

Curriculum Vitae

ADDRESS:

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PERSONAL DATA:

Born: February, 1961, Taipei, Taiwan

EDUCATION:

1990 Ph.D. in Biology, Carnegie Mellon University, Pittsburgh, PA, USA
Advisor: Professor John Woolford
1985 M.S. in Botany, National Taiwan University, Taipei, Taiwan
1983 B.S. in Botany, National Taiwan University, Taipei, Taiwan

PRESENT POSITION:

Distinguished Research Fellow, Institute of Molecular Biology, Academia Sinica, Taipei, Taiwan

RESEARCH AND PROFESSIONAL EXPERIENCE:

2016- Distinguished Research Fellow, Institute of Molecular Biology, Academia Sinica, Taiwan
2019-2020 Acting director, Institute of Molecular Biology, Academia Sinica, Taiwan
2019-2020 Coordinator of Genome and Systems Biology Degree Program, National Taiwan University and Academia Sinica, Taiwan
2013-2016 Coordinator of Taiwan International Graduate Program in Molecular and Cell Biology, Academia Sinica, Taiwan
2011-2014 Deputy Director, Institute of Molecular Biology, Academia Sinica
2009-2016 Research Fellow, Institute of Molecular Biology, Academia Sinica, Taiwan
1999-2009 Associate Research Fellow, Institute of Molecular Biology, Academia Sinica, Taiwan
1994-1999 Assistant Research Fellow, Institute of Molecular Biology, Academia Sinica, Taiwan
1990-1993 Postdoctoral Associate, Department of Biology, University of California at San Diego, Sponsor: Professor Nigel Crawford

2006-now Affiliate Associate Professor/Professor, Institute of Molecular and Cellular Biology, National Taiwan University, Taiwan
1999-now Affiliate Associate Professor/Professor, Department of Life Science and Institute of Genome Science, National Yang-Ming University, Taiwan
2000-2006 Affiliate Associate Professor, Institute of Botany, National Taiwan University, Taiwan

2009-2010 Visiting Scholar, Department of Biology, University of California at San Diego, CA
2002/7-2002/9 Visiting Scholar, Bioscience and Biotechnology Center, Nagoya University, Japan

HONORS AND AWARDS:

2024, Academician, Academia Sinica, Taiwan
2024, TWAS award in Biology, TWAS
2022-2027, Frontier Science Grant, National Science Council, Taiwan
2021, International Member of the National Academy of Sciences, USA

2021, Shang-Fa Yang Memorial Lecture Award, Taiwan
 2019, ASPB Enid MacRobbie Corresponding Membership Award, USA
 2019, CTCI Science and Technology Contribution Award, Taiwan
 2019-2023, Investigator Award from Academia Sinica, Taiwan
 2018, Taiwan Outstanding Woman in Science, Taiwan
 2016, KIA (Khwarizmi International Award) Laureate, Iran
 2014, Hou Chin Dui Outstanding Honor Award, Taiwan
 2014-2019, Frontier Science Grant, National Science Council, Taiwan
 2014-2018, Investigator Award from Academia Sinica, Taiwan
 2013, 57th Academic Awards from Ministry of Education, Taiwan
 2010, Outstanding Research Award from National Science Council, Taiwan
 2009-2014, Frontier Science Grant, National Science Council, Taiwan
 2003, Outstanding Research Award from National Science Council, Taiwan
 2002-2006, Frontier Science Grant, National Science Council, Taiwan
 2000, Outstanding Young Researcher Award from Academia Sinica, Taiwan

ACADEMIC ACTIVITIES:

1. 2021- 2022 Associate Editor for **Plant Physiology**
2. 2021- Section head for the Plant Biochemistry & Physiology section in **Faculty Opinions**
3. 2018-2021 Contributing member for **F1000/Faculty Opinions**
4. 2011-2020 Monitoring Editor for **Plant Physiology**
5. 2011- Associate Editor for **Frontiers** in Plant Traffic and Transport
6. 2009-2010 Guest editor for **Annual Review of Plant Biology**, Vol. 62
7. Guest editor for PNAS.
8. ADHOC reviewers for journals: Nature, PNAS, Plant Cell, Trends in Plant Science, Plant Physiology, Plant Journal, Plant and Soil, Plant and Cell Physiology, Journal of Experimental Botany, Plant Molecular Biology, Biochimica et Biophysica Acta, Annals of Botany, Journal of Plant Research, Journal of Plant Physiology, Gene, etc
9. ADHOC reviewers for grants: European Research Council (ERC), National Science Foundation (NSF) US, and Human Frontier Science Program (HFSP); Australian Research Council (ARC).
10. Actively involved in Taiwan International Science Fair (Intel ISEF) for high school students since 2007
11. Establish an internship program between Philippine Society of Biochemistry and Molecular Biology (PSBMB) and Institute of Molecular Biology, Academia Sinica, since 2015
12. Speakers for High School Girl Science Education Tour Plan in 2019, 2020, 2023, 2024
13. Chair of the organizing committee for **JTPB 2019** in Nagoya, Japan
14. Organizing committee for **Plant Vascular Biology** 2019 meeting in US
15. Organizing committee and session chair for **International Workshop on Plant Membrane Biology** 2019 meeting in Glasgow, UK
16. Review panel for Taiwan Outstanding Woman in Science 2020, 2022, 2024
17. Co-Editor for a Focus Issue of Plant Cell Physiology on “Transport Systems of Mineral Elements in Plants: Transporters, Regulation and Utilization”, Sept. 2021
18. Chief editor for a Focus Issue of **Plant Physiology** on “Transport and Signaling”, Dec. 2021
19. Chair of organizing committee for **International Workshop on Plant Membrane Biology** 2022 meeting in Taipei, Taiwan, March 2023
20. Organizing committee and session chair for **the 13th International Plant Molecular Biology (IPMB) Congress** meeting in Cairns, Australia, June 2024
21. Organizing committee and session chair for **Plant Vascular Biology** 2025 meeting in Japan, July, 2025

INVITED LECTURES at International Conferences /University (since 2010):

- 2010 Seminar given at Department of Plant Biology, **University of California, Davis, CA, USA**
 2010 Invited speaker at **SDCMA 10TH ANNIVERSARY SYMPOSIUM**, San Diego, CA, USA
 2010 Seminar given at Department of Botany and Plant Sciences, **University of California, Riverside, CA, USA**

- 2010 Invited speaker at **Nitrogen 2010**, Inuyama, Japan.
- 2010 Plenary speaker at **International Workshop on Plant Membrane Biology XV**, the University of Adelaide, Australia
- 2010 Seminar given at College of Resources and Environmental Sciences, **Nanjing Agricultural University**, Nanjing, China.
- 2011 Keynote speaker at **Annual Plant Biotech Denmark Meeting 2011**, Copenhagen, Denmark
- 2011 Invited speaker at the **9th Cross-Strait Symposium on Plant Molecular Biology and Biotechnology**, Taichung, Taiwan
- 2011 Invited speaker at **the 8th Cross-Strait Symposium on Cell Biology**, Tainan, Taiwan
- 2011 Invited speaker at **the 2nd International Conference on Plant Metabolism**, Qingdao, China
- 2011 Seminar given at Institute of Plant Physiology and Ecology, **Shanghai Institutes for Biological Sciences**, Chinese Academy of Sciences, Shanghai, China.
- 2012 Invited speaker at Plant Growth, **Nutrition and Environment Interactions 2012**, Vienna, Austria.
- 2012 Seminar given at **Institut für Biologie und Biotechnologie der Pflanzen, Universität Münster, Münster**, Germany.
- 2012 Invited speaker at **the 3rd Banff Conference on Plant Metabolism**, Banff, Alberta, Canada.
- 2012 Invited speaker at **the 10th International Plant Molecular Biology (IPMB) Congress**. Jeju. Republic of Korea
- 2012 Invited speaker at **International Workshop on Agriculture Resource Utilization and Soil Quality Improvement**, Nanjing, China
- 2013 Invited speaker at **International Workshop on Plant Membrane Biology 2013**, Kurashiki, Japan
- 2013 Invited Speaker at **2013 International Symposium on Agricultural Biotechnology: Emerging Topics on Plant Stress Biology**, Taipei, Taiwan
- 2013 Keynote speaker at The 30th **Annual Interdisciplinary Plant Group Symposium**, University of Missouri, US
- 2013 Invited Speaker at the 2nd International Symposium on the **Nitrogen Nutrition of Plants**, Puerto Varas, Chile
- 2014 Seminar given at **ZheJiang University**, Hangzhou, China
- 2014 Seminar given at **INRA Center de Versailles-Grignon**, Versailles, France
- 2014 Seminar given at **University of Washington**, Seattle, US
- 2015 Invited speakers at **Plant Responses to Stress**, Beijing, China
- 2015 Seminar given at International Conference on Arabidopsis Research 2015, Paris, France
- 2015 Chair for two sessions and invited speaker at **International Plant Molecular Biology 2015**, Iguazú Falls, Argentina-Brazil
- 2015 Plenary lecture at **Philippine Society of Biochemistry and Molecular Biology**, Manila, Philippines
- 2016 Seminar given at **Iranian Research Organization for Science and Technology**, Tehran, Iran
- 2016 Seminar given at **University of Maryland**, College Park, US
- 2016 Session Chair at International Workshop on **Plant Membrane Biology 2016**, Maryland, US
- 2016 Plenary lecture at International Conference on **Arabidopsis Research 2016**, Gyeongju, Republic of Korea
- 2016 Invited speaker at **EMBO conference: The Nitrogen Nutrition of Plants**, Montpellier, France
- 2016 Seminar given at **Fujian Agriculture and Forestry University**, Fujian, China
- 2017 Seminar given by PhD student Yu-Hsuan Cheng at **ASPB 2017**, Hawaii, US
- 2017 Session chair and speaker at **Taiwan-Japan Plant Biology 2017**, Taipei, Taiwan
- 2017 Plenary lecture at **Philippine Society of Biochemistry and Molecular Biology**, Manila, Philippines
- 2018 Plenary lecture at **International Plant Molecular Biology 2018**, Montpellier, France
- 2019 Invited speaker at **the 60th Annual Meeting of The Japanese Society of Plant Physiologists**. Nagoya, Japan
- 2019 Seminar given at **Okayama University**, Kurashiki, Japan
- 2019 Session Chair at **International Workshop on Plant Membrane Biology 2019** meeting in Glasgow, UK
- 2022 Speaker at section meeting of the **2022 Annual Meeting, National Academy of Science**, DC, USA
- 2022 Invited speaker at **Plant Vascular Biology 2022**, Berlin, Germany
- 2022 Plenary lecture at **International Conference German Society for Plant Sciences**, Bonn, Germany
- 2022 Invited speaker at **Universität Würzburg**, Würzburg, Germany
- 2022 Invited speaker at **Carnegie-Mellon University**, Pittsburgh, USA
- 2022 Nathan Edward Tolbert Memorial Lecture at **Michigan State University**, East Lansing, USA

2023 Invited speaker at **Gordon Conference, Organellar Channels and Transporters**, Castelldefels, Spain
 2023 Plenary lecture at the 5nd International Symposium on the **Nitrogen Nutrition of Plants**, Sydney, Australia
 2024 Invited speaker at Nagoya University, Japan
 2024 Invited speaker at **Gordon Conference, Plant Molecular Biology**, Holderness, USA
 2024 Invited speaker at **International Plant Molecular Biology 2024**, Cairns, Australia
 2024 Invited speaker at **University of California, San Diego**, USA
 2025 Invited speaker at **International Plant and Animal Genome Conference (PAG32)**, San Diego, USA
 2025 Invited speaker at **Plant Vascular Biology 2025**, Osaka, Japan

GRANT SUPPORTS

1/2023-12/2025 Academia Sinica Sustainability Science Research Program (SSRP), Academia Sinica,
Combining Machine Learning, Traditional Breeding and Gene Editing to Improve Nitrogen Use Efficiency in Rice,
 NT\$2,800,000 - 3,849,000 per year

8/2022-7/2027 Frontier Science Research Program, MOST
Study of novel transporters involved in retrieving nitrate from Vacuole, NT\$ 6,000,000 per year.

PUBLICATIONS:

1. **Tsay, Y.-F.**, Thompson, J. R., Rotenberg, O. M., Larkin, J. C., and Woolford, J. L.* (1988) Ribosomal protein synthesis is not regulated at the translation level in *Saccharomyces cerevisiae*: balanced accumulation of ribosomal proteins L16 and rp59 is mediated by turnover of excess protein. **Genes & Development** 2: 664-676. (Cited 107) (IF 7.5)
2. Woolford, J. L.*, Rotenberg, M. O., Larkin, J. C., Moritz, M., **Tsay, Y.-F.**, and Thompson, J. R. (1988) Genetic analysis of yeast ribosome biogenesis and function. in: **Genetics of Translation**, eds. M. F. Tuite et al. p131-145.
3. Moritz, M., Paulovich, A. G., **Tsay, Y.-F.**, and Woolford, J. L.* (1990) Depletion of ribosomal proteins L16 or rp59 disrupts ribosome assembly and nucleolar structure. **J. Cell Biol.** 111:2261-2274. (Cited 145) (IF 7.3)
4. LaBrie, S. T., Wilkinson, J. Q., **Tsay, Y.-F.**, Feldmann, K. A., and Crawford, N. M.* (1992) Identification of two tungstate-sensitive molybdenum cofactor mutants, *chl2* and *chl7*, of *Arabidopsis thaliana*. **Mol. Gen. Genet.** 233:169-176. (Cited 34) (IF 2.3)
5. **Tsay, Y.-F.**, Schroeder, J. I., Feldmann, K. A., and Crawford, N. M.* (1993) The herbicide sensitivity gene *CHL1* of *Arabidopsis* encodes a nitrate-inducible nitrate transporter. **Cell** 72:705-713. (Cited 992) (IF 45.6)
6. **Tsay, Y.-F.**, Frank, M. J., Page, T., Dean, C., and Crawford, N. M.* (1993) Identification of a mobile endogenous transposon in *Arabidopsis thaliana*. **Science** 260:342-344. (Cited 135) (IF 44.8)
7. Deshmukh, M., **Tsay, Y.-F.**, Paulovich, A. G., and Woolford, J. L.* (1993) Yeast ribosomal protein L1 is required for the stability of 5S rRNA and assembly of 60S subunits. **Mol. Cell. Biol.** 13(5):2835-2845. (Cited 184) (IF 5.3)
8. **Tsay, Y.-F.**, Shankweiler, G., Lake, J., and Woolford, J. L.* (1994) Localization of *Saccharomyces cerevisiae* ribosomal protein L16 on the surface of 60S by immunoelectron microscopy. **J. Biol. Chem.** 269(10):7579-7586. (Cited 17) (IF 4.0)
9. Huang, N.-C., Chiang, C.-S., Crawford, N. M., and **Tsay, Y.-F.*** (1996) *CHL1* encodes a component of the low-affinity nitrate uptake system in *Arabidopsis* and shows cell-type-specific expression in roots. **Plant Cell** 8(12):2183-2191. (Cited 261) (IF 10.0)
10. Frank, M. J., Liu, D., **Tsay, Y.-F.**, Ustach, C., and Crawford, N. M.* (1997) *Tag1* is an autonomous transposable element that shows somatic excision in both *Arabidopsis* and Tobacco. **Plant Cell** 9(10):1745-1756. (Cited 44) (IF 10.0)
11. Liu, K.-H., Huang, C.-Y., and **Tsay, Y.-F.*** (1999) CHL1 is a dual-affinity nitrate transporter of *Arabidopsis* involving in multiple phases of nitrate uptake. **Plant Cell** 11(5):865-874. (Cited 639) (IF 10.0)

12. Huang, N.-C., Liu, K.-H., Ho, H.-J., and **Tsay, Y.-F.*** (1999) Cloning and functional characterization of an Arabidopsis nitrate transporter gene that encodes a constitutive component of low-affinity uptake. *Plant Cell* 11(8):1381-1392. (Cited 475) (IF 10.0)
13. Lin, C.-M., Koh, S., Stacey, G., Yu, S.-M., Lin, T.-Y., and **Tsay, Y.-F.*** (2000) Cloning and functional characterization of a constitutively expressed nitrate transporter gene, OsNRT1, from rice. *Plant Physiol.* 122:379-388. (Cited 230) (IF 6.6)
14. Liu, K. H., and **Tsay, Y.-F.*** (2003) Switching between the two action modes of the dual-affinity nitrate transporter CHL1 by phosphorylation. *EMBO J.* 22:1005-1013. (Recommended by Faculty1000, 6 Stars) (Cited 644) (IF 9.5)
15. Jeong, J., Suh, S., Guan, C., **Tsay, Y.-F.**, Moran, N., Chang, J.-O., Chung, S.-A., Demchenko K. N., Pawlowski, K. and Lee Y.* (2004) A Nodule-specific Dicarboxylate Transporter from Alder is a member of the Peptide Transporter Family. *Plant Physiol.* 134:969-978. (Cited 130) (IF 6.6)
16. Chiang, C.-S., Stacey, G., and **Tsay, Y.-F.*** (2004) Mechanisms and functional properties of two peptide transporters, AtPTR2 and iPTR2. *J Biol Chem.* 279:30150-30157. (Cited 107) (IF 4.0)
17. Chiu, C.-C., Lin, C.-S., Hsia, A.-P., Su, R.-C., Lin, H.-L. and **Tsay, Y.-F.*** (2004) Mutation of a Nitrate Transporter, AtNRT1.4, Results in a Reduced Petiole Nitrate Content and Altered Leaf Development. *Plant and Cell Physiol.* 45:1139-1148. (Cited 281) (IF 4.0)
18. **Tsay, Y.-F.***, Chiu, C.-C., Tsai, C.-B., Ho, C.-H., and Hsu, P.-K. (2007) Nitrate transporters and peptide transporters. *FEBS Lett.* 581(12):2290-300. (Cited 711) (IF 3.0)
19. Lin, S.-H., Kuo, H.-F., Canivenc, G., Lin, C.-S., Lepetit, M., Hsu, P.-K., Tillard, P., Lin H.-L., Wang, Y.-Y., Tsai, C.-B. and **Tsay, Y.-F.*** (2008) Mutation of the Arabidopsis NRT1.5 nitrate transporter causes defective root-to-shoot nitrate transport. *Plant Cell* 20(9): 2514-2528. (Recommended by Faculty1000) (Cited 583) (IF 10.0)
20. Almagro, A., Lin, S.-H., and **Tsay, Y.-F.*** (2008) Characterization of AtNRT1.6 reveals a role of nitrate in early embryo development. *Plant Cell* 20(12):3289-3299. (Cited 243) (IF 10.0)
21. Hu, H.-C., Wang, Y.-Y., and **Tsay, Y.-F.*** (2009) AtCIPK8, a CBL-interacting protein kinase, regulates the low-affinity phase of the primary nitrate response. *Plant J.* 57(2):264-78. (Cited 391) (IF 6.2)
22. Ho, C.-H., Lin, S.-H., Hu, H.-C., and **Tsay, Y.-F.*** (2009) CHL1 functions as a nitrate sensor in plants. *Cell* 138, 1184-1194. (Recommended by Faculty1000, 12 stars) (Cited 1443) (IF 45.6)
23. Fan, S.-C., Lin, C.-S., Hsu, P.-K., Lin, S.-H., and **Tsay, Y.-F.*** (2009) The Arabidopsis nitrate transporter NRT1.7, expressed in phloem, is responsible for source-to-sink remobilization of nitrate. *Plant Cell* 21: 2750-2761. (Recommended by Faculty1000) (Cited 421) (IF 10.0)
24. Krouk, G.*, Crawford, N. M., Coruzzi, G. M., **Tsay, Y.-F.*** (2010) Nitrate signaling: adaptation to fluctuating environments. *Curr. Opin. Plant Biol.* 13(3):266-73. (Cited 425) (IF 8.3)
25. Ho, C.-H., and **Tsay, Y.-F.*** (2010) NO₃⁻, NH₄⁺, K⁺ sensing and signaling. *Curr. Opin. Plant Biol.* 13(5):604-10. (Cited 159) (IF 8.3)
26. **Tsay, Y.-F.***, and Hsu, P.-K. (2011) The Role of Plasma Membrane Nitrogen Transporters in Nitrogen Acquisition and Utilization. *Plant Cell Monographs.* 19: 223-236. (Cited 10)
27. **Tsay, Y.-F.***, Ho, C.-H., Chen, H.-Y., and Lin, S.-H. (2011) Integration of Nitrogen and Potassium Signaling. *Annu. Rev. Plant Biol.* 62: 207-226. (Cited 156) (IF 21.4)
28. Wang, Y.-Y., and **Tsay, Y.-F.*** (2011) Arabidopsis nitrate transporter NRT1.9 is important in phloem nitrate transport. *Plant Cell* 23: 1945-1957. (Cited 277) (IF 10.0)
29. Wang, Y.-Y., Hsu, P.-K., and **Tsay, Y.-F.*** (2012) Uptake, Allocation and Signaling of Nitrate. *Trends in Plant Science* 17(8):458-467. (Cited 784) (IF 17.4)
30. Schroeder, J. I., Delhaize, E., Frommer, W. B., Lou Guerinot, M., Harrison, M. J., Herrera-Estrella, L., Horie, T., Kochian, L. V., Munns, R., Nishizawa, N. K., **Tsay, Y.-F.**, Sanders, D. (2013) Using Membrane Transporters to Improving Crops for Sustainable Food Production. *Nature* 497 (7447):60-66. (Recommended by Faculty1000) (Cited 623) (IF 50.5)

31. Hsu, P.-K., and **Tsay, Y.-F.*** (2013) Two Phloem Nitrate Transporters, NRT1.11 and NRT1.12, Are Important for Redistributing Xylem-borne Nitrate to Enhance Plant Growth. *Plant Physiol.* 163(2):844-56. (Recommended by Faculty1000) (Cited 214) (IF 6.6)
32. L  ran, S., Varala, K., Boyer, J. C., Chiurazzi, M., Crawford, N., Daniel-Vedele, F., David, L., Dickstein, R., Fernandez, E., Forde, B., Gassmann, W., Geiger, D., Gojon, A., Gong, J.M., Halkier, B.A., Harris, J.M., Hedrich, R., Limami, A.M., Rentsch, D., Seo, M., **Tsay, Y.-F.**, Zhang, M., Coruzzi, G., Lacombe, B.* (2014) A unified nomenclature of NITRATE TRANSPORTER 1/PEPTIDE TRANSPORTER family members in plants. *Trends Plant Sci.* 19(1):5-9. (Cited 724) (IF 17.4)
33. **Tsay, Y.-F.*** (2014) How to switch affinity? *Nature* 507(7490):44-5. (Cited 39) (IF 50.5)
34. Chen, W.-J., Hsieh, F.-C., Hsu, F.-C., **Tsay, Y.-F.**, Liu, J.-R., and Shih, M.-C.* (2014). Characterization of insecticidal toxin and pathogenicity of *Pseudomonas taiwanensis* against insects. *PLoS Pathogens* 10(8): e1004288. (Cited 53) (IF 5.5)
35. Li, Y., Ouyang, J., Wang, Y.-Y., Hu, R., Xia, K., Duan, J., Wang, Y., **Tsay, Y.-F.** and Zhang, M.* (2015) Disruption of the rice nitrate transporter OsNPF2.2 hinders root-to-shoot nitrate transport and vascular development. *Scientific Rep.* 5: 9635. (Cited 124) (IF 3.8)
36. Long, S.R., Kahn, M., Seefeldt, L., **Tsay, Y.-F.**, and Kopriva, S. (2015). Nitrogen and Sulfur. In **Biochemistry & Molecular Biology of Plants**, B.B. Buchanan, W. Gruissem, and R.L. Jones, eds (West Sussex, UK: John Wiley & Sons, Ltd.) (Cited 40)
37. Lin, Y.-L. and **Tsay, Y.-F.*** (2017) Influence of differing nitrate and nitrogen availability on flowering control in Arabidopsis. *J Exp. Bot.* 68(10):2603-2609. (Cited 136) (IF 5.8)
38. Li, Z., Wang, R., Gao, Y., Wang, C., Zhao, L., Xu, N., Chen, K.-E., Qi, S., Zhang, M., **Tsay, Y.-F.**, Crawford, N. M. and Wang, Y.* (2017) The *Arabidopsis* CPSF30-L gene plays an essential role in nitrate signaling and regulates the nitrate transceptor gene NRT1.1. *New Phytol.* 216:1205-1222. (Cited 75) (IF 8.3)
39. Wang, Y.-Y., Cheng, Y.-H. Chen, K.-E. and **Tsay, Y.-F.*** (2018) Nitrate transport, signaling and NUE. *Annu. Rev. Plant Biol.* 69:85-122. (Cited 608) (IF 21.4)
40. Chen, K.-E., Chen, H.-Y., Tseng, C.-S., and **Tsay, Y.-F.*** (2020) Improving nitrogen use efficiency by manipulating nitrate remobilization in plants. *Nature Plants* 6(9):1126-1135 (Cited 175) (IF 15.8)
41. Chen, H.-Y., Lin, S.-H., Cheng, L.-H. Wu, J.-J. Lin, Y.-C., and **Tsay, Y.-F.*** (2021) Potential transceptor AtNRT1.13 modulates shoot architecture and flowering time in a nitrate-dependent manner. *Plant Cell* 33: 1492-1505 (Cited 33) (IF 10.0)
42. Ma, J.-F.*, and **Tsay, Y.-F.** (2021) Transport systems of mineral elements in plants: Transporter, regulations and utilization. *Plant and Cell Physiol.* 62:539-540 (Cited 23) (IF 4.0)
43. **Tsay, Y.-F.***, Blatt MR, Gilliam M, Maurel C, von Wir  n N. (2022) Integrating membrane transport, signaling and physiology. *Plant Physiol.* 188(2): 921-923 (IF 6.6)
44. **Tsay, Y.-F.**, and Radutoiu, S. (2022). Chapter 12: Assimilation of Inorganic Nutrients. In **Plant Physiology and Development**, 7th Edition, Taiz, L., Zeiger, E., M  ller, I. M., and Murphy, A., eds (Oxford University Press)
45. Lin, Y.-C. and **Tsay, Y.-F.*** (2023) Study of vacuole glycerate transporter NPF8.4 reveals a new role of photorespiration in C/N balance. *Nature Plants* 9(5):803-816 (Cited 15) (IF 15.8)
46. Cheng, Y.-H., Durand, M., Brehaut, V., Hsu, F.-C., Kelemen, Z., Texier, Y., Krapp, A.*, **Tsay, Y.-F.*** (2023) Interplay between NIN-Like proteins 6 and 7 in nitrate signaling. *Plant Physiol.* 192(4):3049-3068 (Cited 25) (IF 6.6)
47. Wang M.-J. and **Tsay, Y.-F.*** (2025) NRT1.1 is a versatile coordinator of nutrient and hormone signaling in plants. *Developmental Cell* 2025 Nov 3;60(21):2847-2849.
48. Yen, C.-Y., Huang, Y.-S., Lin, MG, Sun, X.-H., **Tsay, Y.-F.**, Sun, Y.-J., Hsiao, C.-D.* Structural and mechanistic insights into nitrate transport in AtNRT1.1: The impact of His356 protonation and Thr101 phosphorylation effect. *Protein Sci.* 2026 Jan;35(1):e70435.

49. Wang M.-J., Tsai, Y.-T. and Tsay, Y.-F.* (2025) A novel vacuole nitrate efflux transporter in Arabidopsis. (submitted)

* Corresponding author

H index = 36, i10 index=43, total cites: 12944 (using Google Scholar)

PATENT ISSUED:

1. Method for Changing Nitrogen Utilization Efficiency in Plants, Taiwan Patent, Patent No.: I4186322, Date of Patent: Dec. 11, 2013
2. Method for Changing Nitrogen Utilization Efficiency in Plants, United States Patent, Patent No.: US 9,228,196 B2, Date of Patent: Jan. 5, 2016 (Cited 6)

RESEARCH ACCOMPLISHMENTS (Past 5 years)

A. Transceptor NRT1.13 monitor nitrate content in the xylem to modulate shoot architecture and flowering time in a nitrate-dependent manner. *Plant Cell* 33: 1492-1505 (Chen et al., 2021)

NRT1.1 (CHL1), the first nitrate transceptor identified, monitor external nitrate level and induced transcriptional responses (named as primary nitrate response) in a concentration dependent manner. The next key question is how internal nitrate is sensed? To address this question, we characterized a transceptor, NRT1.13/NPF4.4 in the *NRT1/PTR/NPF* family. Without the conserved proline residue essential for nitrate transport activity, NRT1.13 showed no nitrate transport activity. NRT1.13 S487P regained nitrate uptake activity, suggesting that wild-type NRT1.13 cannot transport nitrate but can bind it. NRT1.13 is expressed at the parenchyma cells next to xylem. At normal nitrate, *nrt1.13* showed no severe growth phenotype. However, at low nitrate, *nrt1.13* showed delayed flowering, increased node number, retarded branch outgrowth, and reduced lateral nitrate allocation to nodes. In addition to light and temperature, nutrients also play an important role in regulating flowering. FLC acts in the down stream of NRT1.13 for the nitrate-dependent regulation of flowering control. Study of NRT1.13 indicated that NRT1.13 is required for low nitrate acclimation and that internal nitrate is monitored near xylem to regulate shoot architecture and flowering time.

B. Interplay between NIN-like proteins NLP6 and 7 in nitrate signaling. *Plant Physiology* 192(4):3049-3068 (Cheng et al., 2023)

Transcription factor NLP7 (NIN-Like protein 7) is required primary nitrate (transcriptional) response (PNR), and RWP-RK domain of NLP7 can bind to the nitrate-responsive cis element. NLP6 is the closest homologue of NLP7, but *in planta* function of NLP6 remain unclear. In this study, we elucidate the *in vivo* function of NLP6 and its interplay with NLP7. Our four major findings about NLP6/7 are:

1) NLP6 and 7 are positive regulators for nitrate response, and NLP7 plays a more dominant role in regulating PNR.

60% of nitrate responsive genes (292 out of 483 genes) in PNR are regulated by NLP6 and/or NLP7. NLP7 plays a more dominant role in regulating PNR. There are two types of responses; in type I (200 genes), *nlp6nlp7* shows the similar effect as *nlp7*; while in type II (78 genes), *nlp6nlp7* shows the synergistic effect compared to *nlp6* or *nlp7*. These patterns indicate that NLP6 and NLP7 function in parallel to regulate type II genes while only NLP7 is required to regulate type I genes.

2) NLP6 and NLP7 act as repressor under ammonium condition to regulate different set of genes.

For this regulation, NLP6 and NLP7 are functional redundant. When ammonium is the sole nitrogen source, expression levels of 209 genes in *nlp6nlp7* double mutants are 2 fold higher, compared to wild type, while no gene shows altered expression in *nlp6* or *nlp7* single mutant. The activator and repressor activity of NLP6/7 are confirmed by CHIP-PCR and promoter assays. Taken together, functionalities of NLP6/7 and the cooperation patterns between NLP6 and NLP7 depend on the nitrogen sources.

C. Study of vacuole glycerate transporter NPF8.4 reveals a new role of photorespiration in C/N balance. *Nature Plant* 9(5):803-816 (Lin and Tsay, 2023)

Photorespiration is known to be involved in carbon recycling during RuBisCo oxygenation, but our study on glycerate transporter NPF8.4 revealed novel function of photorespiration in nitrogen flux. NPF8.4 is a tonoplast glycerate influx transporter responsible for sequestering the photorespiratory carbon intermediate glycerate into vacuoles during nitrogen depletion. Short-term N deficiency causes stimulated photorespiration and expression of *NPF8.4*. The ammonium released from increased photorespiration upon N depletion potentially serves as an immediate N source for compositional shift among amino acids, enabling survival under N stress. Mutant *npf8.4* shows growth retardation and early senescence phenotype upon N depletion, indicating that sequestering excess carbon glycerate into vacuoles by NPF8.4 plays an important role in alleviating the impact of high C/N ratio under N deficiency.

FUTURE DIRECTIONS:

A. The roles of DTXs in Regulating Vacuole Nitrate Homeostasis and Nitrate Distribution

After the first nitrate transporter gene being isolated in 1993, nitrate transporters in four families including NRT1, NRT2, SLAC and CLC have been subsequently found and characterized. Despite of studying nitrate transport at the molecular level for thirty years, transporter for vacuole nitrate efflux remains unknown. By identifying vacuole nitrate efflux transporter, we can put the missing piece of the puzzle to complete the comprehensive picture of nitrate homeostasis regulation, and provide new markers for molecular breeding to improve NUE for sustainable agriculture.

We employed a reverse genetic approach to screen for mutant defective in vacuole nitrate retrieval, and identified DTX16, a member of the Multidrug and Toxic Compound Extrusion (MATE) transporter family. The loss-of-function mutant *dtx16* accumulated more nitrate in vacuole and exhibited growth retardation during nitrate starvation, demonstrating that retrieving nitrate from the vacuole is a critical process for sustaining plant growth under nitrogen-limiting conditions. *DTX16* expression reaches its maximum at dusk. Further studies revealed that retrieving nitrate from the vacuole is not only a survival strategy during nitrogen starvation but also a daily process to maximize plant growth and nitrogen utilization efficiency. Even when external nitrate supply is sufficient, DTX16 cooperates with NRT1.7 to retrieve nitrate from vacuole at dusk and then remobilize nitrate from old leaves to young leaves on a daily basis, ensuring optimal nitrate distribution to developing leaves.

Evolutionary analyses coupled with functional characterization of MpMATE1, the liverwort orthologue of AtDTX16, show that vacuolar nitrate retrieval is present in bryophytes. Structural modeling and site-directed mutagenesis reveal a motif for nitrate transport activity mainly in streptophyte lineages, suggesting a link of nitrate retrieval to terrestrial adaptation.

By genome-wise associate studies (GWAS) of nitrate content ratio between old and young leaf, we identify another DTX transporter DTX19. Similar to DTX16, DTX19 also exhibits nitrate transport activity and is located in the tonoplast. DTX16 is expressed in mesophyll cells but DTX19 is specifically expressed in guard cells. Vacuole nitrate content in guard cells should only contribute very small portion of total leaf nitrate content. This makes us speculate that nitrate homeostasis in guard cell may play some role in regulating nitrate distribution among leaves. We will elucidate this signaling role of DTX19.

B. Molecular Mechanisms of Nitrogen Signaling and Their Interplay with Other Signals

Plants need to integrate external and internal nitrogen (N) status to maximize utilization efficiency and growth. N signaling and other nutrient signals must be coordinated for this optimization. We are interested to use two modules to address this key issue.

The transporter CHL1 functions as a transceptor to monitor external nitrate and trigger a transcriptional response known as the primary nitrate response (PNR) in a concentration-dependent manner. How signals perceived in the plasma membrane are transmitted to the nucleus is an interesting and unresolved question in transceptor signaling. NLP7 is the major transcription factor for the primary nitrate response. Our evidence shows that the transceptor CHL1 can interact with NLP7. Leaving the plasma membrane is dependent on nitrate- and CHL1-, and is critical for NLP7 to trigger primary nitrate

response. Moreover, NLP7 acts as a positive regulator in the presence of nitrate, but as a negative regulator in the presence of ammonium. In this study, we will employ molecular, biochemical, and genetic approaches to find out how NLP7 is modulated by CHL1 to trigger the transcriptional responses in a concentration dependent manner, and how NLP7 switched between being positive and negative regulator in response to different N sources.

The second module is ATM, which encodes serine hydroxymethyltransferase (SHMT). SHMT adds one-carbon and converts the two-carbon compound glycine back to the three-carbon compound serine during photorespiration. However, ATM, a unique SHMT, does not process enzyme activity and is instead located in the nucleus regulating gene expression. In this study, we seek to understand how ATM functions as a one-carbon sensor to regulate the crosstalk among carbon, sulfate, and ammonium.

C. Searching for key genes regulating nitrogen utilization efficiency of rice

Worldwide, 110 million tons of nitrogen fertilizers are consumed each year. The production of nitrogen fertilizer consumes 2% of global energy. Nevertheless, the nitrogen utilization efficiency (NUE) of most crop cultivars is quite low with only 30-50 % of the nitrogen fertilizer applied being utilized by crops. The nitrogen fertilizer left in the soil causes severe environmental problems. Taiwan ranks eighth on the list of the countries that use excessive amounts of nitrogen fertilizer. Rice is the major crop in Taiwan, and we aim to identify new genes and strategies to enhance nitrogen utilization efficiency in Taiwan.

Building on observations that *indica* rice exhibits higher NUE than *japonica*, and preliminary transcriptome analysis suggesting NPF4.10 is closely associated with NUE traits, this proposal investigates NPF4.10's role in increased root-to-shoot nitrate translocation in *indica*. Functional validation will involve gene editing, promoter analysis, and transport assays.

Additional candidate genes will be identified through comparative transcriptome analysis of *indica* and *japonica* cultivars under varying nitrogen levels. We will also analyze physiological and transcriptomic responses in key Taiwanese rice cultivars to identify gene-trait associations linked to NUE. Finally, we will study the high-NUE AZ358 mutant, which exhibits increased tillering and grain yield under low nitrogen conditions, to identify the underlying genetic mechanisms.

Validated genes and alleles will be introduced into TN11, Taiwan's leading rice variety, to develop high-NUE lines, promoting sustainable agriculture and reducing environmental nitrogen pollution. On the other hand, our previous study showed that introducing chimeric hyperactive nitrate transporter NC4N driven by NRT1.7 promoter can enhance nitrate remobilization and therefore enhance nitrogen utilization efficiency in rice by 8-11%. Since GMO is still an issue in Taiwan as well as a lot of countries, we will collaborate with Prof. Yi-Chen Lin at Fu Jen Catholic University and Choun-Sea Lin at ABRC, Academia Sinica to introduce hyperactive nitrate transporter by gene editing.