

## Commentary

# A long drink of water: how xylem changes with depth

From the top of a coast redwood to roots deep within subterranean caves, water transport in trees is in the news. Evidence is accumulating that the distance water must travel within trees determines many of their structural properties. A recent study of some of the world's tallest trees demonstrated that maximum tree height appears to be limited by gravity and the resistance of the xylem pathway (Koch *et al.*, 2004). Rooting depth, by contrast, shows no such limitation, as revealed in this issue (see pp. 507–517). McElrone *et al.* (2004) gained access to deep tree roots through caves down to 20 m below the soil surface, matching roots to their above-ground shoots by comparing sequences of ribosomal DNA. Their study examines how differences between stems, shallow roots, and deep roots in key aspects of xylem structure enhance water transport from great depths up to the canopy. The study also provides indirect but compelling evidence for the cohesion-tension theory of water ascent in plants by demonstrating that patterns of tension in the xylem and vulnerability to cavitation are reflected in the structure of the conducting elements.

### Xylem anatomy

Plant anatomists have known for some time that xylem conduits (vessels and tracheids) within a plant tend to increase in diameter in a basipetal direction, from terminal branches down to the roots (Tyree & Zimmermann, 2002). According to Vernon Cheadle (1953), vessels themselves first evolved in roots, replacing less efficient tracheids. Differences in conduit diameter for stem and root xylem have been reported for a wide range of species; a typical example is provided by a quick examination of two-year-old saplings of basswood (*Tilia americana*), in which vessels in the second-year xylem are 1.8 times as wide in the roots as in the stem ( $P < 0.001$ ;  $n = 4$ ). Due to difficulties in root excavation, differences in conduit size along the length of roots have been less frequently observed, with a few exceptions. The desert shrub (and invasive species in arid soils) *Retama raetama* has horizontal roots up to 10 m long, with vessel elements increasing in width and length at increasing distances from the base of the stem (Fahn, 1990). Interestingly, these roots occupy a vertically restricted zone near the surface of the soil, where the gradient in soil moisture would be relatively slight. In a study of the hydraulic architecture

of trees in the Proteaceae, Pate *et al.* (1995) report increases in vessel diameter between shallow roots and so-called sinker roots and along sinker roots with increasing depth. The deepest roots sampled by Pate *et al.* were at 2 m below the soil surface, whereas McElrone *et al.* collected roots at depths from 7 to 20 m below the surface. For the conifer *Juniperus ashei*, tracheids in shallow roots and deep roots were about three and four times wider, respectively, than tracheids in stems; for the three dicotyledonous trees investigated, vessels in roots were an average of 1.5 (shallow) and 2.3 (deep) times wider than vessels in stems (Fig. 1). Such differences in xylem anatomy have profound consequences for water transport, as McElrone *et al.* discuss, due to the relationship between volumetric flow and conduit diameter raised to the fourth power.

### Water transport in the roots

If wide tracheids and vessels are so efficient at moving water, why are they more common in deep roots than elsewhere in trees? One argument put forward by McElrone *et al.* is that large conduits are necessary to minimize the hydraulic resistance associated with the great path length from deep roots to the canopy. For relatively short-statured trees such as those from the arid western USA, the depth of the roots can greatly exceed the height of the shoots, thus an adaptive premium is placed on minimizing below-ground hydraulic resistance. In other words, it behooves a tree to maximize the hydraulic conductance ( $K_b$ ;  $\text{m}^4 \text{MPa}^{-1} \text{s}^{-1}$ ) of its deepest roots. Based on the Ohm's law analogue, and ignoring direction and the gravitational component, the rate of water flow ( $F$ ;  $\text{m}^3 \text{s}^{-1}$ ) through the xylem in a plant axis can be expressed as

$$F = K_b (\Delta P_x / L)$$

where  $\Delta P_x$  (MPa) is the difference in pressure between the two ends of the axis and  $L$  (m) is the axis length (Tyree & Zimmermann, 2002). This simplified equation is useful to show that, as McElrone *et al.* state, large values of  $K_b$  can help maintain water flow despite large values of  $L$ . In addition, large  $\Delta P_x$  would not be required for water uptake by deep roots, and steep gradients in tension along the xylem could be avoided. Specific hydraulic conductivity,  $K_s$ , which is  $K_b$  divided by the transverse area of the conducting tissue (the stele in this case), for deep roots was 7–38 times greater than for stems and 1.2–2.4 times greater than for shallow roots (Fig. 1). While not as large as would be predicted on the basis of differences in conduit diameter,  $K_s$  measured

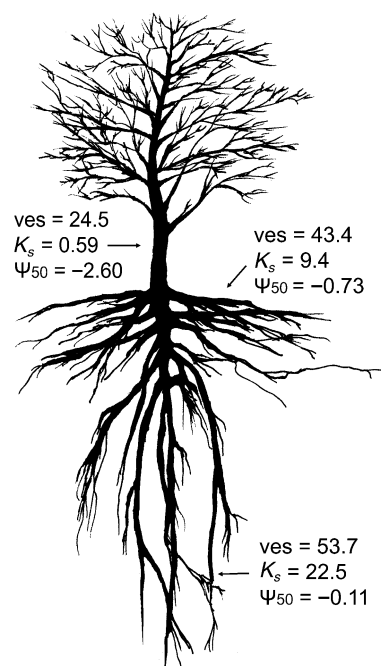
by McElrone *et al.* for deep roots would help offset their great distance from the leaves.

## The soil environment

Other reasons why xylem conduits are wider in deep roots than elsewhere within trees involve constraints that are relaxed due to the soil environment. As discussed by McElrone *et al.* deep roots experience biomechanical release: they are supported by the soil and unlike shallow roots are relatively unaffected by mechanical forces acting on the shoot. The reduced need for the xylem to provide structural support allows deep roots to be specialized for transport, with fewer xylem fibers, fewer rays (Pate *et al.*, 1995), more vessels or tracheids per transverse area, and conduits with larger lumens than in shallow roots and stems. Such specialization results not only in more efficient water uptake but also in reduced carbon allocation per unit length of root. Construction costs are lower due to more lumen and less cell wall per unit volume, and respiration costs are also lower due to the lower proportion of rays, fibers, and other living cells. Despite their lower construction and respiratory costs, deep roots are probably limited in length by carbon due to allometric considerations.

Constraints due to temperature are also relaxed in the soil environment of deep roots. A freeze-thaw episode is the environmental cause of embolism that has been linked most directly and consistently to conduit diameter (Ewers, 1985), and the lack of such episodes may account for the relative scarcity of wide-vesseled lianas in temperate regions. On an annual basis, a typical soil may vary by  $\pm 6^\circ\text{C}$  at 1 m below the surface but by only  $\pm 1^\circ\text{C}$  at 4 m (Nobel, 1999), thus deep roots of the Texas trees sampled by McElrone *et al.* never encounter freezing temperatures and are thus spared this cause of embolism. In addition, deep roots are also buffered against excessively high temperatures, which are associated with reduced vessel diameter in developing wheat roots (Huang *et al.*, 1991).

Perhaps the most important environmental constraint that is relaxed for deep roots is the availability of soil water. At the cave sites investigated by McElrone *et al.* an underground stream assures a nearly continuous supply of water to deep roots (although the trees are not phreatophytes – their roots do not tap directly into water). Differences in water availability directly and indirectly account for the structural differences observed in the xylem of stems, shallow roots, and deep roots. As a direct response, vessel diameter in water stressed roots of sorghum is significantly smaller than in non-stressed roots (Cruz *et al.*, 1992), as are root primordia in general, which may in turn lead to narrower vessels and tracheids. Indirectly, vulnerability to stress-induced cavitation may select for smaller conduits in organs routinely exposed to drying conditions, because wide conduits tend to embolize more readily (whether because of their greater



**Fig. 1** Next to the stem, shallow roots, and deep roots of the tree are the values for vessel diameter (ves;  $\mu\text{m}$ ), specific hydraulic conductivity ( $K_s$ ;  $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ ), and vulnerability to cavitation ( $\Psi_{50}$ ; MPa) measured for *Bumelia lanuginosa* by McElrone *et al.* (pp. 507–517).

diameter or the greater likelihood of air-seeding through pores in the pit membranes of large conduits is a matter for further research; Hacke *et al.*, 2000; Martínez-Vilalta *et al.*, 2002). For long roots in particular, reductions in  $K_b$  due to embolism can be even more limiting to water uptake than is radial resistance (between the soil and the root xylem), which tends to limit water uptake for young roots in moist soil (North & Peterson, in press).

## Perspectives

In two of the species examined by McElrone *et al.* the ranking of plant axes with respect to vulnerability to embolism is the same as their ranking in conduit diameter,  $K_s$ , and access to water: deep roots were greatest, then shallow roots, then stems (Fig. 1). As McElrone *et al.* discuss, the greater vulnerability of roots may be tolerable due to the possibility of conduit refilling via root pressure. This gradient in vulnerability, as well as the gradients in conduit width and hydraulic conductivity, is most readily understood within the framework of the cohesion-tension theory of water ascent in trees. For example, such differences in xylem structure and function would not be expected if water flow were driven predominantly by forces other than transpirational pull, such as radial pressure applied by tissues or cells alongside the conduits. The differences in xylem structure and function within the tree species in this study thus provide

some of the best whole-plant evidence gathered to date in support of the cohesion-tension theory.

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**Key words:** cavitation, cohesion-tension theory, long-distance transport, ribosomal DNA, xylem

# Phenotypic plasticity – contrasting species-specific traits induced by identical environmental constraints

Can it be assumed that a specific environmental constraint imposed on different species leads to a convergence in, for

example, morphology? A phenotype expressed in response to external stimuli (e.g. size-reduction in response to mechanical stress) should be adaptive regardless of species – this is largely intuitive, but has been poorly studied. In this issue (pp. 651–660), Puijalón & Bornette reveal exciting new data that suggest that phenotypic plastic responses to identical environmental constraints may indeed be species-specific (Puijalón & Bornette, 2004).

## Phenotypic plasticity – background

Early twentieth century research on phenotypic plasticity has been largely overlooked, with some exceptions (e.g. Bradshaw, 1965), until the last few decades. Not until recently has the concept of phenotypic plasticity become an important and integrated part of modern evolutionary and ecological research (Pigliucci, 1996; see Box 1). The past few decades have seen a large amount of interdisciplinary research being carried out on various aspects of phenotypic plasticity and reaction norms (e.g. Moran, 1992; Dudley & Schmitt, 1996; Lachmann & Lablonka, 1996; Preston, 1999; Pigliucci, 2002), together with a number of reviews (e.g. Coleman *et al.*, 1994; DeWitt *et al.*, 1998). Debates have also focused on evolution of phenotypic plasticity, including traits, models and gene expression (see De Jong, 1995 for an overview). Today, it seems clear that phenotypic plasticity must be recognised as central to evolution rather than a minor phenomenon, secondary to ‘real’ genetic adaptation (Sultan, 1992).

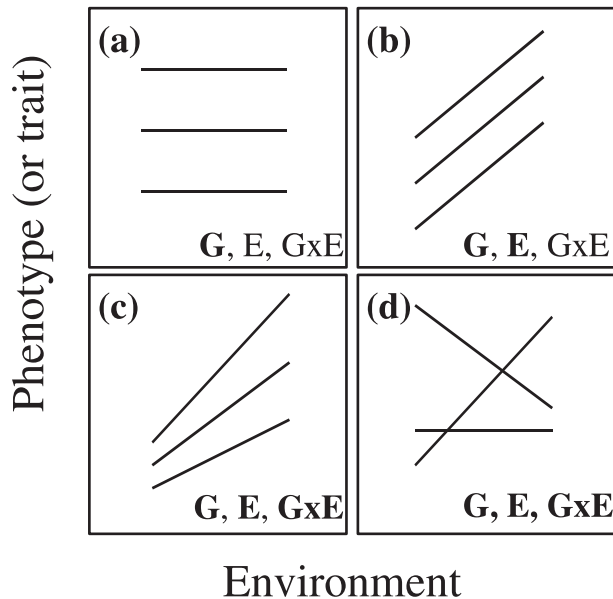
## Current research

An interesting aspect of ongoing research is a closer coupling between genetics and ecologists (e.g. Jasienski *et al.*, 1997), where molecular evolutionary geneticists work together with plant ecologists. This is likely to be a fruitful cross-pollination that will reduce the risks of research ‘inbreeding’ and increase the development of healthy new insights in complex and dynamic ecological systems. It is unfortunate if genetic and functional aspects of plasticity are studied separately: they should be complementary.

In addition to investigating the genetic and evolutionary basis for, and effects of, phenotypic plasticity, it might be viewed in the context of species interactions, plant community structure and food-web dynamics. Reciprocal phenotypic change between individuals of interacting species (Agrawal, 2001) is an area of research that should lead to a greater understanding, not only of phenotypic plasticity, but also of species interactions and how these are affected by, and affect, the environment. The new findings of Puijalón & Bornette should stimulate research on the significance of species-specific plastic responses and how these affect distribution and abundance of individuals and species. It is possible that different species have different ‘starting points’ (i.e. genetic conditions), leading to different expressions of adaptive

**Box 1. What is phenotypic plasticity?**

**Phenotypic plasticity** is the ability of individual genotypes to express diverse phenotypes, by altering, for example, morphology or physiology, in response to changes in environmental conditions (Schlichting, 1986; Bradshaw, 1965; Stearns, 1989; Schlichting & Pigliucci, 1998). The function or relationship that describes the phenotypes produced by a given genotype when exposed to a certain range of environments is called the reaction norm (Pigliucci, 1996). The reaction norm can be viewed graphically in a phenotype–environment space (Fig. 1) or as an equation:  $V_P = V_G + V_E + V_{G \times E} + V_{err}$ .  $V_P$  is the total phenotypic variation of a trait,  $V_G$  is the genetic variance,  $V_E$  is the environmental variance,  $V_{G \times E}$  is the genotype–environment interaction variance, and  $V_{err}$  is the residual error variance. The reaction norm is what is actually inherited (i.e. the ability to express different phenotypes). However, it has been pointed out that plasticity can also be produced by allelic effects that vary across environments (Via, 1993).



**Fig. 1** Conceptual graphic presentation of reaction norms (phenotypic expressions across environments for different genotypes or species). Bold letters (G, E, GxE) indicate significant genetic, environmental, or gene–environment interaction variance. (a) No phenotypic plasticity (denoted by flat reaction norms) but with significant genetic effects (space between genotypes). (b) Plasticity and genetic variation for traits (sloped and separated reaction norms), but no interaction variance (parallel slopes). (c) Differently sloped (positive) interaction norms indicating genetic variation for plasticity (genotype–environment interaction). (d) Differently sloped interaction norms (both positive and negative) indicating genetic variation for plasticity. Opposite slopes indicating that the phenotypic expression across the environmental gradient goes in different directions depending on genotype (or species). Figure and text partly modified from Schlichting & Pigliucci (1998) and DeWitt & Scheiner (2004).

plasticity in traits in a given environment. Reduction in stem length as a response to increased flow velocity might be adaptive. But if the species is genetically limited in this aspect (i.e. does not have the ability to effect plasticity in stem length) it is likely that an alternative response (e.g. decreased rigidity) might also be adaptive. In a competition situation the magnitude and cost of plasticity might be factors that decide the outcome.

Aquatic macrophytes are likely to be a good group of plant to focus on considering their evolutionary history with several distantly related taxa, exposed to several specific environmental constraints caused by adaptations to aquatic life. It is possible that inherent phenotypic plasticity might be a major factor explaining observed distribution patterns and shifts in dominance between species.

An applied aspect of plasticity research is the question as to why some species are invasive and others not. It has been suggested that invasive species are invasive just because they are more plastic (Agrawal, 2001). Again, aquatic plants are relevant since invasive species are frequent in aquatic habitats and often outcompete the native flora in lakes and rivers (e.g. *Elodea canadensis* in Europe, *Myriophyllum spicatum* in North America and *Salvinia* spp. and *Eichornia crassipes* in large parts of the tropics). From a nature conservation point of view, a better understanding about the ecology of invasive species is paramount, including the species-specific phenotypic plasticity.

Finally it is important to note that many phenotypic traits of plants change dramatically over the course of plant growth – a phenomenon termed ontogenetic drift (Evans, 1972). Therefore any studies concerning phenotypic plasticity must take into account size-dependent variation, in order not to confuse this with true phenotypic plasticity. The interpretation of variation in many phenotypic traits will therefore depend on whether comparisons are made as a function of plant age, size or developmental stage (Coleman *et al.*, 1994). Allometric studies where difference in size is accounted for is necessary for the correct interpretation of results concerning phenotypic plasticity (Schlichting & Pigliucci, 1998).

## Perspectives

The work of Puijalon & Bornette opens up new, interesting areas of research, including further studies on difference in plastic responses between species, but also, for example, differences in responses between life-history stages (both within and between species), and how this might affect competition and plant community structure and dynamics. A first step should be further studies to examine whether different responses to an environmental change between species

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.

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

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## Letters

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### 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.

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

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## Editorial

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### 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

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

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## Letters

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### 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, Brimmer & 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.

Brimmer & 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

potential to disrupt entire ecosystems through changes in the native soil community' or 'likely all fungi, including mycorrhizal fungi, that have cell walls composed of chitin, would be at risk for attack from *G. virens*' are not supported by published data. The data cited show only that, in some cases, some fungi used as BCAs are antagonistic to fungi other than the target plant pathogens, or have negative effects on the host plants, but their nontarget activities are not correlated with any 'significant environmental impact'.

In the case of *Ampelomyces quisqualis*, Brimner & Boland state that '... it may be possible for this BCA to attack nontarget fungal species and until its host range is identified, it is difficult to determine the risk to beneficial fungi and other soil organisms'. However, *A. quisqualis*, a highly specialized intracellular mycoparasite of powdery mildews, is one of the best known BCAs in terms of its host range (Falk *et al.*, 1995; Kiss, 1998; Kiss *et al.*, 2004) and, in addition, has nothing to do with soil organisms because its entire life cycle takes place on the aerial plant surfaces.

Brimner & Boland also state that 'cultivated mushrooms are also at risk' because it is known that some *Trichoderma* strains have been responsible for a disease of the commercially grown *Agaricus* while some other *Trichoderma* strains have long been used as commercial BCAs. However, the authors add that the disease-causing *Trichoderma* strains, recently described as belonging to a new species, *T. aggressivum* (Samuels *et al.*, 2002), have never been used for biocontrol purposes. Therefore, the warning concerning the attack of commercially grown mushrooms by BCAs is unsupported.

Another example of an 'undesired effect' of a BCA is even more disturbing. Based on a long-term field experiment carried out by Gerlach *et al.* (1999), Brimner & Boland mention that the application of some *Trichoderma* strains against *S. sclerotiorum* result in the increase of the disease instead of achieving control. This data was used to demonstrate that BCAs may contribute to the spread of plant pathogens. However, the authors do not mention that this data came from only a single, small-scale experiment; *Trichoderma* strains have never been used as BCAs of *S. sclerotiorum* in an extensive way in plant protection practice; and Gerlach *et al.* (1999) excluded the treatments with *Trichoderma* from the 5-yr experiment 3 yr after its start because they showed no promise for practical control.

Some parts of the review raise conceptual problems. For example, Brimner & Boland write that 'the most likely nontarget effect of BCAs is a reduction in the diversity and/or abundance of other fungi in an ecosystem'. However, fungal BCAs used for plant disease control have usually been applied in agricultural systems or in forestry, where the presence of other fungi has always been controlled to some extent by human activity. These locations should not be confused with natural ecosystems. Another conceptual problem is the statement that 'several species of fungi commonly found in soils control plant diseases by preying on patho-

genic soil microorganisms, such as nematodes (Jansson *et al.*, 2000), pathogenic fungi (Foley & Deacon, 1986; Huang & Kokko, 1987; Falk *et al.*, 1995, ...' Fungi parasitize, and do not 'prey on', microorganisms; nematodes are not microorganisms; and the paper written by Falk *et al.* (1995) and cited here deals exclusively with powdery mildews and *A. quisqualis* mycoparasites, which are not soil fungi.

Unfortunately, the Brimner & Boland review might be interpreted by decision makers as evidence of the harmful effects of BCAs and this might easily result in a more negative attitude towards their use in the plant protection practice. However, as the examples as selected show, there is good reason to mistrust the conclusions of the review. The 'precautionary principle' might be, at least to some extent, acceptable when little is known about the nontarget effects of a novel method. However, it is unreasonable to insist on ideas that are not backed up by well-founded data. It is well known that fungi may produce toxic metabolites and may parasitize each other. However, this is not a reason to stop using them to produce beer, wine, bread and antibiotics, or to control plant diseases, whenever a careful scientific investigation has shown that this is a feasible method and has no major nontarget effects.

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**Key words:** *Ampelomyces*, biological control, fungal biocontrol agents, environmental hazards, safety regulations, nontarget effects, *Trichoderma*.

## Nontarget effects of biological control agents

Kiss (2004) raises several concerns over aspects of our review on the non-target effects of fungi being used as biological control agents of plant diseases (Brimmer & Boland, 2003). We welcome the opportunity to provide additional comment and clarification. In our opinion, the most important point raised by Kiss is the assertion that the use of biological control agents 'is considered, in general, as a safe and environmentally friendly alternative for plant disease control compared to the application of conventional pesticides' (Kiss, 2004). We agree that this perception is common, but such assumptions are often unsubstantiated by scientific evidence. If biological control products are to live up to this perception, it is important that we confirm such assumptions scientifically, and do not avoid the need for toxicology and environmental fate data that can contribute to the identification of potential environmental and health risk (Whipps & Lumsden, 2001).

There is increasing published scientific evidence that microorganisms being used as biological controls can have significant, measurable effects, both direct and indirect, on non-target organisms. These effects include displacement of non-target microorganisms, allergenicity to humans and other animals, toxigenicity to non-target organisms, and pathogenicity to non-target organisms (Cook *et al.*, 1996; Brimmer & Boland, 2003; and references therein). There is a growing awareness for the need to consider these issues when developing biological control products. The commercial development of biological controls for plant diseases is a relatively new field and can arguably be compared with the early stages of pesticide development when often limited evaluations of target and non-target effects preceded more widespread application. It was only through more widespread use that epidemiological and environmental repercussions of using such products were identified. Furthermore, there are well documented examples in other areas of biological control, such as invasive animal and plant species, where introduced biological control strategies have become problematic.

Several aspects of our review appear to have contributed to miscommunication. We used the term 'environment' to include both physical and biological aspects of the environment, and the term 'microorganisms' to include bacteria, fungi,

amoebae, flagellates, nematodes, etc. as is commonly used in the literature. Our use of the term 'significant' was, in most cases, consistent with a statistical detection between or among treatments. Similarly, due to the limitations of space, we did not point out the strengths or weaknesses of individual studies underlying the points we made, but did provide citations to the literature for other researchers to consider. Some studies are obviously more substantial and convincing than others, and the apparent shortage of articles on non-target assessment does not dismiss specific experiments if such studies are representative of the available information, or test an important hypothesis. Subsequent studies will support or refute these often exploratory studies. Unfortunately, much of the available evidence on non-target effects of biological controls is not published because of the tendency not to publish the results of experiments that do not show significant differences between or among treatments, or because data are often generated for purposes of commercial registration and are considered confidential. These considerations may produce a bias in the literature towards identification of possible risks.

The host range of parasitic fungi can be particularly difficult to determine and typically relies on compilation of anecdotal records from the literature, by conducting ecological surveys, and/or by inoculations of specific combinations of hosts and parasites. *Ampelomyces quisqualis* is considered a strict parasite of powdery mildews based on evidence compiled from the literature and, within the Erysiphaceae, has a wide host range (Kiss, 1998). However, specific host–parasite–hyperparasite interactions have seldom been conducted and, at least to some degree, are confounded by taxonomic delineations and a lack of basic ecological data. Inundative biological controls are often used at high rates of application, and may be used both within and outside of the indigenous habitats of the microorganisms being used. Such usage will result in new interactions of biological control microorganisms with non-target organisms, although differences in registration requirements may constrain the use of non-indigenous microorganisms in some regions (Whipps & Lumsden, 2001). The study by Kiss (1998) provides an example of how extensive survey data can contribute to our understanding of the role of mycoparasitism in the natural ecology of fungal communities in general, and to the known host associations of this fungus in particular. Taxonomic delineation of fungal species is another important area of concern in assessing non-target effects of biological control products, and one that is of particular concern to regulatory agencies because of the relationship between the identification of a microorganism and the scientific literature. For example, until recently, strains Th4 and Th2 of *Trichoderma harzianum* were associated with a green mold disease of *Agaricus bisporus*, which caused both real and perceived concern regarding the potential use of biological control products containing *T. harzianum* in surrounding agricultural and horticultural industries. In our article, we specifically noted that the relationship between

*T. harzianum* and *A. bisporus* was highly specialized and dependent on the strain of the antagonist. More recently, the strains of *Trichoderma* associated with green mold disease were reclassified as a new species, *Trichoderma aggressivum* (Samuels *et al.*, 2002), and this report provides an example of how taxonomic clarification can contribute to improved risk assessment, and supports the use of biocontrol strains of *Trichoderma* spp. that are non-pathogenic to *A. bisporus*.

In contrast to the statement by Kiss, there have been numerous studies on the potential use of *Trichoderma* spp. for the management of *Sclerotinia* spp., and *Trichoderma* spp. have a recognized role in the natural ecology of sclerotia of *Sclerotinia* spp. (Willetts & Wong, 1980; Adams & Ayers, 1979; Zhou & Boland, 1998). Our review did not focus on the results of biological control efficacy to target organisms but did include brief mention of the study by Gerlagh *et al.* (1999) because of the unexpected result where applications of the biocontrol agent resulted in an increased production of apothecia – an unexpected and possible non-target effect in itself. In our view, this was not a ‘small-scale experiment’ (Kiss, 2004) as it examined 12 biological control and crop treatments in a factorial design in 5 × 5 m plots with 10 replications over a five year period. The results made a substantial contribution to the *in situ* comparative efficacy of the biological controls that were compared. The *Trichoderma* treatment was dropped from the experiment after three years due to lack of efficacy although there were relatively few significant differences among the number of apothecia or disease in any of the treatments assessed during these years. In at least two plots, including bean and chicory, that had been treated with *Trichoderma* spp., diseased crops developed up to 2.6 times more apothecia than the untreated control. The authors advanced no reason for these unexpected results and additional experimentation would be required to determine if this was a spurious effect, as suggested by Kiss (2004), or an initial observation of a more substantial biological phenomenon. In our view, it is too early to discriminate between these possibilities.

Perhaps one of the most challenging aspects of risk assessment for biological control organisms is to discriminate between significant, measurable effects on other organisms and important, long-lasting perturbations of other species. This has become an important discussion in several arenas of risk assessment and often requires considerable study and discussion to resolve. Because of the often inadequate amount of published information on risk assessment of biological controls for plant diseases to date, we consider it premature to distinguish effectively between what are significant vs. important non-target effects, whether this effect be in agricultural, forestry or natural ecosystems. There is increasing recognition that above-ground–below-ground communities can be important factors in terrestrial ecosystems, with both positive and negative feedbacks on species abundance and diversity (Wardle *et al.*, 2004). In contrast to the view of

Kiss (2004), non-target effects in any of these environments can potentially be important, and it seems evident that biological control microorganisms can move from areas of application to surrounding areas. As pointed out by Whipps & Lumsden (2001), the key determinants of whether biological controls are advantageous or not are influenced by scientific facts or observations, public opinion and perception, and commercial or financial considerations.

In conclusion, Kiss draws attention to ‘decision makers’ and the possible repercussions of non-target assessments on pest control product registration policies. We agree that ‘this is not a reason to stop using them ... whenever a careful scientific investigation has shown that this is a feasible method and has no major non-target effects’ (Kiss, 2004). The challenge, of course, is for those of us involved in biological control research to provide scientific evidence to support these assumptions. Indeed, it was through discussions with regulatory agencies in Canada that one of the authors (GJB) became aware of many of the issues summarized in our article. The regulatory approval process for many countries requires substantial documentation of potential effects to non-target organisms, and on the environmental fate and persistence of the biological control microorganism. Such data can be challenging to collect and there is a need for more discussion on the most appropriate protocols for assessing the safety of such products. The letter by de Jong (1992) summarizes one example of how quantitative risk assessment in plant pathology and biological control can contribute to effective risk analysis and policy development.

We remain optimistic that an increased understanding of these questions can contribute to the successful understanding and development of microorganisms as effective and environmentally benign biological controls for plant disease, and we believe that our review raises important issues that must be considered when developing or using biological control products.

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**Key words:** biological control agents, fungi, nontarget effects, plant disease, regulation.



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