

are in fact adaptive in both cases (i.e. can different and even opposite trait responses increase fitness in different species under a given set of external stimuli?). Proof of adaptive plasticity also requires analysis of fitness in multiple environments.

John A. Strand^{1*} and Stefan E. B. Weisner²

¹The Rural Economy and Agricultural Society of Halland, Lilla Boslid, SE -310 31 Eldsberga, Sweden; ²Wetland Research Centre, Halmstad University, Box 823, SE -301 18 Halmstad, Sweden (*Author for correspondence: tel +46 (0)35 46518; fax +46 (0)35 46529; email John.Strand@hs.halland.net)

References

- Agrawal AA. 2001. Phenotypic plasticity in the interaction and evolution of species. *Science* 294: 321–326.
- Bradshaw AD. 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* 13: 115–155.
- Coleman JS, McConnaughay KDM, Ackerly DD. 1994. Interpreting phenotypic variation in plants. *Trends in Ecology and Evolution* 9: 187–191.
- De Jong G. 1995. Phenotypic plasticity as a product of selection in a variable environment. *American Naturalist* 145: 493–512.
- DeWitt TJ, Scheiner SM. 2004. *Phenotypic plasticity: functional and conceptual approaches*. New York, NY, USA: Oxford University Press.
- DeWitt TJ, Sih A, Wilson DS. 1998. Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution* 13: 77–82.
- Dudley SA, Schmitt J. 1996. Testing the adaptive plasticity hypothesis: density-dependent selection on manipulated stem length in *Impatiens capensis*. *American Naturalist* 147: 445–465.
- Evans GC. 1972. *The quantitative analysis of plant growth*. Berkeley, CA, USA: University of California Press.
- Jasienski M, Ayala FJ, Bazzaz FA. 1997. Phenotypic plasticity and similarity of DNA among genotypes of an annual plant. *Heredity* 78: 176–181.
- Lachmann M, Lablonka E. 1996. The inheritance of phenotypes: an adaptation to fluctuating environments. *Journal of Theoretical Biology* 181: 1–9.
- Moran NA. 1992. The evolutionary maintenance of alternative phenotypes. *American Naturalist* 139: 971–989.
- Pigliucci M. 1996. How organisms respond to environmental changes: from phenotypes to molecules (and vice versa). *Trends in Ecology and Evolution* 11: 168–173.
- Pigliucci M. 2002. Touchy and bushy: phenotypic plasticity and integration in response to wind stimulation in *Arabidopsis thaliana*. *International Journal of Plant Science* 163: 399–408.
- Preston KA. 1999. Can plasticity compensate for architectural constraints on reproduction? Patterns of seed production and carbohydrate translocation in *Perilla frutescens*. *Journal of Ecology* 87: 697–712.
- Puijalon S, Bornette G. 2004. Morphological variation of two taxonomically distant plant species along a natural flow velocity gradient. *New Phytologist* 163: 651–660.
- Schlichting CD. 1986. The evolution of phenotypic plasticity in plants. *Annual Review of Ecology and Systematics* 17: 667–693.
- Schlichting CD, Pigliucci M. 1998. *Phenotypic evolution: a reaction norm perspective*. Sunderland, MA, USA: Sinauer Associates Inc.
- Stearns SC. 1989. The evolutionary significance of phenotypic plasticity. *Bioscience* 29: 436–445.
- Sultan SE. 1992. What has survived of Darwin's theory? *Evolutionary Trends in Plants* 6: 61–71.
- Via S. 1993. Adaptive phenotypic plasticity: target or by-product of selection in a variable environment? *American Naturalist* 142: 352–365.

Key words: adaptation, aquatic macrophytes, evolution, morphology, phenotypic plasticity.

Letters

The Cohesion-Tension Theory

In the June 2004 (162: 3) issue of *New Phytologist*, U. Zimmermann *et al.* published a Tansley review that criticizes the work of many scientists involved in the study of long-distance water transport in plants (Zimmermann *et al.*, 2004). Specifically, the review attempts to 'show that the arguments of the proponents of the Cohesion Theory are completely misleading'. We, the undersigned, believe that this review is misleading in its discussion of the many

recent papers which demonstrate that the fundamentals of the Cohesion-Tension theory remain valid (Holbrook *et al.*, 1995; Pockman *et al.*, 1995; Steudle, 1995; Milburn, 1996; Sperry *et al.*, 1996; Tyree, 1997; Melcher *et al.*, 1998; Comstock, 1999; Stiller & Sperry, 1999; Tyree, 1999; Wei *et al.*, 1999a; Wei *et al.*, 1999b; Cochard *et al.*, 2000; Cochard *et al.*, 2001a; Cochard *et al.*, 2001b; Richter, 2001; Steudle, 2001; Cochard, 2002; Tyree & Zimmermann, 2002; Tyree, 2003; Tyree & Cochard, 2003; Tyree *et al.*, 2003). We wish the readers of *New Phytologist* to know that the Cohesion-Tension theory is widely supported as the only theory consistent with the preponderance of data on water transport in plants.

Guillermo Angeles, Instituto de Ecología, A.C., Mexico
Barbara Bond, Oregon State University, USA
John S. Boyer, University of Delaware, USA
Tim Brodribb, Harvard University, USA
J. Renée Brooks*, U.S. EPA, Oregon, USA
Michael J. Burns, formerly Harvard University, USA
Jeannine Cavender-Bares, University of Minnesota, USA
Mike Clearwater, HortResearch, New Zealand
Hervé Cochard, INRA, Clermont-Ferrand, France
Jonathan Comstock, Cornell University, USA
Stephen D. Davis, Pepperdine University, USA
Jean-Christophe Domec, Oregon State University, USA
Lisa Donovan, University of Georgia, USA
Frank Ewers, Michigan State University, USA
Barbara Gartner, Oregon State University, USA
Uwe Hacke, University of Utah, USA
Tom Hinckley, University of Washington, USA
N. Michelle Holbrook, Harvard University, USA
Hamlyn G. Jones, University of Dundee, UK
Kathleen Kavanagh, University of Idaho, USA
Bev Law, Oregon State University, USA
Jorge López-Portillo, Instituto de Ecología, A.C., Mexico
Claudio Lovisolo, University of Turin, Italy
Tim Martin, University of Florida, USA
Jordi Martínez-Vilalta, University of Edinburgh, UK
Stefan Mayr, University Innsbruck, Austria
Fredrick C. Meinzer, U.S. Forest Service, Oregon, USA
Peter Melcher, Ithaca College, USA
Maurizio Mencuccini, University of Edinburgh, UK
Stephen Mulkey, University of Florida, USA
Andrea Nardini, University of Trieste, Italy
Howard S. Neufeld, Appalachian State University, USA
John Passioura, CSIRO Plant Industry, Australia
William T. Pockman, University of New Mexico, USA
R. Brandon Pratt, Pepperdine University, USA
Serge Rambal, CNRS, Montpellier, France
Hanno Richter, Institute of Botany, Austria
Lawren Sack, University of Hawaii, USA
Sebastiano Salleo, University of Trieste, Italy
Andrea Schubert, University of Turin, Italy
Paul Schulte, University of Nevada, USA
Jed P. Sparks, Cornell University, USA
John Sperry, University of Utah, USA
Robert Teskey, University of Georgia, USA
Melvin Tyree, U.S. Forest Service, Vermont, US

(*Author for correspondence:
tel +1 541 7544684; fax +1 541 7544799;
email Brooks.ReneeJ@epa.gov)

References

- Cochard H. 2002. A technique for measuring xylem hydraulic conductance under high negative pressures. *Plant, Cell & Environment* 25: 815–819.
- Cochard H, Ameglio T, Cruiziat P. 2001a. The cohesion theory debate continues. *Trends in Plant Science* 6: 456.
- Cochard H, Bodet C, Ameglio T, Cruiziat P. 2000. Cryo-scanning electron microscopy observations of vessel content during transpiration in walnut petioles. Facts or artifacts? *Plant Physiology* 124: 1191–1202.
- Cochard H, Forestier S, Ameglio T. 2001b. A new validation of Scholander pressure chamber technique based on stem diameter variations. *Journal of Experimental Botany* 52: 1361–1365.
- Comstock JP. 1999. Why Canny's theory doesn't hold water. *American Journal of Botany* 86: 1077–1081.
- Holbrook NM, Burns MJ, Field CB. 1995. Negative xylem pressures in plants: a test of the balancing pressure technique. *Science* 270: 1193–1194.
- Melcher PJ, Meinzer FC, Yount DE, Goldstein GH, Zimmermann U. 1998. Comparative measurements of xylem pressure in transpiring and non-transpiring leaves by means of the pressure chamber and the xylem pressure probe. *Journal of Experimental Botany* 49: 1757–1760.
- Milburn JA. 1996. Sap ascent in vascular plants: Challengers to the Cohesion Theory ignore the significance of immature xylem and the recycling of Munch water. *Annals of Botany* 78: 399–407.
- Pockman WT, Sperry JS, O'Leary JW. 1995. Sustained and significant negative water pressure in xylem. *Nature* 378: 715–716.
- Richter H. 2001. The cohesion theory debate continues: the pitfalls of cryobiology. *Trends in Plant Science* 6: 456–457.
- Sperry JS, Saliendra NZ, Pockman WT, Cochard H, Cruiziat P, Davis SD, Ewers FW, Tyree MT. 1996. New evidence for large negative xylem pressures and their measurement by the pressure chamber method. *Plant, Cell & Environment* 19: 427–436.
- Stedle E. 1995. Trees under tension. *Nature* 378: 663–664.
- Stedle E. 2001. The cohesion-tension mechanism and the acquisition of water by plant roots. *Annual Review of Plant Physiology and Molecular Biology* 52: 847–875.
- Stiller V, Sperry JS. 1999. Canny's Compensating Pressure Theory fails a test. *American Journal of Botany* 86: 1082–1086.
- Tyree MT. 1997. The Cohesion-Tension theory of sap ascent: current controversies. *Journal of Experimental Botany* 48: 1753–1765.
- Tyree MT. 1999. The forgotten component of plant water potential: a reply. Tissue pressures are not additive in the way M.J. Canny suggests. *Plant Biology* 1: 598–601.
- Tyree MT. 2003. The ascent of water. *Nature* 423: 923.
- Tyree MT, Cochard H. 2003. Vessel content of leaves after excision: a test of the Scholander assumption. *Journal of Experimental Botany* 54: 2133–2139.
- Tyree MT, Cochard H, Cruiziat P. 2003. The water-filled versus air-filled status of vessels cut open in air: The 'Scholander assumption' revisited. *Plant, Cell & Environment* 26: 613–621.
- Tyree MT, Zimmermann MH. 2002. *Xylem structure and the ascent of sap*. Berlin, Germany: Springer Verlag.
- Wei C, Stedle E, Tyree MT. 1999a. Water ascent in plants: do ongoing controversies have a sound basis? *Trends in Plant Science* 4: 372–375.
- Wei C, Tyree MT, Stedle E. 1999b. Direct measurement of xylem pressure in leaves of intact maize plants. A test of the Cohesion-Tension theory taking hydraulic architecture into consideration. *Plant Physiology* 121: 1191–1205.
- Zimmermann U, Schneider H, Wegner LH, Haase A. 2004. Water ascent in tall trees: does evolution of land plants rely on a highly metastable state? *New Phytologist* 162: 575–615.

Key words: cohesion-tension theory, Tansley reviews, long-distance transport, water transport, xylem.