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DAFTAR PUSTAKA

Alotaibi, S. S. (2021). Developing specific leaf promoters tools for genetic use in transgenic plants towards food security. *Saudi Journal of Biological Sciences*, *28*(9), 5187–5192. https://doi.org/10.1016/j.sjbs.2021.05.046

Amack, S. C., & Antunes, M. S. (2020). CaMV35S promoter – A plant biology and biotechnology workhorse in the era of synthetic biology. *Current Plant Biology*, *24*, 100179. https://doi.org/10.1016/j.cpb.2020.100179

An, Y., Zhou, Y., Han, X., Shen, C., Wang, S., Liu, C., Yin, W., & Xia, X. (2020). The GATA transcription factor GNC plays an important role in photosynthesis and growth in poplar. *Journal of Experimental Botany*, *71*(6), 1969–1984. https://doi.org/10.1093/jxb/erz564

Bakery, A., Vraggalas, S., Shalha, B., Chauhan, H., Benhamed, M., & Fragkostefanakis, S. (2024). Heat stress transcription factors as the central molecular rheostat to optimize plant survival and recovery from heat stress. *New Phytologist*, *244*(1), 51–64. https://doi.org/10.1111/nph.20017

Bercu, R., Bavaru, A., & Broasca, L. (2011). Anatomical aspect of *Phalaenopsis amabilis* (L.) Blume. *Annals of the Romanian Society for Cell Biology*, *XVI*(2), 102–109. https://www.researchgate.net/publication/267985849

Bhardwaj, A., Agarwal, D., Bhatt, U., Parihar, S., & Soni, V. (2025). The secrets of variegated leaves: Molecular to physiological and ecological insights. *Flora*, *331*, 152815. https://doi.org/10.1016/j.flora.2025.152815

Bhoite, R., Onyemaobi, O., Halder, T., Shankar, M., & Sharma, D. (2025). Transcription factors – Insights into abiotic and biotic stress resilience and crop improvement. *Current Plant Biology*, *41*, 100434. https://doi.org/10.1016/j.cpb.2025.100434

Bresso, E. G., Chorostecki, U., Rodriguez, R. E., Palatnik, J. F., & Schommer, C. (2018). Spatial control of gene expression by miR319-regulated TCP transcription factors in leaf development. *Plant Physiology*, *176*(2), 1694–1708. https://doi.org/10.1104/pp.17.00823

Byrne, M. E., Imlay, E., & Ridza, N. N. B. (2024). Shaping leaves through TALE homeodomain transcription factors. *Journal of Experimental Botany*, *75*(11), 3220–3232. https://doi.org/10.1093/jxb/erae118

Cao, X., Wei, Y., Shen, B., & Liu, L. (2024). Interaction of the transcription factors BES1/BZR1 in plant growth and stress response. *International Journal of Molecular Sciences*, *25*, 6836. https://doi.org/10.3390/ijms25136836

Chai, X., Chen, J., Fu, C., Zhang, J., Zhao, X., Lyu, H. N., Xia, S., Li, X., Suo, Y., Shi, Q., Wang, J., & Xu, C. (2026). Exploring leaf variegation in *Arabidopsis yellow variegated2* by single-cell RNA sequencing. *The Plant Journal*, *125*(2),

UNIVERSITAS GADJAH MADA
Perbandingan Struktur Gen dan Aktivitas Transien Promoter Putatif VARIEGATED2 (VAR2) pada Zona Hijau dan Kuning Daun Anggrek Phalaenopsis Sogo Vivien
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1–14. https://doi.org/10.1111/tpj.70659

Chen, J., Wang, L., Chen, J., Huang, J., Liu, F., Guo, R., Yang, L., Grabon, A., & Zhao, K. (2018). *Agrobacterium tumefaciens*-mediated transformation system for the important medicinal plant *Dendrobium catenatum* Lindl. *In Vitro Cellular and Developmental Biology - Plant*, *54*, 228–239. https://doi.org/10.1007/s11627-018-9903-4

Chen, M., Choi, Y. D., Voytas, D. F., & Rodermel, S. (2000). Mutations in the Arabidopsis *VAR2* locus cause leaf variegation due to the loss of a chloroplast FtsH protease. *Plant Journal*, *22*(4), 303–313. https://doi.org/10.1046/j.1365-313X.2000.00738.x

Chen, M., Ji, M., Wen, B., Liu, L., Li, S., Chen, X., Gao, D., & Li, L. (2016). *GOLDEN 2-LIKE* transcription factors of plants. *Frontiers in Plant Science*, *7*, 1509. https://doi.org/10.3389/fpls.2016.01509

Chew, Y. C., Abdullah, W. M. A. N. W., Kok, D. X. A., Ong-Abdullah, J., Mahmood, M., & Lai, K. S. (2019). Development of an efficient particle bombardment transformation system for the endemic orchid, *Phalaenopsis bellina*. *Sains Malaysiana*, *48*(9), 1867–1877. https://doi.org/10.17576/jsm-2019-4809-07

Chiang, Y. H., Zubo, Y. O., Tapken, W., Kim, H. J., Lavanway, A. M., Howard, L., Pilon, M., Kieber, J. J., & Schaller, G. E. (2012). Functional characterization of the GATA transcription factors GNC and CGA1 reveals their key role in chloroplast development, growth, and division in *Arabidopsis*. *Plant Physiology*, *160*(1), 332–348. https://doi.org/10.1104/pp.112.198705

Chow, C. N., Lee, T. Y., Hung, Y. C., Li, G. Z., Tseng, K. C., Liu, Y. H., Kuo, P. L., Zheng, H. Q., & Chang, W. C. (2019). Plantpan3.0: A new and updated resource for reconstructing transcriptional regulatory networks from chip-seq experiments in plants. *Nucleic Acids Research*, *47*(D1), D1155–D1163. https://doi.org/10.1093/nar/gky1081

Conklin, P. A., Strable, J., Li, S., & Scanlon, M. J. (2019). On the mechanisms of development in monocot and eudicot leaves. *New Phytologist*, *221*(2), 706–724. https://doi.org/10.1111/nph.15371

Corpet, F. (1988). Multiple sequence alignment with hierarchical clustering. *Nucleic Acids Research*, *16*(22), 10881–10890. https://doi.org/10.1093/nar/16.22.10881

Croft, H., & Chen, J. M. (2017). Leaf pigment content. In *Comprehensive Remote Sensing* (Vols. 1–9, pp. 117–142). Elsevier. https://doi.org/10.1016/B978-0-12-409548-9.10547-0

Datta, S. K. (2025). Plant chimera and its management for the floriculture industry. *Journal of Floriculture and Landscaping*, *11*, 1–10. https://doi.org/10.25081/jfcls.2025.v11.9568

UNIVERSITAS GADJAH MADA
Perbandingan Struktur Gen dan Aktivitas Transien Promoter Putatif VARIEGATED2 (VAR2) pada Zona Hijau dan Kuning Daun Anggrek Phalaenopsis Sogo Vivien
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Universitas Gadjah Mada, 2026 | Diunduh dari http://etd.repository.ugm.ac.id/

Davis, M. W., & Jorgensen, E. M. (2022). ApE, A Plasmid Editor: A freely available DNA manipulation and visualization program. *Frontiers in Bioinformatics*, *2*, 818619. https://doi.org/10.3389/fbinf.2022.818619

de Ruijter, N. C. A., Verhees, J., van Leeuwen, W., & van der Krol, A. R. (2003). Evaluation and comparison of the GUS, LUC and GFP reporter system for gene expression studies in plants. *Plant Biology*, *5*, 103–115. https://doi.org/10.1055/s-2003-40722

Dkhar, J., & Pareek, A. (2014). What determines a leaf's shape? *EvoDevo*, *5*, 47. https://doi.org/10.1186/2041-9139-5-47

Dolgikh, V. A., Pukhovaya, E. M., & Zemlyanskaya, E. V. (2019). Shaping ethylene response: The role of EIN3/EIL1 transcription factors. *Frontiers in Plant Science*, *10*, 1030. https://doi.org/10.3389/fpls.2019.01030

Donaldson, L. (2020). Autofluorescence in plants. *Molecules*, *25*(10), 2393. https://doi.org/10.3390/molecules25102393

El-Tanbouly, R., Hassan, H., Awd, L. M., Makhlouf, A. A., Shalabi, H. G., & El-Messeiry, S. (2024). Molecular validation of genetically transformed *Catharanthus roseus* plants via different strains of *Agrobacterium tumefaciens*. *Heliyon*, *10*(23), e40589. https://doi.org/10.1016/j.heliyon.2024.e40589

Fibriani, S. uwind., Agustien, I., Sawitri, W. D., & Sugiharto, B. (2019). Transformasi genetik dan ekspresi mutan *sucrose phosphate synthase* pada tanaman tomat. *Jurnal Bioteknologi & Biosains Indonesia*, *6*(1), 130–138. https://doi.org/10.29122/jbbi.v6i1.3341

Frangedakis, E., Yelina, N. E., Billakurthi, K., Hua, L., Schreier, T., Dickinson, P. J., Tomaselli, M., Haseloff, J., & Hibberd, J. M. (2024). MYB-related transcription factors control chloroplast biogenesis. *Cell*, *187*(18), 4859–4876. https://doi.org/10.1016/j.cell.2024.06.039

Fransiska, J., Sedjati, S., & Endrawati, H. (2023). Kadar pigmen klorofil dan karotenoid pada *Nannochloropsis* sp. dengan perlakuan penyinaran ultraviolet. *Buletin Oseanografi Marina*, *12*(3), 340–346. https://doi.org/10.14710/buloma.v12i3.42285

Gao, J., Liang, D., Xu, Q., Yang, F., & Zhu, G. (2020). Involvement of *CsERF2* in leaf variegation of *Cymbidium sinense* 'Dharma.' *Planta*, *252*(2), 29. https://doi.org/10.1007/s00425-020-03426-x

Gao, R., Helfant, L. J., Wu, T., Li, Z., Brokaw, S. E., & Stock, A. M. (2021). A balancing act in transcription regulation by response regulators: Titration of transcription factor activity by decoy DNA binding sites. *Nucleic Acids Research*, *49*(20), 11537–11549. https://doi.org/10.1093/nar/gkab935

Ghosh, D., Thakur, S., Bali, S., Sharma, S., & Dogra, V. (2026). Comparative genome-wide analysis in *Setaria italica* and *Arabidopsis thaliana* revealed

UNIVERSITAS GADJAH MADA
Perbandingan Struktur Gen dan Aktivitas Transien Promoter Putatif VARIEGATED2 (VAR2) pada Zona Hijau dan Kuning Daun Anggrek Phalaenopsis Sogo Vivien
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Universitas Gadjah Mada, 2026 | Diunduh dari http://etd.repository.ugm.ac.id/

functional conservation of specific FtsH proteases under high light and heat stress. *Plant Cell Reports*, *45*(83), 1–20. https://doi.org/10.1007/s00299-026-03754-4

Gondalia, N., Brychkova, G., Quiroz, L. . F. F., Mckeown, P. C., Lai, L., Singh, A. K., Khan, M., Brychkova, G., Mckeown, P. C., Chatterjee, M., & Spillane, C. (2025). Harnessing promoter elements to enhance gene editing in plants : perspectives and advances. *Plant Biotechnology Journal*, *23*(5), 1375–1395. https://doi.org/10.1111/pbi.14533

Grace, M. L., Chandrasekharan, M. B., Hall, T. C., & Crowe, A. J. (2004). Sequence and spacing of TATA Box elements are critical for accurate from the *β-Phaseolin* promoter. *Journal of Biological Chemistry*, *279*(9), 8102–8110. https://doi.org/10.1074/jbc.M309376200

Grob, U., & Stuber. K. (1987). Discrimination of phytochrome dependent light inducible from non-light inducible plant genes. Prediction of a common light-responsive element (LRE) in phytochrome dependent light inducible plant genes. *Nucleic Acids Research*, *15*(23), 9957–9973. https://doi.org/10.1093/nar/15.23.9957

Grunennvaldt, R. L., Degenhardt-Goldbach, J., Gerhardt, I. R., & Quoirin, M. (2015). Promoters used in genetic transformation of plants. *Research Journal of Biological Sciences*, *10*(1–2), 1–9. https://doi.org/10.36478/rjbsci.2015.1.9

Gunadi, A., Dean, E. A., & Finer, J. J. (2019). Transient transformation using particle bombardment for gene expression analysis. In S. Kumar, P. Barone, & M. Smith (Eds.), *Transgenic Plants: Methods and Protocols, Method in Molecular Biology* (Vol. 1864, pp. 67–79). Springer Nature. https://doi.org/10.1007/978-1-4939-8778-8_5

Guo, X., Li, R., Ding, Y., Mo, F., Hu, K., Ou, M., Jiang, D., & Li, M. (2024). Visualization of the infection and colonization process of *Dendrobium officinale* using a Green Fluorescent Protein-tagged isolate of *Fusarium oxysporum*. *Phytopathology*, *114*(8), 1791–1801. https://doi.org/10.1094/PHYTO-12-23-0495-R

Guo, Z., Gao, X., Cai, H., Yu, L., Gu, C., & Zhang, S. L. (2021). Genome-wide identification, evolution and expression analysis of the FtsH gene during fruit development in pear (*Pyrus bretschneideri*). *Plant Biotechnology Reports*, *15*(4), 537–550. https://doi.org/10.1007/s11816-021-00686-1

Gupta, S. K., Sharma, M., Deeba, F., & Pandey, V. (2017). Role of reactive oxygen species in photophosphorylation and damage to D1 protein: Past and present. In *Reactive Oxygen Species in Plants: Boon Or Bane - Revisiting the Role of ROS* (pp. 165–186). https://doi.org/10.1002/9781119324928.ch9

Hajibarat, Z., & Saidi, A. (2023). Filamentation temperature-sensitive (FtsH); Key player in response to multiple environmental stress conditions and developmental stages in potato. *Journal of Plant Growth Regulation*, *42*(7),

UNIVERSITAS GADJAH MADA
Perbandingan Struktur Gen dan Aktivitas Transien Promoter Putatif VARIEGATED2 (VAR2) pada Zona Hijau dan Kuning Daun Anggrek Phalaenopsis Sogo Vivien
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Universitas Gadjah Mada, 2026 | Diunduh dari http://etd.repository.ugm.ac.id/

4223–4239. https://doi.org/10.1007/s00344-022-10885-x

Han, G., Li, Y., Qiao, Z., Wang, C., Zhao, Y., Guo, J., Chen, M., & Wang, B. (2021). Advances in the regulation of epidermal cell development by C2H2 Zinc Finger proteins in plants. *Frontiers in Plant Science*, *12*, 754512. https://doi.org/10.3389/fpls.2021.754512

Heisler, M. G., Jönsson, H., Wenkel, S., & Kaufmann, K. (2022). Context-specific functions of transcription factors controlling plant development: From leaves to flowers. *Current Opinion in Plant Biology*, *69*, 102262. https://doi.org/10.1016/j.pbi.2022.102262

Hernandez-Garcia, C. M., & Finer, J. J. (2016). A novel *cis*-acting element in the *GmERF3* promoter contributes to inducible gene expression in soybean and tobacco after wounding. *Plant Cell Reports*, *35*(2), 303–316. https://doi.org/10.1007/s00299-015-1885-7

Hernández-Verdeja, T., & Lundgren, M. R. (2024). GOLDEN2-LIKE transcription factors: A golden ticket to improve crops? *Plants People Planet*, *6*(1), 79–93. https://doi.org/10.1002/ppp3.10412

Higo, K., Ugawa, Y., Iwamoto, M., & Korenaga, T. (1999). Plant *cis*-acting regulatory DNA elements (PLACE) database: 1999. *Nucleic Acids Research*, *27*(1), 297–300. https://doi.org/10.1093/nar/27.1.297

Hou, X., Wang, S., Zhou, S., & Liu, W. (2025). Identification of two new GRAS transcription factors and expression analysis of these genes in *Chenopodium quinoa*. *Frontiers in Plant Science*, *16*, 1579338. https://doi.org/10.3389/fpls.2025.1579338

Hraška, M., Rakouský, S., & Čurn, V. (2006). Green fluorescent protein as a vital marker for non-destructive detection of transformation events in transgenic plants. *Plant Cell, Tissue and Organ Culture*, *86*(3), 303–318. https://doi.org/10.1007/s11240-006-9131-1

Hsing, H. X., Lin, Y. J., Tong, C. G., Li, M. J., Chen, Y. J., & Ko, S. S. (2016). Efficient and heritable transformation of *Phalaenopsis* orchids. *Botanical Studies*, *57*, 30. https://doi.org/10.1186/s40529-016-0146-6

Hu, B., Jin, J., Guo, A. Y., Zhang, H., Luo, J., & Gao, G. (2015). GSDS 2.0: An upgraded gene feature visualization server. *Bioinformatics*, *31*(8), 1296–1297. https://doi.org/10.1093/bioinformatics/btu817

Huang, Y., Cao, L., Chen, T., Chang, X., & Fang, Y. (2024). Genome-wide identification of the ATP- dependent zinc metalloprotease (FtsH) in *Triticeae species* reveals that *TaFtsH-1* regulates cadmium tolerance in *Triticum aestivum*. *PLoS ONE*, *19*(12), e0316486. https://doi.org/10.1371/journal.pone.0316486

Ijaz, U., Pervaiz, T., Ahmed, T., Seemab, R., Shahid, M., Noman, M., Nadeem, M., & Azeem, F. (2020). Plant *cis*-regulatory elements: methods of identification

UNIVERSITAS GADJAH MADA
Perbandingan Struktur Gen dan Aktivitas Transien Promoter Putatif VARIEGATED2 (VAR2) pada Zona Hijau dan Kuning Daun Anggrek Phalaenopsis Sogo Vivien
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Universitas Gadjah Mada, 2026 | Diunduh dari http://etd.repository.ugm.ac.id/

and applications. *Asian Journal of Agriculture and Biology*, *8*(2), 207–222. https://doi.org/10.35495/ajab.2019.08.352

Inal, B., Muslu, S., Yigider, E., Kasapoglu, A. G., Ilhan, E., Ciltas, A., Yildirim, E., & Aydin, M. (2025). *In silico* analysis of *Phaseolus vulgaris* L. metalloprotease *FtsH* gene: characterization and expression in drought and salt stress. *Genetic Resources and Crop Evolution*, *72*(1), 1065–1088. https://doi.org/10.1007/s10722-024-02031-1

Iqbal, S., Hafeez, A., Chang, M. S., Suthar, V., Khaskheli, M. A., Zahra, L. T., Qadir, F., Naeem, H., Pervaiz, H., Aslam, P., Bukhari, H., & Rasool, G. (2026). Identification of differential expression of the *FTSH* gene family to produce heat-resilient cotton cultivar (upland cotton) for sustainable agriculture. *International Journal of Agriculture and Biosciences*, *15*(3), 1053–1062. https://doi.org/10.47278/journal.ijab/2026.021

Janska, H., Kwasniak, M., & Szczepanowska, J. (2013). Protein quality control in organelles - AAA/FtsH story. *Biochimica et Biophysica Acta - Molecular Cell Research*, *1833*(2), 381–387. https://doi.org/10.1016/j.bbamcr.2012.03.016

Järvi, S., Suorsa, M., Tadini, L., Ivanauskaite, A., Rantala, S., Allahverdiyeva, Y., Leister, D., & Aro, E. M. (2016). Thylakoid-bound FtsH proteins facilitate proper biosynthesis of Photosystem I. *Plant Physiology*, *171*(2), 1333–1343. https://doi.org/10.1104/pp.16.00200

Jiang, F., Guo, M., Yang, F., Duncan, K., Jackson, D., Rafalski, A., Wang, S., & Li, B. (2012). Mutations in an AP2 transcription factor-like gene affect internode length and leaf shape in maize. *PLoS ONE*, *7*(5), e37040. https://doi.org/10.1371/journal.pone.0037040

Kabeya, Y., & Miyagishima, S. Y. (2013). Chloroplast DNA replication is regulated by the redox state independently of chloroplast division in *Chlamydomonas reinhardtii*. *Plant Physiology*, *161*(4), 2102–2112. https://doi.org/10.1104/pp.113.216291

Kato, Y., Miura, E., Ido, K., Ifuku, K., & Sakamoto, W. (2009). The variegated mutants lacking chloroplastic FtsHs are defective in D1 degradation and accumulate reactive oxygen species. *Plant Physiology*, *151*(4), 1790–1801. https://doi.org/10.1104/pp.109.146589

Kato, Y., Miura, E., Matsushime, R., & Sakamoto, W. (2007). White leaf sector in *yellow variegated2*are formed by viabel cells with undifferentiated plastids. *Plant Physiology*, *144*, 952–960. http://dx.doi.org/10.1016/j.jaci.2012.05.050

Kavita, P., & Burma, P. K. (2008). A comparative analysis of green fluorescent protein and β-glucuronidase protein-encoding genes as a reporter system for studying the temporal expression profiles of promoters. *Journal of Bioscience*, *33*, 337–343. https://doi.org/10.1007/s12038-008-0053-4

Komenda, J., Tichý, M., Prášil, O., Knoppová, J., Kuviková, S., de Vries, R., &

UNIVERSITAS GADJAH MADA
Perbandingan Struktur Gen dan Aktivitas Transien Promoter Putatif VARIEGATED2 (VAR2) pada Zona Hijau dan Kuning Daun Anggrek Phalaenopsis Sogo Vivien
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Universitas Gadjah Mada, 2026 | Diunduh dari http://etd.repository.ugm.ac.id/

Nixon, P. J. (2007). The exposed N-terminal tail of the D1 subunit is required for rapid D1 degradation during photosystem II repair in *Synechocystis* sp PCC 6803. *Plant Cell*, *19*(9), 2839–2854. https://doi.org/10.1105/tpc.107.053868

Kui, L., Chen, H., Zhang, W., He, S., Xiong, Z., Zhang, Y., Yan, L., Zhong, C., He, F., Chen, J., Zeng, P., Zhang, G., Yang, S., Dong, Y., Wang, W., & Cai, J. (2017). Building a genetic manipulation tool box for orchid biology: Identification of constitutive promoters and application of *CRISPR/Cas9* in the orchid, *Dendrobium officinale*. *Frontiers in Plant Science*, *7*, 2036. https://doi.org/10.3389/fpls.2016.02036

Kummari, D., Palakolanu, S. R., Kishor, P. B. K., Bhatnagar-Mathur, P., Singam, P., Vadez, V., & Sharma, K. K. (2020). An update and perspectives on the use of promoters in plant genetic engineering. *Journal of Biosciences*, *45*, 119. https://doi.org/10.1007/s12038-020-00087-6

Kurniawan, F. Y. (2023). *Karakterisasi Fenotipik dan Genotipik Pola Varigata Pada Daun Anggrek* Dendrobium *Burana Green dan* Phalaenopsis *Sogo Vivien.* Universitas Gadjah Mada.

Kurniawan, F. Y., Putri, S. U., Linggabuwana, A., Lawrie, M. D., Purwantoro, A., & Semiarti, E. (2024). Mutation of the *VAR2* gene plays a role as one of the causes of leaf variegation in the moth orchid *Phalaenopsis* Sogo Vivien. *Horticulture, Environment, and Biotechnology*, *65*, 119–130. https://doi.org/10.1007/s13580-023-00543-w

Kushwaha, A., Singh, S., Zheng, B. S., Tripathi, D. K., Gupta, R., & Singh, V. P. (2025). MpRR-MYB2 and MpRR-MYB5 New players of chloroplast biogenesis. *Journal of Integrative Plant Biology*, *67*(4), 884–886. https://doi.org/https://doi.org/10.1111/jipb.13868

Lacroix, B., & Citovsky, V. (2019). Pathways of DNA transfer to plants from *Agrobacterium tumefaciens* and related bacterial species. *Annual Review of Phytopathology*, *57*, 231–251. https://doi.org/10.1146/annurev-phyto-082718-100101

Lan, Y., Gong, F., Li, C., Xia, F., Li, Y., Liu, X., Liu, D., Liang, G., Fang, C., & Cai, P. (2024). New insights into the evolution analysis of *trihelix* gene family in eggplant (*Solanum melongena* L.) and expression analysis under abiotic stress. *BMC Genomics*, *25*(1). https://doi.org/10.1186/s12864-024-10959-y

Lee, D. W., O'Keefe, J., Holbrook, N. M., & Feild, T. S. (2003). Pigment dynamics and autumn leaf senescence in a New England deciduous forest, eastern USA. *Ecological Research*, *18*(6), 677–694. https://doi.org/10.1111/j.1440-1703.2003.00588.x

Lescot, M., Déhais, P., Thijs, G., Marchal, K., Moreau, Y., Van De Peer, Y., Rouzé, P., & Rombauts, S. (2002). PlantCARE, a database of plant *cis*-acting regulatory elements and a portal to tools for in silico analysis of promoter sequences. *Nucleic Acids Research*, *30*(1), 325–327.

UNIVERSITAS GADJAH MADA
Perbandingan Struktur Gen dan Aktivitas Transien Promoter Putatif VARIEGATED2 (VAR2) pada Zona Hijau dan Kuning Daun Anggrek Phalaenopsis Sogo Vivien
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https://doi.org/10.1093/nar/30.1.325

Lev-Yadun, S., & Niemelä, P. (2017). Leaf pseudo-variegation: Definition, common types, and probably the defended models for real defensive leaf variegation mimicking them? *Flora*, *226*, 82–88. https://doi.org/10.1016/j.flora.2016.11.010

Li, C. H., Fang, Q. X., Zhang, W. J., Li, Y. H., Zhang, J. Z., Chen, S., Yin, Z. G., Li, W. J., Liu, W. D., Yi, Z., Mu, Z. S., & Du, J. D. (2021). Genome-wide identification of the *CCCH* gene family in rose (*Rosa chinensis* Jacq.) reveals its potential functions. *Biotechnology and Biotechnological Equipment*, *35*(1), 517–526. https://doi.org/10.1080/13102818.2021.1901609

Li, C., Lu, Y., Xu, J., Cui, J., Liu, Y., & Yu, W. (2025). MIKC-type *MADS-box* genes regulate phytohormone-dependent fruit ripening in tomatoes. *Horticulturae*, *11*(5), 487. https://doi.org/10.3390/horticulturae11050487

Li, J., Wen, J., Wu, K., Li, L., & Fang, L. (2024). Integrating physiology, cytology, and transcriptome to reveal the leaf variegation mechanism in *Phalaenopsis* Chia E Yenlin variegata leaves. *Biomolecules*, *14*, 963. https://doi.org/10.3390/biom14080963 Academic

Li, M., Zhu, X., Yu, Q., Yu, A., Chen, L., Kang, J., Wang, X., Yang, T., Yang, Q., & Long, R. (2024). FtsH proteases confer protection against salt and oxidative stress in *Medicago sativa* L. *Plant Science*, *338*, 111915. https://doi.org/10.1016/j.plantsci.2023.111915

Li, Q., Chen, J., McConnell, D. B., & Henny, R. J. (2007). A simple and effective method for quantifying leaf variegation. *HortTechnology*, *17*(3), 285–288. https://doi.org/10.21273/horttech.17.3.285

Li, X., Li, J., Cai, M., Zheng, H., Cheng, Z., & Gao, J. (2020). Identification and evolution of the wuschel-related homeobox protein family in Bambusoideae. *Biomolecules*, *10*, 739. https://doi.org/10.3390/biom10050739

Li, X., & Schmitz, R. J. (2025). *Cis*-regulatory dynamics in plant domestication. *Trends in Genetics*, *41*(11), 1–11. https://doi.org/10.1016/j.tig.2025.02.005

Li, Y., He, N., Hou, J., Xu, L., Liu, C., Zhang, J., Wang, Q., Zhang, X., & Wu, X. (2018). Factors influencing leaf chlorophyll content in natural forests at the biome scale. *Frontiers in Ecology and Evolution*, *6*, 1–10. https://doi.org/10.3389/fevo.2018.00064

Li, Y., Liu, H., Wang, X., & Wang, B. (2025). Genome-wide identification and comprehensive analysis of the *FtsH* gene family in wheat. *Molecular Biology Reports*, *52*(1). https://doi.org/10.1007/s11033-025-10243-6

Lin, M., Yan, J., Ali, M. M., Wang, S., Tian, S., Chen, F., & Lin, Z. (2022). Isolation and functional characterization of a green-tissue promoter in Japonica rice (*Oryza sativa* subsp. *Japonica*). *Biology*, *11*, 1092. https://doi.org/10.3390/biology11081092

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GADJAH MADA
**Perbandingan Struktur Gen dan Aktivitas Transien Promoter Putatif VARIEGATED2 (VAR2) pada Zona Hijau
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Lindahl, M., Tabak, S., Cseke, L., Pichersky, E., Andersson, B., & Adam, Z. (1996). Identification, characterization, and molecular cloning of a homologue of the bacterial FtsH protease in chloroplasts of higher plants. *Journal of Biological Chemistry*, *271*(46), 29329–29334. https://doi.org/10.1074/jbc.271.46.29329

Liu, D., Cui, Y., Li, S., Bai, G., Li, Q., Zhao, Z., Liang, D., Wang, C., Wang, J., Shi, X., Chen, C., Feng, G., & Liu, Z. (2019). A new chloroplast DNA extraction protocol significantly improves the chloroplast genome sequence quality of Foxtail millet (*Setaria italica* (L.) P. Beauv.). *Scientific Reports*, *9*, 16227. https://doi.org/10.1038/s41598-019-52786-2

Liu, H., Duang, L., Tang, C., Ma, J., Jin, J. Q., Chen, J., He, W., Yao, M., & Chen, L. (2025). A single-base mutation in promoter of *CsTPR* enhances the negative regulation on mechanical-related leaf drooping in tea plants. *Horticulture Research*, *12*, uhaf098. https://doi.org/10.1093/hr/uhaf098

Liu, R., Feng, Y., Li, Q., Wu, H., Guo, S., Li, J., Liu, X., Zhang, Y., Tang, X., & Cao, S. (2025). Genome-wide analysis of CPP transcription factor family in endangered plant *Phoebe bournei* and its response to adversity. *Plants*, *14*(5), 1–18. https://doi.org/10.3390/plants14050803

Liu, X., Rodermel, S. R., & Yu, F. (2010). A *var2* leaf variegation suppressor locus, *SUPPRESSOR OF VARIEGATION3*, encodes a putative chloroplast translation elongation factor that is important for chloroplast development in the cold. *BMC Plant Biology*, *10*, 287. https://doi.org/10.1186/1471-2229-10-287

Lu, J., Tong, P., Xu, Y., Liu, S., Jin, B., Cao, F., & Wang, L. (2023). SA-responsive transcription factor GbMYB36 promotes flavonol accumulation in *Ginkgo biloba*. *Forestry Research*, *3*(19), 1–12. https://doi.org/10.48130/FR-2023-0019

Ma, S., Tang, Q., Wang, X., Chi, F., & Song, Y. (2026). Molecular mechanism of ethylene signaling response gene *VcERF061* to promote anthocyanin synthesis in blueberry (*Vaccinium corymbosum*). *BMC Plant Biology*, *26*, 1–15. https://doi.org/10.1186/s12870-025-07712-2

Macalister, C. A., & Bergmann, D. C. (2011). Sequence and function of bHLHs required for stomatal development in *Arabidopsis* are deeply conserved in land plants. *Evolution and Development*, *13*(2), 182–192. https://doi.org/10.1111/j.1525-142X.2011.00468.x

Malmberg, M. M., Spangenberg, G. C., Daetwyler, H. D., & Cogan, N. O. I. (2019). Assessment of low-coverage nanopore long read sequencing for SNP genotyping in doubled haploid canola (*Brassica napus* L .). *Scientific Reports*, *9*(8688), 1–12. https://doi.org/10.1038/s41598-019-45131-0

Maoka, T. (2020). Carotenoids as natural functional pigments. *Journal of Natural Medicines*, *74*(1), 1–16. https://doi.org/10.1007/s11418-019-01364-x

UNIVERSITAS GADJAH MADA
Perbandingan Struktur Gen dan Aktivitas Transien Promoter Putatif VARIEGATED2 (VAR2) pada Zona Hijau dan Kuning Daun Anggrek Phalaenopsis Sogo Vivien
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Universitas Gadjah Mada, 2026 | Diunduh dari http://etd.repository.ugm.ac.id/

Marcotrigiano, M. (1997). Chimeras and variegation: Patterns of deceit. In *HortScience* (Vol. 32, Issue 5, pp. 773–784). https://doi.org/10.21273/hortsci.32.5.773

Martínez-Zapater, J. M. (1993). Genetic analysis of variegated mutants in *Arabidopsis*. *Journal of Heredity*, *84*(2), 138–140. https://doi.org/10.1093/oxfordjournals.jhered.a111298

Matsuo, K., Fukuzawa, N., & Matsumura, T. (2016). A simple agroinfiltration method for transient gene expression in plant leaf discs. *Journal of Bioscience and Bioengineering*, *122*(3), 351–356. https://doi.org/10.1016/j.jbiosc.2016.02.001

Maugarny-Calès, A., & Laufs, P. (2018). Getting leaves into shape: A molecular, cellular, environmental and evolutionary view. *Development (Cambridge)*, *145*(13), dev161646. https://doi.org/10.1242/dev.161646

Mishra, L. S., & Funk, C. (2021). The FtsHi enzymes of *Arabidopsis thaliana*: Pseudo-proteases with an important function. *International Journal of Molecular Sciences*, *22*(11), 5917. https://doi.org/10.3390/ijms22115917

Mithra, S. V. A., Kulkarni, K., & Srinivasan, R. (2017). Plant promoters: Characterization and applications in transgenic technology. In M. Abdin, U. Kiran, Kamaluddin, & A. Ali (Eds.), *Plant Biotechnology: Principles and Applications* (pp. 117–170). Springer. https://doi.org/10.1007/978-981-10-2961-5

Moose, S. P., & Sisco, P. H. (1996). *Glossy15*, an *APETALA2-like* gene from maize that regulates leaf epidermal cell identity. *Genes & Development*, *5*, 3018–3027. https://doi.org/10.1101/gad.10.23.3018

Mufti, F. U. D., Aman, S., Banaras, S., Shinwari, Z. K., & Shakeel, S. (2015). Actin gene identification from selected medicinal plants for their use as internal controls for gene expression studies. *Pakistan Journal of Botany*, *47*(2), 629–635. https://www.researchgate.net/publication/275335218

Murray, M. G., & Thompson, W. F. (1980). Rapid isolation of high molecular weight plant DNA. *Nucleic Acids Research*, *8*(19), 4321–4326. https://doi.org/10.1093/nar/8.19.4321

Mursyanti, E., Purwantoro, A., Moeljopawiro, S., & Semiarti, E. (2016). Micropropagation of mini orchid hybrid *Phalaenopsis* "Sogo Vivien." *Journal of Tropical Biodiversity and Biotechnology*, *1*(1), 45–53. https://doi.org/10.22146/jtbb.12933

Nanjareddy, K., Arthikala, M. K., Aguirre, A. L., Gómez, B. M., & Lara, M. (2017). Plant promoter analysis: Identification and characterization of root nodule specific promoter in the common bean. *Journal of Visualized Experiments*, e56140. https://doi.org/10.3791/56140

Nishimura, K., Kato, Y., & Sakamoto, W. (2016). Chloroplast proteases: Updates

UNIVERSITAS GADJAH MADA
Perbandingan Struktur Gen dan Aktivitas Transien Promoter Putatif VARIEGATED2 (VAR2) pada Zona Hijau dan Kuning Daun Anggrek Phalaenopsis Sogo Vivien
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Universitas Gadjah Mada, 2026 | Diunduh dari http://etd.repository.ugm.ac.id/

on proteolysis within and across suborganellar compartments. *Plant Physiology*, *171*(4), 2280–2293. https://doi.org/10.1104/pp.16.00330

Nopitasari, S., Setiawati, Y., Lawrie, M. D., Purwantoro, A., Widada, J., Sasongko, A. B., Yoshioka, Y., Matsumoto, S., Ninomiya, K., Asano, Y., & Semiarti, E. (2020). Development of an *Agrobacterium*-delivered *CRISPR/Cas9* for *Phalaenopsis amabilis* (L.) Blume genome editing system. *AIP Conference Proceedings*, *2260*, 060014. https://doi.org/10.1063/5.0015868

Oboni, K. A., & Hossain, M. A. (2025). Exploring the diversity, propagation, impacts, and market dynamics of houseplants: current trends and future prospects. *Technology in Horticulture*, *5*(1), e010. https://doi.org/10.48130/tihort-0025-0005

Oda-Yamamizo, C., Mitsuda, N., Sakamoto, S., Ogawa, D., Ohme-Takagi, M., & Ohmiya, A. (2016). The NAC transcription factor ANAC046 is a positive regulator of chlorophyll degradation and senescence in *Arabidopsis* leaves. *Scientific Reports*, *6*, 1–12. https://doi.org/10.1038/srep23609

Ogura, T., Tomoyasu, T., Yuki, T., Morimura, S., Begg, K. J., Donachie, W. D., Mori, H., Niki, H., & Hiraga, S. (1991). Structure and function of the *fisH* gene in *Escherichia coli*. *Research in Microbiology*, *142*(2–3), 279–282. https://doi.org/10.1016/0923-2508(91)90041-8

Oljira, M. T., & Barka, G. D. (2021). Bioinformatic analysis of promoter, motifs and CpG islands of genes encoding potassium transporters in crop plants. *Biotechnology and Biotechnological Equipment*, *35*(1), 1809–1819. https://doi.org/10.1080/13102818.2021.2022533

Olson, J., & Clark, M. (2021). Characterization of anatomical and physiological effects of variegation mutation on grapevine. *HortScience*, *56*(10), 1251–1257. https://doi.org/10.21273/HORTSCI15929-21

Pan, J., Song, J., Sharif, R., Xu, X., Li, S., & Chen, X. (2024). A mutation in the promoter of the yellow stripe-like transporter gene in cucumber results in a yellow cotyledon phenotype. *Journal of Integrative Agriculture*, *23*(3), 849–862. https://doi.org/10.1016/j.jia.2023.11.024

Pao, S. H., Liu, J. W., Yang, J. Y., Chesson, P., & Sheue, C. R. (2020). Uncovering the mechanisms of novel foliar variegation patterns caused by structures and pigments. *Taiwania*, *65*(1), 74–80. https://doi.org/10.6165/tai.2020.65.74

Park, S. H., Yi, N., Kim, Y. S., Jeong, M. H., Bang, S. W., Choi, Y. D., & Kim, J. K. (2010). Analysis of five novel putative constitutive gene promoters in transgenic rice plants. *Journal of Experimental Botany*, *61*(9), 2459–2467. https://doi.org/10.1093/jxb/erq076

Park, S. I., Kim, H. B., Jeon, H. J., & Kim, H. (2021). *Agrobacterium*-mediated *Capsicum annuum* gene editing in two cultivars, Hot Pepper CM334 and Bell Pepper Dempsey. *International Journal of Molecular Sciences*, *22*, 3921.

UNIVERSITAS GADJAH MADA
Perbandingan Struktur Gen dan Aktivitas Transien Promoter Putatif VARIEGATED2 (VAR2) pada Zona Hijau dan Kuning Daun Anggrek Phalaenopsis Sogo Vivien
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https://doi.org/10.3390/ijms22083921

Porra, R. J., Thompson, W. A., & Kriedemann, P. E. (1989). Determination of accurate extinction coefficients and simultaneous equations for assaying chlrophylls a and b extracted with four different solvents: verification of the concentration of chlorophyll standards by atomic absorption spectroscopy. *Biochimia et Biophysica Acta*, *975*(3), 384–394. https://doi.org/10.1016/S0005-2728(89)80347-0

Porto, M. S., Pinheiro, M. P. N., Batista, V. G. L., dos Santos, R. C., Filho, P. A. M., & de Lima, L. M. (2014). Plant promoters: An approach of structure and function. *Molecular Biotechnology*, *56*(1), 38–49. https://doi.org/10.1007/s12033-013-9713-1

Prajapati, M., Chaudhary, D., Jaiwal, P. K., Jaiwal, R., & Ahlawat, Y. K. (2024). Optimizing *Agrobacterium*-mediated transformation efficiency in an Indian cultivar of *Trifolium alexandrinum* L. *Grass Research*, *4*, e019. https://doi.org/10.48130/grares-0024-0018

Primasiwi, D. H., Purwestri, Y. A., & Semiarti, E. (2024). Improving transient gene expression and agroinfiltration-based transformation effectiveness in Indonesian orchid *Phalaenopsis amabilis* (L.) Blume. *Indonesian Journal of Biotechnology*, *29*(3), 111–120. https://doi.org/10.22146/ijbiotech.80555

Pu, T., Mo, Z., Su, L., Yang, J., Wan, K., Wang, L., Liu, R., & Liu, Y. (2022). Genome-wide identification and expression analysis of the ftsH protein family and its response to abiotic stress in *Nicotiana tabacum* L. *BMC Genomics*, *23*, 503. https://doi.org/10.1186/s12864-022-08719-x

Purwantoro, A., Irsyadi, M. B., Sawitri, W. D., Fatumi, N. C., & Fajrina, S. N. (2023). Efficient floral dip transformation method using *Agrobacterium tumefaciens* on *Cosmos sulphureus* Cav. *Saudi Journal of Biological Sciences*, *30*(7), 103702. https://doi.org/10.1016/j.sjbs.2023.103702

Putarjunan, A., Liu, X., Nolan, T., Yu, F., & Rodermel, S. (2013). Understanding chloroplast biogenesis using second-site suppressors of *immutans* and *var2*. *Photosynthesis Research*, *116*(2–3), 437–453. https://doi.org/10.1007/s11120-013-9855-9

Putri, S. U., Linggabuwana, A., Kurniawan, F. Y., Lawrie, M. D., & Semiarti, E. (2023). Morphological and molecular characterization of variegated-leaf pattern in *Dendrobium* Burana Green based on the structure of *VAR2* gene. *Proceedings of the 3rd International Conference on Smart and Innovative Agriculture (ICoSIA 2022)*, 524–539. https://doi.org/10.2991/978-94-6463-122-7_50

Rawlings, N. D., & Barrett, A. J. (1995). Evolutionary families of metallopeptidases. *Methods in Enzimology*, *248*, 183–228. https://doi.org/10.1016/0076-6879(95)48015-3

UNIVERSITAS GADJAH MADA
Perbandingan Struktur Gen dan Aktivitas Transien Promoter Putatif VARIEGATED2 (VAR2) pada Zona Hijau dan Kuning Daun Anggrek Phalaenopsis Sogo Vivien
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Universitas Gadjah Mada, 2026 | Diunduh dari http://etd.repository.ugm.ac.id/

Reese, M. G. (2001). Application of a time-delay neural network to promoter annotation in the *Drosophila melanogaster* genome. *Computers and Chemistry*, *26*(1), 51–56. https://doi.org/10.1016/S0097-8485(01)00099-7

Ruzin, S. E. (1999). *Plant Microtechnique and Microscopy*. Oxford University Press.

Schuiteman, A. (2021). Leopard spots, chequerboards and spider's webs: Classification, systematics and function of variegated leaves in Orchidaceae. *Rheedea*, *31*(3), 105–132. https://doi.org/10.22244/rheedea.2021.31.03.02

Semiarti, E., Indrianto, A., Purwantoro, A., Machida, Y., & Machida, C. (2011). *Agrobacterium*-mediated transformation of Indonesian orchids for micropropagation. In M. Alvarez (Ed.), *Genetic Transformation* (pp. 215–240). InTech. https://doi.org/10.5772/24997

Semiarti, E., Nopitasari, S., Setiawati, Y., Lawrie, M. D., Purwantoro, A., Widada, J., Ninomiya, K., Asano, Y., Matsumoto, S., & Yoshioka, Y. (2020). Application of CRISPR/Cas9 genome editing system for molecular breeding of orchids. *Indonesian Journal of Biotechnology*, *25*(1), 61–68. https://doi.org/10.22146/ijbiotech.39485

Semiarti, E., Purwantoro, A., & Purnomo. (2024). *Produksi planlet tanaman anggrek* Dendrobium macrophyllum *dengan metode agroinfiltrasi* (IDP000095582). Kementrian Hukum dan Hak Asasi Manusia.

Setiawati, Y., Nopitasari, S., Lawrie, M. D., Purwantoro, A., Widada, J., Sasongko, A. B., Ninomiya, K., Asano, Y., Matsumoto, S., Yoshioka, Y., & Semiarti, E. (2020). *Agrobacterium*-mediated transformation facillitates the *CRISPR/Cas9* genome editing system in *Dendrobium macrophyllum* A. Rich orchid. *AIP Conference Proceedings*, *2260*, 060016. https://doi.org/10.1063/5.0016200

Shan, Q., Zhou, B., Wang, Y., Hao, F., Zhu, L., Liu, Y., Wang, N., Wang, F., Li, X., Dong, Y., Xu, K., Zhou, Y., Li, H., Liu, W., & Gao, H. (2023). Genome-wide identification and comprehensive analysis of the *FtsH* gene family in soybean (*Glycine max*). *International Journal of Molecular Sciences*, *24*(23), 16996. https://doi.org/10.3390/ijms242316996

Shengcai, L., Tianliu, H., Yingxiao, H., Weijia, L., Mengbo, Y., Rui, Z., & Ning, L. (2025). CaNAC014 transcription factor enhances salt stress tolerance in pepper by regulating the activity of the *CaSOS1* promoter. *Plant Stress*, *18*, 101025. https://doi.org/10.1016/j.stress.2025.101025

Sheue, C. R., Pao, S. H., Chien, L. F., Chesson, P., & Peng, C. I. (2012). Natural foliar variegation without costs? The case of *Begonia*. *Annals of Botany*, *109*(6), 1065–1074. https://doi.org/10.1093/aob/mcs025

Shihan, M. H., Novo, S. G., Le Marchand, S. J., Wang, Y., & Duncan, M. K. (2021). A simple method for quantitating confocal fluorescent images. *Biochemistry and Biophysics Reports*, *25*, 100916. https://doi.org/10.1016/

UNIVERSITAS GADJAH MADA
Perbandingan Struktur Gen dan Aktivitas Transien Promoter Putatif VARIEGATED2 (VAR2) pada Zona Hijau dan Kuning Daun Anggrek Phalaenopsis Sogo Vivien
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j.bbrep.2021.100916

Srivastava, R., Rai, K. M., Srivastava, M., Kumar, V., Pandey, B., Singh, S. P., Bag, S. K., Singh, B. D., Tuli, R., & Sawant, S. V. (2014). Distinct role of core promoter architecture in regulation of light-mediated responses in plant genes. *Molecular Plant*, *7*(4), 626–641. https://doi.org/10.1093/mp/sst146

Su, J., Jiao, Q., Jia, T., & Hu, X. (2024). The photosystem-II repair cycle: updates and open questions. *Planta*, *259*(20), 1–16. https://doi.org/10.1007/s00425-023-04295-w

Su, Z. L., Li, A. M., Wang, M., Qin, C. X., Pan, Y. Q., Liao, F., Chen, Z. L., Zhang, B. Q., Cai, W. G., & Huang, D. L. (2025). The role of AP2/ERF transcription factors in plant responses to biotic stress. *International Journal of Molecular Sciences*, *26*(10), 4921. https://doi.org/10.3390/ijms26104921

Subchan, A. N., Nopitasari, S., Setiawati, Y., Zubaidah, L., Nikmah, N., Lawrie, M. D., Sasongko, A. B., Matsumoto, S., Yoshioka, Y., & Semiarti, E. (2022). *Agrobacterium*-mediated transformation by using immerse and agroinfiltration method for genome editing of orchids with *CRISPR/Cas9*. *Acta Horticulturae*, *1334*, 263–271. https://doi.org/10.17660/ActaHortic.2022.1334.32

Takechi, K., Sodmergen, Murata, M., Motoyoshi, F., & Sakamoto, W. (2000). The *YELLOW VARIEGATED* (*VAR2*) locus encodes a homologue of FtsH, an ATP-dependent protease in *Arabidopsis*. *Plant and Cell Physiology*, *41*(12), 1334–1346. https://doi.org/10.1093/pcp/pcd067

Tamura, K., Stecher, G., & Kumar, S. (2021). MEGA11: Molecular Evolutionary Genetics Analysis Version 11. *Molecular Biology and Evolution*, *38*(7), 3022–3027. https://doi.org/10.1093/molbev/msab120

Tao, R., Ma, J., Qian, J., Liu, Y., Zhang, W., Lavelle, D., Wang, X., Yan, W., Michelmore, R. W., Chen, J., & Kuang, H. (2025). Differential methylation of a retrotransposon upstream of a *MYB* gene causes variegation of lettuce leaves, which is abolished by the presence of an $(AT)_5$ repeat in the promoter. *The Plant Journal*, *122*, e70123. https://doi.org/10.1111/tpj.70123

Tee, C. S., Marziah, M., Tan, C. S., & Abdullah, M. P. (2003). Evaluation of different promoters driving the GFP reporter gene and selected target tissues for particle bombardment of *Dendrobium* Sonia 17. *Plant Cell Reports*, *21*(5), 452–458. https://doi.org/10.1007/s00299-002-0539-8

Telfer, A. (2020). Photosynthesis without β-carotene. *ELife*, *9*, 1–16. https://doi.org/10.7554/ELIFE.58984

Tian, F., Yang, D. C., Meng, Y. Q., Jin, J., & Gao, G. (2020). PlantRegMap: Charting functional regulatory maps in plants. *Nucleic Acids Research*, *48*(D1), D1104–D1113. https://doi.org/10.1093/nar/gkz1020

Tian, J., Jiang, W., Si, J., Han, Z., Li, C., & Chen, D. (2022). Developmental

UNIVERSITAS
GADJAH MADA
**Perbandingan Struktur Gen dan Aktivitas Transien Promoter Putatif VARIEGATED2 (VAR2) pada Zona Hijau
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Universitas Gadjah Mada, 2026 | Diunduh dari http://etd.repository.ugm.ac.id/

characteristics and auxin response of epiphytic root in *Dendrobium catenatum*. *Frontiers in Plant Science*, *13*, 935540. https://doi.org/10.3389/fpls.2022.935540

Tong, C. G., Wu, F. H., Yuan, Y. H., Chen, Y. R., & Lin, C. S. (2020). High-efficiency *CRISPR/Cas*-based editing of *Phalaenopsis* orchid *MADS* genes. *Plant Biotechnology Journal*, *18*(4), 889–891. https://doi.org/10.1111/pbi.13264

Toshoji, H., Katsumata, T., Takusagawa, M., Yusa, Y., & Sakai, A. (2012). Effects of chloroplast dysfunction on mitochondria: White sectors in variegated leaves have higher mitochondrial DNA levels and lower dark respiration rates than green sectors. *Protoplasma*, *249*(3), 805–817. https://doi.org/10.1007/s00709-011-0325-y

Tsai, C. C., Wu, Y. J., Sheue, C. R., Liao, P. C., Chen, Y. H., Li, S. J., Liu, J. W., Chang, H. T., Liu, W. L., Ko, Y. Z., & Chiang, Y. C. (2017). Molecular basis underlying leaf variegation of a moth orchid mutant (*Phalaenopsis aphrodite* subsp. *formosana*). *Frontiers in Plant Science*, *8*, 1333. https://doi.org/10.3389/fpls.2017.01333

Tsukaya, H. (2014). Comparative leaf development in angiosperms. *Current Opinion in Plant Biology*, *17*(1), 103–109. https://doi.org/10.1016/j.pbi.2013.11.012

Tsukaya, H., Okada, H., & Mohamed, M. (2004). A novel feature of structural variegation in leaves of the tropical plant *Schismatoglottis calyptrata*. *Journal of Plant Research*, *117*(6), 477–480. https://doi.org/10.1007/s10265-004-0179-x

Valoroso, M. C., Lucibelli, F., & Aceto, S. (2022). Orchid NAC transcription factors: A focused analysis of *CUPULIFORMIS* genes. *Genes*, *13*(12), 2293. https://doi.org/10.3390/genes13122293

Varchenko, O. I., Kuchuk, M. V., Parii, M. F., & Symonenko, Y. V. (2020). Comparison of *gfp* gene expression levels after *Agrobacterium*-mediated transient transformation of *Nicotiana rustica* L. by constructs with different promoter sequences. *Cytology and Genetics*, *54*(6), 531–538. https://doi.org/10.3103/S0095452720060110

Villao-Uzho, L., Chávez-Navarrete, T., Pacheco-Coello, R., Sánchez-Timm, E., & Santos-Ordóñez, E. (2023). Plant promoters: their identification, characterization, and role in gene regulation. *Genes*, *14*(6), 1226. https://doi.org/10.3390/genes14061226

Wahyuningsih, S., Lawrie, M. D., Daryono, B. S., Moeljopawiro, S., Jang, S., & Semiarti, E. (2017). Early detection of the orchid flowering gene *PaFT1* in tobacco cells using a *GFP* reporter. *Indonesian Journal of Biotechnology*, *21*(1), 12. https://doi.org/10.22146/ijbiotech.26781

UNIVERSITAS GADJAH MADA
Perbandingan Struktur Gen dan Aktivitas Transien Promoter Putatif VARIEGATED2 (VAR2) pada Zona Hijau dan Kuning Daun Anggrek Phalaenopsis Sogo Vivien
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Universitas Gadjah Mada, 2026 | Diunduh dari http://etd.repository.ugm.ac.id/

Wang, H., Niu, H., Li, C., Shen, G., Liu, X., Weng, Y., Wu, T., & Li, Z. (2020). *WUSCHEL-related homeobox1 (WOX1)* regulates vein patterning and leaf size in *Cucumis sativus*. *Horticulture Research*, *7*, 182. https://doi.org/10.1038/s41438-020-00404-y

Wang, J., Liu, L., Luo, R., Zhang, Q., Wang, X., Ling, F., & Wang, P. (2024). Genome-wide analysis of *filamentous temperature-sensitive H protease* (*ftsH*) gene family in soybean. *BMC Genomics*, *25*(1), 1–13. https://doi.org/10.1186/s12864-024-10389-w

Wang, L., Chen, W., Zhao, Z., Li, H., Pei, D., Huang, Z., Wang, H., & Xiao, L. (2025). Genome-wide identification, conservation, and expression pattern analyses of the *BBR-BPC* gene family under abiotic stress in *Brassica napus* L. *Genes*, *16*(1), 36. https://doi.org/10.3390/genes16010036

Wang, Y., Jensen, R. C., & Stumph, W. E. (1996). Role of TATA box sequence and orientation in determining RNA polymerase II/III transcription specificity. *Nucleic Acids Research*, *24*(15), 3100–3106. https://doi.org/10.1093/nar/24.15.3100

Wei, T., & Heping, D. (2014). Quantification of GFP Signals by Fluorescent Microscopy and Flow Cytometry. In W. Xiao (Ed.), *Yeast Protocols: Methods in Molecular Biology* (Vol. 1163, pp. 23–31). Humana Press. https://doi.org/10.1007/978-1-4939-0799-1

Wetzel, C. M., Jiang, C. Z., Meehan, L. J., Voytas, D. F., & Rodermel, S. R. (1994). Nuclear—organelle interactions: the immutans variegation mutant of *Arabidopsis* is plastid autonomous and impaired in carotenoid biosynthesis. *The Plant Journal*, *6*(2), 161–175. https://doi.org/10.1046/j.1365-313X.1994.6020161.x

Woo, H. R., Kim, J. H., Kim, J., Kim, J., Lee, U., Song, I. J., Kim, J. H., Lee, H. Y., Nam, H. G., & Lim, P. O. (2010). The RAV1 transcription factor positively regulates leaf senescence in *Arabidopsis*. *Journal of Experimental Botany*, *61*(14), 3947–3957. https://doi.org/10.1093/jxb/erq206

Wu, L., Cao, L., Chu, Z., Dong, L., Sun, J., Li, S., Yang, Y., Liu, S., Tong, S., Tang, M., Zhatova, H., & Meng, L. (2026). Identification of the *FtsH* gene family in chrysanthemums and functional analysis of CmFtsH-15 under cadmium stress. *Frontiers in Plant Science*, *17*, 1768126. https://doi.org/10.3389/fpls.2026.1768126

Wu, Y., Wu, W., Zhang, L., Ni, S., Shen, J., Kong, D., Zhang, Z., Ma, C., Peng, L., Huang, J., & Ming, F. (2026). PeFtsH1 and PeFtsH2 form a heteromeric hexamer and play conserved roles in chloroplast development and leaf variegation in *Phalaenopsis equestris*. *Plant Journal*, *125*(6), 1–13. https://doi.org/10.1111/tpj.70776

Xi, Z., Jia, H., Li, Y., Ma, J., Lu, M., Wang, Z., Kong, D., & Deng, W. (2024). Identification and functional analysis of *PR* Genes in leaves from variegated

UNIVERSITAS GADJAH MADA
Perbandingan Struktur Gen dan Aktivitas Transien Promoter Putatif VARIEGATED2 (VAR2) pada Zona Hijau dan Kuning Daun Anggrek Phalaenopsis Sogo Vivien
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Universitas Gadjah Mada, 2026 | Diunduh dari http://etd.repository.ugm.ac.id/

tea plant (*Camellia sinensis*). *Agronomy*, *14*, 156. https://doi.org/10.3390/agronomy14010156

Xiao, K., Zhang, C., Harrison, M., & Wang, Z. Y. (2005). Isolation and characterization of a novel plant promoter that directs strong constitutive expression of transgenes in plants. *Molecular Breeding*, *15*(2), 221–231. https://doi.org/10.1007/s11032-004-5679-9

Xue, M., Long, Y., Zhao, Z., Huang, G., Huang, K., Zhang, T., Jiang, Y., Yuan, Q., & Pei, X. (2018). Isolation and characterization of a green-tissue promoter from common wild rice (*Oryza rufipogon* Griff.). *International Journal of Molecular Sciences*, *19*(7), 2009. https://doi.org/10.3390/ijms19072009

Yang, F., Lu, C., Wei, Y., Wu, J., Ren, R., Gao, J., Ahmad, S., Jin, J., Xv, Y., Liang, G., & Zhu, G. (2022). Organ-specific gene expression reveals the role of the *Cymbidium ensifolium-miR396/Growth-Regulating Factors* module in flower development of the orchid lant *Cymbidium ensifolium*. *Frontiers in Plant Science*, *12*, 799778. https://doi.org/10.3389/fpls.2021.799778

Yang, K., An, J. P., Li, C. Y., Shen, X. N., Liu, Y. J., Wang, D. R., Ji, X. L., Hao, Y. J., & You, C. X. (2021). The apple C2H2-type zinc finger transcription factor MdZAT10 positively regulates JA-induced leaf senescence by interacting with MdBT2. *Horticulture Research*, *8*(1), 159. https://doi.org/10.1038/s41438-021-00593-0

Yang, R., Huang, T., Song, W., An, Z., Lai, Z., & Liu, S. (2023). Identification of WRKY gene family members in amaranth based on a transcriptome database and functional analysis of *AtrWRKY42-2* in betalain metabolism. *Frontiers in Plant Science*, *14*(1), 1300522. https://doi.org/10.3389/fpls.2023.1300522

Yang, Y., Chen, X., Xu, B., Li, Y., Ma, Y., & Wang, G. (2015). Phenotype and transcriptome analysis reveals chloroplast development and pigment biosynthesis together influenced the leaf color formation in mutants of *Anthurium andraeanum* 'Sonate.' *Frontiers in Plant Science*, *6*, 1–16. https://doi.org/10.3389/fpls.2015.00139

Yasmeen, E., Wang, J., Riaz, M., Zhang, L., & Zuo, K. (2023). Designing artificial synthetic promoters for accurate, smart, and versatile gene expression in plants. *Plant Communications*, *4*(4), 100558. https://doi.org/10.1016/j.xplc.2023.100558

Ye, R., Zhou, F., & Lin, Y. (2012). Two novel positive cis-regulatory elements involved in green tissue-specific promoter activity in rice (*Oryza sativa* L ssp.). *Plant Cell Reports*, *31*(7), 1159–1172. https://doi.org/10.1007/s00299-012-1238-8

Yeung, E. C. (1998). A beginner's guide to the study of plant structure. In S. J. Karcher (Ed.), *Tested Studies For Laboratory Teaching* (pp. 125–143). Association for Biology Laboratory Education (ABLE).

UNIVERSITAS GADJAH MADA
Perbandingan Struktur Gen dan Aktivitas Transien Promoter Putatif VARIEGATED2 (VAR2) pada Zona Hijau dan Kuning Daun Anggrek Phalaenopsis Sogo Vivien
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Universitas Gadjah Mada, 2026 | Diunduh dari http://etd.repository.ugm.ac.id/

Yi, L., Liu, B., Nixon, P. J., Yu, J., & Chen, F. (2022). Recent advances in understanding the structural and functional evolution of FtsH proteases. *Frontiers in Plant Science*, *13*, 1–16. https://doi.org/10.3389/fpls.2022.837528

Yu, F., Fu, A., Aluru, M., Park, S., Xu, Y., Liu, H., Liu, X., Foudree, A., Nambogga, M., & Rodermel, S. (2007). Variegation mutants and mechanisms of chloroplast biogenesis. *Plant, Cell and Environment*, *30*(3), 350–365. https://doi.org/10.1111/j.1365-3040.2006.01630.x

Yu, F., Park, S., & Rodermel, S. R. (2004). The *Arabidopsis* FtsH metalloprotease gene family: interchangeability of subunits in chloroplast oligomeric complexes. *The Plant Journal*, *37*, 864–876. https://doi.org/10.1111/j.1365-313X.2003.02014.x

Yu, H., Zhang, L., Wang, W., Tian, P., Wang, W., Wang, K., Gao, Z., Liu, S., Zhang, Y., Irish, V. F., & Huang, T. (2021). TCP5 controls leaf margin development by regulating KNOX and BEL-like transcription factors in *Arabidopsis*. *Journal of Experimental Botany*, *72*(5), 1809–1821. https://doi.org/10.1093/jxb/eraa569

Zhang, D., Zhao, X. W., Li, Y. Y., Ke, S. J., Yin, W. L., Lan, S., & Liu, Z. J. (2022). Advances and prospects of orchid research and industrialization. *Horticulture Research*, *9*, uhac220. https://doi.org/10.1093/hr/uhac220 Review

Zhang, J. H., Zeng, J. C. C., Wang, X. M., Chen, S. F. F., Albach, D. C., & Li, H. Q. (2020). A revised classification of leaf variegation types. *Flora*, *272*, 151703. https://doi.org/10.1016/j.flora.2020.151703

Zhang, S., Wang, L., Sun, X., Li, Y., Yao, J., van Nocker, S., & Wang, X. (2019). Genome-wide analysis of the *YABBY* gene family in grapevine and functional characterization of *VvYABBY4*. *Frontiers in Plant Science*, *10*, 1207. https://doi.org/10.3389/fpls.2019.01207

Zhang, S., Yang, Y., Li, J., Qin, J., Zhang, W., Huang, W., & Hu, H. (2018). Physiological diversity of orchids. *Plant Diversity*, *40*(4), 196–208. https://doi.org/10.1016/j.pld.2018.06.003

Zhang, Y., Qiu, L., Zhang, Y., Wang, Y., Fu, C., Dai, S., & Sun, M. (2024). A high-efficiency transient expression system mediated by *Agrobacterium tumefaciens* in *Spinacia oleracea* leaves. *Plant Methods*, *20*(1), 1–13. https://doi.org/10.1186/s13007-024-01218-y

Zhao, M. H., Li, X., Zhang, X. X., Zhang, H., & Zhao, X. Y. (2020). Mutation mechanism of leaf color in plants: A review. *Forests*, *11*, 851. https://doi.org/10.3390/f11080851

Zheng, L., Yang, J., Chen, Y., Ding, L., Wei, J., & Wang, H. (2021). An improved and efficient method of *Agrobacterium* syringe infiltration for transient transformation and its application in the elucidation of gene function in poplar.

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BMC Plant Biology, *21*, 54. https://doi.org/10.1186/s12870-021-02833-w

Zhu, X., Yu, A., Zhang, Y., Yu, Q., Long, R., Kang, J., Yang, Q., Guo, C., & Li, M. (2023). Genome-wide identification and characterization of filamentation temperature-sensitive H (FtsH) genes and expression analysis in response to multiple stresses in *Medicago truncatula*. *Molecular Biology Reports*, *50*(12), 10097–10109. https://doi.org/10.1007/s11033-023-08851-1

Zou, X., & Sun, H. (2023). DOF transcription factors: Specific regulators of plant biological processes. *Frontiers in Plant Science*, *14*, 1044918. https://doi.org/10.3389/fpls.2023.1044918