



ISSN : 2347 - 2243

Indo - American Journal of Life Sciences and Biotechnology



<https://iajlb.org>

Email : editor@iajlb.com or iajlb.editor@gmail.com



Long Non-Coding RNAs in Plant Stress Responses: Mechanisms and Prospects

Giulia Bellandi¹●, Elin Lindqvist²●, Javier Larranaga³●

¹Senior Scientist, Department of Biotechnology, Monti Lepini Institute of Life Sciences, Frosinone, Italy.

²Senior Scientist, Department of Plant Molecular Biology, Dalarna Institute of Environmental Biology, Falun, Sweden.

³Research Associate, Department of Biotechnology, Rioja Institute of Biotechnology, Logrono, Spain.

Email: ¹g.bellandi@mlils.it, ²e.lindqvist@dieb.se, ³j.larranaga@ribt.es

ORCID: ¹0000-0001-2057-8983, ²0000-0001-4083-5609, ³0000-0001-0476-6642

Received: September 16, 2025 Accepted: January 23, 2026 Published: May 2, 2026

DOI: [10.62644/iajlb.2026.v23.i2.pp11-18](https://doi.org/10.62644/iajlb.2026.v23.i2.pp11-18)

ABSTRACT

Plants meet drought, salinity, temperature extremes, nutrient shortage and pathogens without the option of moving away, and their answer is a broad reprogramming of gene expression. Long non-coding RNAs, transcripts longer than about 200 nucleotides with little or no protein-coding capacity, have been added to the list of regulators involved. This narrative mini review summarises what the published literature shows about how such transcripts act in stress responses, drawing on well-studied cases in cold, heat, drought, salt, phosphate starvation and immunity. Mechanisms described include guiding chromatin-modifying complexes, interfering with transcription of neighbouring genes, acting as decoys for microRNAs, modulating splicing and helping to assemble transcriptional co-activators. The strongest evidence comes from a small number of Arabidopsis loci, whereas most lncRNAs listed in crop surveys are supported only by changes in expression. We discuss why that gap exists, what an adequate functional test would involve, and how genome editing and structural work might narrow it. No new data are reported.

Keywords: Long non-coding RNA; Abiotic stress; Biotic stress; Chromatin regulation; Target mimicry; Plant gene expression; Narrative review

Citation: Bellandi, Lindqvist and Larranaga [2026]. Long Non-Coding RNAs in Plant Stress Responses: Mechanisms and Prospects. *Indo-Am. J. Life Sci. Biotechnol.* 23(2):11-18. DOI: [10.62644/iajlb.2026.v23.i2.pp11-18](https://doi.org/10.62644/iajlb.2026.v23.i2.pp11-18)

Article Class: Mini Review

1. Introduction

A plant that meets drought, salt, frost or a fungal pathogen cannot walk away from it. What it can do is change which genes are switched on, and by how much, and a great deal of work has gone into understanding the signalling and transcription factors behind those changes (1, 2). Small RNAs, microRNAs in particular, were an early

addition to that picture (3); longer non-coding transcripts came later and are still harder to place.

Long non-coding RNAs (lncRNAs) are usually defined as transcripts longer than about 200 nucleotides that do not appear to encode a protein (4, 5). Most look much like messenger RNAs, although plants also use two specialised polymerases that make



non-coding transcripts (6). General accounts exist (7, 8), as do reviews on stress (9, 10).

Genome-wide surveys in Arabidopsis, maize, poplar and wheat have shown that the pool of lncRNAs changes when plants are stressed (11, 12, 13, 14, 15, 16). That observation is real, and it is also easy to over-read. A transcript whose level rises under drought may be doing something, or it may simply be switched on with its neighbours. This review therefore tries to keep two things apart: the few lncRNAs for which a mechanism has been worked out, and the much larger number known only from expression data. The aim is a fair account of what has been shown, as against what has merely been repeated. This is a narrative mini review of published work; the authors report no data of their own and examples are drawn from wherever the evidence is strongest.

2. Literature Review

2.1 What Counts as a Plant lncRNA

Classification is mostly by position. A lncRNA may lie between genes, run antisense to a protein-coding gene, arise inside an intron, or begin as read-through from a neighbour (4, 17). Table 1 gives the main classes with a characterised plant example of each. The boundaries are not sharp, and one lncRNA can belong to more than one class. Position also hints at mechanism: an antisense transcript is likely to act on its sense partner, whereas an intergenic one may act far from where it is made, and that difference shapes how each kind can be tested.

Two features make plant lncRNAs awkward to study. Most are expressed at low levels and in narrow sets of tissues or conditions, and their sequences are poorly conserved between species, so it is hard to say whether a transcript in one crop corresponds to one in another (12, 24, 25).

Table 1. Classes of plant long non-coding RNAs by genomic context, with a characterised example of each.

Class	Genomic context	Example
Natural antisense	Transcribed from the opposite strand of a protein-coding gene	COOLAIR at FLC (18, 19)
Intronic	Arises from within an intron of a host gene	COLDAIR at FLC (20)
Intergenic	Own promoter, between genes	DRIR (21)
Read-through	Upstream transcription runs on into a neighbour	SVALKA (22)
Target mimic	Binds a microRNA without being cleaved	IPS1 (23)

Note: Classification follows genomic position; examples are those discussed in the text and one locus can fit more than one class.

2.2 How lncRNAs Act

The best-understood plant lncRNAs act on chromatin. At the Arabidopsis locus FLC, long cold exposure leads to a silenced state, and at least two sets of transcripts are involved: antisense transcripts collectively called COOLAIR (18, 19, 26), and an intronic transcript called COLDAIR that has been linked to recruitment of a Polycomb complex (20, 27). The relative contributions of the transcripts, of transcription itself and of the chromatin machinery are still being worked out, a reminder that even a famous lncRNA is not fully explained.

A second route goes through DNA methylation: transcripts made by RNA polymerase V serve as scaffolds that help bring silencing complexes to chromatin (6, 28), and others shape chromatin loops, in one case through an R-loop (29, 30); wider accounts are available (31, 32, 33).

Other lncRNAs work after transcription. IPS1 carries a sequence that pairs with the microRNA miR399 but is not cleaved by



it, so it acts as a decoy that holds the microRNA away from its real targets (23). A nuclear lncRNA interacts with splicing regulators and changes alternative splicing (34). Natural antisense transcripts can control a neighbouring gene directly, as proposed for a heat-induced antisense RNA at the heat shock factor gene HSFB2a (35) and for one at MAF4 (36); antisense transcription is widespread and light-responsive (37).

Finally, lncRNAs can influence transcription directly. In the cold, read-through of the lncRNA SVALKa generates a cryptic antisense transcript that limits expression of the neighbouring CBF1 gene, a mechanism that may keep the cold response in proportion (22). The immune-induced ELENA1 associates with the Mediator complex and enhances expression of defence genes (38). Figure 1 places these routes on a generic pathway. Names such as these tend to stick, which is part of why single examples carry so much weight.

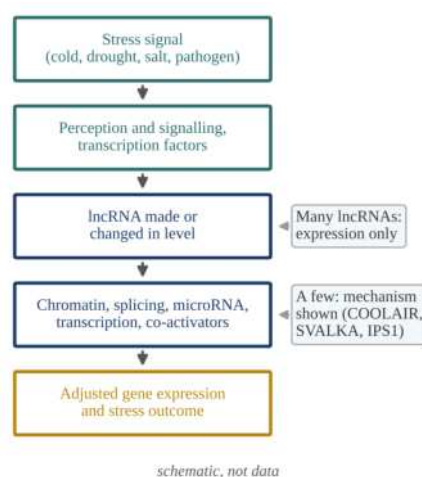


Figure 1. From stress signal to physiological outcome, with the points at which lncRNAs have been placed (schematic, not data).

2.3 Stress Contexts and Overlap with Development

Cold is the best-studied case, partly because of FLC and partly because

SVALKa bears directly on the CBF pathway of cold acclimation. COOLAIR, however, belongs to the developmental response to prolonged cold, vernalization, and not strictly to cold damage (18, 19); arguments built on it should say so. The cold response is therefore the best-lit corner of a largely dark room.

For heat, the clearest proposal is the antisense control of HSFB2a (35), while a wheat survey reported lncRNAs responding to heat and to powdery mildew (14). For drought and salinity, the most informative case is DRIR, a nuclear Arabidopsis lncRNA whose overexpression raised tolerance to both and altered many stress-related genes (21); surveys in maize and poplar listed candidates but, as surveys do, did not test them (15, 16). Phosphate shortage induces the decoy IPS1 (23), and Fusarium infection changes many Arabidopsis lncRNAs (39). The same transcripts also turn up in development, for example in photoperiod-sensitive male sterility in rice (40), so a stress phenotype may be a side effect of a developmental role. That distinction sounds pedantic until a breeding programme has to choose which transcript to chase.

3. Materials and Methods

3.1 Scope

The review asks what the published literature establishes about how lncRNAs contribute to plant stress responses, and how firmly. It covers abiotic stress and the immune response to pathogens in land plants.

3.2 Literature Assembly

This is a narrative synthesis. No formal systematic search was made, no database list or search string is claimed, and no screening or quality scoring was done; the authors chose sources for relevance, influence and clarity of methods, so the



selection reflects judgement. Every work cited was published in or before 2026.

3.3 Appraisal Framework

To compare claims of different strength, we sorted them along the ladder in [Figure 2](#), a simple scale of evidence and not a scoring system. A claim sits on the lowest rung if a transcript was only detected or changed in abundance, higher if loss or gain of function altered a phenotype, higher again if a mechanism was demonstrated, and highest if the effect held in more than one genetic background or condition.

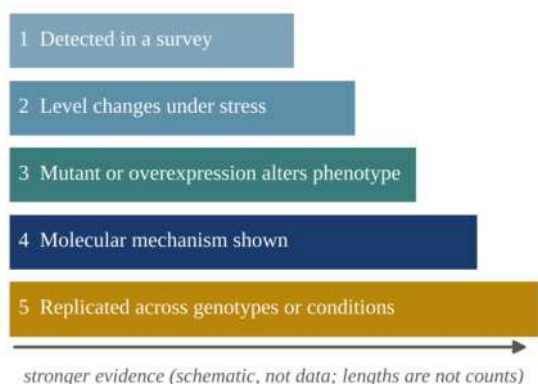


Figure 2. Ladder of evidence used to appraise lncRNA claims (schematic; step heights are not counts).

4. Results

4.1 Where the Evidence Is Strongest

The sorting yields a few well-supported cases and many candidates. COOLAIR, COLDAIR, SVALKA, IPS1, DRIR and ELENA1 have supporting genetic or molecular evidence of some kind, though not all of equal depth (18, 20, 21, 22, 23, 38). Most of what is reported for crops sits lower down, as expression change in response to stress (14, 15, 16). [Table 2](#) sets the cases side by side.

Nearly all the best-supported examples come from Arabidopsis, where mutants are cheap and the genome is well annotated.

Even among them the evidence is uneven: for some the transcript matters, for others it is the act of transcription that appears to do the work (22), and an RNA that works only through its transcription cannot be rescued by supplying it in trans.

Table 2. Stress contexts in which lncRNAs have been studied and how firmly each case is supported.

Stress	lncRNA or survey	Proposed role	Evidence
Cold	COOLAIR, COLDAIR (20, 26)	Silencing of FLC after cold	Genetic and molecular
Cold	SVALKA (22)	Tunes CBF1 by interference	Genetic and molecular
Drought, salt	DRIR (21)	Raises tolerance; affects stress genes	Mainly overexpression
Phosphate	IPS1 (23)	Decoy for miR399	Genetic and molecular
Immunity	ELENA1 (38)	Boosts defence gene expression	Genetic and molecular
Crop surveys	Maize, poplar, wheat (14, 15, 16)	Candidates only	Expression changes

Note: Evidence descriptions are the authors' qualitative reading of the cited papers, not a formal grading.

4.2 Recurring Mechanistic Patterns

Across these cases a few patterns recur ([Figure 3](#)). Chromatin silencing is prominent in the cold, transcriptional interference in the cold acclimation example, microRNA decoying in nutrient stress, and co-activator assembly in immunity. Drought and salt, by contrast, are represented by a case in which the effect is clear but the mechanism is not (21). The pattern is probably partly an accident of where researchers have looked.



A transcript studied in one stress is rarely examined in another, so the apparent specialisation of each example may reflect the experiment as much as the biology, and a lncRNA that looks cold-specific could prove to respond to several signals once someone checks.

The patterns suggest that lncRNAs often modulate the strength or timing of a response already under protein control (22, 38); such effects are small and easily lost in a mutant grown under mild conditions. Seen this way, a stress lncRNA is less a switch than a dial.

	Cold	Heat	Phosphate	Immunity
Chromatin silencing	COOLAIR COLDAIR			
Transcriptional interference	SVALKA			
microRNA decoy			IPS1	
Co-activator assembly				ELENA1
Antisense control		HSFB2a		

blank: no characterised example discussed here; not data

Figure 3. Mechanisms by stress context, with the characterised example in each cell (qualitative matrix, not data).

4.3 Gaps and Limitations in the Evidence

The literature also shows consistent weaknesses (Table 3). Expression change is the commonest evidence and the weakest, because a change in level is not a function (10, 25). Low abundance hampers detection and knock-down (12), poor conservation hampers transfer from Arabidopsis to crops (24, 41), and catalogues built with different pipelines cannot easily be merged (9).

Striking results from overexpression lines are easier to publish than modest or null results from mutants, so the record

probably overstates how many stress lncRNAs have large effects; a case tested under more than one stress, or in more than one species, is far stronger than one tested once (8).

Table 3. Recurring limitations in the lncRNA literature and what would address them.

Limitation	Why it matters	What would help
Expression only	Change in level is not a function (10, 25)	Mutant or edited lines
Low abundance	Hard to detect and to knock down (12)	Sensitive, replicated assays
Poor conservation	Orthologues hard to call (24)	Synteny and structure (41)
Act or product	Transcription may matter more than the RNA (22)	Promoter and terminator tests
Few species	Mechanisms rest on Arabidopsis (8)	Crop-based functional work

Note: Limitations are those discussed in the cited reviews and surveys and are not attributed to any single study.

5. Discussion

5.1 Interpretation

The central point is a mismatch of scale. Surveys report lncRNAs in large numbers, and mechanistic studies explain a handful. It would be wrong to conclude that most are unimportant, and equally wrong to assume that they matter; for most we do not know. What the well-studied cases show is that lncRNAs can add a layer of control that proteins alone would not provide, consistent with long non-coding RNAs in other kingdoms (5, 17).

There is a practical side to this as well. Because several of the best-characterised transcripts act on a neighbouring gene, or through the act of transcription itself, a lncRNA cannot be assumed to behave like a protein-coding gene when it is moved into a crop: the same sequence placed elsewhere in the genome may lose the



effect it had at its home locus (21, 22). For breeders, that is a reason to ask what a transcript does at its native position before asking whether it can be transferred. The question is plainly harder than a list of differentially expressed transcripts can answer.

5.2 Limitations

This review shares the limitations of its form. Selection was by judgement, no systematic search was done, and relevant recent papers, particularly in crops, will have been missed. It quotes no numerical results, because these could not be checked against the primary papers for this article. Much of the mechanistic material comes from one model species, and the appraisal ladder is our own device and has not been validated.

5.3 Future Work

Three needs stand out: functional tests in edited or mutant lines, with promoter, transcript and act of transcription tested separately; better comparison across species using synteny and structure as well as sequence (41); and replication under fluctuating, field-like conditions where modulating effects are most likely to show. That is slow work, but it is the work that turns a list into an explanation.

6. Conclusion

Long non-coding RNAs take part in plant responses to stress, and a few have been shown to act through chromatin, microRNA decoying, interference with transcription or co-activator assembly. Most of the literature still consists of catalogues of transcripts whose expression changes under stress, and readers should treat these as leads, not conclusions. The route from such a transcript to a reliable trait runs through the kind of evidence this review has tried to separate from the rest.

7. Acknowledgements

The authors thank colleagues who commented on earlier drafts of this review.

8. Funding

This work received no specific grant from any funding agency in the public, commercial or not-for-profit sectors.

9. Conflict of Interest

The authors declare no conflict of interest.

10. Author Contributions

G.B. conceived the review and wrote the sections on classification and chromatin mechanisms. E.L. wrote the sections on abiotic stress and plant molecular biology. J.L. wrote the sections on appraisal, limitations and future work. All authors revised the manuscript and approved the final version.

11. Ethics Statement

This is a review of published literature. No human participants, animals or field sites were involved and no ethical approval was required.

12. Data Availability

No new data were generated. All sources are cited in the reference list.

13. References

1. Hirayama, T., & Shinozaki, K. (2010). Research on plant abiotic stress responses in the post-genome era: Past, present and future. *The Plant Journal*, 61(6), 1041–1052. DOI: [10.1111/j.1365-3113X.2010.04124.x](https://doi.org/10.1111/j.1365-3113X.2010.04124.x)
2. Zhu, J.-K. (2016). Abiotic stress signaling and responses in plants. *Cell*, 167(2), 313–324. DOI: [10.1016/j.cell.2016.08.029](https://doi.org/10.1016/j.cell.2016.08.029)
3. Sunkar, R., Li, Y.-F., & Jagadeeswaran, G. (2012). Functions of microRNAs in plant stress responses. *Trends in Plant Science*, 17(4), 196–203. DOI: [10.1016/j.tplants.2012.01.010](https://doi.org/10.1016/j.tplants.2012.01.010)
4. Ma, L., Bajic, V. B., & Zhang, Z. (2013). On the classification of long non-coding RNAs. *RNA Biology*, 10(6), 925–933. DOI: [10.4161/rna.24604](https://doi.org/10.4161/rna.24604)



5. Rinn, J. L., & Chang, H. Y. (2012). Genome regulation by long noncoding RNAs. *Annual Review of Biochemistry*, 81, 145–166. DOI: [10.1146/annurev-biochem-051410-165902](https://doi.org/10.1146/annurev-biochem-051410-165902)
6. Wierzbicki, A. T., Haag, J. R., & Pikaard, C. S. (2008). Noncoding transcription by RNA polymerase Pol IVb/Pol V mediates transcriptional silencing of overlapping and adjacent genes. *Cell*, 135(4), 635–648. DOI: [10.1016/j.cell.2008.09.035](https://doi.org/10.1016/j.cell.2008.09.035)
7. Liu, X., Hao, L., Li, D., Zhu, L., & Hu, S. (2015). Long non-coding RNAs and their biological roles in plants. *Genomics, Proteomics & Bioinformatics*, 13(3), 137–147. DOI: [10.1016/j.gpb.2015.02.003](https://doi.org/10.1016/j.gpb.2015.02.003)
8. Chekanova, J. A. (2015). Long non-coding RNAs and their functions in plants. *Current Opinion in Plant Biology*, 27, 207–216. DOI: [10.1016/j.pbi.2015.08.003](https://doi.org/10.1016/j.pbi.2015.08.003)
9. Nejat, N., & Mantri, N. (2018). Emerging roles of long non-coding RNAs in plant response to biotic and abiotic stresses. *Critical Reviews in Biotechnology*, 38(1), 93–105. DOI: [10.1080/07388551.2017.1312270](https://doi.org/10.1080/07388551.2017.1312270)
10. Jha, U. C., Nayyar, H., Jha, R., Khurshid, M., Zhou, M., Mantri, N., & Siddique, K. H. M. (2020). Long non-coding RNAs: Emerging players regulating plant abiotic stress response and adaptation. *BMC Plant Biology*, 20, 466. DOI: [10.1186/s12870-020-02595-x](https://doi.org/10.1186/s12870-020-02595-x)
11. Ben Amor, B., Wirth, S., Merchan, F., Laporte, P., d'Aubenton-Carafa, Y., Hirsch, J., ... Crespi, M. (2009). Novel long non-protein coding RNAs involved in *Arabidopsis* differentiation and stress responses. *Genome Research*, 19(1), 57–69. DOI: [10.1101/gr.080275.108](https://doi.org/10.1101/gr.080275.108)
12. Liu, J., Jung, C., Xu, J., Wang, H., Deng, S., Bernad, L., ... Chua, N.-H. (2012). Genome-wide analysis uncovers regulation of long intergenic noncoding RNAs in *Arabidopsis*. *The Plant Cell*, 24(11), 4333–4345. DOI: [10.1105/tpc.112.102855](https://doi.org/10.1105/tpc.112.102855)
13. Di, C., Yuan, J., Wu, Y., Li, J., Lin, H., Hu, L., ... Lu, Z. J. (2014). Characterization of stress-responsive lncRNAs in *Arabidopsis thaliana* by integrating expression, epigenetic and structural features. *The Plant Journal*, 80(5), 848–861. DOI: [10.1111/tpj.12679](https://doi.org/10.1111/tpj.12679)
14. Xin, M., Wang, Y., Yao, Y., Xie, C., Peng, H., Ni, Z., & Sun, Q. (2011). Identification and characterization of wheat long non-protein coding RNAs responsive to powdery mildew infection and heat stress by using microarray analysis and SBS sequencing. *BMC Plant Biology*, 11, 61. DOI: [10.1186/1471-2229-11-61](https://doi.org/10.1186/1471-2229-11-61)
15. Zhang, W., Han, Z., Guo, Q., Liu, Y., Zheng, Y., Wu, F., & Jin, W. (2014). Identification of maize long non-coding RNAs responsive to drought stress. *PLoS ONE*, 9(6), e98958. DOI: [10.1371/journal.pone.0098958](https://doi.org/10.1371/journal.pone.0098958)
16. Shuai, P., Liang, D., Tang, S., Zhang, Z., Ye, C.-Y., Su, Y., ... Yin, W. (2014). Genome-wide identification and functional prediction of novel and drought-responsive lincRNAs in *Populus trichocarpa*. *Journal of Experimental Botany*, 65(17), 4975–4983. DOI: [10.1093/jxb/eru256](https://doi.org/10.1093/jxb/eru256)
17. Kopp, F., & Mendell, J. T. (2018). Functional classification and experimental dissection of long noncoding RNAs. *Cell*, 172(3), 393–407. DOI: [10.1016/j.cell.2018.01.011](https://doi.org/10.1016/j.cell.2018.01.011)
18. Swiezewski, S., Liu, F., Magusin, A., & Dean, C. (2009). Cold-induced silencing by long antisense transcripts of an *Arabidopsis* Polycomb target. *Nature*, 462(7274), 799–802. DOI: [10.1038/nature08618](https://doi.org/10.1038/nature08618)
19. Csorba, T., Questa, J. I., Sun, Q., & Dean, C. (2014). Antisense COOLAIR mediates the coordinated switching of chromatin states at *FLC* during vernalization. *Proceedings of the National Academy of Sciences*, 111(45), 16160–16165. DOI: [10.1073/pnas.1419030111](https://doi.org/10.1073/pnas.1419030111)
20. Heo, J. B., & Sung, S. (2011). Vernalization-mediated epigenetic silencing by a long intronic noncoding RNA. *Science*, 331(6013), 76–79. DOI: [10.1126/science.1197349](https://doi.org/10.1126/science.1197349)
21. Qin, T., Zhao, H., Cui, P., Albeshier, N., & Xiong, L. (2017). A nucleus-localized long non-coding RNA enhances drought and salt stress tolerance. *Plant Physiology*, 175(3), 1321–1336. DOI: [10.1104/pp.17.00574](https://doi.org/10.1104/pp.17.00574)
22. Kindgren, P., Ard, R., Ivanov, M., & Marquardt, S. (2018). Transcriptional read-through of the long non-coding RNA *SVALKA* governs plant cold acclimation. *Nature Communications*, 9, 4561. DOI: [10.1038/s41467-018-07010-6](https://doi.org/10.1038/s41467-018-07010-6)
23. Franco-Zorrilla, J. M., Valli, A., Todesco, M., Mateos, I., Puga, M. I., Rubio-Somoza, I., ... Paz-Ares, J. (2007). Target mimicry provides a new mechanism for regulation of microRNA activity. *Nature Genetics*, 39(8), 1033–1037. DOI: [10.1038/ng2079](https://doi.org/10.1038/ng2079)
24. Li, L., Eichten, S. R., Shimizu, R., Petsch, K., Yeh, C.-T., Wu, W., ... Springer, N. M. (2014). Genome-wide discovery and characterization of maize long non-coding RNAs. *Genome Biology*, 15(2), R40. DOI: [10.1186/gb-2014-15-2-r40](https://doi.org/10.1186/gb-2014-15-2-r40)
25. Kung, J. T. Y., Colognori, D., & Lee, J. T. (2013). Long noncoding RNAs: Past, present, and future. *Genetics*, 193(3), 651–669. DOI: [10.1534/genetics.112.146704](https://doi.org/10.1534/genetics.112.146704)
26. Liu, F., Marquardt, S., Lister, C., Swiezewski, S., & Dean, C. (2010). Targeted 3' processing of antisense transcripts triggers *Arabidopsis* *FLC* chromatin silencing. *Science*, 327(5961), 94–97. DOI: [10.1126/science.1180278](https://doi.org/10.1126/science.1180278)



27. Kim, D.-H., Xi, Y., & Sung, S. (2017). Modular function of long noncoding RNA, COLDAIR, in the vernalization response. *PLoS Genetics*, 13(7), e1006939. DOI: [10.1371/journal.pgen.1006939](https://doi.org/10.1371/journal.pgen.1006939)
28. Matzke, M. A., & Mosher, R. A. (2014). RNA-directed DNA methylation: An epigenetic pathway of increasing complexity. *Nature Reviews Genetics*, 15(6), 394–408. DOI: [10.1038/nrg3683](https://doi.org/10.1038/nrg3683)
29. Ariel, F., Jegu, T., Latrasse, D., Romero-Barrios, N., Christ, A., Benhamed, M., & Crespi, M. (2014). Noncoding transcription by alternative RNA polymerases dynamically regulates an auxin-driven chromatin loop. *Molecular Cell*, 55(3), 383–396. DOI: [10.1016/j.molcel.2014.06.011](https://doi.org/10.1016/j.molcel.2014.06.011)
30. Ariel, F., Lucero, L., Christ, A., Mammarella, M. F., Jegu, T., Veluchamy, A., ... Crespi, M. (2020). R-loop mediated *trans* action of the APOLO long noncoding RNA. *Molecular Cell*, 77(5), 1055–1065. DOI: [10.1016/j.molcel.2019.12.015](https://doi.org/10.1016/j.molcel.2019.12.015)
31. Mercer, T. R., & Mattick, J. S. (2013). Structure and function of long noncoding RNAs in epigenetic regulation. *Nature Structural & Molecular Biology*, 20(3), 300–307. DOI: [10.1038/nsmb.2480](https://doi.org/10.1038/nsmb.2480)
32. Wang, K. C., & Chang, H. Y. (2011). Molecular mechanisms of long noncoding RNAs. *Molecular Cell*, 43(6), 904–914. DOI: [10.1016/j.molcel.2011.08.018](https://doi.org/10.1016/j.molcel.2011.08.018)
33. Quinn, J. J., & Chang, H. Y. (2016). Unique features of long non-coding RNA biogenesis and function. *Nature Reviews Genetics*, 17(1), 47–62. DOI: [10.1038/nrg.2015.10](https://doi.org/10.1038/nrg.2015.10)
34. Bardou, F., Ariel, F., Simpson, C. G., Romero-Barrios, N., Laporte, P., Balzergue, S., ... Crespi, M. (2014). Long noncoding RNA modulates alternative splicing regulators in *Arabidopsis*. *Developmental Cell*, 30(2), 166–176. DOI: [10.1016/j.devcel.2014.06.017](https://doi.org/10.1016/j.devcel.2014.06.017)
35. Wunderlich, M., Gross-Hardt, R., & Schöffl, F. (2014). Heat shock factor HSFB2a involved in gametophyte development of *Arabidopsis thaliana* and its expression is controlled by a heat-inducible long non-coding antisense RNA. *Plant Molecular Biology*, 85(6), 541–550. DOI: [10.1007/s11103-014-0202-0](https://doi.org/10.1007/s11103-014-0202-0)
36. Zhao, X., Li, J., Lian, B., Gu, H., Li, Y., & Qi, Y. (2018). Global identification of *Arabidopsis* lncRNAs reveals the regulation of MAF4 by a natural antisense RNA. *Nature Communications*, 9, 5056. DOI: [10.1038/s41467-018-07500-7](https://doi.org/10.1038/s41467-018-07500-7)
37. Wang, H., Chung, P. J., Liu, J., Jang, I.-C., Kean, M. J., Xu, J., & Chua, N.-H. (2014). Genome-wide identification of long noncoding natural antisense transcripts and their responses to light in *Arabidopsis*. *Genome Research*, 24(3), 444–453. DOI: [10.1101/gr.165555.113](https://doi.org/10.1101/gr.165555.113)
38. Seo, J. S., Sun, H.-X., Park, B. S., Huang, C.-H., Yeh, S.-D., Jung, C., & Chua, N.-H. (2017). ELF18-INDUCED LONG-NONCODING RNA associates with Mediator to enhance expression of innate immune response genes in *Arabidopsis*. *The Plant Cell*, 29(5), 1024–1038. DOI: [10.1105/tpc.16.00886](https://doi.org/10.1105/tpc.16.00886)
39. Zhu, Q.-H., Stephen, S., Taylor, J., Helliwell, C. A., & Wang, M.-B. (2014). Long noncoding RNAs responsive to *Fusarium oxysporum* infection in *Arabidopsis thaliana*. *New Phytologist*, 201(2), 574–584. DOI: [10.1111/nph.12537](https://doi.org/10.1111/nph.12537)
40. Ding, J., Lu, Q., Ouyang, Y., Mao, H., Zhang, P., Yao, J., ... Zhang, Q. (2012). A long noncoding RNA regulates photoperiod-sensitive male sterility, an essential component of hybrid rice. *Proceedings of the National Academy of Sciences*, 109(7), 2654–2659. DOI: [10.1073/pnas.1121374109](https://doi.org/10.1073/pnas.1121374109)
41. Hawkes, E. J., Hennelly, S. P., Novikova, I. V., Irwin, J. A., Dean, C., & Sanbonmatsu, K. Y. (2016). COOLAIR antisense RNAs form evolutionarily conserved elaborate secondary structures. *Cell Reports*, 16(12), 3087–3096. DOI: [10.1016/j.celrep.2016.08.045](https://doi.org/10.1016/j.celrep.2016.08.045)