Contribution of pre-flowering stored stem reserves to developing seeds of different field crops: a review

S. K. Roy and M. P. Rolston

Herbage Seed Section, AgResearch, PO Box 60, Lincoln, New Zealand

Abstract

Apparent contribution of pre-flowering stored stem reserves to developing seeds of maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), perennial ryegrass (*Lolium perenne* L.) and mustard (*Brassica juncea* L.) were studied in separate experiments after partial modification of the predictive formula of Gallagher *et al.* (1976), i.e.,

$$\text{Translocation } (\%) = ((\Delta TDM - \Delta GDM)/\Delta GDM) \times 100$$

where, ΔTDM and ΔGDM are the increases in total and seed dry matter, respectively, from silking to maturity in maize, from anthesis to maturity in wheat and ryegrass, and from end of flowering to the pod maturity stage in mustard. The paper compiles the results of different trials which are discussed in detail. From various experiments, pre-flowering reserve contributions in maize were 1-29%, wheat 20-65%, ryegrass 14-51%, and mustard 16-22% to rapidly developing seeds. This suggests that stresses late in growth may be partly compensated by stem reserves translocation to the seed, although complete compensations are unlikely. The method may be extrapolated to estimate apparent translocation of pre-flowering stem reserves to developing seeds of other field crops.

Additional key words: apparent translocation, wheat, maize, ryegrass, mustard.

Introduction

Grain growth depends mostly on gross photosynthesis rates, stored materials at the end of flowering, initial grain dry weight, grain growth rates and nutrient supply (Thornley, 1979). When photosynthetic performance is inhibited by post-flowering stress caused by nutrient starvation, drought, defoliation or foliar diseases, grain growth becomes increasingly dependent on plant reserves stored prior to flowering (Wardlaw, 1967; Rawson and Evans, 1971, Gallagher *et al.*, 1975, 1976; Rawson *et al.*, 1977; Austin *et al.*, 1980; Hawkins and Cooper, 1981; Fischer, 1983; Blum *et al.*, 1983; Roy, 1985). Genetic variation exists. For example Austin *et al.* (1977) reported greater translocation of stored pre-anthesis stem reserves into growing grains in varieties that lost more stem and leaf dry weight after flowering. Rawson and Evans (1971) found variations among varieties in the rate of translocation from stems to ears; the rate was proportional to the length of the period from termination of stem growth to the initiation of grain growth. In some cases pre-flowering assimilates are temporarily stored in the stem (Gallagher *et al.*, 1975; Rawson and Evans, 1971; Wardlaw and Willenbrink, 1994) and may be translocated in the second phase of grain growth if harsh environments limit current photosynthesis (Biscoe *et al.*, 1975; Pheloung and Siddique, 1991).

Leaf removal after flowering was found to affect grain growth differentially among various genetic material (Bremner, 1972). Severe post-flowering drought and heat stress that restrict grain growth are common in mediterranean and tropical environments (Blum *et al.*, 1983). The mobilization of temporarily stored plant reserves is a major stress tolerance factor, especially when the tolerance of the plant to water or nutrient deficits was considered. However, most of the studies were confined to single experiments and inter- or intra-species comparisons of translocation ability were not made.

Several studies on cereal crops reported by Yoshida (1972) indicated that 20-40% of the final grain weight in rice can be provided by translocation from the stem of materials assimilated before flowering. Such large amounts of translocation are associated with nutrient-starvation, in particular, nitrogen. Yoshida concluded that under usual field conditions such translocation is unlikely because the rice flag leaf remains green even at maturity. However, post-anthesis foliar disease is common in a tropical environment and with post-anthesis leaf blight disease, as much as 50% of the pre-anthesis

stem reserves may be translocated to the rice grain (Yoshida, 1972). Biscoe *et al.* (1975) reported that as much as 30% of final grain weight in Proctor barley was accounted for from translocation of pre-anthesis material. A significant positive relationship between the rate of stem dry matter loss after anthesis and grain production capacity under conditions of drought stress, across varied genetic material has also been recorded (Rawson *et al.*, 1977; Hunt, 1979). Translocation of pre-flowering stem reserves also depends on availability, and post-flowering assimilate demand, of the developing seed (Roy, 1985). Once seed growth has ceased it is unlikely that the stored reserves in partially filled seeds will be used, and thus wide variation in translocating ability exists. The amounts of pre-anthesis stored materials translocated to developing grains of different cereal crops as estimated by different authors are given in Table 1. From the data it is apparent that large amounts of assimilate formed before anthesis appear to be available for translocation to the developing grain.

Sources of assimilate

In general there are two sources of assimilate for the developing grain: current assimilate and that stored before flowering. The contribution of these two sources of assimilate can be examined by comparing the growth rate of the whole stand as well as the individual plant after flowering, with the grain growth rate measured in the same unit. After flowering, ear or pod dry weight increases are almost entirely accounted for by the filling of the grain. Near the end of grain filling, current photosynthesis almost ceases following leaf or assimilatory surface senescence (Biscoe *et al.*, 1975), but ear or pod growth continues. This increase in dry weight can be accounted for only by translocation of assimilate stored elsewhere in the plant. This assumes that the roots neither provide nor accept assimilate while the grain is filling, and that shedding of leaf or other plant parts during this period is negligible. The respiratory loss which is estimated to be about 39% (Wardlaw and Porter, 1967) is ignored, with the assumption that assimilate (either current or stored) is the end product after metabolic losses. Grain or floret weight at flowering is very small in relation to final weight and may be neglected without introducing serious error.

More accurate measurement of the translocation of pre-flowering stored stem reserves to developing seeds can be made using tracer elements like ^{14}C or $^{14}CO_2$ (Bidinger *et al.*, 1977; Austin *et al.*, 1977). However,

Table 1. Estimates of apparent translocation of pre-anthesis stored materials in rice, wheat, barley and maize.

Crop	Authors	Apparent translocation (% of grain weight)	Method used
Rice	Yoshida (1972)	20-40	^{14}C labelling
Wheat	Wardlaw (1967)	30-50	^{14}C labelling
	Rawson and Evans (1971)	3-12	^{14}C labelling
	Gallagher *et al.*(1976)	35-57	Growth analysis
	Austin *et al.* (1977)	10-15	^{14}C labelling
	Bidinger *et al.* (1977)	13-27	^{14}C labelling
	Brocklehurst *et al.* (1978)	20-30	Growth analysis
	Blum *et al.* (1983)	10-32	Growth analysis
	Fischer (1983)	20-30	^{14}C labelling
	Borrell *et al.* (1989)	25-43	Growth analysis
	Bell and Incoll (1990)	5-15	^{14}C labelling
	Pheloung and Siddique (1991)	15-20	^{14}C labelling
	Wardlaw and Willenbrink (1994)	30-40	^{14}C labelling
Barley	Gallagher *et al.* (1975)	2-74	Growth analysis
	Bidinger *et al.* (1977)	12-17	^{14}C labelling
	Austin *et al.* (1980)	15-60	^{14}C labelling
	Bonnett and Incoll (1992)	25-43	Growth analysis
Maize	Hawkins and Cooper (1981)	20-50	Growth analysis
	Setter and Meller (1984)	25-45	^{14}C labelling

Gallagher *et al.* (1975) devised a predictive formula,

$$\Delta W_g /N = \Delta W_t /N - \Delta W_s /N \qquad (1)$$

where, ΔW_g, ΔW_t and ΔW_s are the increases or changes in grain, total and stem dry weights, respectively, (all from anthesis to maturity), and N is the number of grains per unit area. The increase in weight per grain ($\Delta W_g/N$) is considered to be the difference between total dry matter production per grain ($\Delta W_t/N$) after anthesis, and the change in stem weight per grain ($\Delta W_s/N$) over the same period. When $\Delta W_t/N$ exceeds $\Delta W_g/N$, $\Delta W_s/N$ will be positive, i.e., the stem will increase in weight after flowering. If $\Delta W_t/N$ is less than $\Delta W_g/N$ the stem may decrease in weight so that $\Delta W_s/N$ is a negative quantity. $\Delta W_g/N$ is regarded as the sum of two terms; $\Delta W_t/N$ related to photosynthesis after anthesis and $(-)\Delta W_s/N$ related to photosynthesis before anthesis. Thus $\Delta W_s/\Delta W_g$ represents the fraction of grain weight which may be supplied by the translocation of material stored in the stem before anthesis. If $\Delta W_t/N = 0$, then $\Delta W_s/\Delta W_g = -1$, i.e., all the grain weight is provided by the decrease in the weight of the stem. As N is a constant, in subsequent studies Gallagher *et al.* (1976) modified the formula to $\Delta W_g = (\Delta W_t - \Delta W_s)$ and estimated the apparent translocation (AT) of pre-flowering stem reserves to the developing seed as, $-\Delta W_s/\Delta W_g$, where $-\Delta W_s = (\Delta W_t - \Delta W_g)$. We have further modified the formula to AT(%) = $((\Delta TDM - \Delta GDM)/\Delta GDM) * 100$ where, ΔTDM and ΔGDM are the changes in total and grain dry matters, respectively, from anthesis to maturity, with the assumption that assimilate produced after flowering is mostly used by the seeds, and that loss of plant parts (leaves and flowers) were minimal. This formula has been applied for a number of crops, including cereals, mustard and perennial ryegrass seed (Table 2).

Table 2. Estimates of apparent translocation (AT) of pre-flowering stored stem reserves of different crops using the formula ((ΔTDM - ΔGDM)/ΔGDM) * 100. Data are from different experiments.

Crop/Authors	Experiment	AT(%)
Wheat (*Triticum aestivum* L.)		
Roy (1985)	Effect of drought during different developmental phases on growth and yield of wheat in a glasshouse	9-13
	Response of wheat to plant population, nitrogen, thinning and suppression of photosynthesis in the field	15-30
	Response of wheat to nitrogen in growth cabinets	8-45
	Response of tillering, yield and yield components of wheat to irradiance during different developmental phases	0-50
Roy *et al.* (1991)	Effect of nitrogen and planting geometry on tillering,growth and yield of wheat	35-55
Roy *et al.* (1993)	Effect of additional nitrogen at anthesis on plant development and yield components of four cultivars of wheat	25-40
Roy and Salahuddin (1994)	Effect of spikelet thinning on individual seed weight and yield of wheat under two sowing dates	28-38
Maize (*Zea mays* L.)		
Roy and Quasem (1987)	Effect of population and leaf pruning on yield and yield attributes of maize	18-29
Roy and Biswas (1992)	Effect of population and detopping following silking on cob growth, fodder and grain yield of maize	17-22
Mustard (*Brassica campestris* L.)		
Roy *et al.* (1994)	Effect of leaf and flower removal on seed yield and its components in three cultivars of mustard	16-22
Ryegrass (*Lolium perenne* L.) at AgResearch, Lincoln		
Unpublished data (1994)	Irrigated	14-48
	Rainfed	14-50

General implications

The review and discussion in this paper puts an emphasis on events before flowering as important determinants of grain yield. A crop variety able to draw on large amounts of material assimilated before flowering and translocated from the stem under adverse conditions for grain filling, has an advantage over a variety which does not. The degree to which a variety is able to do is called compensatory ability. Here compensatory translocation has been shown to occur in wheat, maize, perennial ryegrass and mustard; this property in barley has been discussed in detail by Gallagher *et al.* (1975) and Bidinger *et al.* (1977). Donald (1968) described an idealized cereal plant, and considered that maximum transfer of materials from the stem to the ear was desirable in every season. The degree to which a variety compensates for poor photosynthesis after flowering, by translocating material from its stem, may be an important varietal characteristic (Austin *et al.*, 1980; Wardlaw and Willenbrink, 1994).

Apparent translocation may be estimated from appropriate dry weight and yield component measurements. When a variety shows high compensatory ability, it should then be possible, by combining appropriate genetic material and cultural practices, to ensure a high and fairly uniform grain number and grain weight from season to season and location to location. In so doing it might be possible to achieve a varietal character of great economic importance. Knowledge of translocating ability of different field crops could be incorporated in computer models to predict yield or yield losses due to post-flowering stress. Translocating abilities of different crops may be incorporated into a database for modelling, and in selecting appropriate varieties for an environment where yield loss due to post-flowering stress is common.

Conclusions

It appears that translocation of 10-20% of stored stem assimilate is common, even in a normally growing crop. The translocating ability is greatly enhanced if there is post-anthesis stress, where up to 60% of the stored stem reserves may be translocated. The apparent translocation of stored pre-flowering stem reserves has been largely overlooked or bypassed in seed production research in New Zealand. This short review suggests that the translocation of pre-flowering stored stem reserves can contribute significantly to yield and could be an important varietal characteristic.

References

Austin, R.B., Edrich, J.A., Ford, M.A. and Blackwell, R.D. 1977. The fate of dry matter, carbohydrates and ^{14}C loss from leaves and stems of wheat during grain filling. *Annals of Botany, London* **41**, 1309-1321.

Austin, R.B., Morgan, R.B., Ford, M.A. and Blackwell, R.D. 1980. Contribution of grain yield from pre-anthesis assimilation in tall and dwarf barley genotypes in two contrasting seasons. *Annals of Botany, London* **45**, 309-319.

Bell, C.J. and Incoll, L.D. 1990. The redistribution of assimilate in field-grown winter wheat. *Journal of Experimental Botany* **41,** 949-960.

Bidinger, F., Musgrave, R.B. and Fischer, R.A. 1977. Contribution of stored pre-anthesis assimilate to grain yield in wheat and barley. *Nature* **270**, 431-433.

Biscoe, P.V., Gallagher, J.N., Littleton, E.J., Scott, R.K. and Monteith, J.L. 1975. Barley and its environment. IV. Contributions to yield. *Journal of Applied Ecology* **12**, 295-318.

Blum, A., Poiarkova, H., Golan, G. and Mayer, J. 1983. Chemical desiccation of wheat plant as a simulator of post-anthesis stress. I. Effects on translocation and kernel growth. *Field Crops Research* **6,** 51-58.

Borrell, A.K., Incoll, L.D., Simpson, R.J. and Dalling, M.J. 1989. Partitioning of dry matter and the deposition and use of stem reserves in a semi-dwarf wheat crop. *Annals of Botany* **63**, 527-539.

Bonnett, G.D. and Incoll, L.D. 1992. The potential pre-anthesis and post-anthesis contributions of stem internodes to grain yield in crops of winter barley. *Annals of Botany* **39,** 106-114.

Bremner, P.M. 1972. Accumulation of dry matter and nitrogen in grains of different positions of the wheat ear as influenced by shading and defoliation. *Australian Journal of Biological Sciences* **25,** 657-668.

Brocklehurst, P.A., Moss, J.P. and Watkin Williams 1978. Effects of irradiance and water supply on grain development in wheat. *Annals of Applied Biology* **90**, 265-276.

Donald, C.M. 1968. The breeding of crop ideotypes. *Euphytica* **17**, 385-403.

Fischer, R.A. 1983. Wheat. *In* Potential Productivity of Field Crops Under Different Environments. pp. 130-154. IRRI, Los Banos, Laguna, Philippines.

Gallagher, J.N., Biscoe, P.V. and Scott, R.K. 1975. Barley and its environment. V. Stability of grain weight. *Journal of Applied Ecology* **12**, 319-336

Gallagher, J.N., Biscoe, P.V. and Hunter, B. 1976. Effects of drought on grain growth. *Nature* **264**, 541-542.

Hawkins, R.C. and Cooper, P.J.M. 1981. Growth, development and grain yield of maize. *Experimental Agriculture* **17**, 203-207.

Hunt, L.A. 1979. Stem weight changes during grain filling in wheat from diverse sources. *In* Proceedings of the 5th International Wheat Genetic Symposium. pp. 923-929. IARI, New Delhi, India.

Pheloung, P.C. and Siddique, K.H.M. 1991. Contribution of stem dry matter to grain yield in wheat cultivars. *Australian Journal of Plant physiology 18*, 53-64.

Rawson, H.M. and Evans, L.T. 1971. The contribution of stem reserves to grain development in a range of wheat cultivars of different height. *Australian Journal of Agricultural Research 22*, 851-863.

Rawson, H.M., Bagga, A.K. and Bremner, P.M. 1977. Aspects of adaptation by wheat and barley to soil moisture deficits. *Australian Journal of Plant Physiology 4*, 389-401.

Roy, S.K. 1985. Environmental control of tillering and yield of wheat. Ph.D. Thesis, Lincoln College, University of Canterbury, New Zealand. 231 pp.

Roy, S.K. and Quasem, A. 1987. Effect of population and leaf pruning on yield and yield attributes of maize. *Bangladesh Journal of Agronomy 2*, 64-67.

Roy, S.K., Maniruzzaman, A.F.M. and Saifuzzaman, M. 1991. Effect of nitrogen and planting geometry on tillering, growth and yield of wheat. *Indian Journal of Agronomy 36*, 32-39.

Roy, S.K. and Biswas, P.K. 1992. Effect of population and detopping following silking on cob growth, fodder and grain yield of maize. *Journal of Agricultural Science 119*, 297-301.

Roy, S.K., Biswas, P.K., Jalaluddin, M. and Mohammad H Mondal 1993. Effect of additional nitrogen at anthesis on plant development, growth and yield components of four cultivars of wheat. *Indian Journal of Agricultural Science*: accepted

Roy, S.K. and Salahuddin, A.B.M. 1994. Effect of spikelet thinning on individual seed weight and seed yield of wheat under two sowing dates. *Journal of Applied Seed Production 12*, In press

Roy, S.K., Akteruzzaman, M. and Salahuddin, A.B.M. 1994. Effect of leaf and flower removal on seed yield and its components of three cultivars of mustard. *Journal of Applied Seed Production 12*, In press

Setter, T.L. and Meller, V.H. 1984. Reserve carbohydrate in maize stem. [^{14}C]glucose and [^{14}C]sucrose uptake characteristics. *Plant Physiology 75*, 617-622.

Thornley, J.H.M. 1979. Wheat grain growth: anthesis to maturity. *Australian Journal of Plant Physiology 6*, 187-194.

Wardlaw, I.F. 1967. The effect of water stress on translocation in relation to photosynthesis and growth. I. Effect during grain development in wheat. *Australian Journal of Biological Sciences 20*, 25-39.

Wardlaw, I.F. and Porter, H.K. 1967. The redistribution of stem sugars in wheat during grain development. *Australian Journal of Biological Sciences 20*, 309-318.

Wardlaw, I.F. and Willenbrink, J. 1994. Carbohydrate storage and mobilisation by the culm of wheat between heading and grain maturity: the relation to sucrose synthase and sucrose-phosphate synthase. *Australian Journal of Plant Physiology 21*, 255-271.

Yoshida, S. 1972. Physiological aspects of grain yield. *Annual Review of Plant Physiology 23*, 437-464.