PHOTOSYNTHESIS AND ASSIMILATE DISTRIBUTION IN *LOLIUM MULTIFLORUM* LAM. FOLLOWING DIFFERENTIAL TILLER DEFOLIATION

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Abstract

The rate of net CO_2 exchange and the distribution of ^{14}C-assimilates was studied in single plants of *L. multiflorum*. Defoliation of tillers, while leaving the main shoot intact, diverted some of the ^{14}C assimilated by leaf 10 of the main shoot to the regrowing tillers. The level of this diversion continued to increase throughout a 9-day experiment when regrowth was trimmed daily, but reached a peak after 2 days when the regrowth was allowed to remain on the plant. The diversion of assimilate to defoliated tillers was largely at the expense of the main shoot when the stress was mild but also at the expense of the roots for the more severe treatments.

For a leaf in a phase of declining net photosynthesis the first effect of tiller defoliation on the gas-exchange properties of main shoot leaves was a reduction of gas-phase resistance. Continued regrowth trimming maintained this low gas-phase resistance and also prevented the increase of residual resistance with age which was evident in control plants. For a leaf which had not quite reached full expansion when the tiller defoliation–regrowth trimming procedure started, the major source of the higher net photosynthesis rate after 10 days (relative to the controls) was a low gas-phase resistance.

These experiments confirm that although established tillers are usually independent of the main shoot for assimilate, when under stress they again become dependent on the main shoot. This support was sustained if the stress was sustained, and the enhanced demand for assimilate from the main shoot delayed the normal decline of photosynthesis rate with age in main-shoot leaves.

I. INTRODUCTION

In young plants of *Lolium multiflorum* Lam. (Marshall and Sagar 1965; Marshall 1967) and other grasses such as *Phleum pratense* L. (Williams 1964; St. Pierre and Wright 1972) the primary tillers soon lose their dependence on the main shoot for carbohydrate and become virtually independent. Temporary re-integration, with respect to photosynthate, of well-developed tillers with the main shoot is possible, however, when they are defoliated (Forde 1966; Marshall and Sagar 1965, 1968; Williams 1968), but the defoliated tillers regain their physiological independence within a few days as leaf area is re-established. This contrasts with what would be expected if the tillers were truly independent units competing for resources such as light: then a stressed tiller would be at a competitive disadvantage and be suppressed.

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One question examined in this paper is whether the intact main shoot of *L. multiflorum* will continue to support stressed tillers when the stress is prolonged over many days, or whether support is given only for a short period. Another is whether the support provided by the intact tiller is merely a matter of diversion of some of its assimilates to the stressed tiller or whether its photosynthetic rate is also enhanced. Evidence in the literature (e.g. Brougham 1956; King *et al.* 1967; Neales and Incoll 1968; Hodgkinson *et al.* 1972) suggests that some enhancement of photosynthetic rate might be expected.

II. Materials and Methods

Plants of *L. multiflorum* cv. S22 (Italian ryegrass) were grown singly in 12·5-cm pots of perlite in a naturally lit glasshouse with day length extended by low intensity incandescent light to give a 16-hr photoperiod. The pots were watered twice daily, with Hoagland nutrient solution in the morning and with demineralized water in the afternoon. Temperatures were maintained at 24°C from 8.30 a.m. to 4.30 p.m. and at 19°C for the remaining 16 hr of the day. Experiments were made on plants 6–8 weeks after sowing. Plants were defoliated as in previous work (Marshall and Sagar 1965, 1968) with only the tillers being cut, the main shoot always remaining intact. The plants were vegetative throughout.

The net CO_2 exchange rate per unit leaf area and diffusion resistances of the selected leaves of the main shoot were followed using an open air circuit gas-analysis system. Air recirculation on each side of the leaf blade gave a linear velocity of about 350 cm s^{-1} in the leaf chamber. Leaf temperature, determined by three thermocouples (42 s.w.g.) pressed on the underside of the leaf, was maintained at 25·5±0·5°C by recirculating the chamber air over a cool heat-exchanger. By continuous mixing of moistened and dried CO_2-enriched and CO_2-free air, humidity was maintained at 65–75% and CO_2 concentration at 503±15 ng cm^{-3} in the chamber. The plant and leaf chamber were placed in an artificially lit (L.B.) growth cabinet (Morse and Evans 1962), set at 21°C. Fluorescent lighting (VHO) was supplemented by a Philips HPLR high-pressure mercury vapour lamp. Ultraviolet radiation was filtered out by a glass window in the leaf chamber. The height of the leaf chamber was adjusted to give 150 W m^{-2} of visible radiation (400–700 nm) on the upper leaf surface. Carbon dioxide was determined with a Grubb-Parsons SB2 infrared gas analyser calibrated with Wösthoff mixing pumps, and humidity was measured with a thermocouple–wet-bulb psychrometer similar to the design of Slatyer and Bierhuizen (1964). Gas phase resistance to CO_2 diffusion (r_a+r_s) was calculated from the equation

$$(r_a/1{\cdot}46+r_s/1{\cdot}56) = (e_l-e_a)/E,$$

where r_a is the boundary layer resistance and r_s the stomatal resistance to CO_2 diffusion, e_l is the saturated humidity (g cm^{-3}) at leaf temperature, e_a is the leaf chamber humidity (g cm^{-3}), E is the transpiration rate (g cm^{-2} s^{-1}) and the factors 1·46 and 1·56 are for conversion of the resistances to water vapour diffusion to the equivalent terms for CO_2 diffusion. Substomatal CO_2 concentration was calculated from

$$C_s = C_a-P(r_a+r_s),$$

where C_a is the ambient CO_2 concentration in the leaf chamber (g cm^{-3}) and P is the net CO_2 exchange rate per unit leaf area (g cm^{-2} s^{-1}). "Residual resistance" (r_r) to CO_2 uptake was calculated from the equation

$$r_r = (C_s-C_p)/P,$$

where C_p is the CO_2 compensation point. The CO_2 compensation point did not vary significantly with treatments or age of leaf in this study and had an average value of 90 ng cm^{-3}. One hour before a plant was due for measurement it was transferred from the glasshouse to the growth cabinet for equilibration. After measurement of gas-exchange parameters the plants were returned to well-illuminated, widely spaced positions in the glasshouse.

The pattern of assimilate distribution was determined by supplying the selected leaves on the main shoot with $^{14}CO_2$ and harvesting the plants after 24 hr. Leaves of all replicates were

enclosed in a common chamber inside an L.B. type growth cabinet and $^{14}CO_2$, generated by adding excess 50% lactic acid to $Ba^{14}CO_3$ containing 6 or 10 μCi ^{14}C per leaf, was circulated through the leaf chamber in a closed air circuit for 20 min after which the leaves were removed from the chamber. Light intensity within the chamber was 60 W m^{-2} from mixed mercury vapour (Philips HPLR) and fluorescent (VHO) sources. At harvest the plants were cut into component parts, dried, weighed, and 30 mg powdered aliquots counted for radioactivity by the procedure of O'Brien and Wardlaw (1961). There were at least four replicates of each treatment.

III. Results

(*a*) *Net CO_2 Exchange Rate*

Net CO_2 exchange and transpiration measurements were made on main shoot leaves 6, 8, and 10 (numbering from the base) in three experiments. The first measurements (day 0) were taken 10–15 days after emergence of the ligule. At the end of day 0 (i.e. about 6 p.m.) tillers were defoliated and their sheaths cut back to 5 cm. Tiller regrowth was removed daily. On the days photosynthetic measurements were made, regrowth was removed after the measurement. The main shoot remained intact throughout. In the experiments using leaves 8 and 10, the tillers of the control plants were held loosely back to avoid shading of the leaf studied.

TABLE 1

MEAN DATA FOR NET CO_2 EXCHANGE RATE, GAS-PHASE RESISTANCE (r_a+r_s), AND RESIDUAL RESISTANCE (r_r) FOR ALL THREE EXPERIMENTS

The defoliation treatment was carried out at the end of day 0 after measurements were completed. Statistically significant differences between day 0 and day 1 values at $P < 0{\cdot}05$ and $P < 0{\cdot}01$ indicated by * and ** respectively; n.s., not significant

Parameter	Control		Tillers defoliated	
	Day 0	Day 1	Day 0	Day 1
Net CO_2 exchange rate (ng cm^{-2} s^{-1})	60	57 (n.s.)	60	69**
(r_a+r_s) (s cm^{-1})	2·3	2·2 (n.s.)	2·3	1·4*
r_r (s cm^{-1})	4·7	5·1**	4·7	4·5 (n.s.)

Similar results were obtained for all three experiments. Net CO_2 exchange rate per unit blade area was, on average, 15% greater the day after tiller defoliation than just before defoliation (Table 1) whereas the control plants showed a slight (non-significant) decrease of net CO_2 exchange over the 24-hr period. This rapid reaction to tiller defoliation was largely a stomatal response, the gas-phase resistance having dropped from 2·3 to 1·4 s cm^{-1}. The small decline in net CO_2 exchange rate of the controls, on the other hand, was due to a rise of residual resistance while gas-phase resistance remained constant. The enhanced net CO_2 exchange rates were maintained, throughout the experiments, above the values on day 0 by daily trimming of tiller regrowth, while the rates for the control plants declined (Fig. 1). This decline with time for the leaves of the control plants was due to increase of both gas phase and residual resistance (Fig. 2). The maintenance of the relatively high exchange rates for the tiller-defoliated plants throughout each experiment was

due to the constancy of residual resistance with time and the maintenance of gas-phase resistance less than or equal to its value prior to defoliation of the tillers (Fig. 2).

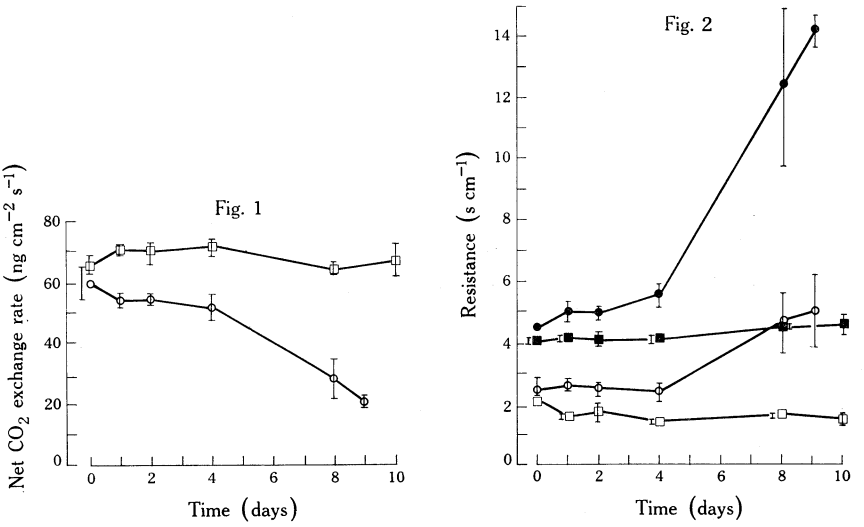

Fig. 1.—Time course of net CO_2 exchange rate of leaf 10 of the main shoot when tillers were defoliated after the measurement on day 0 and the regrowth trimmed daily (□) or when the tillers were left intact (○). Each point is the mean of four replicates. Vertical bars are twice the standard error.

Fig. 2.—Time course of resistance parameters for leaf 10. Defoliated as in Figure 1 (squares); intact (circles). Gas-phase resistance (open symbols); residual resistance (closed symbols).

In the experiment using leaf 10, the gas-exchange properties of leaf 13, also of the main shoot, were examined on day 10 of the study. The ligule of leaf 13 emerged on day 0, the day the tillers were defoliated. On day 10, leaf 13 had a net CO_2 exchange rate 39% greater than leaf 13 of the control, and this difference was attributable almost entirely to the gas-phase resistance, as shown in the following tabulation (values given are means of four plants):

	Control	Tillers defoliated 10 days earlier
Net CO_2 exchange rate (ng cm^{-2} s^{-1})	56	77*
(r_a+r_s) (s cm^{-1})	3·4	1·4*
r_r (s cm^{-1})	4·1	3·8 (n.s.)

* Significantly different from control at $P < 0{\cdot}05$.

(*b*) *Assimilate Distribution*

Two experiments were performed to study the distribution of ^{14}C, assimilated by leaf 10 of the main shoot, to various parts of the plant when the tillers were defoliated. The first experiment was for the same conditions as the above photosynthesis experiment (Figs. 1 and 2). On day 0, 15 days after emergence of the ligule of leaf 10, the tillers were defoliated, the sheaths trimmed back to 5 cm, and the

regrowth was removed daily. On days 1, 3, 6, and 9, leaf 10 was labelled with $^{14}CO_2$ and the distribution of ^{14}C between fed leaf, main shoot, tillers, and roots examined 24 hr later.

Tiller defoliation markedly enhanced the proportion of ^{14}C leaving leaf 10 to go to the tillers (Table 2); initially this was largely at the expense of the proportion going to other parts of the main shoot. As the experiment proceeded the proportion of ^{14}C going to the tillers continued to rise and by the end this was at the expense of the root system as well as the main shoot. The proportion of ^{14}C retained by the fed leaf was also reduced by tiller defoliation relative to the controls (bottom line of Table 2).

TABLE 2

PERCENTAGE DISTRIBUTION AND EXPORT OF RADIOCARBON AFTER 24 HR FROM LEAF 10 OF THE MAIN SHOOT WITH TIME IN UNDEFOLIATED CONTROLS AND PLANTS WHICH WERE DEFOLIATED DAILY

Mean of four replicates (±S.E.)

Plant part	Control plants: days to supplying $^{14}CO_2$				Defoliated plants: days from initial defoliation to supplying $^{14}CO_2$			
	1	3	6	9	1	3	6	9
Main shoot	33·4 ±2·0	33·9 ±4·9	36·1 ±4·8	40·0 ±4·6	12·0 ±3·9	14·9 ±4·7	20·0 ±4·1	16·8 ±2·7
Tillers	11·1 ±2·0	13·1 ±1·5	23·0 ±2·9	18·3 ±6·6	35·6 ±6·0	28·3 ±2·7	53·4 ±6·8	69·8 ±5·0
Roots	55·3 ±2·9	53·0 ±5·8	40·9 ±7·7	41·7 ±3·9	52·4 ±2·5	56·8 ±5·6	26·5 ±4·8	13·4 ±3·2
Export (%)	74·6 ±3·9	60·0 ±4·6	53·3 ±4·5	67·6 ±4·3	79·7 ±2·4	75·5 ±1·5	73·7 ±4·3	81·7 ±3·6

In the second ^{14}C-distribution experiment the tillers were defoliated (without later trimming of regrowth) 2 days after the ligule of leaf 10 had emerged, i.e. when leaf 10 was just fully expanded. $^{14}CO_2$ was fed to leaf 10, 1, 48, or 96 hr after defoliation and the distribution of label was determined after 24 hr. Two levels of defoliation were applied; in one all tillers were cut back to 5 cm of sheath and in the other only the fully expanded leaf blades were removed.

Tiller defoliation caused an immediate re-directing of much of the ^{14}C exported from leaf 10 to the stressed tillers (Table 3). The degree of the effect was greater for the severe defoliation than for the relatively mild defoliation. But for both mild and severe defoliation the peak level of support of tiller regrowth by leaf 10 was about 2 days after the treatment, after which time a decline in support set in. The increased proportion of support of tillers, after their defoliation, by leaf 10 was primarily at the expense of the portion going to the main shoot. Although supply of ^{14}C assimilates to the root system was rather variable, the severe defoliation also reduced the proportion of ^{14}C assimilate acquired by the roots in 48 hr whereas the mild defoliation did not have this effect. After 96 hr the ^{14}C-distribution pattern for the lesser defoliation treatment was approaching the pattern for the control whereas the pattern for the severe treatments after 96 hr was the same as for the mild treatment after only

48 hr. The proportion of the ^{14}C retained by the fed leaf was unaffected by the defoliation treatments in this experiment (bottom line of Table 3).

TABLE 3

PERCENTAGE DISTRIBUTION AND EXPORT OF RADIOCARBON AFTER 24 HR FROM LEAF 10 OF THE MAIN SHOOT WITH TIME IN UNDEFOLIATED CONTROL AND DEFOLIATED PLANTS (SINGLE DEFOLIATION)

Mean of four replicates (±S.E.)

Plant part	Control plants: time to supplying $^{14}CO_2$ (hr)			Plants with all tiller leaves removed: time from defoliation to supplying $^{14}CO_2$ (hr)			Plants with expanded tiller leaves only removed: time from defoliation to supplying $^{14}CO_2$ (hr)		
	1	48	96	1	48	96	1	48	96
Main shoot	37·8	42·8	42·1	12·8	17·8	28·5	20·8	29·6	35·3
	±4·1	±6·0	±5·4	±1·2	±2·1	±4·6	±2·5	±1·5	±7·6
Tillers	24·7	29·6	28·9	61·9	65·3	48·9	32·4	46·7	41·9
	±3·1	±4·8	±2·8	±3·6	±1·5	±2·8	±3·3	±3·1	±5·1
Roots	35·1	26·2	28·1	25·3	16·9	22·6	46·8	23·7	22·8
	±3·9	±1·3	±2·7	±3·0	±1·8	±3·8	±2·9	±2·6	±2·5
Export (%)	83·0	84·5	86·1	87·5	87·7	86·5	82·6	86·9	82·9
	±1·9	±0·5	±3·8	±1·5	±3·0	±1·7	±3·2	±1·7	±1·5

IV. DISCUSSION

The pattern of assimilate distribution from leaf 10 of *L. multiflorum* at the newly expanded stage was greatly and rapidly altered in favour of the tillers by tiller defoliation (Table 3). This agrees with previous autoradiographic work on earlier leaves than leaf 10 (Marshall and Sagar 1965), and with quantitative studies on export from wholly labelled main shoots of plants at an earlier stage than in the present investigation (Marshall and Sagar 1968). Further it was shown that the more severe the defoliation the greater was the support given to the tillers—both in the amount of ^{14}C supplied and in the duration of the supply. When leaf 10 was 2 weeks older, in the phase of declining photosynthesis rate (Fig. 1), its assimilate was still directed towards the defoliated tillers (Table 2). When the carbohydrate stress on the tillers was maintained by daily regrowth trimming, the degree of tiller support by leaf 10, relative to its support of the rest of the plant, was not only maintained for many days, but was also increased with time. This shows that the support given by the mother shoot to stressed tillers, formerly virtually independent of the mother shoot, can be maintained if the need arises. Presumably the transitory nature of the tiller support following only a single defoliation reflects the re-establishment of the tillers' own leaf surface.

On the basis of autoradiographic work (Marshall and Sagar 1965) it is evident that most of the ^{14}C accumulated by the tiller fraction in the controls (Tables 2 and 3) is restricted to the younger tillers still dependent on the main shoot; the established tillers are virtually independent for carbohydrate. Further, comparing the data for intact control plants in Table 3 (leaf 10 newly expanded) and Table 2 (leaf 10 over 2 weeks old), the proportion of ^{14}C supplied to these tillers was substantially reduced

with leaf age—a situation reported also by Ryle (1972). There was no effect of defoliation on the proportion of export of assimilates from a young leaf (Table 3), but at a later stage of development when the degree of assimilate export had decreased, defoliation resulted in an increase in the proportion of ^{14}C exported out of the leaf. Similar increases in this proportion have been found by Hartt *et al.* (1964), Khan and Sagar (1969), Lovell *et al.* (1972).

Taking the relative ^{14}C distribution data in Tables 2 and 3 at face value one obtains the picture that after mild defoliation the tillers are supported at the expense of carbon accumulation in the main shoot, but after severe defoliation of tillers the root system also suffers. However, whether or not the main shoot and root system are deprived of assimilate from the main shoot leaves in absolute terms will depend on the level of photosynthetic enhancement and the degree to which assimilates are exported from the leaf. For example, on day 9 in Figure 1, net CO_2 exchange rate of leaf 10 for the defoliation treatment is about 66 ng cm^{-2} s^{-1} compared with 21 ng cm^{-2} s^{-1} for the control. Partitioning these values in accordance with the proportions exported from the leaf 10 (Table 2) (82% for defoliated; 68% for control) and with the proportion of import by the root (13% for defoliated; 42% for control) we obtain 7·2 ng cm^{-2} s^{-1} for the defoliated and 5·9 ng cm^{-2} s^{-1} for control plants as an approximation to the absolute amounts (per unit leaf area) being exported from leaf 10 to the roots. Thus in absolute terms the level of support given to the root system by the main shoot probably did not fall (cf. Marshall and Sagar 1968) and may have increased as a result of tiller defoliation. But it is unlikely that this enhanced support could make up losses due to reduction of leaf area—rate of root growth is usually reduced after defoliation (see Milthorpe and Davidson 1966).

The progressive decline in net CO_2 exchange rate of the leaf after about 2 weeks from full emergence has also been reported for other temperate grasses like tall fescue (*Festuca arundinacea*) (Jewiss and Woledge 1967) and barley (Thorne 1963). Also there are reports of declining net CO_2 exchange rate with leaf age for many dicotyledenous species (e.g. Ludlow and Wilson 1971; Hodgkinson *et al.* 1972). In the present study the decline with time was due to changes in both gas-phase and residual resistances. Residual resistance was two to three times greater than gas-phase resistance and was therefore the more dominant determinant of the decline in net CO_2 exchange rate with time.

There were two effects of tiller defoliation on net CO_2 exchange rate of a leaf which had commenced its phase of decline. The first immediate effect was stomatal opening. This had occurred by the next morning following tiller defoliation the previous evening. The stomatal opening was sufficient to have a significant effect on net CO_2 exchange rate (Table 1). The second effect was the prevention of the decline in both gas-phase and residual resistance with time. This behaviour contrasts with the findings of Hodgkinson *et al.* (1972) who studied the gas exchange of stubble leaves of lucerne after cutting off the top of the shoot. They found no effect of defoliation on gas-phase resistance, either immediate or long term, but observed a steady decline of residual resistance for 8 days after defoliation leading to a two- to threefold increase of net CO_2 exchange rate to the value found for a young leaf at its maximum. Although this seems very different from our results the only major difference may be that in the senesced stubble leaves of lucerne the stomata had not closed somewhat

as they did in the ryegrass. Gas-phase resistance was so low for these old lucerne leaves that there was little scope for further opening following defoliation.

Residual resistance of the lucerne stubble leaves, on the other hand, was initially very high in contrast to residual resistance in the ryegrass leaves, which were not far beyond their peak net CO_2 exchange rate (Fig. 1). The failure of the present work to detect any significant decline of residual resistance after defoliation may be because it was already close to the minimal value possible. Neales *et al.* (1971) examined the increase in photosynthesis rate of the remaining leaves after partial defoliation of another legume species, *Phaseolus vulgaris*. As for lucerne, so too for *P. vulgaris* had residual resistance declined 3 days after defoliation. But for the latter stomatal resistance had also declined, although residual resistance was the dominant factor.

The response of leaf 13 [see tabulation, Section III(*a*)] for which the enhanced demand for assimilate, due to tiller defoliation, commenced before it reached its maximum photosynthetic capacity, differed from the response of the other leaves which experienced enhanced demand when they were already in a phase of declining photosynthesis (Fig. 1). The continued exposure to tiller defoliation maintained the gas-phase resistance at the same low level ($1 \cdot 4$ s cm^{-1}) that the leaves at a later stage in their aging cycle opened to when their tillers were initially defoliated (Table 1). Perhaps this was the lowest gas-phase resistance possible for the particular stomatal and boundary layer geometry of the system. The residual resistance, on the other hand, was lower for leaf 13 ($3 \cdot 8$ s cm^{-1}) than was ever achieved during rejuvenation of any of the other leaves; these other leaves had an average minimum residual resistance of about $4 \cdot 5$ s cm^{-1} and did not exhibit any trend of decrease over a prolonged period as found by Hodgkinson *et al.* (1972) for lucerne stubble leaves.

Our observation, that defoliation initially caused stomatal opening in the remaining leaves, fits in with the hypothesis of Wareing *et al.* (1968) that partial defoliation reduces the competition between leaves for cytokinins produced in the roots (Mothes 1964; Weiss and Vaadia 1965). Kinetin is known to cause rapid stomatal opening in leaves of barley (Livne and Vaadia 1965; Meidner 1967; Cooper *et al.* 1972) and oats (Luke and Freeman 1968; Pallas and Box 1970). Kinetin also retards leaf senescence, probably via an effect on protein metabolism (Richmond and Lang 1957; Woolhouse 1967), hence the prevention, following partial defoliation, of the steady increase of residual resistance with aging could also be attributable to cytokinin effects on carboxylase activity (Neales *et al.* 1971).

Overall the results show that the stress imposed by defoliation is efficiently buffered by the rapid re-organization in the carbon economy of the plant. The increase in the rate of photosynthesis by the remaining leaves, in the proportion of assimilate exported from the older leaves, and the change of distribution pattern allow the tillers to receive maximum support from the intact part of the shoot. Further, the results emphasize the importance of the source–sink balance in the physiological organization of the plant.

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