

different nutrient forms of N regardless of the charge (NO_3^- , NH_4^+ , N_2 , glutamine), across all macronutrient deficiencies, under water stress and when S:R increases under reduced irradiance or CO_2 conditions when sucrose levels are likely to decrease substantially regardless of N availability [3,5–7]. The proposal of Hermans *et al.* [4] cannot explain the increase in S:R associated with decreased leaf sucrose concentration under reduced irradiance or CO_2 supply or an increase in S:R with increased N supply at low irradiance when leaf sucrose concentrations are negligible [6,7]. The strength of the relationship between S:R and leaf protein concentration across different environmental variables was highlighted in a recent study. When tobacco (*Nicotiana tabacum*) was supplied with (i) different concentrations of N, P, K, S and Mg, (ii) different N forms (NO_3^- , glutamine, urea, NH_4NO_3) or (iii) NO_3^- under low and high irradiance the S:R was not significantly correlated with plant dry weight, but a linear regression model incorporating leaf soluble-protein concentration could explain 82% of the variation in S:R within and across all treatments [3]. Only the values for the low P treatment fell slightly outside the line, which indicates that, for tobacco, there might be a P-specific effect. However, this P effect was not found with a range of other species [2,6]. Also, for *Lolium multiflorum* under extreme Mg deficiency, S:R was exceptionally high [6]. It is possible that this was in part due to a Mg-specific effect, such as impaired photosynthate export in the phloem [4].

Our view is that normally, shoot growth is co-limited by the availability of the C and N substrates. It is proposed that the shoot soluble-protein concentration is of particular importance as this reflects the availability of the N substrate and N catalyst for shoot growth. Thus, the increase in S:R observed with increased leaf soluble-protein concentration across a wide range of environmental conditions, is due to an increase in N relative to the C substrate for shoot growth in conjunction with the proxi-

mity of the shoot to the C and energy supplies [3]. The proximity of the shoot to the C and energy sources results in the shoots acquiring an increased proportion of photosynthate for growth if the supply of N substrate increases relative to the C substrate for growth. The greater the proportion of photosynthate utilized in shoot growth, the smaller the proportion available for transport to the root, and, as a result, the S:R increases.

In conclusion, we propose that root growth is not positively correlated with leaf sucrose concentration across different N supplies but S:R is positively correlated with leaf protein concentration across a wide range of environmental variables including N, P, K and Mg deficiency. A mechanism involving the relative availability of the C and N substrates for growth in shoots can explain how shoot protein concentration could determine shoot growth and, hence, root growth and S:R.

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Letters Response

Response to Andrews *et al.*: correlations and causality

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We thank Mitchell Andrews and colleagues for their interest in our recent article published in the December 2006 issue of *Trends in Plant Science* [1]. In their letter, Andrews *et al.* [2] seem to disagree with some of the points made in our review. They focus on the hypothesis that increased sugar concentrations in the leaves of plants grown at low nitrogen (N) and phosphorus (P) supply are linked mechanistically to an increased partitioning

of dry matter to roots. First, they suggest that this hypothesis ‘fails to consider . . . that the root is smaller on low than on high N supply. . . and. . . there are many reports of strong positive correlations between S:R [shoot:root biomass ratio] and plant/shoot N’. Second, they assert that this hypothesis ‘cannot explain the increase in S:R associated with decreased leaf sucrose concentration under reduced irradiance or CO_2 supply or an increase in S:R with increased N supply at low irradiance when leaf sucrose concentrations are negligible’.

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Here, we briefly reiterate the thinking behind the hypothesis. Addressing the first statement: in Hermans *et al.* [1], we report that plant S:R decreases under N deficiency (i.e. when shoot N concentrations are decreasing) and also observe that nitrate content in leaves, which is directly related to N supply, is negatively correlated with the proportion of carbon (C) allocated to the root. This is entirely consistent with a strong positive correlation between plant S:R and shoot N concentration. Also, at low N supply, C partitioned to the roots might not be used for root growth owing to N-limitation and, consequently, roots can be smaller than those of N-replete plants, but S:R is still greater than N-replete plants.

Addressing the second statement: in Hermans *et al.* [1], we propose that C fluxes in the phloem are the currency for changes in S:R and suggest that an increase in shoot sucrose leads to a decrease in plant S:R – provided that it can be translocated to the root. Again, this is entirely consistent with the observation that a decrease in leaf sucrose concentration, as reported under reduced irradiance or CO₂ supply, leads to an increase in S:R. Under these circumstances proportionally less photosynthate will be translocated to the root.

Although it was not the focus of our review, we did note that ‘some of the effects of N deficiency on plant growth and gene expression seem to be related to the C:N ratio in the tissue rather than carbohydrate status alone. Carbon metabolites and plant C:N status both regulate the expression of several genes involved in N acquisition and metabolism, and nitrate regulates many genes assigned to sugar metabolism.’ Thus, the relative availabilities of C and N affect the poise of plant carbohydrate metabolism and N assimilation. We propose that sucrose is both the product and indicator of imbalances between N (and P) supply and photosynthesis. Thus, we suggest that sucrose behaves not only as a C source for root growth, but also as a phloem-mobile signal initiating acclimatory responses of roots to N and P deficiencies, and the remodeling of specific aspects of root architecture. Considerable support now exists for the latter hypothesis [3–8]. For balance, we noted that other systemic signals, such as phytohormones, also participate in orchestrating the morphological responses of plant roots

to mineral availability. These are considered in more detail in a recent review by Potters *et al.* [9].

In the final section of their letter, Andrews *et al.* [2] promote a view that shoot growth is co-limited by the availability of C and N, and that shoot protein synthesis determines plant S:R. This view is based on the impressive correlation between S:R and leaf soluble protein concentration when plants are grown with many diverse mineral supplies [10]. However, it should be remembered that a correlation does not imply causality and it is unlikely (although not impossible) that changes in shoot protein concentrations *per se* provide the systemic signal for changes in root morphology.

In summary, the letter of Andrews *et al.* [2] affirms the conclusions of Hermans *et al.* [1] that C fluxes in the phloem determine S:R, and makes the valuable suggestion that the relative supply of essential elements, and in particular the C:N ratio, determines the relative partitioning of C to shoot metabolism or phloem export.

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