RESEARCH PAPER

Distribution of current photosynthate in two Guinea grass (Panicum maximum Jacq.) cultivars

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Abstract

In a glasshouse experiment, different tiller categories (main, young primary, and old primary) of two Guinea grass cultivars, Mombaca and Tanzania, were 14C-labelled to investigate C translocation between tillers. In both cultivars, young primary tillers retained less radiocarbon (79%) than main (86%) and old primary (87%) labelled tillers, suggesting that the photosynthetic capacity of the young tillers exceeds their capacity either to store or use that photosynthate for growth and maintenance. In cv. Tanzania the old primary tillers translocated more photoassimilate to their daughter tillers and to the rest of the plant than cv. Mombaca, suggesting either higher vascular connectivity between tillers or stronger diurnal fluctuations in sink–source balance in Tanzania than Mombaca. For unlabelled tillers, specific activities were almost always higher in roots than in shoots, although total radiocarbon uptake by roots was reduced in younger tillers with low root mass. Where young primary tillers were labelled, the largest single repository of exported photoassimilate was the main tiller roots, indicating that daughter tillers may make an important contribution to the maintenance of older roots on mature tillers.

Key words: Carbon translocation, Panicum maximum, source–sink, specific activity, tiller hierarchy.

Introduction

Historically, measurement of carbon translocation within the grass plant has provided basic physiological information on source–sink relationships within individual tillers, between tillers of different hierarchical positions, or between reproductive and vegetative tillers. For example, Clifford et al. (1973) measured the percentage recovery from the main shoot of radiocarbon applied to a young leaf of a lateral tiller and vice versa in Lolium multiflorum, and concluded from observations of reciprocal transfer that mature tillers maintain vascular continuity with their roots and daughter tillers, and that photoassimilate exported to roots is not redistributed later. Similarly, Dankwerts and Gordon (1987) studied the fate of exported photoassimilate over longer time periods (up to 22 d) showing that most reached a final destination within 4–6 d and respired; any remobilization of stored photoassimilate was from stem bases, not roots. Colvill and Marshall (1984) used a 14C tracer to demonstrate in Lolium perenne, that competition between young tillers and reproductive organs for current assimilate during stem elongation and head emergence is important in determining tiller lifespan. Information from such studies is often drawn upon in reviews (for example, Robson et al., 1988) where the aim is to provide an overview of whole plant function. Similarly, information on photoassimilate distribution patterns can assist in understanding whether or not leaf, root or daughter tiller formation of plants in the field may be limited by competition for assimilate arising from growth activity in other parts of the plant (Lemaire and Chapman, 1996). The majority of published studies of this type have used small temperate grasses, such as perennial ryegrass (L. perenne) or tall fescue (Festuca arundinacea).

Assimilated C may be used in situ, stored, or exported to other plant parts via the phloem/xylem system (Simpson et al., 1982). Current understanding of the functioning of phloem (through which the majority of photoassimilate is redistributed within the plant) is much hindered as phloem...
function is often lost, or at best altered, as soon as the system is disturbed during measurement. Direct measurements of translocation rates are difficult, however some informative studies using the short-lived but easily detectable radiocarbon isotopes ($^{14}$C) and recently NMR, have been conducted (Peuke et al., 2001; Minchin et al., 2002; Minchin and Thorpe, 2003; Minchin and Lacointe, 2005). These studies indicate that the Munich theorem of phloem translocation, mass flow driven by osmotic differentials generated by osmolyte loading by companion cells in source tissue and unloading in sink tissues, is consistent with experimental data, and can be used to describe sink–source dynamics in growing plants. Current models suggest that phloem is a dynamic and diffuse network, allowing transport of nutrients and assimilate to any organ, either up or down the stem depending upon the demands of the sink–source system. This diffusivity should allow the free transport of nutrients and photoassimilate between stems and tillers provided that the vascular connections between these stems are extant and do not represent a bottleneck for mass flow.

The present study was conducted as part of a series of experiments to collect ecophysiological data, similar to that already extant for L. perenne and F. arundinacea, for a tropical grass species widely used in Brazil (Guinea grass, Panicum maximum). P. maximum is the second most widely used forage grass for pastoral production in Brazil, with an estimated at 5.5 million ha (Bono et al., 2000). The species was introduced to Brazil from tropical Africa during the 18th century (Parsons, 1972). In the 1980s a French germplasm collection of 426 apomictic and 417 sexual accessions was transferred to a Brazilian research entity EMBRAPA (Empresa Brasileira de Pesquisa Agropecuária) (Jank, 1994). The P. maximum cultivars used in this study, Tanzânia and Mombça, are direct selections from the French accessions, released in 1990 and 1993, respectively, by CNPGC (Centro Nacional de Pesquisa de Gado de Corte).

A number of recent studies have attempted to define the morphological basis for yield, by measurement of tiller dry weight and tiller number in parallel with herbage accumulation (Gomide, 1997; Santos, 1997; Carvalho et al., 1999). A consensus to emerge from these studies is that Mombça consistently has larger tiller and plant dry weight than Tanzânia, but paradoxically Tanzânia produces more new tillers than Mombça, and maintains a higher tiller density. For example, in one experiment (Carvalho et al., 1999), leaf number per plant increased by 0.0055 leaves per growing degree day (GDD) with a site-filling ratio of 0.186 tillers per leaf for Mombça, and by 0.0075 leaves per GDD with a site-filling ratio of 0.153 for Tanzânia. As estimated by the product of leaf appearance and site filling, the respective tiller appearance interval for whole plants in this experiment is 34 GDD for Mombça and 20 GDD for Tanzânia. In a subsequent experiment, tiller number after 7 months growth averaged over three cutting heights was 41 and 48 tillers plant$^{-1}$ ($P$ < 0.01) for Mombça and Tanzânia, respectively, but with a consistent tendency ($P$ < 0.05) for Mombça to have increased root mass per plant (Carvalho, 2002). It was also found that individual tillers tend to be longer lived in Tanzânia than in Mombça (Carvalho, 2002).

These observations of consistent differences in plant size and in tillering habit of the two P. maximum cultivars Mombça and Tanzânia, led to the formation of the hypothesis that there may be cultivar differences in patterns of photoassimilate distribution within and between tillers, and an experiment was designed to test this possibility, using $^{14}$C-labelled CO$_2$ as a tracer.

**Materials and methods**

The experiment was carried out in a greenhouse, located at the Plant Growth Unit, Massey University, Palmerston North (40°16′S, 175°17′E) from May–July 1999 (Southern Hemisphere winter). Over the experimental period, daily minimum and maximum temperatures were maintained between approximately 18 °C and 32 °C, respectively.

Seeds of the two Guinea grass cultivars, cvs Tanzânia and Mombça, were germinated in soil in flat trays for 2 weeks in a greenhouse maintained at 25 °C. At this point, pairs of similar-sized seedlings were transplanted to 4.0 l plastic pots filled with a mixture of sand and soil (1:1) from the B horizon of an alluvial silt deposit (Karipoti soil series). A controlled release fertilizer was added (3 g pot$^{-1}$, Osmocote brand) containing 15% N, 4.8% P, 10.8% K, 1.2% Mg, 3.0% S, 0.4% Ca plus trace elements, B, Cu, Fe, Mn, Mo, and Zn. One week later seedlings were thinned to one per pot to leave seedlings of similar size in all pots. Plants were grown for a further 5 weeks, then one adult tiller in each plant was randomly selected for application of $^{14}$C treatments. In replicate plants, different categories of tiller were labelled; the main tiller (TM); the first or second most recently developed primary tiller on the main stem, with at least three fully emerged leaves (TY); and an old primary tiller (TO), the fourth or fifth tiller on the main stem with at least two daughter tillers (Treatments TM, TY, and TO; Table 1). These treatments were replicated four times, making a total of 12 plants for each cultivar.

The labelled tillers were enclosed in a plastic bag with a clip seal, and silicon rubber used to seal bags around the base of the stem. Atmospheric $^{14}$CO$_2$ enrichment was achieved by injecting with a hypodermic syringe 1 ml dilute NaH$^{14}$CO$_3$ (Amersham product CFA2, diluted to a specific activity of approximately 740 KBq ml$^{-1}$) into a pocket in the plastic bag, followed by an equal quantity of 10% (v/v) acetic acid to release $^{14}$CO$_2$ gas inside the plastic bag for uptake by the enclosed tiller. This would result in a transiently higher concentration of CO$_2$ inside the bag, however, this would ensure that the tiller had adequate $^{14}$CO$_2$ during labelling. In previous studies with temperate plants such as Lolium perenne, a typical dose rate would be 37 KBq (1 μCi) tiller$^{-1}$, and the dose rate used here of 740 KBq tiller$^{-1}$ was estimated, based on the much larger size of tropical grass tillers, as the dose required to achieve specific activities in labelled tillers similar to those previously used in studying photoassimilate distribution in temperate grasses. The needle holes in labelled tillers similar to those previously used in studying photoassimilate distribution in temperate grasses. The needle holes were sealed with petroleum jelly and bags were left in place for 20 h until Geiger counter readings showed that radioactivity had transferred from solution to the tiller being labelled. Since the $^{14}$CO$_2$ was present in the labelling bags until near the end of the labelling period, in quantities detectable by Geiger counter, it is
unexpectedly that the labelled tillers suffered from CO₂ starvation during the labelling process. Plants were destructively harvested 24 h after the end of labelling, dissected, and roots and shoots separated into the categories detailed in Table 1. Before separating tillers into groups as described in Table 1, all primary and secondary tillers per plant were counted for further comparison among cultivars. Samples were placed in paper bags and dried in an oven for 48 h at 60 °C for later scintillation counting.

All samples were ground in a kitchen coffee grinder and a 90 mg subsample was combusted in a Harvey OX 400 oxidizer. ¹⁴CO₂ was trapped in scintillation vials using the method described by Jeffay and Alvarez (1961), and scintillation counting was performed on a liquid scintillation counter (Wallac 1409). Two calibration discs (CF 101, Amersham product) were used to adjust the quench correction of the scintillation counter.

For analysing ¹⁴C allocation, since different treatments were subject to different dissections, each of the three treatments (TM, TY, TO) was treated as a separate experiment, with two cultivars and four replicates. The quantity of ¹⁴C recovered represents the quantity of net assimilate remaining in the plant at the end of the 24 h chase period. The standard errors for percentages of ¹⁴C recovered from each tiller category (expressed as a percentage of the total in the whole plant) are shown and t tests were used to test for cultivar differences in the distribution of ¹⁴C, except where specifically noted. Specific activity (Bq mg⁻¹) for the different categories of tillers was similarly assessed. For certain other measurements, including total ¹⁴C recovered and plant total dry weight, the experiment was analysed by 2-way ANOVA, as a factorial design with three treatments, two cultivars, and four replicates.

### Results

#### Tiller number and dry weight
On average, total tiller number per plant was 22% higher in Tansánia than Mombaça (15.7±0.57, and 12.8±0.57, P <0.01) with secondary tillers accounting for this difference rather than primary tillers. The mean plant dry mass was 28% higher in Mombaça (17.3±0.81 and 13.5±0.89 g plant⁻¹; P=0.009, for Mombaça and Tansánia, respectively) however, no differences in plant mass were noted between treatments (P=0.616, 2-way ANOVA). Both shoot (14.3±0.73 and 10.8±0.75 g plant⁻¹; P=0.005) and root (3.2±0.14 and 2.7±0.16 g plant⁻¹, P=0.04) dry mass were higher in Mombaça than Tansánia. Neither main shoot, primary tiller nor old tiller masses varied between treatments, however, genotypic differences were noted in the main shoot and primary tiller masses (P >0.05 and P=0.001, respectively, 2-way ANOVA). The difference in root–shoot ratios approached significance between the two genotypes (0.229±0.011 and 0.255±0.007; P=0.0519, for Mombaça and Tansánia, respectively). Table 2 shows the breakdown of shoot and root masses for each tiller group within the three treatments. The tiller masses for each of the three treatments are similar, although differences between cultivars in one treatment were not always evident in the other treatments. For example, in the treatment TM, the masses of both the main stem and the root associated with it were significantly different between cultivars, with Mombaça being heavier than either older tillers or the main stem. In treatment TY, however, only the root masses exhibit significant difference, and in TO only the stem masses are statistically different. Root masses were, in most cases, significantly lower than the shoot mass for each tiller group.

#### Distribution of radiocarbon
528±70 and 428±58 kBq plant⁻¹ (P=0.059, 2-way ANOVA) were recovered from Tansánia and Mombaça plants, respectively. TM treatments tended to exhibit a higher recovery than plants in TY and TO treatments (566±115, 350±37, and 322±40, and 649±106, 500±169, and 436±67 kBq plant⁻¹, for Mombaça and Tansánia, respectively), although within cultivars this was not significant (P=0.341, 2-way ANOVA). Only when the two cultivars were pooled were the TM and TY recoveries significantly different. Generally, the proportion of exported carbon from a labelled tiller was in the order of 10–22% (Table 3) of the total ¹⁴C recovered from the plant; there were no significant differences in the proportion of C exported either between cultivars (P=0.543) or treatments (P=0.189, 2-way ANOVA). This value tended to be numerically higher (although not statistically different), for young tillers than either older tillers or the main stem (20.5±3.1%, 14.3±3.1%, and 12.6±3.1%), respectively.
Figures 1 to 3 show schematically, for each treatment (TM, TY and TO), the position of the various tiller groups, and the vascular pathways between them. Tiller categories are represented as opposing pairs of triangles (except the main stem where the shoots and roots are at opposite ends of the tiller axis), the upper triangle representing the leaf and pseudostem, and the lower triangle representing attached roots. The area of triangles is scaled in proportion to the dry weight of shoot and root fractions for each tiller category, and the percentage of recovered radiocarbon in each fractions is indicated. In reality, axis length between the shoot and root is very short (about 10 mm long). Here, the axis is expanded for clarity and drawn horizontally to allow illustration of root and shoot fractions of each tiller category. The shoot and root triangles in the top right of each figure represent the secondary tillers (these were not separated into subgroups attached to PI and PO tillers, because of their comparatively small contribution to total plant mass). However, secondary tillers present on labelled tillers in the TO treatment (i.e. on POL tillers) were analysed for specific activity, and are represented by a second axis in Fig. 3. Bold triangles represent the labelled tiller. The overall average specific activity for all labelled tillers was 367 Bq mg⁻¹ and for unlabelled tillers was 11 Bq mg⁻¹. Individual tiller specific activities are shown in Table 4.

For all three treatments, within individual tillers that had not been labelled, specific activity was almost always numerically higher in roots than in shoots. However, coefficients of variation were typically high enough to

<table>
<thead>
<tr>
<th>Treatment TM Cultivar</th>
<th>Fraction</th>
<th>Tiller group</th>
</tr>
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<tbody>
<tr>
<td></td>
<td></td>
<td>Main</td>
</tr>
<tr>
<td>Mombaca</td>
<td>Shoot</td>
<td>2.27 (0.15)</td>
</tr>
<tr>
<td></td>
<td>Root</td>
<td>1.40 (0.09)**</td>
</tr>
<tr>
<td>Tanzaibia</td>
<td>Shoot</td>
<td>1.54 (0.11)</td>
</tr>
<tr>
<td></td>
<td>Root</td>
<td>0.79 (0.07)**</td>
</tr>
<tr>
<td>Significance</td>
<td>Shoot</td>
<td>0.01</td>
</tr>
<tr>
<td>(Tan. v. Mom.)</td>
<td>Root</td>
<td>&lt;0.01</td>
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</table>

<table>
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<th>Treatment TY Cultivar</th>
<th>Fraction</th>
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<td></td>
<td>Main</td>
</tr>
<tr>
<td>Mombaca</td>
<td>Shoot</td>
<td>2.16 (0.19)</td>
</tr>
<tr>
<td></td>
<td>Root</td>
<td>1.22 (0.06)*</td>
</tr>
<tr>
<td>Tanzaibia</td>
<td>Shoot</td>
<td>1.63 (0.29)</td>
</tr>
<tr>
<td></td>
<td>Root</td>
<td>0.71 (0.05)*</td>
</tr>
<tr>
<td>Significance</td>
<td>Shoot</td>
<td>ns</td>
</tr>
<tr>
<td>(Tan. v. Mom.)</td>
<td>Root</td>
<td>&lt;0.01</td>
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<th>Tiller group</th>
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</thead>
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<td></td>
<td></td>
<td>Main</td>
</tr>
<tr>
<td>Mombaca</td>
<td>Shoot</td>
<td>2.30 (0.13)</td>
</tr>
<tr>
<td></td>
<td>Root</td>
<td>0.95 (0.03)**</td>
</tr>
<tr>
<td>Tanzaibia</td>
<td>Shoot</td>
<td>1.52 (0.15)</td>
</tr>
<tr>
<td></td>
<td>Root</td>
<td>0.88 (0.07)*</td>
</tr>
<tr>
<td>Significance</td>
<td>Shoot</td>
<td>0.01</td>
</tr>
<tr>
<td>(Tan. v. Mom.)</td>
<td>Root</td>
<td>ns</td>
</tr>
</tbody>
</table>

Table 3. Percentage of radiocarbon recovered in shoot and root fractions of labelled and non-labelled tillers in plants subjected to different treatments TM (main tiller labelled), TY (young primary tiller labelled), and TO (old primary tiller labelled) in two Guinea grass cultivars Mombaca and Tanzaibia

Asterisks represent a difference between Mombaca and Tanzaibia at P<0.05 (±SE).
make root:shoot differences non-significant in Mombaca and in the TY treatment in Tanzania, whereas root-shoot differences in specific activity were usually significant in Tanzania, treatments TM and TO (Table 4).

In treatment TM (Fig. 1; Table 3), 87% and 85% of recovered radiocarbon was found in the labelled tillers for Mombaca and Tanzania, respectively, with 18% and 14% of that recovered from the roots. Transfer from labelled tissues to roots thus represented 54% and 45% of the C exported from the labelled tissues for the two genotypes. The labelled tillers always had the highest specific activity (Table 4), except for young tiller roots of Tanzania, which had a numerically higher (although not statistically different) specific activity than the main stem roots. Hence, the main tiller exported 13% and 15% of fixed C to other tillers in Mombaca and Tanzania, respectively, making total export of radiocarbon to all attached primary and secondary shoots and their roots approximately equal to the C translocated from the main tiller.

In the TM plants of Mombaca, a gradation in the photoassimilate partitioning between primary tillers was evident. PY tillers were the youngest and were also physically connected closest to the photoassimilate source from the main stem leaves. Of the radiocarbon exported from the main stem, these tillers received 41.2% (Fig. 1), despite their low mass (Table 2). Conversely, PO tillers (the oldest tillers and most distant from the source leaves) received only 16.2% of the radiocarbon exported from the main stem, irrespective of their high mass. PI tillers, of intermediate age, received an intermediate amount, 28.7% of radiocarbon exported. The interaction of sink strength and sink size is indicated by the fact that an approximate 3-fold difference between PY and PO tiller shoots, and an approximate 10-fold difference between PY and PO tillers in total radiocarbon allocation (Fig. 1) was associated with an approximate 5-fold difference in specific activity of PY and PO tiller shoots, and an approximate 5-fold difference in specific activity of PY and PO tillers in specific activity of their roots. Secondary tillers do not have a direct connection to the main stem, and could only receive 14C indirectly through the primary tiller (which is connected to the main stem) to which they were connected. Despite this indirect vascular pathway, secondary tillers received 14.0% of radiocarbon exported from the main tiller and had specific activities very similar to the average of the PI and PO tillers to which they were attached (Table 4).

The simple basipetal gradation of 14C recovery between primary tillers, as seen in Mombaça, did not occur in Tanzania. For TM plants of cultivar Tanzania, the PY...
tillers, located closest to the source, received 37.2% of the radiocarbon exported from the main stem, whilst the PI tillers received 21.4%, these allocations being similar to Mombaca. However, the PO tillers of Tanzania tended to have larger total weight than in Mombaca (Table 2) and received 34.5% of the radiocarbon exported from the main tiller, more than double the percentage allocation observed in Mombaca. Consistent with this, roots and shoots of all primary tillers of Tanzania TM plants tended to have higher specific activities than Mombaca, and in the case of the PO tiller roots, this difference approached significance (P=0.058, Table 4). For Tanzania, the ratio of PY:PO specific activities was also higher than in Mombaca (>10 for shoots, >15 for roots). Thus, photosynthate translocated from the main tiller was more localized in Tanzania than Mombaca. Secondary tillers in Tanzania also tended to have higher specific activity than those of Mombaca (Table 4), but in contrast to observations for PO tillers, lower average mass (Table 2).

In TY plants (Fig. 2; Table 4), shoot systems of young labelled tillers retained 78% of recovered radiocarbon, in both cultivars. In this treatment, the root systems of labelled tillers were very small, giving a recovery on a whole tiller basis of under 80% in both cultivars, a reduction compared to treatment TM. However, despite the diminished total recovery of radiocarbon from labelled PY tillers in treatment TY, these tillers had a specific activity about three to five times the specific activities of either the labelled main stem or the labelled old primary tillers of treatments TM and TO (Table 4).

In Mombaca TY plants, 21.6% of recovered radiocarbon was exported from the labelled PY tillers. Of the exported C, 20.0% was recovered from the main stem shoots, and 4.2%, 6.0%, and 17.6%, respectively, from unlabelled PY, PI, and PO tillers. A further 18.1% of exported C was recovered in Sec tillers. PO tillers comprise a high proportion of total plant mass (approximately 33% total plant dry weight, Table 2), and presumably also form the largest tiller-based sink, but what is notable is the generally lower and comparatively similar specific activity across primary tiller categories in the TY plants (range 1.6–17 Bq mg⁻¹) compared with the TM plants (range 2.5–119 Bq mg⁻¹; Table 4). Notable in TY plants, however, was that the main tiller roots received 34.3% of the radiocarbon exported from the labelled tillers (7.4% of total recovered radiocarbon).

Tanzania presented patterns similar to Mombaca, with respect to redistribution of photoassimilate from labelled young primary tillers. 19.1% of recovered radiocarbon had been exported from young tillers. Of this, percentages recovered from main tiller shoots, PY, PI, PO, and Sec tillers, respectively, were 20.4%, 6.8%, 13.6%, 11.0%, and 10.5%. As with Mombaca, main tiller roots received a high allocation (36.5%) of radiocarbon exported from labelled PY tillers (7.0% total recovered radiocarbon, Fig. 4). As in treatment TM, primary tiller specific activity in treatment TY diminished basipetally down the main axis, being highest in the PY category and lowest in the PO category, but there was much less concentration of exported radiocarbon in PY tillers with unlabelled PY:PO tiller specific activity ratios close to five, and no indication of this ratio being systematically higher in roots than in shoots or in Tanzania than in Mombaca.

For treatment TO, the percentage of recovered radiocarbon found in the labelled tillers was 90.8% and 83.0% for Mombaca and Tanzania, respectively, or 92.3% and 91.5%, respectively, when including secondary tillers attached to labelled tillers (Fig. 3), with 6.6% and 15.3%, of that recovered in the roots. Hence, characteristics of this treatment were a comparatively high retention of the recovered radiocarbon in the labelled tiller, and a difference between cultivars in distribution of radiocarbon, with increased allocation to roots and secondary tillers attached to labelled PO tillers of Tanzania. Of the radiocarbon exported from labelled PY tillers in treatment TO, approximately 25% was found in the main tiller, and the remaining 75% (about 6% of the total radiocarbon recovered) was distributed to PY, PI, and PO tillers approximately in proportion to tiller weight, with the result that broadly similar specific activities were observed for all primary tiller shoots or roots of a given cultivar, irrespective of age (Table 4). However, roots were supplied preferentially
over shoots, and this effect was more pronounced in Tanzania than in Mombaca, with root:shoot specific activity differences being statistically significant in five out of the seven tiller categories, and cultivar differences in root specific activity (i.e. Tanzania > Mombaca) being significant at P < 0.10 in all seven tiller categories (Table 4).

**Discussion**

Most 14C-labelling studies of translocation in grasses involve labelling individual leaves to observe the effects of position, age, and efficiency of the leaf labelled in relation to the rest of the plant (Clifford et al., 1973; Lloyd, 1980; Chapman et al., 1991; Ahmad and Marshall, 1997; Fetene et al., 1997; Osaki et al., 2004; Thornton et al., 2004). In the present study, however, the main aim was to quantify the translocation of recent photoassimilate from the tiller as a unit and to understand the interdependency of tillers in a hierarchical cluster. Comparatively few previous studies on translocation patterns within grass plants discriminate between tiller functional categories. It was hypothesized that cultivar differences in translocation between tillers may underlie differences in tillering habit of the two cultivars. Hence, in this study, tillers were grouped according to age/position on the main axis, and dry weight and specific activity for shoots and roots separately measured for each ‘functional’ category of tiller. This experiment therefore provides the possibility of new insight, although care is also required in the interpretation of these results. For example, the labelling procedure used, adapted from earlier UK studies of Chapman et al. (1991), would have subjected labelled tillers to changes in humidity, temperature, and CO2 concentration not experienced by the rest of the plant. It is felt that these factors were managed so as not to affect translocation patterns, but scrutiny is appropriate, even so.

The total amount of radiocarbon recovered was 24% greater in Tanzania than Mombaca. It is not clear if this arises from a differential uptake during labelling or greater respiratory losses in Mombaca. Total radiocarbon recovery for TM plants was 40% and 57% higher than TY and TO plants, which may be related to either greater efficiency in 14C incorporation by the main tiller compared with primary and old tillers, or lower respiratory losses

**Table 4. Specific activity (Bq mg\(^{-1}\)) of shoot and root fractions of each tiller category for the three treatments TM, TY, and TO in two Guinea grass cultivars, Mombaca and Tanzania (±SE)**

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Fraction</th>
<th>Tiller group</th>
<th>Main</th>
<th>PY</th>
<th>PL</th>
<th>PO</th>
<th>Sec</th>
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<tbody>
<tr>
<td><strong>TM</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mombaca</td>
<td>Shoot</td>
<td>171.6 (34.8)</td>
<td>13.6 (7.0)</td>
<td>4.0 (1.1)</td>
<td>2.5 (0.6)</td>
<td>2.7 (0.6)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Root</td>
<td>65.5 (33.7)</td>
<td>40.8 (9.9)</td>
<td>12.4 (5.9)</td>
<td>3.7 (1.1)</td>
<td>4.9 (0.6)</td>
<td></td>
</tr>
<tr>
<td>Tanzania</td>
<td>Shoot</td>
<td>321.9 (65.2)</td>
<td>20.8 (6.8)</td>
<td>4.7 (0.7)</td>
<td>3.3 (0.4)</td>
<td>3.2 (0.4)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Root</td>
<td>96.7 (19.4)</td>
<td>118.6 (56.2)</td>
<td>12.4 (2.5)*</td>
<td>7.0 (0.6)**</td>
<td>7.0 (2.8)</td>
<td></td>
</tr>
<tr>
<td>Significance Shoot</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
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</tr>
<tr>
<td>(Tan. v. Mom.) Root</td>
<td>ns</td>
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<td><strong>TY</strong></td>
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<tr>
<td>Mombaca</td>
<td>Shoot</td>
<td>8.2 (4.9)</td>
<td>1049.6 (98.4)</td>
<td>10.9 (8.1)</td>
<td>2.5 (0.7)</td>
<td>1.6 (0.3)</td>
<td>2.0 (0.2)</td>
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<td></td>
<td>Root</td>
<td>3.7 (1.3)</td>
<td>1079.8 (179.8)</td>
<td>6.8 (1.3)</td>
<td>3.3 (0.4)</td>
<td>2.0 (0.3)</td>
<td>2.4 (0.4)</td>
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<tr>
<td>Tanzania</td>
<td>Shoot</td>
<td>3.6 (11.0)</td>
<td>879.9 (178.1)</td>
<td>17.0 (4.5)</td>
<td>8.1 (2.3)</td>
<td>3.9 (1.4)</td>
<td>5.3 (1.6)</td>
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<tr>
<td></td>
<td>Root</td>
<td>36.1 (11.0)</td>
<td>1094.6 (98.4)</td>
<td>10.9 (8.1)</td>
<td>2.5 (0.7)</td>
<td>1.6 (0.3)</td>
<td>2.0 (0.2)</td>
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<td>Significance Shoot</td>
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<td>ns</td>
<td>ns</td>
<td>ns</td>
<td></td>
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<tr>
<td>(Tan. v. Mom.) Root</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
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<td></td>
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<td></td>
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</tr>
<tr>
<td>Mombaca</td>
<td>Shoot</td>
<td>2.0 (0.9)</td>
<td>1.4 (0.4)</td>
<td>0.9 (0.4)</td>
<td>166.7 (51.3)</td>
<td>1.5 (0.1)</td>
<td>2.4 (0.9)</td>
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<td>Root</td>
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<td>2.6 (0.8)</td>
<td>2.7 (1.4)</td>
<td>42.3 (18.0)</td>
<td>2.1 (0.3)</td>
<td>4.2 (1.8)</td>
</tr>
<tr>
<td>Tanzania</td>
<td>Shoot</td>
<td>2.6 (0.2)</td>
<td>3.4 (0.4)</td>
<td>3.2 (0.2)</td>
<td>266.6 (41.1)</td>
<td>2.2 (0.2)</td>
<td>6.2 (1.5)</td>
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<tr>
<td></td>
<td>Root</td>
<td>6.1 (0.4)***</td>
<td>6.4 (0.3)***</td>
<td>7.0 (0.6)**</td>
<td>139.0 (37.6)</td>
<td>3.4 (0.3)*</td>
<td>33.4 (11.0)</td>
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<td>Significance Shoot</td>
<td>ns</td>
<td>0.019</td>
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<td>0.086</td>
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<td>(Tan. v. Mom.) Root</td>
<td>0.003</td>
<td>0.027</td>
<td>0.084</td>
<td>0.078</td>
<td>0.041</td>
<td>0.074</td>
<td>0.005</td>
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</table>
from the main stem. These results contrast with data obtained with Bahia grass (Paspalum notatum) where no statistical difference was found in the amount of $^{14}$C recovered in plants on which young, mature or old tillers were labelled (Beaty et al., 1974).

As noted in the Introduction, a number of factors are important in determining the source–sink relationships within plants. Distance is known to be important in determining the flux between two pools, with more distal sinks receiving less photosynthate than more proximal sinks (Matthew and Kemball, 1997; Osaki et al., 2004), since flow resistance increases with the distance between the source and sink. Individual source and sink strengths are also important in determining the redistribution of photosynthate within the plant. The strength of any given source or sink will be determined by the balance between the organs growth potential and its ability to provide the photosynthate for that growth. Differential vascular architecture between genotypes may also contribute to differences in photosynthate distribution. It has been suggested, for example, that young tillers of $L$. perenne cv. ‘Ellett’, may develop a vascular connection with their parent tiller at an earlier stage than young tillers of $L$. perenne cv. ‘Grasslands Ruanui’ (Matthew et al., 1991). With these provisos, a synthesis of the results for radiocarbon distribution for the three categories of labelled tiller is now offered.

Firstly, these results do not show a substantive and consistent difference in physiological behaviour across all categories of labelled tiller for the two cultivars that would explain the consistently observed differences in tillering behaviour. The situation is considerably more complex, with each category of labelled tiller exhibiting differing patterns of photosynthate distribution, and the cultivar differences in photosynthate distribution most clearly evident in labelled PO tillers.

When the main tiller was labelled (treatment TM), there was an approximately equal allocation of radiocarbon between main tiller roots and main tiller primary shoots. Although this result would not have been predicted in advance, it is logical in hindsight, since each phytomer or segment on the tiller axis of a grass generates both tiller buds and root primordia, and daughter tiller connections and roots are interspersed along the tiller axis. Root:shoot allocation of radiocarbon within the main tiller was 0.22 in Mombaça and 0.16 in Tanzania, similar to the root:shoot partitioning of dry matter commonly expected in grasses. Specific activities in the primary tillers diminished basipetally with increasing distance from the source leaves, in line with conventional source–sink models, and a preferential allocation of imported $^{14}$C to roots was noted (Table 4). In Mombaça, the diminishing basipetal allocation pattern was also observed for the total radiocarbon allocation to primary tillers; however, in Tanzânia, the PO tillers received a total radiocarbon allocation similar to PY tillers and greater than the more proximal PI tillers. It is not easy to propose a mechanism that would explain this observation, but a higher growth rate of secondary tillers could produce this effect, since the secondary tillers are mainly found on PO tillers.

When PY tillers were labelled (treatment TY), specific activities in labelled tillers were extremely high (Table 4), reflecting concentration of the $^{14}$C label into an organ of much smaller size but higher growth rate than the main tiller. The majority of C used in new growth derives either from current photosynthesis or from short-term C stores (Lattanzi et al., 2005). Labelled PY tillers retained less, and exported more radiocarbon label than either labelled main tillers or labelled PO tillers. Young, small tillers have high photosynthetic capacity, a high growth rate, and a comparatively high proportion of meristematic tissue to total leaf mass. Young tillers, with their small size and high growth rate have little capacity for C storage. Hence, results for the TY treatment are consistent with high photosynthetic rate in young tissue and a low capacity for C storage. In the temperate grass $L$. multiflorum (Clifford et al., 1973), it has been established that such flows between a daughter and parent tiller are reciprocal, though to our knowledge it is not known if the flow direction oscillates on a diurnal basis or is simultaneously bidirectional. Since an equal quantity of radiocarbon was applied to each category of labelled tiller, comparison of the absolute amount of radiocarbon exported by PY tillers in treatment TY, with import by equivalent tillers in treatments TM and TO may be a crude estimate of the net balance of reciprocal flows. Based on this study’s results, the net position is that young tillers supply excess photosynthate to the rest of the plant during the day, although it seems likely that since they have little capacity for C storage they are net C sinks during the night. Approximately one-third of radiocarbon exported by PY tillers was recovered from main tiller roots, and specific activity of main tiller roots in PY plants was among the highest recorded for any unlabelled tillers in this experiment, second only to the reciprocal case of roots of PY tillers on TM treatment plants (Table 4). However, considering the more than 10-fold dry weight difference (Table 2), this indicates a significant level of subsidy by the PY tillers to the parent tiller roots. Moreover, based on tiller axis maps for the temperate grasses $L$. perenne and $F$. arundinacea (Yang et al., 1998), the point of attachment of PY tillers to the main tiller axis would be near to that of younger roots, so it is likely that those rapidly elongating, young main-tiller roots would have benefited most from the C supplied by PY tillers, and that specific activities of these particular roots would have been much higher than the average of all main-tiller roots, recorded in Table 4. Follow up work would be of interest to confirm this presumed concentration of imported $^{14}$C in younger main-tiller roots. These findings highlight the complexity of interaction between interconnected clusters of tillers within a grass plant.
An interesting, and initially paradoxical set of results suggests that whilst approximately 45–54% of exported main-stem photoassimilate is recovered in roots, this is far lower for C exported from the young primary tiller. Only 32–34% of the C exported from young primary tillers was recovered in the main-tiller roots, with 65%+ being recovered in above-ground biomass. This makes little apparent sense, especially if current models of phloem transport are accurate and allow rapid translocation of C between plant organs. However, if tiller age and size are taken into account, especially their differing capacities for photosynthesis and C storage, an apparent resolution presents itself. The plants were labelled for a period of 20 h, followed by a further 24 h period to allow redistribution of C, incorporating both light and dark periods. As noted earlier in the text, young tillers have little capacity for C storage; however, their instantaneous C fixation rates are higher than their C demand for growth. During the day, young tillers export C to the rest of the plant, some proportion of the exported carbon is used by the roots, and the remainder translocated to above-ground material where it was used either for growth, or stored. At night, the young tillers have little reserves of assimilated C, the majority having been incorporated into structural material or exported. Thus at night, young tillers do not supply photoassimilate to the roots. The main stem, however, is far larger and has both a higher photosynthetic rate and higher capacity to store C, especially since the main stem has a lower relative growth rate. At night, the roots continue to require carbon; young tillers are unable to supply photosynthesize, however, reserves from the main stem can be used, which, it is proposed, increases the amount of recent assimilate recovered from the root from 32–34% from the young primary tillers up to the 50% noted for the main stem.

In labelled PO tillers (treatment TO), less than 10% of radiocarbon was exported beyond the labelled tiller (including secondary tillers), in both cultivars; this may reflect diminishing efficiency of older vascular connections between tillers. However, it was in the PO labelled tillers, that cultivar differences in pattern of radiocarbon distribution were clearly defined, with both SecL roots and shoots of the labelled tiller itself, and roots and shoots of importing primary tillers elsewhere on the main-tiller axis, all showing a tendency for greater concentration of radiocarbon in these tissues of Tanzânia than Mombaça. Again it is not easy to propose a mechanism that could explain the various observations, but here too, a greater sink strength in importing tillers of Tanzânia than Mombaça would be predicted to produce many of the results seen in this experiment. This hypothesis sits logically with agronomic observations of increased tiller numbers per plant in Tanzânia compared to Mombaça, but is counterintuitive with respect to the smaller size of Tanzânia plants, unless a greater sink strength in subordinate tillers has a net effect of reducing relative growth rate in dominant tillers that produce the bulk of the plant total dry weight.

**Conclusion**

This study compared two *P. maximum* cultivars with differing agronomic behaviour, cv. Mombaça consistently having fewer tillers per plant but higher total plant dry weight, than cv. Tanzânia, but did not find a common physiological trait expressed in all categories of tiller that would explain agronomic performance differences between the two cultivars. The situation seems to be far more complex than first suspected, with cultivar differences in radiocarbon distribution clearly demonstrated only in old primary tillers, and indicating quite complex interactions between parent and daughter tillers, such as the preferential feeding of young parent tiller roots by daughter tillers or differential diurnal sink–source behaviours. A mechanism that would account for both the observed agronomic behaviour differences and radiocarbon distribution differences between cultivars is greater sink strength in Tanzânia in tillers that are net importers of photosynthate, however, this must be regarded as a speculative hypothesis for future study, and not as a definitive research finding.

**Acknowledgement**

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**References**


Yang JZ, Matthew C, Rowland RE. 1998. Tiller axis observations for perennial ryegrass (*Lolium perenne* L.) and tall fescue (*Festuca arundinacea* Schreb.): number of active phytomers, probability of tiller appearance, and frequency of root appearance per phytomer for three cutting heights. *New Zealand Journal of Agricultural Research* 41, 11–17.