

The mechanism of the nitrate effect on shoot to root ratio of herbaceous plants: an hypothesis

M. Andrews

Department of Plant Science, Lincoln University, Canterbury, N.Z.

Abstract

For many herbaceous species, shoot to root dry weight ratio (S:R) increases with increased external nitrate (NO_3^-) concentration in the range 0.1 to 20 mol m^{-3} . This paper reviews the various proposals for the mechanism of the NO_3^- effect on S:R. It is argued that none of the proposed mechanisms fully explains all data available. It is proposed that the NO_3^- effect on S:R can be explained primarily by the effect of increased NO_3^- assimilation and protein synthesis on photosynthesis and hence growth/development and secondarily by competition between the NO_3^- assimilation/protein synthesis processes and growth for energy derived from photosynthesis. Any major change in S:R with increased NO_3^- supply above that which gives greatest growth is likely to be a toxic effect.

Additional key words: Nitrate assimilation, photosynthesis, growth.

Introduction

Nitrate (NO_3^-) is often the major form of inorganic nitrogen (N) taken up and assimilated by higher plants (Andrews, 1986a). Under natural conditions, NO_3^- concentration in the interstitial water of undisturbed soils is usually <1 mol m^{-3} but in agricultural soils it ranges from 1 to 20 mol m^{-3} (Barber, 1984; Haynes *et al.*, 1986; Wild, 1988). It has been shown for many herbaceous species that shoot to root dry weight ratio (S:R) increases greatly with increased external NO_3^- concentration over part of the range 0.1 to 20 mol m^{-3} (e.g. Sutherland *et al.*, 1985; Andrews, 1986b; Andrews *et al.*, 1992a,b). This paper reviews the various proposals for the controlling mechanism of the NO_3^- effect on S:R. It is argued that none of the proposals fully explain all data available. An alternative explanation is given.

Previous Explanations for the NO_3^- Effect

Brouwer (1962) proposed that when a nutrient becomes limiting, shoot growth will decrease more than root growth as the shoot is further away from the nutrient supply. Thornley (1972 a,b) developed this theory into a mathematical model based on two assumptions. Firstly, utilisation of substrate for growth depends upon local substrate concentration and secondly, transport of substrate between two places in the plant is given by the substrate concentration difference divided by a resistance. Bastow-Wilson (1988) concluded that the response of

S:R to deficits of major inorganic nutrients, water, light and CO_2 and to defoliation and root pruning usually conform to the Thornley model.

Increased growth with increased NO_3^- availability is dependent on increased NO_3^- assimilation (Khamis and Lamaze, 1990; Zhen and Leigh, 1990). There is strong evidence that for many species, the root is the main site of NO_3^- assimilation at external NO_3^- concentrations around 1 mol m^{-3} or less and that shoot NO_3^- assimilation increases in importance as external NO_3^- concentration increases in the range 1 to 20 mol m^{-3} (Andrews, 1986a; Andrews *et al.*, 1992b). This change in partitioning of NO_3^- assimilation between root and shoot is compatible with the Brouwer/Thornley model. However, evidence is also strong that for many other species, the shoot is the main site of NO_3^- assimilation at low and high external NO_3^- concentrations (Andrews, 1986a). The Brouwer/Thornley model can not explain a decrease in S:R with decreased NO_3^- supply for species which have the shoot as their main site of NO_3^- assimilation regardless of NO_3^- supply.

Boote (1977) argued that for *T. aestivum* and *Pisum sativum* L., shoot NO_3^- assimilation increases but root NO_3^- assimilation decreases with increased NO_3^- supply. Consequently, on high NO_3^- supply, roots are reliant on shoots for their reduced-N and this may at least partly explain why root growth is depressed relative to shoot growth as N fertility increases. There is good evidence for some grain legumes and cereals, that root NO_3^- assimilation decreases with increased applied NO_3^- .

concentration over part of the range 1 to 20 mol m⁻³ due to decreased carbon (C) supply and/or decreased levels of reductant (Minotti and Jackson, 1970; Andrews *et al.*, 1992b; Oaks, 1992). However, it has been shown for grain legumes and cereals, that at high external NO₃⁻ concentrations, there is substantial cycling of reduced-N between shoot and root and it is highly unlikely that root growth is N limited on high NO₃⁻ supply (Layzell *et al.*, 1979; Lambers *et al.*, 1982; Cooper and Clarkson, 1989).

Vessey and Layzell (1987) proposed a mechanism by which the NO₃⁻ effect on S:R is mediated by N circulation round the plant. It was proposed that decreased NO₃⁻ supply results in a decrease in NO₃⁻ uptake and hence decreases in root NO₃⁻ assimilation and root respiration. Consequently, the concentration of N in the xylem sap, shoot N pool and phloem sap all decrease. However, of the N translocated to the root in the phloem, a much higher proportion is unloaded in order to maintain root N content. Maintenance of root N content coupled with decreased root respiration would promote root growth. This proposal does not explain the increase in S:R with additional NO₃⁻ over the range in which, for several species, root NO₃⁻ assimilation appears to decrease (Minotti and Jackson, 1970; Andrews *et al.*, 1992b; Oaks, 1992).

Starch/sucrose Control of S:R

Although NO₃⁻ availability can affect growth greatly, N is likely to be < 4% of total plant dry weight (d.wt.). Carbon and oxygen (O) obtained via CO₂ fixation and incorporated into a range of organic compounds make up ~90% of plant d.wt. There is considerable evidence that the amount of photosynthate (specifically sucrose) translocated to the root determines root growth (Farrar and Minchin, 1991). The question therefore is how can NO₃⁻ availability differentially affect the amount of C retained by the shoot and that translocated to the root. It has been proposed that S:R is determined by the partitioning of photosynthate between sucrose and starch during the photoperiod (Huber, 1983; Geiger and Servaites, 1991). Specifically, the greater proportion of photosynthate utilised in starch production, the greater the proportion of C retained for shoot growth. It was argued that during the day, roots and shoots receive C equally. However, at night, the main source of C for growth is sucrose produced from starch mobilisation and that due to proximity to source and possibly greater sink activity, the shoot obtains the greater proportion of this sucrose. It is not known whether NO₃⁻ availability affects the partitioning of photosynthate between starch and sucrose. However, on the data available, it appears

unlikely that NO₃⁻ effects on S:R can be fully explained by a change in the partitioning of photosynthate between starch and sucrose for at least three reasons. Firstly, starch synthesis appears to increase relative to sucrose synthesis under conditions where photosynthesis is reduced (Baysdorfer and Robinson, 1985; Mooney and Winner, 1991) while S:R can increase with NO₃⁻ availability when growth and photosynthetic rate (unpub.) increase, change little or decrease. Secondly, additional NO₃⁻ has been shown to increase the activity of sucrose phosphate synthase, a key enzyme in sucrose biosynthesis (Huber, Kerr and Rufty, 1985). Thirdly, additional NO₃⁻ can cause an increase in S:R of cereal seedlings developing in darkness (Andrews *et al.*, 1991; Lieffering *et al.*, 1992). This effect is associated with increased rate of mobilisation of seed reserves and could not be explained by a differential partitioning of photosynthate between starch and sucrose.

Alternative Explanation for the NO₃⁻ Effect

In most reports, increased S:R with additional NO₃⁻ was associated with increased growth (Bastow-Wilson, 1988, and references therein). Usually, for herbaceous species, S:R increases with increased growth/development thus at least part of the NO₃⁻ effect is likely to have been an ontogenetic effect. The effect of increased applied NO₃⁻ concentration from 0.1 to 20 mol m⁻³ on S:R and d.wt of *Triticum aestivum* L. is shown in Fig. 1. For *T. aestivum* (Fig. 1), a range of temperate pasture grasses (Porter, Andrews and Lucas, 1992) and *Phaseolus vulgaris* L. (unpub.), S:R increased with

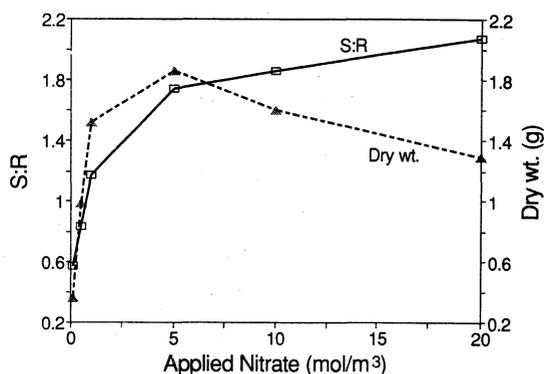


Figure 1. Effect of NO₃⁻ concentration on (S:R) and total plant dry wt. of *T. aestivum*. Modified from Andrews *et al.* (1992b).

additional NO_3^- from 0.1 to 20 mol m^{-3} but plant d.wt peaked in the range 1 to 5 mol m^{-3} . This shows that there is a NO_3^- effect which is independent of growth as for the same plant d.wt at NO_3^- concentrations above and below that which gave maximum growth, S:R was greater at high than at low NO_3^- . In a separate study of *T. aestivum*, it was shown that reduced-N content of shoots approximately doubled with increased applied NO_3^- from 5 to 10 mol m^{-3} despite growth peaking at around 5.0 mol m^{-3} (Dastgheib and Andrews, unpub.). Similarly, for *Vicia faba* L., reduced-N content of leaf, stem and root increased substantially with additional NO_3^- concentration above that which gave maximum growth (Fig. 2). As NO_3^- assimilation and protein synthesis are energy requiring processes, this indicates that energy derived from photosynthesis was used for the production of amino acids and proteins as opposed to the production of dry matter.

It is proposed that the NO_3^- effect on S:R can be explained primarily by the effect of increased NO_3^- assimilation and protein synthesis on photosynthesis and hence growth and secondarily by competition between the NO_3^- assimilation/protein synthesis processes and growth for energy derived from photosynthesis. Increased NO_3^- assimilation/protein synthesis results in an increased proportion of energy derived from photosynthesis being utilised in these processes at the expense of growth. This is reflected in an increase in tissue N content (Fig. 2b). Over part of the external NO_3^- concentration range 0.1 to 20 mol m^{-3} , the effect of increased NO_3^- assimilation/protein synthesis on photosynthesis is

so great that increased photosynthate is available for growth (Fig. 1). Over this range, the increase in S:R is likely to be at least partly an ontogenetic effect. It is suggested that the increase in shoot d.wt relative to root d.wt is due to proximity of the shoot to the C source. As NO_3^- assimilation/protein synthesis increases, N use efficiency decreases (Hocking and Meyer, 1991). When NO_3^- assimilation/protein synthesis increases to a point where photosynthate available for dry matter production decreases, S:R will still increase as the shoot will realise a greater proportion of its growth potential due to its proximity to the source of C and the availability of reduced N for growth. In studies of temperate cereals and pasture grasses, the change in S:R with additional NO_3^- above that which gave maximum growth, was much less than that associated with increased NO_3^- over the range which gave increased growth, except in cases where growth was severely restricted by high NO_3^- (Fig. 1; Andrews *et al.*, 1992b; Porter *et al.*, 1992). It is suggested that this indicates that the NO_3^- effect on S:R is primarily an ontogenetic effect. However, it is acknowledged that serial harvest experiments are required to confirm this. Major changes in S:R with increased NO_3^- supply above that which gives greatest growth are likely to be toxic effects (Andrews *et al.*, 1992b). The proposed explanation for NO_3^- effects on S:R of photosynthesising plants could also hold for seedlings developing in darkness, if roots obtain a substantial proportion of their seed derived C via the shoot. The pathway of carbon translocation from seed to root in developing cereal seedlings remains to be determined.

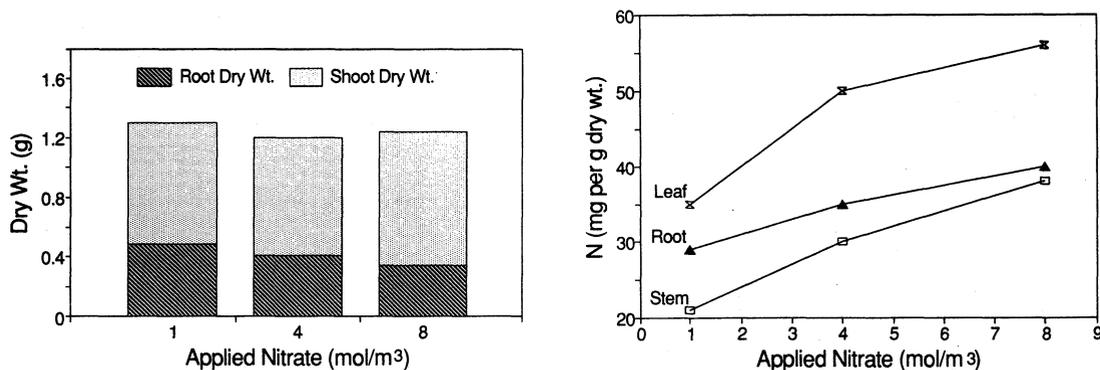


Figure 2. Effect of different concentrations of applied NO_3^- on a) shoot and root dry wt. and b) leaf, stem and root reduced-N content of *Vicia faba* L. Modified from Sutherland *et al.*, 1985.

References

- Andrews, M. 1986a. The partitioning of nitrate assimilation between root and shoot of higher plants. *Plant, Cell and Environment* **9**, 511-519.
- Andrews, M. 1986b. Nitrate and reduced-N concentrations in the xylem sap of *Stellaria media*, *Xanthium strumarium* and six legume species. *Plant, Cell and Environment* **9**, 605-608.
- Andrews, M., Hill, G.D., Raven, J.A. and Sprent, J.I. 1992a. Nitrate effects on leaf growth of grain legumes prior to nodulation: species differences relate to nitrate uptake. *Proceedings of the 1st European Conference on Grain Legumes*, 139-140.
- Andrews, M., Morton, J.D., Lieffering, M. and Bisset, L. 1992b. The partitioning of nitrate assimilation between root and shoot of a range of temperate cereals and pasture grasses. *Annals of Botany* **70**, 271-276.
- Andrews, M., Scott, W.R. and McKenzie, B.A. 1991. Nitrate effects on pre-emergence growth and emergence percentage of wheat (*Triticum aestivum* L.) from different sowing depths. *Journal of Experimental Botany* **42**, 1449-1454.
- Barber, S.A. 1984. Soil nutrient bioavailability. A mechanistic approach. John Wiley & Sons, New York.
- Bastow-Wilson, J. 1988. A review of evidence on the control of shoot: root ratio in relation to models. *Annals of Botany* **61**, 433-449.
- Baysdorfer, C. and Robinson, M.J. 1985. Sucrose and starch synthesis in spinach plants grown under long and short photosynthetic periods. *Plant Physiology* **79**, 838-842.
- Boote, K.J. 1977. Root:shoot relationships. *Proceedings of the Soil and Crop Science Society of Florida* **36**, 15-23.
- Brouwer, R. 1962. Nutritive influences on the distribution of dry matter in the plant. *Netherlands Journal of Agricultural Science* **10**, 399-408.
- Cooper, H.D. and Clarkson, D.T. 1989. Cycling of amino-nitrogen and other nutrients between shoots and roots in cereals - a possible mechanism integrating shoot and root in the regulation of nutrient uptake. *Journal of Experimental Botany* **40**, 753-762.
- Farrar, J.F. and Minchin, P.E.H. 1991. Carbon partitioning in split root systems of barley: relation to metabolism. *Journal of Experimental Botany* **42**, 1261-1269.
- Geiger, D.R. and Servaites, J.C. 1991. Carbon allocation and response to stress. In *Response of Plants to Multiple Stresses* (eds. H.A. Mooney, W.E. Winner and E.J. Pell), pp. 103-127. Academic Press Inc., San Diego, California.
- Haynes, R.J., Cameron, K.C., Goh, K.M. and Sherlock, R.R. 1986. Mineral nitrogen in the plant-soil system. Academic Press Inc., Orlando, Florida.
- Hocking, P.J. and Meyer, C.P. 1991. Effects of CO₂ enrichment and nitrogen stress on growth, and partitioning of dry matter and nitrogen in wheat and maize. *Australian Journal of Plant Physiology* **18**, 339-356.
- Huber, S.C. 1983. Relation between photosynthetic starch formation and dry weight partitioning between the shoot and root. *Canadian Journal of Botany* **61**, 2709-2716.
- Huber, S.C., Kerr, P.S. and Rufty, T.W. 1985. Diurnal changes in sucrose phosphate synthase activity in leaves. *Physiologia Plantarum* **64**, 81-87.
- Khamis, S. and Lamaze, T. 1990. Maximal biomass production can occur in corn (*Zea mays*) in the absence of NO₃ accumulation in either leaves or roots. *Physiologia Plantarum* **78**, 388-394.
- Lambers, H., Simpson, R.J., Beilharz, V.C., Dalling, M.J. 1982. Growth and translocation of C and N in wheat grown with a split root system. *Physiologia Plantarum* **56**, 421-429.
- Layzell, D.B., Pate, J.S., Atkins, C.A., Canvin, D.T. 1979. Partitioning of carbon and nitrogen and the nutrition of root and shoot apex in a nodulated legume. *Plant Physiology* **67**, 30-36.
- Lieffering, M., Andrews, M. and McKenzie, B.A. 1992. Seed reserve mobilisation and partitioning of dry matter in barley seedlings prior to emergence. *Proceedings Agronomy Society of New Zealand* **22**, 83-86.
- Minotti, P.L. and Jackson, W.A. 1970. Nitrate reduction in the roots and shoots of wheat seedlings. *Planta* **95**, 36-44.
- Mooney, H.A. and Winner, W.E. 1991. Partitioning response of plants to stress. In *Response of Plants to Multiple Stresses* (eds. H.A. Mooney, W.E. Winner and E.J. Pell), pp. 129-141. Academic Press Inc., San Diego, California.
- Oaks, A. 1992. A re-evaluation of nitrogen assimilation in roots. *Bioscience* **42**, 103-111.
- Porter, D., Andrews, M. and Lucas, R.J. 1992. The partitioning of dry matter between root and shoot of a range of temperate annual and perennial grasses. *Proceedings Agronomy Society of New Zealand* **22**, 87-90.
- Sutherland, J.M., Andrews, M., McInroy, S. and Sprent, J.I. 1985. The distribution of nitrate assimilation between root and shoot of *Vicia faba*. *Annals of Botany* **56**, 259-265.
- Thornley, J.H.M. 1972a. A model to describe the partitioning of photosynthate during vegetative plant growth. *Annals of Botany* **36**, 419-430.
- Thornley, J.H.M. 1972b. A balanced quantitative model for root:shoot ratios in vegetative plants. *Annals of Botany* **36**, 431-441.
- Vessey, J.K. and Layzell, D.B. 1987. Regulation of assimilate partitioning in soybean: initial effects following change in nitrate supply. *Plant Physiology* **83***, 341-48.
- Wild, A. 1988. Plant nutrients in soil:nitrogen. In *Russell's Soil Conditions and Plant Growth* (ed. A.Wild), pp. 652-694. Longman Scientific and Technical, Essex, U.K.
- Zhen, R.G. and Leigh, R.A. 1990. Nitrate accumulation by wheat (*Triticum aestivum*) in relation to growth and tissue N concentrations. *Plant and Soil* **124**, 157-160.