant cells. Sci. Rep. 5, 11058; doi: 10.1038/srep11058 (2015).

This work is licensed under a Creative Commons Attribution 4.0 International License. The images or other third party material in this article are included in the article’s Creative Commons license, unless indicated otherwise in the credit line; if the material is not included under the Creative Commons license, users will need to obtain permission from the license holder to reproduce the material. To view a copy of this license, visit http://creativecommons.org/licenses/by/4.0/