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. Weisner[2]

[1]The Rural Economy and Agricultural Society of Halland,
Lilla Boslid, SE –310 31 Eldsberga, Sweden; [2]Wetland
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.

Steudle E. 1995. Trees under tension. *Nature* **378**: 663–664.

Steudle 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, Steudle 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, Steudle 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.

© *New Phytologist* (2004)

Editorial

Tansley reviews

Authors of Tansley reviews, which are fully peer-reviewed papers, are asked to consider two major themes in their writing. First, to deal with major research topics in some depth – to provide a 'touchstone' for those intending to enter the field. Second, to consider the review less as an exercise in literature documentation and more as a forum for the presentation of ideas. The balance between these two themes varies widely, depending on the subject and the individual, but we aim to make the distinction clear.

Where views and opinions are expressed in a Tansley review, or indeed any *New Phytologist* paper, these naturally belong to the authors. This is, we believe, clearly the case in the writing of the Tansley review by Zimmermann *et al.* in our June 2004 (162: 3) issue (Zimmermann *et al.*, 2004).

The Tansley reviews and our forum section encourage debate in *New Phytologist*. We therefore welcome discussion, in this instance concerning the work of Zimmermann *et al.* through the comments of Angeles *et al.* (2004), which complement recent and relevant publications in *New Phytologist* by Brodribb & Holbrook (2004) and Sperry (2004).

Ian Woodward
Editor-in-Chief

References

Angeles G, Bond B, Boyer JS, Brodribb T, Brooks JR, Burns MJ, Cavender-Bares J, Clearwater M, Cochard H, Comstock J, Davis SD, Domec J-C, Donovan L, Ewers F, Gartner B, Hacke U, Hinckley T, Holbrook NM, Jones HG, Kavanagh K, Law B, López-Portillo J, Lovisolo C, Martin T, Martínez-Vilalta J, Mayr S, Meinzer FC, Melcher P, Mencuccini M, Mulkey S, Nardini A, Neufeld HS, Passioura J, Pockman WT, Pratt RB, Rambal S, Richter H, Sack L, Salleo S, Schubert A, Schulte P, Sparks JP, Sperry J, Teskey R, Tyree M. 2004. The Cohesion-Tension Theory. *New Phytologist* **163**: 451–452.

Brodribb TJ, Holbrook NM. 2004. Stomatal protection against hydraulic failure: a comparison of coexisting ferns and angiosperms. *New Phytologist* **162**: 663–670.

Sperry JS. 2004. Coordinating stomatal and xylem functioning – an evolutionary perspective. *New Phytologist* **162**: 568–570.

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: Tansley reviews, peer review, forum, cohesion-tension theory, long-distance transport, water transport, xylem.

Letters

How dangerous is the use of fungal biocontrol agents to nontarget organisms?

Biological control of plant pathogens is a method based on the antagonism between microorganisms (Andrews, 1992) – fungi or bacteria known to be antagonistic to a given plant pathogen are artificially multiplied and then released into an agricultural field to control a plant disease. Most biocontrol agents (BCAs) of plant diseases, similar to most plant pathogens they control, are fungi. Their use is considered, in general, as a safe and environmentally friendly alternative for plant disease control compared to the application of conventional pesticides (Whipps & Lumsden, 2001). Recently, Brimner & Boland (2003) published a review of the nontarget effects of fungal BCAs of plant pathogens in which they attempt to demonstrate the way in which many hazards may be associated with the use of fungi as BCAs of plant diseases. However, as the examples highlighted here indicate, their case was based mainly on unsubstantiated statements, which might mislead and be detrimental to the application of BCAs in the future.

Brimner & Boland (2003) use expressions such as 'significant environmental impacts', 'significant threat' and 'unforeseen ecological repercussions' in order to dramatize suggested damaging effects of fungal BCAs. However, none of the data reviewed in the paper support these serious warnings. Similarly, key statements such as 'released BCAs have the

This is supplementary material to

G. Angeles, B. Bond, J.S. Boyer, T. Brodribb, J.R. Brooks, M.J. Burns, J. Cavender-Bares, M. Clearwater, H. Cochard, J. Comstock, S.D. Davis, J-C Domec, L. Donovan, F. Ewers, B. Gartner, U. Hacke, T. Hinckley, N.M. Holbrook, H.G. Jones, K. Kavanagh, B. Law, J. Lopez-Portillo, C. Lovisolo, T. Martin, J. Martinez-Vilalta, S. Mayr, F.C. Meinzer, P. Melcher, M. Mencuccini, S. Mulkey, A. Nardini, H.S. Neufeld, J. Passioura, W.T. Pockman, R.B. Pratt, S. Rambal, H. Richter, L. Sack, S. Salleo, A. Schubert, P. Schulte, J.P. Sparks, J. Sperry, R. Teskey, M. Tyree, "The Cohesion-Tension Theory", *New Phytologist* **163**: 451–452 (2004).

Ian Woodward, "Tansley reviews", *New Phytologist* **163**: 453 (2004).

Comment on "Water ascent in tall trees: does evolution of land plants rely on a highly metastable state?" by Ulrich Zimmermann, Heike Schneider, Lars H. Wegner, and Axel Haase (*New Phytologist 162*: 575–615.)

Abstract:
The critique given by Zimmermann *et al.* (2004) of Holbrook *et al.* (1995) is fundamentally flawed. Figure 1 of Holbrook *et al.* (1995) is a stick figure schematic illustration of the experiment presented in the paper, with the leaf chamber size and details given in footnote 13. Zimmermann *et al* display a fundamental misunderstanding of the correct application of the centrifugal force equation used in the experiment. Their imaginary scenario produces tensions 1/225th to 1/2500th of those needed to produce the 1:1 observations of Holbrook *et al.*, rather than produce tensions capable of providing an alternative path to the observed 1:1 observation. In addition, they mislead the reader by failing to point out that the water potential of the control leaves was independent of the angular velocity.

Details:

On page 615 of the article "Water ascent in tall trees: does evolution of land plants rely on a highly metastable state?" by Ulrich Zimmermann, Heike Schneider, Lars H. Wegner, and Axel Haase (*New Phytologist* **162**: 575–615), the authors state:

> "The experiment of Holbrook *et al.* (1995) is faced with the same shortcomings as the various 'vulnerability' methods. They used an excised stem segment with a single leaf at its midpoint, and mounted the midpoint of the stem on the rotating axis of a centrifuge-like set-up placed in a closed chamber. After centrifugation the authors removed the leaf and determined the balancing pressure value. In the light of the discussion in section III.3 tension in the xylem should be released instantaneously upon cutting (provided that no breakage of the water columns had occurred). Nevertheless, the authors found a 1 : 1 relationship between the (relative) pressure calculated from the centrifugation force and the balancing pressure. A possible explanation for the 1 : 1 correlation is that water was shifted into the periphery of the leaf (including the intercellular spaces) during centrifugation. Then, Newton's law that action has to equal reaction requires that the same force is needed to push water back from the tissue into the xylem. The problem for interpreting the data is the control experiment of Holbrook *et al.* (1995). It is obvious from the sketch in Fig. 1 of their paper that the control leaf, being not attached to the branch, was spun simultaneously, but not fixed close to the rotor axis of the centrifuge. In

> this case, the leaf is pressed against the wall of the chamber during rotation and, in turn, the centrifugal forces may act in a different way on the water in the control leaf compared to the fixed leaf. This could explain why the *P*b-values of the control leaves were significantly lower than those of the attached leaves by 0.2 to 0.4 MPa. A correlation with the calculated rotational tension can also not be expected under these conditions. However, the finding that the *P*b-values of the control leaves were significantly higher than the values of untreated leaves (0.05 MPa relative to atmosphere) evidences clearly that the control experiments were not properly designed."

To propose their hypothetical "flaw", Zimmermann *et al.* ignore the data in footnote 13 and instead propose an imaginary scenario they believe will produce the result they desire. *Taking Zimmerman et al.'s statements at face value*, the forces Zimmermann *et al.* describe shifting the water to "…the periphery of the leaf (including the intercellular spaces) during centrifugation" range from factors 2-3 orders of magnitude ***too small*** to account for the 1:1 relationship of the Scholander reading to the "calculated rotational tension" presented in Figure 2 of Holbrook *et al.* As clearly stated in footnote 13 of Holbrook *et al.*, the lengths of the *Cercis occidentalis* branches ranged from 30-100cm, thus the R’s used to calculate the "calculated rotational tension" (x-axis of Figure 2) ranged from 15-50cm while the maximum extension from the rotation axis any part of a leaf even using Zimmermann *et al.*'s incorrect description of the *Cercis occidentalis* leaves is 1cm, limited by the chamber size clearly stated in footnote 13. The induced tension in the water column at the rotation center is $T=0.5\sigma\omega^2 R^2$, where σ is the density of water, ω the angular velocity, and *R* is the distance from the axis of rotation to the end of the water column, which Holbrook *et al.*'s Figure 2 x-axis, was half the branch length. Zimmerman’s imaginary scenario results in a discrepancy of a factor of the square of half the total branch length to the square of the 1 cm leaf chamber radius, thus a discrepancy of 15^2:1 to 50^2:1 (225:1 - 2500:1) from the observed 1:1 ratio. In other words, since the x-axis of Figure 2 of Holbrook*et al.* is ***a calculated value*** using*R*'s of 15-50cm, and the induced tensions *anywhere* there is an intact water column depend on the water column R^2, leaves with a maximum moment arm (*R*) of 1cm cannot have tensions induced between their centers and peripheries sufficient to come anywhere near the calculated values where *R* ranged from 15 to 50cm. (The 1:1 line of Figure 2 of Holbrook *et al.)* Zimmermann *et al.*'s (erroneous) scenario could, based on simple physics any High School physics student would understand, induce tensions 1/225th to 1/2500th of those needed to produce the observed 1:1 observations of Holbrook *et al.* Thus **Zimmermann *et al.'s* imaginary "possible explanation" results in tensions *2 -3 orders of magnitude too small* to produce the observed 1:1 ratio of Figure 2**. Furthermore, had Zimmermann et al.'s imaginary scenario been valid, it would have had to also occur in the test leaves which would have resulted in the test leaves being indistinguishable from the control leaves, in direct contradiction with the actual observations.

In addition, had Zimmermann *et al.* looked up what *Cercis occidentalis* leaves look like, it would have been obvious that both the test and control leaves had to be wrapped together around the inner chamber walls, thus experiencing exactly the same forces and thus precluding their proposed scenario from occurring even with its deficiencies. In other words, the experiment of Holbrook *et al.* is even more robust than it may appear to an inattentive reader.

Given the overall tenor of Zimmermann *et al.*, we will leave it to the reader to speculate as to why Zimmermann *et al.* would advance the critique on Holbrook *et al.* that they did, hidden in the second appendix their paper and without presenting any estimates for the magnitude of the hypothesis they proposed despite such estimates being in a realm that any High School physics student could easily calculate.

Holbrook *et al.* (1995) - "Negative Xylem Pressures in Plants: A Test of the Balancing Pressure Technique", N. Michele Holbrook, Michael J. Burns, and Christopher B. Field, *Science* ***270***, 1193 (1995)

Zimmermann *et al.* (2004) -"Water ascent in tall trees: does evolution of land plants rely on a highly metastable state?", Ulrich Zimmermann, Heike Schneider, Lars H. Wegner, and Axel Haase *New Phytologist* ***162***: 575 (2004).)