The effect of leaf age and decapitation of the cane apex on the translocation of assimilates in the weed, *Rubus cuneifolius*

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The percentage absorption of ^{14}C-sucrose applied to the adaxial surface of detached *Rubus cuneifolius* (bramble) leaves was highest in senescing leaves. Incubation for more than six hours did not result in a significant increase in the percentage radiotracer absorbed. Leaves situated at different positions on intact bramble plants exported assimilates to different sink regions. Translocation of assimilates exported from apically situated leaves was predominantly acropetal to the cane apex sink region while that from basal leaves was predominantly basipetal into the root sink region. Leaves situated midway down the canes exported assimilates both acropetally and basipetally. Assimilates which would normally have been transported acropetally were transported in a basipetal direction once the cane apex was removed.

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Na die aanwending van ^{14}C-sukrose aan die adaksiale oppervlakke van afgeplukte *Rubus cuneifolius* (braam) blare het die oudste blare die hoogste persentasie opname getoon. Inkubering vir langer as ses uur het nie tot 'n betekenisvolle toename in die persentasie geabsorbeerde radioisotoop gelei nie. Assimilaat uit blare wat op verskillende posisies op ongeskonde braamplante geleë was, is na verskillende swelgpunte vervoer. Vervoer van assimilaat van apikaalgeleë blare was hoofsaaklik akropetaal na die stingelgroeipunt, terwyl dié vanaf basaal geleë blare hoofsaaklik basipetaal na die wortels was. Assimilaat uit die tussenliggende blare is beide op- en afwaarts vervoer. Verwydering van die stingelgroeipunt het tot gevolg gehad dat assimilaat wat normaalweg akropetaal vervoer is, in 'n basipetale rigting vervoer is.

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Introduction

As previously stated (Erasmus & van Staden 1983), *Rubus cuneifolius* Pursh (bramble) is a serious weed in Natal. Not only do the dense infestations result in a lower grazing capacity but the thorn covered canes form a natural obstacle, thereby limiting accessibility to infested areas such as forest plantations and grazing veld.

Since the area of infestation has increased, chemical control measures presently employed must be inadequate. In Australia the low efficacy of herbicide treatments in other *Rubus* weed species has been attributed to insufficient herbicide reaching the extensive root system (Richardson 1976). Consequently regrowth of the canes occurs, respraying in subsequent years is required and control costs escalate.

Evidence suggests that foliar applied systemic herbicides are translocated along with assimilates in the phloem (Crafts & Crisp 1971; Richardson 1977). It has also been shown that the translocation direction of assimilates is controlled by sink regions (Eschrich 1975; Herold 1980) and that the direction can be manipulated (Gersani *et al.* 1980a; Herold 1980). Wardlaw (1968) showed that leaves at different positions on a plant contribute photosynthetic assimilates to different sink regions and Richardson (1975) suggested that absorption of foliar applied solutions by *Rubus procerus* leaves of different ages varied.

Bearing the above-mentioned aspects in mind, the possible manipulation of assimilate transport direction and the absorption and translocation of radiotracer by leaves at different ages and, therefore, different positions on bramble plants, were investigated in an attempt to predict the likely absorption and translocation of foliar applied systemic herbicides.

Materials and Methods

^{14}C-sucrose application and radioassay

In all experiments the adaxial surface of the leaf to be treated was first wetted to near run-off with 0,25% (v/v) Polyoxyethylene sorbitan monolaurate (Tween 20) (Richardson 1980). Subsequently ^{14}C-sucrose (specific activity 45,10 MBq mg^{-1}) was applied by micro syringe to the wetted leaf surface. After the incubation period, as detailed for each experiment, the plant material was sampled, dried and radioassayed as previously described (Erasmus & van Staden 1983).

The effect of leaf age on the absorption of ^{14}C-sucrose

The absorption of ^{14}C-sucrose applied to the adaxial surface of detached leaves was compared in newly formed, fully expanded and senescing bramble leaves. Newly formed leaves

were excised from cane apices, fully expanded leaves from half-way down the canes and senescing leaves from the base of canes of plants grown from root cuttings in a greenhouse. The cut end of each petiole was immediately immersed in distilled water in a vial. The vials containing the detached leaves were placed in the laboratory under continuous light (spectral irradiance = 3,62 W m^{-2}) and at 26 ± 2 °C and 65% relative humidity.

The adaxial surface of each trifoliate detached leaf was treated with 3 mm^3 ^{14}C-sucrose as described above. Three leaves of each age class were sampled 2 h, 6 h and 12 h after treatment. The sampled leaves were rinsed by agitation in 15 cm^3 80% ethanol (v/v) aliquots for 1 min to remove unabsorbed radiotracer. The leaf samples were then dried and radioassayed. The individual ethanol leaf wash aliquots and the water in the vials were evaporated to dryness, 10 cm^3 Beckman Ready Solve E.P. scintillation cocktail was added and the radioactivity was determined using a liquid scintillation counter.

Leaf discs to indicate leaf age were punched from leaves corresponding in age to those used for the absorption experiment. Chlorophyll was extracted from the discs in 100% methanol for 24 h in the dark (Talling & Driver 1963). A sample from each of the three age classes was scanned from 350 nm to 700 nm on a Varian 90 double beam (UV-Vis) spectrophotometer to determine the chlorophyll absorbance peaks. Two absorbance peaks were found, one at 435 nm and the other at 664 nm. Thereafter five replicates in each leaf age class were tested for absorbance at these two wavelengths.

Absorption and translocation of assimilates in cane portions

To investigate absorption and translocation of assimilates in a larger system than the detached leaves, cane lengths were used. The canes selected were all primocanes and varied in length from 30 – 35 cm. These canes were bisected to give two portions from each cane (Figure 1). The basal cut end of each cane portion i.e. the shoot and decapitated stem, was immediately placed in distilled water in a beaker.

A single leaf on each portion of the cane was treated with 4 mm^3 ^{14}C-sucrose (Figure 1) as described above. Triplicate shoots and decapitated stems were incubated for 48 h and 168 h in the laboratory under the same conditions as described for the detached leaf experiment. At sampling the shoots were sectioned into treated leaf, apex, cane and leaves while the decapitated stems were sectioned into treated leaf, cane and leaves (Figure 1). In each case the excised treated leaves were rinsed to remove unabsorbed ^{14}C as described for the detached leaves. Again the leaf wash aliquots and the water in the beakers were evaporated and the radioactivity determined. The plant material was then dried and radioassayed.

The effect of leaf position and apical decapitation on the translocation of assimilates in intact plants

Translocation of ^{14}C-sucrose applied to leaves located at different positions on intact canes was investigated in bramble plants grown from horizontal root cuttings in a greenhouse. Four-month-old morphologically uniform plants with primocanes approximately 30 cm in height were selected for treatment. ^{14}C-sucrose (5 mm^3) was applied to the wetted adaxial surface of:

(i) the first leaf below the 5 cm cane apex ('control'),
(ii) a leaf half-way down the length of the primocane (middle leaf),
(iii) a leaf at the base of the primocane (basal leaf), and
(iv) the uppermost leaf of a cane from which the 5 cm primocane apex had been excised (decapitated),

as illustrated in Figure 2.

In each case three plants were treated and incubated for 72 h in the greenhouse before sampling.

At sampling each treated leaf was excised and rinsed in 80% ethanol to remove unabsorbed ^{14}C-sucrose. Each plant was

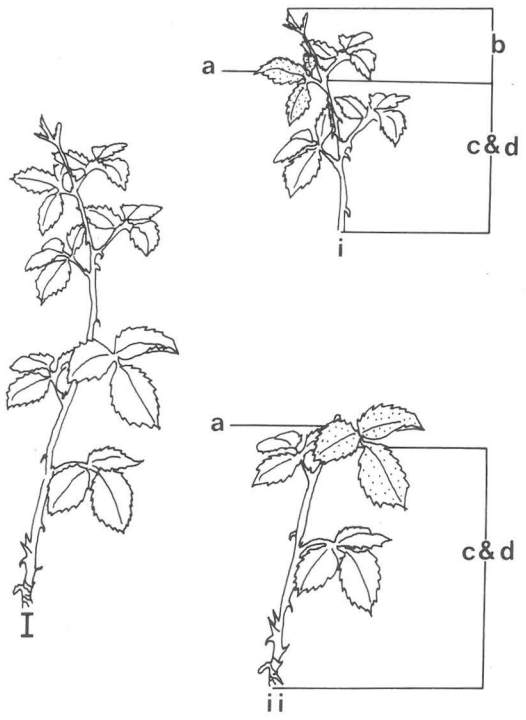

Figure 1 A detached *Rubus cuneifolius* primocane (I) was bisected to obtain the shoots (i) and decapitated stems (ii). The radiotracer was applied to a single leaf (▨) on each portion. Samples radioassayed: (a) treated leaf, (b) apex, (c) cane and (d) leaves.

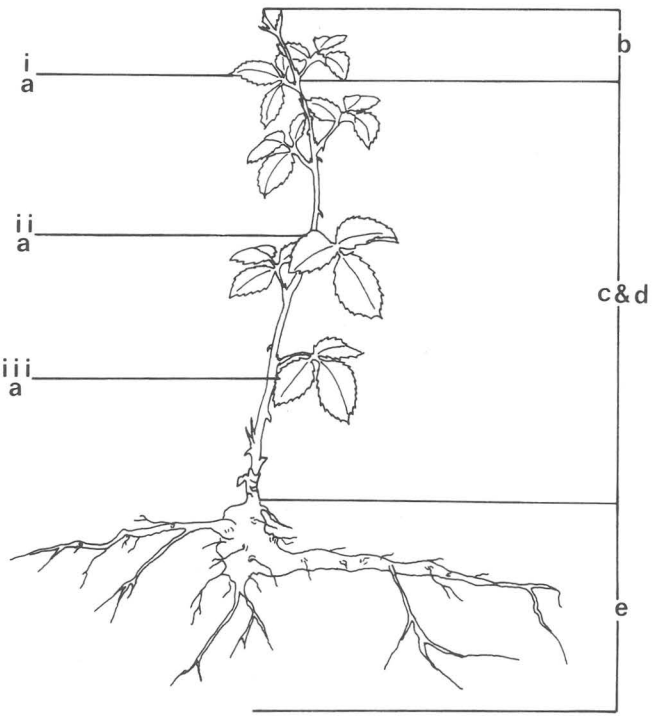

Figure 2 Position of the treated leaf where (i) is the 'control', (ii) middle leaf and (iii) the basal leaf treatments. For the decapitated plants, the apical region of the cane above (i) was excised and a leaf in the position (i) was treated. Samples radioassayed: (a) treated leaf, (b) apex, (c) cane, (d) leaves and (e) roots.

divided into the following samples for radioassay: treated leaf, apex, cane, leaves and roots. In the decapitated plants there was no apex sample.

Results and Discussion

The effect of leaf age on the absorption of ^{14}C-sucrose

The chlorophyll content, as determined by absorbance, was highest in the fully expanded leaves at both wavelengths measured (Table 1). The senescing leaves contained the least chlorophyll. The decrease in chlorophyll content in senescing leaves is frequently used as an indicator of leaf age (Woolhouse 1967; Friedrich & Huffaker 1980).

Table 1 Chlorophyll as determined by absorbance at 435 nm and 660 nm, of new, fully expanded and senescing *Rubus cuneifolius* leaves (Mean ± S.E.)

Wavelength (nm)	Absorbance/leaf sample		
	New leaf	Expanded leaf	Senescing leaf
435	0,84 ± 0,07	1,19 ± 0,06	0,41 ± 0,03
660	0,49 ± 0,04	0,69 ± 0,03	0,20 ± 0,01

The influence of leaf age and incubation time on the absorption of radiotracer applied to the adaxial surface of detached bramble leaves is presented in Table 2. In all three leaf age classes, and for each incubation time, the majority of the recovered radioactivity was in the 80% ethanol leaf rinse. The percentage radiotracer absorbed was similar in both the new and fully expanded leaves and did not vary with time. In the senescing leaves the percentage radioactivity detected in the leaf wash was significantly less than in the new and fully expanded leaf washes. Conversely, the percentage absorbed by the senescing leaves was significantly greater than that absorbed by the new and fully expanded leaves. Furthermore, the percentage radioactivity absorbed by the senescing leaves increased with incubation time. After 2 h 13% of the recovered radioactivity had penetrated into the senescing leaves, 21% after 6 h and nearly 23% after 12 h. A small percentage radioactivity was recovered from the 6-h senescing leaf and 2-h expanded leaf water source samples. No radiotracer was detected in any other water source sample.

These results obtained for detached bramble leaves show that the senescing leaves absorbed greater quantities of surface applied ^{14}C-sucrose than did the younger leaves. The rate of radiotracer absorption also differed with leaf age. In the new and expanded leaves there was no increase in absorption after 2 h incubation, while in the senescing leaves absorption continued for 6 h after which time very little radiotracer moved into the leaves. The senescing leaves used in this experiment correspond to the *R. procerus* autumn leaves used by Richardson (1975) who found that these leaves absorbed 2,4,5-trichlorophenoxyacetic acid (2,4,5-T) more rapidly than did summer leaves (expanded leaves). Although it is commonly agreed that chemicals penetrate young leaves more rapidly than older leaves (Hull 1970), Richardson (1975) suggested that weathering of the cuticle on old leaves results in an increased uptake of solutes. The results obtained for the detached *R. cuneifolius* leaves are similar to those of the seasonal translocation study (Erasmus & van Staden 1983) where increased age of the treated leaf resulted in an increased percentage of radiotracer being recovered from the experimental plants.

Absorption and translocation of assimilates in cane portions

As in the detached leaves, the majority of the recovered radioactivity was detected in the leaf wash samples (Table 3). In both the shoots and decapitated stems radioactivity was detected in all the samples radioassayed, with the exception of the water source samples. In the shoots, increased incubation time resulted in an increased percentage of radiotracer being detected in the leaves. Increased incubation time of the decapitated stems resulted in a significant increase of the percentage of radiotracer in the treated leaf samples and a converse decrease in the leaf wash samples (Table 3).

Absorption of the surface applied ^{14}C-sucrose by the treated leaves and subsequent translocation of the exported radiotracer did occur in both shoots and decapitated stems since radioactivity was detected in samples other than the treated leaf. However, no source/sink transport of assimilates was apparent. A possible reason for the results obtained may be the gross interference with the plants i.e. severing the canes from the root system followed by bisection of these canes. This may have induced changes in the assimilate distribution as has been found in other plants (Neales & Incoll 1968; Gersani *et al.* 1980b; Herold 1980). Furthermore, the severed cane ends were immersed in distilled water, consequently no nutrients were available for sustaining growth. Therefore, in retrospect, it was decided that the use of cane portions in translocation experiments was impractical. However, the results obtained emphasize that before detached plant portions are used in experiments, the possible physiological changes induced by cutting should be considered.

The effect of leaf position and apical decapitation on the translocation of assimilates in intact plants

For clarity, the middle and basal leaf treatments will first be compared with the 'control', followed by a comparison of the 'control' and decapitation treatments.

Table 2 Absorption of radiotracer by detached new, fully expanded and senescing *Rubus cuneifolius* leaves 2, 6 and 12 h after application of ^{14}C-sucrose to the adaxial surface (Mean ± S.E.)

Samples radioassayed	Percentage recovered radioactivity/sample								
	New leaf			Expanded leaf			Senescing leaf		
	Incubation time (h)								
	2	6	12	2	6	12	2	6	12
Leaf	6,1 ± 0,4	5,2 ± 1,9	5,9 ± 0,1	5,5 ± 1,8	6,4 ± 1,3	5,1 ± 0,4	13,0 ± 3,7	21,3 ± 2,6	22,6 ± 1,0
Wash	94,0 ± 0,5	94,8 ± 1,9	94,1 ± 0,1	94,5 ± 1,8	93,6 ± 1,3	94,9 ± 0,4	87,0 ± 3,7	78,6 ± 2,7	77,4 ± 1,0
Water source	0,0	0,0	0,0	a	0,0	0,0	0,0	0,2 ± 0,2	a

[a]Low percentage radioactivity detected

Table 3 Percentage of the total recovered radioactivity in samples of *Rubus cuneifolius* shoots and decapitated stems 48 and 168 h after ^{14}C-sucrose application to the adaxial surface of a single leaf (Mean ± S.E.)

Samples radioassayed	Percentage of total recovered radioactivity/sample			
	Shoot		Decapitated stem	
	Treatment time (h)			
	48	168	48	168
Apex	0,7 ± 0,3	0,4 ± 0,2	–	–
Treated leaf	9,5 ± 1,4	8,1 ± 1,4	7,7 ± 0,6	11,1 ± 0,3
Leaf wash	83,7 ± 0,4	82,0 ± 2,7	84,1 ± 0,4	79,9 ± 0,5
Cane	1,3 ± 0,2	1,3 ± 0,1	2,7 ± 0,6	3,4 ± 0,3
Leaves	4,8 ± 0,9	8,0 ± 1,8	5,5 ± 0,4	5,6 ± 0,5
Water source	0,0	0,0	0,0	0,0

Although the majority of the recovered radioactivity was detected in the treated leaf samples, the position of the treated leaf apparently influenced the export of radioactivity (Table 4). In the 'control', the exported radiotracer was detected in the apex, cane and leaves. No radioactivity was detected in the root samples of these plants. Where radiotracer was applied to a leaf midway down the cane, radioactivity was detected in all the samples including the roots. Significantly less radiotracer was detected in the apex samples of the basal leaf treated plants than those of the 'control' and middle leaf treatments. Furthermore, the percentage radioactivity in the root samples of the basal leaf treated plants was significantly greater than that of the middle leaf treated plants.

Table 4 Percentage of the total recovered radioactivity in samples of *Rubus cuneifolius* plants grown in a greenhouse, following ^{14}C-sucrose application to the adaxial surface of (i) the first leaf below the 5 cm cane apex ('control'); (ii) a leaf midway down the cane (middle leaf); (iii) a leaf at the basal region of the cane (basal leaf) and (iv) the top leaf of decapitated canes (decapitated) (Mean ± S.E.)

Samples radioassayed	Application site and percentage of recovered radioactivity/sample			
	'Control'	Middle leaf	Basal leaf	Decapitated
Apex	3,2 ± 2,0	1,8 ± 1,6	0,6 ± 0,3	–
Treated leaf	93,5 ± 3,9	93,3 ± 0,6	86,5 ± 3,3	94,9 ± 0,4
Cane	2,1 ± 0,9	1,5 ± 0,7	6,3 ± 2,7	1,4 ± 0,3
Leaves	4,2 ± 3,2	1,4 ± 0,7	1,8 ± 1,4	0,5 ± 0,5
Roots	0,0	1,9 ± 0,7	4,7 ± 0,9	3,3 ± 0,4

Comparing the results obtained for the 'control' and decapitated treatments, the most obvious difference is that radiotracer was detected in the roots of decapitated plants but not in the roots of 'control' plants.

The results obtained for the intact plants depict the translocation of assimilates from the treated leaves. Therefore translocation of assimilates exported from leaves situated near the cane apex was predominantly acropetal. Assimilates exported from leaves situated midway down the cane were translocated acropetally and basipetally since radiotracer was detected in both the apex and root samples. Assimilates exported from leaves situated near the base of canes was predominantly basipetal.

Movement of assimilates in plants is thought to occur from a source (usually photosynthetic tissue) to a sink (region depleting or transforming translocate) (Geiger & Sovonick 1975). In the experiments on intact bramble plants, the treated leaf was the source leaf while the region of highest percentage recovered radiotracer formed the sink region. Since the object of this experiment was to project the likely destination of foliar applied systemic herbicides, the acropetal/basipetal translocation pattern (i.e. from the treated leaf to the cane apex or roots) will be discussed.

The apparent translocation pattern in bramble determined from these results is similar to that reported in other plants (Wardlaw 1968). That is, assimilates exported from leaves situated near the cane apex were transported to the cane apex sink region, those from the basal leaves to the root sink region while assimilates from leaves in an intermediate position were transported in both directions. Relating these results to foliar applied systemic herbicides, suggests that to ensure maximal basipetal translocation into the roots, the basal leaves must be treated with herbicide solution. Merely wetting the upper leaves with the herbicide solution may result in killing off the topgrowth but the root system, which must be killed to ensure good control of this species, may receive little or no herbicide.

It has been shown that the direction of assimilate translocation can be manipulated (Gersani *et al.* 1980a). This was apparently also the case in bramble primocane plants. Radiotracer exported from a source leaf situated near the cane apex of intact bramble plants was transported acropetally to the apical sink region. However, with the removal of this sink region (i.e. decapitation), the exported radiotracer which would normally have been transported acropetally, was translocated basipetally to the root system sink region. It is therefore proposed that decapitation of bramble plants immediately prior to foliar herbicide application may promote movement of the herbicide to the target region; the root system. This would increase the kill rate and prevent regrowth in subsequent years.

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