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Title: MANIPULATION OF ASSIMILATE TRANSPORT PATTERNS AS A METHOD OF STUDYING GLYPHOSATE TRANSLOCATION IN TALL MORNINGGLORY [IPOMOEA PURPUREA (L.) ROTH]

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Glyphosate [N-(phosphonomethyl)glycine] is a translocated herbicide known to move readily via the phloem into natural assimilate sinks. However, reports of its movement in the transpiration stream suggest possible differences between glyphosate and assimilate translocation capabilities. This research was conducted to study the degree of similarity between glyphosate and assimilate translocation.

Translocation patterns were compared in tall morningglory [Ipomoea purpurea (L.) Roth] 24 hours after application of ^{14}C-glyphosate or $^{14}CO_2$ to a mature leaf. Under normal conditions translocated glyphosate moved like ^{14}C-assimilates in a typical source to sink pattern, accumulating in the roots, stem, new leaves, and

shoot tip. Small amounts of both labeled assimilate and glyphosate entered untreated mature leaves. ^{14}C distribution patterns compared on a percentage basis indicated minor differences between glyphosate and assimilate sink partitioning.

The export of either glyphosate or assimilate from a treated leaf was prevented by petiole girdling. Girdles were created by passing a hot copper wire loop along a 2-cm section of stem or petiole 24 hours prior to treatment. Stem girdling below a treated leaf essentially stopped all basipetal translocation of both materials. Stem girdles above the leaf greatly reduced but did not eliminate acropetal transport. Glyphosate demonstrated greater capacity to pass acropetally through a stem girdle than did assimilates (3.7% vs 1.0% of translocated label). Some repartitioning from the apoplast back into the phloem was evident once glyphosate had passed the girdle.

Conversion of any mature leaf into a strong assimilate sink (artificial sink) was accomplished by an application of N^6-benzyladenine, and enclosure in an aluminum foil envelope. Labeled assimilate or glyphosate was imported by these artificial sinks regardless of their location. Greater leakage into the apoplast occurred when glyphosate was translocated acropetally rather than basipetally to an artificial sink.

When applied as small droplets on the stem, large amounts of

glyphosate moved symplastically to natural or artificial sinks, and apoplastically via the transpiration stream into all transpiring tissues above the site of application. Stem girdling below the treated area prevented basipetal transport of glyphosate, but girdles located above the application site appeared to have little effect on acropetal movement. Of the total herbicide translocated, 26.4% was found to have passed through upper girdles.

Results of this study suggest that: (a) glyphosate moves readily via the symplast from assimilate source to sink; (b) a substantial portion of the herbicide is transported via the transpiration stream to all transpiring tissues "downstream" from a site of application; (c) glyphosate transfers from apoplast to the phloem with relative ease; and (d) glyphosate has a tendency for limited leakage from the phloem back into the apoplast.

MANIPULATION OF ASSIMILATE TRANSPORT PATTERNS AS A METHOD OF STUDYING GLYPHOSATE TRANSLOCATION IN TALL MORNINGGLORY[*IPOMOEA PURPUREA* (L.) ROTH]

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INTRODUCTION

Effective chemical weed control requires a working knowledge of herbicide translocation capabilities. In spite of considerable research, certain questions about glyphosate translocation have gone unanswered. For example, glyphosate is generally described as a phloem-mobile herbicide. But it is not certain how closely glyphosate follows changes in assimilate translocation patterns. Uncertainty also exists regarding the amount of glyphosate which is translocated via the transpiration stream.

The primary objective of this research was to compare glyphosate and assimilate translocation patterns under a variety of normal and dramatically altered translocation conditions. At the same time, the tendency for glyphosate to move in the transpiration stream would be studied. Chapters in this thesis are prepared in the general format of manuscripts for Weed Science.

Tall morningglory was selected as a test species because of its relatively simple morphology and source-sink patterns. Chapter One is dedicated to characterizing assimilate translocation in that species. A large portion of that research involved developing or

adapting techniques which effectively and predictably change assimilate distribution patterns. It was of interest to know whether these techniques affected xylem transport, so the effects of assimilate flow manipulation on the translocation of a xylem-mobile herbicide were studied in Chapter Two. A study of glyphosate translocation is reported in Chapter Three, using the assimilate translocation patterns established in Chapter One as standards. Comparing the response of glyphosate and assimilates to various manipulative techniques proved an effective means of identifying certain differences in translocation characteristics, while also serving to reemphasize similarities.

LITERATURE REVIEW

Glyphosate Absorption

Glyphosate [N-(phosphonomethyl)glycine] is a non-selective herbicide, dependent on foliar absorption and translocation for effective weed control. Extensive research has been conducted characterizing its absorptive and translocative properties in efforts to maximize performance.

Glyphosate is normally a negatively charged acid molecule formulated as an isopropylamine salt. The polar molecule is quite water soluble (1.2% at 25 C) and would be expected to have difficulty passing through the lipophilic surface waxes of plant cuticles. Wyrill and Burnside (68) compared absorption of glyphosate and 2,4-D through isolated cuticles of hemp dogbane and common milkweed. 2,4-D is a semi-polar molecule which is less water soluble (.09%) and is readily absorbed by foliage. After 43 hours, up to 58 times more 2,4-D was absorbed than glyphosate. The authors attributed the greater 2,4-D absorption to its semi-polar nature which allowed better diffusion through the lipophilic constituents of the cuticle. Schultz and Burnside (50) compared 2,4-D and glyphosate absorption on intact leaves of hemp dogbane. They also noted greater absorption of 2,4-D, but the difference was not as great. Twenty-four

hours after application, 80.5% of the applied 2,4-D had been absorbed, compared with 29.5% glyphosate absorption.

The total amount of glyphosate absorbed varies considerably. Marquis et al. (36) observed 14.7% absorption, 14 days after application on reed canarygrass. Davis et al. (16), studying absorption on quackgrass, found that 93% of applied glyphosate was taken up within 10 days. Gottrup et al. (23) reported 24-hour absorption values ranging from 7 to 87% on leafy spurge. Jordan (29) recorded absorption extremes from 10 to 70% in bermudagrass 48 hours after glyphosate treatment. Variation in absorption may be explained by many factors which affect the rate of absorption and/or the length of the absorptive period. Several of these factors are species related. Numbers of stomata and trichomes, cuticle thickness, and cuticle chemistry have all been implicated (36,47,49,68,69). But, probably of greater influence are environmental factors, especially those related to the water status of the plant. Relative humidity, soil moisture, and temperature appear to be most influential.

Glyphosate absorption tends to decrease as available soil moisture decreases. Ahmadi et al. (1) demonstrated 3-4 times greater absorption at 40% than 10% soil moisture. McWhorter et al. (39) reported 33% more absorption at 20% than at 12% soil moisture.

Absorption of glyphosate generally increases with increasing temperature (50,66,67). Jordan (29) compared glyphosate absorption

in bermudagrass at temperatures of 22 and 32 C. Uptake was 17-66% greater at 32 C. McWhorter et al. (40) showed absorption in johnsongrass to nearly double as temperature changed from 24 to 35 C. Frost may also promote increased absorption. Davis et al. (16,17) saw a slight increase in absorption (30%) after quackgrass was exposed to frost.

Relative humidity is probably the most important environmental factor influencing glyphosate absorption. Gottrup et al. (23) studied absorption under conditions of low and high relative humidity. Twenty-four hour absorption values of 7.2% and 86.6% were recorded on leafy spurge plants subjected to low and high relative humidity, respectively. High relative humidity on Canada thistle resulted in 3.1-4.4 times more absorption. The effect of relative humidity on absorption was significantly greater than the effect of surfactant. Jordan (29) compared the effects of relative humidity and temperature on absorption, and found RH to be most influential. Absorption was 4.5-6.5 times greater at 100% RH than at 40% RH. Wills (67) studied the effect of temperature, soil moisture, relative humidity and surfactants on the absorption of glyphosate in cotton. He concluded that absorption was most affected by relative humidity. Variations in temperature, soil moisture, or the surfactant produced less than a one fold change in uptake, while an increase in RH from 40 to 100% resulted in a 3 to 6 fold increase in absorption. Though RH had the

greatest influence on absorption, temperature was most important in determining phytotoxicity. McWhorter and Azlin (39) studied glyphosate absorption on johnsongrass and soybeans in response to relative humidity, soil moisture, temperature, and surfactant variables. They found relative humidity and soil moisture to have the greatest influence.

According to McWhorter and Azlin (39), McWhorter et al. (40), and Wills (67) the optimum conditions for glyphosate absorption include high relative humidity, soil moisture, and temperature. These conditions may result in a more hydrated cuticle, which in turn promotes better diffusion of the hydrophylic glyphosate molecule across the cuticle.

The relationship between light and glyphosate absorption is still uncertain. Schultz and Burnside (50) found higher light intensities to reduce glyphosate absorption in hemp dogbane. They attributed this to increased necrosis of treated areas which they observed to be associated with higher light intensity. Whitwell et al. (66) and Kells and Rieck (31) compared glyphosate absorption under light and dark conditions. Both groups observed significantly more absorption in the light. Whitwell et al. (66) concluded that light is involved in the active uptake of glyphosate through production of ATP and other energy sources. Evidence of active uptake was also presented by Leonard and Shaner (33).

Surfactants are known to improve glyphosate performance (23, 30,40,56). According to Richard and Slife (47), surfactants increase the rate of glyphosate absorption but do not extend the absorption period. The degree of increase is dependent on the type of surfactant and environmental conditions. Wyrill and Burnside (69) studied 74 surfactants and found the cationic variety to be most effective in improving glyphosate uptake. Of those surfactants tested, Mon 0818 was the most effective. McWhorter and Azlin (39) and Wills (67) found the effect of surfactant to be more noticeable when plants were subjected to conditions of low relative humidity, low soil moisture, or high temperature.

It has been suggested that surfactants improve herbicide absorption by reducing surface tension and/or enhancing cuticular penetration (4,21,27). McWhorter and Azlin (39) proposed that surfactants promote glyphosate absorption by similar means. Others, however, have presented evidence suggesting that, in the case of glyphosate, the primary role of surfactants may be considerably different. Wyrill and Burnside (68) studied the movement of glyphosate across intact and isolated cuticles of common milkweed and hemp dogbane. Surfactant significantly increased glyphosate absorption in intact leaves, but neither addition of surfactant nor wax removal increased diffusion of glyphosate through the isolated cuticles. Wyrill and Burnside (69) demonstrated that reduction of surface tension was not associated

with greater glyphosate uptake. Comparing the effect of numerous surfactants, they found many of the more effective materials had high contact angles. They concluded that the main influence of surfactant was on the plasma membrane rather than the cuticle. They cite evidence by Sutton and Foy (57) that surfactants can alter membrane permeability, and suggest that movement of the negatively charged glyphosate molecule through the lipid bilayer may be facilitated by its association with a cationic surfactant. Richard and Slife (47) compared absorption of glyphosate by intact leaves and isolated leaf cells. There were no significant differences in absorption even though isolated cells had no cuticle. Adjuvants increased absorption 2.7 fold in both test systems. These authors suggest that even though the cuticle represents a significant barrier, cellular rather than cuticular absorption is the limiting factor in foliar uptake of glyphosate.

Variation in experimental techniques used to apply ^{14}C-labeled glyphosate also contributes to absorption differences. Researchers may apply ^{14}C-glyphosate to a leaf surface as a single drop (5-10 ul), or as multiple small droplets. They may or may not use lanolin to contain the drop(s). Total rates applied also vary considerably. Each of these factors has been shown to significantly influence absorption (23,30,51). Neither is there a standard method of formulating glyphosate. There are examples of ^{14}C-glyphosate applied

in methanol, water, or commercial Roundup. Parent glyphosate may be used with or without isopropylamine. Surfactants also vary widely, and some researchers use no surfactant. Undoubtedly such differences in formulation contribute to variation in absorption.

An abbreviated absorption period and incomplete absorption are characteristic traits of glyphosate. Most reports indicate an initial rapid rate of uptake. Richard and Slife (47) recorded significant absorption in 15 minutes on hemp dogbane. Shultz and Burnside (50), studying hemp dogbane, saw 13-25% absorption in 30 minutes. Sprankle et al. (56) demonstrated 34.2% absorption on quackgrass 4 hours after treatment.

Uptake declines rapidly over time. Within a matter of days absorption approaches zero. Shultz and Burnside (50), comparing 2,4-D and glyphosate on hemp dogbane, concluded that glyphosate absorption failed to continue beyond 3 days while absorption of 2,4-D continued for their entire 12-day study. Zandstra and Nishimoto (70), Segura et al. (52), Marquis et al. (38), and Sandberg et al. (49) all determined glyphosate absorption to cease within 2 to 4 days of application. In each case a considerable amount of glyphosate remained on the leaf surface long after absorption had ended. Schultz and Burnside (50) recovered 46% of the applied glyphosate from the leaf surface after 12 days. Marquis et al. (36) recovered 85% after 14 days.

Reasons for the seemingly premature termination of absorption are still speculative. One explanation might be inavailability due to evaporation of carrier, and subsequent glyphosate crystallization on the leaf surface. Some researchers (30,50,51) support the idea of physiological isolation of unabsorbed glyphosate as a result of spot necrosis under the treated areas. Research by Gottrup et al. (23) is unique in that the authors were able to significantly extend the period of glyphosate uptake (7 days). They used techniques to minimize both spot necrosis and droplet evaporation. The actual cause of incomplete absorption is likely a combination of these and other factors.

Glyphosate Translocation

Research has established that glyphosate translocates, and that good translocation is required for effective weed control (11, 17,18,25,47,56).

The amount of glyphosate translocated varies. Kells and Rieck (31) reported that 4.7% of applied glyphosate was translocated from the site of application after 3 days. Wyrill and Burnside (68) noted translocation of 51% after 24 hours. The time over which translocation occurs also varies. Wyrill and Burnside (68) found most translocation to roots occurs within 24 hours. Chase and Appleby (9) and Sandberg et al. (49) suggested that 3 days be allowed for best

translocation. Kells and Rieck (31) reported continued translocation of significant amounts of glyphosate 6 days after treatment. Marquis et al. (36) reported no change in translocation patterns after 4 hours. Much of the reported variability is the direct result of variation in absorption. The amount translocated is dependent on the quantity absorbed, and therefore will be significantly affected by all factors influencing absorption.

Though much work has been done, there seems to remain a considerable degree of confusion on the subject of glyphosate translocation capabilities. There is general agreement that glyphosate moves in the phloem. In an early study by Rioux et al. (48), glyphosate was translocated from mature quackgrass leaves to rhizomes, and between shoots connected by a common rhizome. The authors concluded that glyphosate moved in the phloem in the same manner as carbohydrate. Sprankle et al. (56) did some of the first translocation work with ^{14}C-glyphosate. Distribution patterns in Canada thistle and quackgrass indicated that glyphosate moved primarily in the phloem, following established source-sink relationships. The authors suggested that any conditions affecting the source-sink movement of assimilates would also affect the translocation of glyphosate. Ahmadi et al. (1) made a similar conclusion. Chase and Appleby (10), Bingham et al. (6), Whitesides (65), and Jordan (30) all reported significant movement of glyphosate from exporting leaves

to assimilate sinks. Richard and Slife (47) and Davis et al. (17) determined intact phloem to be essential for glyphosate translocation.

Apoplastic glyphosate translocation is not as well understood. Glyphosate has been shown to move readily in the transpiration stream, once in the xylem. Richard and Slife (47) and Shaner and Lyon (53) found that glyphosate taken up through cut stems or petioles was rapidly translocated in an apoplastic pattern throughout all tissues. However, glyphosate applied exogeneously to intact plants seems to behave much differently. In the translocation studies by Rioux et al. (48) and Sprankle et al. (56) where glyphosate was applied to leaves of Canada thistle, quackgrass, or field bindweed there was no mention made of any apoplastic translocation. Kells and Rieck (31) reported that glyphosate translocation in johnsongrass was via the phloem, but provided no evidence of apoplastic transport. Haderlie et al. (25) and Sandberg et al. (49) also found glyphosate to move as the assimilate in the phloem. Again, there was no indication of apoplastic translocation.

Other researchers have reported some degree of apoplastic glyphosate transport in intact plants. Though not addressed in their discussions, Wyrill and Burnside (68) and Schultz and Burnside (50) presented data indicating ^{14}C label in mature, untreated leaves below the site of ^{14}C-glyphosate application. Wyrill and Burnside found 1 to 3% of the total translocated label in these leaves, while

Schultz and Burnside recovered 4 to 5%. It was concluded in both cases that glyphosate moved in a typical phloem pattern. Either the authors considered ^{14}C in mature leaves to be a result of typical phloem transport, or discounted it as insignificant apoplastic movement and not worthy of mention. Other researchers, observing limited movement of glyphosate into mature untreated leaves, have described it as apoplastic movement (40,52).

The most easily recognized and most often reported evidence of apoplastic glyphosate translocation occurs in the treated leaf of intact plants. Gottrup et al. (23) first reported this in Canada thistle and leafy spurge. They described glyphosate moving in the apoplast from the point of application to the margins of the treated leaf, and in the symplast from the treated leaf to roots and young leaves. Segura et al. (52) reported the same phenomena in ryegrass and clover. Large amounts of glyphosate moved acropetally in the transpiration stream of the treated leaf before symplastic movement occurred out of the leaf. Translocation throughout the untreated portions of the plant was primarily symplastic with very small amounts observed in untreated mature leaves after 72 hours. Marquis et al. (36), Bingham et al. (6) and Whitwell et al. (66) also showed strong acropetal movement of glyphosate in the transpiration stream of treated grass leaves, either prior to or concurrent with symplastic export. Each reported strong symplastic movement of exported glyphosate

into roots and new leaves with limited transport into mature untreated leaves.

Leakage of ^{14}C-glyphosate from roots of intact plants suggests some apoplastic mobility. Marquis et al. (36), 1 week after a foliar application of ^{14}C-glyphosate to two grass species, found 5-10% of the applied label in the nutrient solution. Schultz and Burnside (50), studying hemp dogbane, reported leakage of 10-20% (of the translocated glyphosate) after 3 days. Coupland and Casely (13) noted glyphosate in guttation fluid as well as root exudate.

Not all apoplastic movement into mature leaves is minor. Zandstra and Nishimoto (70) published autoradiographs of glyphosate-treated purple nutsedge showing substantial label in old untreated leaves. Autoradiographs of bermudagrass by Jordan (29) showed nearly equal amounts of glyphosate in old and new leaves, and Haderlie (24) reported equal glyphosate concentrations in all leaves of soybeans. Lunde-Hoie (34) showed very strong accumulation of glyphosate at transpiring surfaces in ash, indicating transfer into xylem.

Certain environmental factors may affect transport patterns. McWhorter et al. (40) found glyphosate to translocate into johnsongrass rhizomes only at 100% relative humidity. According to Wills (67), higher temperatures resulted in a larger percentage of translocated glyphosate moving into cotton roots. Whitwell et al. (66)

suggested that high transpiration rates in bermudagrass would change the overall pattern of glyphosate distribution. Kells and Rieck (31) observed a 20-fold increase in glyphosate translocation to johnsongrass roots when plants were maintained in light rather than dark conditions, even though absorption was only increased 2.5 times.

Patterns of ^{14}C-glyphosate distribution do not appear affected by overspraying plants with unlabeled glyphosate (50,70). Metabolism does not appear to be a factor in reported ^{14}C-glyphosate distribution patterns. All species tested showed little or no glyphosate metabolism 1-2 weeks after treatment (23,36,49,50,68,70).

The pattern of glyphosate translocation does appear to be very dependent on the site of application. Schultz and Burnside (50) observed strong movement to the roots of hemp dogbane plants when glyphosate was applied to a basal leaf. Treatment of an upper expanded leaf resulted in little transport to the roots, but strong upward movement to new leaves and shoot tip. Wills (67) noted almost no translocation when he applied glyphosate to a young "importing" cotton leaf, but extensive movement to roots and young leaves when a mature leaf was treated. Wills also noted considerably more apoplastic transport into mature leaves when application was made to the stem rather than a leaf. Root-applied glyphosate gave even more extensive apoplastic transport (24).

Assimilate Translocation

Several extensive reviews have been published on the subject of assimilate transport (14,43,61,62,72). Some aspects, such as the mechanism of phloem transport, are still subject to much debate. Others, including patterns of assimilate distribution, are more definitive. The latter topic is most pertinent to the subject of this thesis.

Assimilation may be defined as the energy-requiring biosynthesis of organic molecules from more simple precursors. Referring specifically to plants, it is the transformation or incorporation of CO_2, water, and mineral nutrients into the many organic substances composing a plant. Photosynthesis may be defined as the photochemical assimilation of CO_2 into carbohydrates. The term photosynthate or photo-assimilate is often used to distinguish this more specific class of assimilate. Photosynthate includes sugars, starches, organic acids, and structural carbohydrate. Assimilate refers to photosynthate as well as amino acids, nucleic acids, vitamins, enzymes, and numerous other 'assimilated' organic molecules. Crafts and Crisp (14) list 111 assimilates which have been reported translocated in the phloem.

Patterns of assimilate distribution are often studied through the use of $^{14}CO_2$. Labeled CO_2 is initially converted into carbohydrates,

but will eventually appear in all forms of assimilate. Sucrose is the primary form in which ^{14}C will be translocated throughout the plant. However, small amounts of ^{14}C may also translocate in the form of certain monosaccharides, other disaccharides, amino acids, and other assimilates (14,62).

Assimilate translocation occurs primarily in the phloem, though small quantities may also move in the xylem (5,62). Assimilates found in the xylem include sucrose, certain monosaccharides, organic acids, and amino acids (62).

Translocation follows a characteristic "source to sink" distribution pattern, where assimilate moves from areas of synthesis or remobilization to areas of utilization or storage. A typical ^{14}C translocation pattern following $^{14}CO_2$ assimilation by a mature leaf would consist of export into underground parts, stem, new leaves, and new shoots. Other mature exporting leaves would be largely bypassed (35,37,38,54). Early work by Jones et al. (28) is still used as a representative model of translocation patterns. These researchers exposed a single mature leaf of Nicotiana tabacum to $^{14}CO_2$ for 2-3 hours, then followed its pattern of translocation for 96 hours. They observed translocation of 3-6% into young leaves and the shoot apex. A large percentage appeared to be stored in the stem. The remainder was transported to the roots. Upper leaves translocated a greater percentage of their total ^{14}C to new leaves

and the shoot apex, than did lower leaves. Lower leaves transported more to underground tissues. Mature leaves below the treated leaf failed to import ^{14}C.

It was also noted that tobacco leaves did not export assimilate until they had attained approximately one-half of their full size. Near this stage of physiological maturity the leaf was shown to import and export assimilate simultaneously. More recently Turgeon and Webb (59) determined assimilate export to begin at 35% leaf expansion in Cucurbita pepo, while import continued until 45% expansion. Swanson and Haddinott (58) observed maximum sink strength of bean leaves to occur at 9-10% of full expansion. Sink strength was near zero at 45% expansion. Similar results have been obtained by Silvius et al. (55) in soybeans.

Techniques for altering or manipulating assimilate transport patterns have proven useful tools in better understanding assimilate translocation. They have also been used extensively in comparing the movement of xenobiotics, such as herbicides, with the translocation patterns of assimilate.

One of the earliest used techniques involved ringing or girdling a stem, either with steam or by cutting, to destroy the living conductive tissues. Mason and Maskell (37) found that destruction of the symplast in this manner prevented passage of carbohydrates beyond that point, and demonstrated that sugars were translocated primarily

via the phloem. Girdling has since been used extensively in assimilate and some herbicide translocation studies (15,42,45,60).

Leaf shading or darkening has also been a popular method of altering translocation patterns (19,20,26,37,44,71). Forde (20) shaded the leaves on a stolen of bermudagrass and found that movement of assimilates into the stolen was increased. Fondy and Geiger (19) shaded leaves of sugar beet or bean and saw no change in movement to sink leaves, but a reduction in transport to roots. Hartt (26) compared the effects of leaf darkening with red, green, blue, white, and far-red light on sugar cane. She reported little or no basipetal translocation of ^{14}C from the leaf exposed to $^{14}CO_2$ under conditions of darkness or far-red light. Red or blue light resulted in significantly greater basipetal translocation than occurred with either white or green light.

Defoliation, fruit removal, or shoot pruning have all contributed to dramatic changes in assimilate distribution (2,45,46,70). Cook and Evans (12) demonstrated that removal of competing sinks dramatically increased assimilate movement to a normally weak sink. They also showed that elimination of mature leaves between a distant sink and a ^{14}C-assimilate source could significantly alter ^{14}C translocation patterns. Assimilate demands in the distant sink were normally satisfied with unlabeled carbohydrates from more proximal source-leaves. Upon removal of adjacent source-leaves the sink

became a strong importer of ^{14}C. Forde (20) induced assimilate movement into stolens of bermudagrass by defoliation. A minimum of three defoliations were required to assure import.

Temperature has been effective in altering assimilate flow, especially cold temperatures (63,64). Lang (32) studied the effect of petiole temperature on the phloem transport of ^{137}Cs from a mature leaf. Raising the temperature resulted in increased sustained movement into roots. Lowering petiole temperatures caused an abrupt pause in translocation, followed by gradual increase and eventual resumption of original flow rates. At 4 C little transport occurred during the first hour, with full translocation being regained after 4-5 hours. The authors attributed the temporary disruption of assimilate flow to shock-induced phloem plugging, which was gradually reversed over time. Freezing a section of petiole prevented all translocation as long as the temperature was maintained. Transpiration was also stopped, as evidenced by leaf wilting. Phloem transport did not resume after thawing, presumably because of sieve element damage. Transpiration did resume after thawing. Pickard et al. (44) demonstrated the effects of cold blocks on moonflower. When temperature of a petiole or section of stem was reduced to near freezing, assimilate translocation through that tissue was stopped almost immediately (within 5 minutes). Freezing a section of stem or petiole was equally effective at stopping assimilate movement, but also

stopped transpirational water flow. The authors did not observe resumption of symplastic translocation through cold blocks but failed to monitor the effects beyond 1.5-2 hours.

The use of homones and growth regulators as translocation manipulators is becoming more common (3,7,22). Müller and Leopold (41,42) used exogenously applied cytokinin to direct transport of ^{32}P in corn leaves. Localized application of kinetin resulted in an accelerated transport of ^{32}P to kinetin areas. Kinetin also attracted Na^{22} but failed to influence the movement of Rb^{86}, Cl^{36}, and I^{131}. Kinetin-induced translocation was inhibited by steam girdling. Quinlan and Weaver (45) showed cytokinins to be instrumental in creating strong ^{14}C-assimilate sinks in intact leaves of Vitis vinifera. The strongest sinks resulted from the simultaneous use of cytokinin, steam girdling, and shading.

Ethephon and GA also promote import of ^{14}C-assimilate into treated areas (8). Additionally, ethephon has been shown to affect the translocation of several phloem-mobile herbicides (3,7,22).

Techniques used to study the transport of assimilates, especially girdling, have proven extremely useful in characterizing the translocation properties of herbicides (14,15). But as yet, few of these techniques have been used in studying glyphosate translocation. It is hoped that information derived from the use of transport manipulation techniques will be useful in better defining the translocation

properties of glyphosate and thereby resolve much of the apparent confusion over its degree of apoplastic transport.

CHAPTER 1

An Autoradiographic Study of ^{14}C-Assimilate Translocation in Tall Morningglory [Ipomoea purpurea (L.) Roth]

INTRODUCTION

Extensive translocation research has been conducted on assimilates. Several recent publications review much of the information currently available on this subject (14,61,62,72). As a general rule, assimilates are exported from regions of production or remobilization (sources) to areas of utilization or storage (sinks). However, patterns are changing constantly in response to environmental influences and plant maturation.

Experimental techniques which alter assimilate translocation patterns have contributed much to the present understanding of assimilate transport. Stem girdling was one of the earliest techniques, and is still commonly used in translocation studies today. Through its use Mason and Maskell (37) were among the first to show that carbohydrate moves in the phloem rather than xylem. Permanent girdling may be accomplished by localized heating, freezing, or cutting (32,42,45). Temporary girdles have been formed using cold blocks (32,44).

Leaf darkening or removal also are popular methods of altering

assimilate distribution patterns (12,19,37,71). Both are used to reduce or eliminate the influence of multiple sources. In some instances they have resulted in the creation of weak assimilate sinks (20,45).

Localized application of hormones or growth regulators has proven effective in creating or strengthening sinks. Müller and Leopold (41,42) reported strong movement of assimilates into areas treated with kinetin. Quinlan and Weaver (45) used benzyladenine to successfully create assimilate sinks in mature leaves. Chalmers et al. (8) were able to promote import of assimilates into tissues treated with ethephon or GA.

Assimilate transport is commonly used as a standard of reference in herbicide translocation studies. Accuracy in such comparative studies requires that assimilate translocation patterns in the selected test species be well defined. Tall morningglory was chosen for a future glyphosate translocation study. It was the objective of this research to characterize assimilate translocation in that species, and to demonstrate how techniques of girdling, leaf darkening, and cytokinin application could be used in accomplishing that goal.

MATERIALS AND METHODS

Tall morningglory plants [Ipomoea purpurea (L.) Roth, 'Heavenly Blue'] were grown from seed to approximately 1 m in height (16 days)

in 10-cm plastic pots containing a 3:1 mixture (v/v) of pearlite and a peat-based commercial potting medium (Jiffy Mix Plus). Plants were maintained in growth chambers (14-h photoperiod, photosynthetic photon flux density of 215 $uE\,s^{-1}m^{-2}$, 60 to 65% RH, 26 C constant temperature), and selected for morphological uniformity prior to treatments.

Forty-eight hours before harvest, designated plants were subjected to heat girdling, leaf darkening, and/or localized applications of N^6-benzyladenine. Benzyladenine ($1x10^{-3}$ M with 0.1% Tween 20) was brush-applied to individual leaves until both abaxial and adaxial surfaces were completely wetted. Leaves were darkened by enclosure in an 18- by 28-cm envelope constructed of aluminum foil. When both benzyladenine and shading treatments were applied, the leaf was allowed to dry before covering with foil. Girdling was accomplished by slowly passing an electrically heated 24-guage copper wire loop along a 2-cm length of stem or petiole (Appendix Figures 1 and 2), until a loss of cellular integrity was evident (30-60 s). The 4-mm diameter wire loop was not allowed to come in direct contact with plant tissue during the girdling process.

Twenty-four hours prior to harvest, all plants were exposed to $^{14}CO_2$. Labeled CO_2 was generated in a collapsing polyethylene reservoir of known volume, by the addition of perchloric acid to ^{14}C-labeled barium carbonate. A single leaf on each plant was

enclosed and sealed in a polyethylene bag, into which 0.75 uCi of $^{14}CO_2$ were injected in 5 cc of air using a hypodermic syringe.

At harvest, bags were evacuated and all plants were immediately dissected into 21 parts (two cotyledonary leaves, five true leaves, six nodes, six internodes, root, and shoot tip). A clean blade was used for each cut. Plants were then pressed, dried with forced air (45 C), mounted, and exposed to Kodak X-Omat R X-ray film for 21 days. Plant parts were arranged for all mounts as shown and labeled in Figure 1. Actual internode lengths were greater than depicted in the mounts. Treatments were repeated 2 to 5 times.

RESULTS AND DISCUSSION

The export-import status of each leaf, and the normal patterns of translocation from exporting leaves are shown in a series of plants treated at a uniform growth stage (Figure 2). All exporting leaves translocated ^{14}C to immature sink-leaves and shoot tip, but only lower leaves provided assimilate to roots. Basipetal transport diminished progressively as distance between source-leaf and root increased.

The transition of a leaf from sink to source usually occurs when it has reached 35% to 50% of its mature size (28,55,59). At the growth stage studied, L4 was nearest transition, as evidenced by its capacity both to import and export (Figure 2).

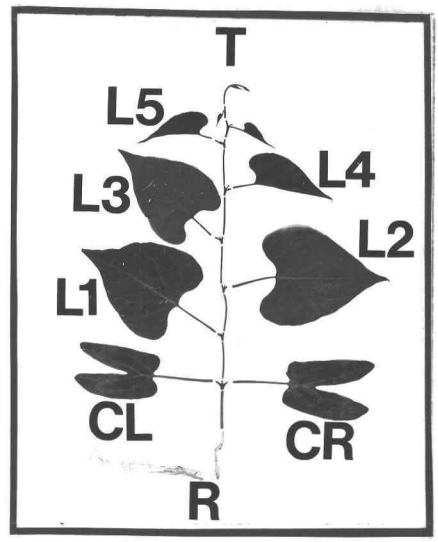

Figure 1. Mounting pattern for all plants used in autoradiographs; root (R), left cotyledon (CL), right cotyledon (CR), first leaf (L1), second leaf (L2), third leaf (L3), fourth leaf (L4), fifth leaf (L5), and shoot tip (T).

Figure 2. Assimilate transport patterns following exposure of a single leaf on each plant to $^{14}CO_2$; (A) representative plant mount, (B) CR exposed, (C) L1 exposed, (D) L2 exposed, (E) L3 exposed, (F) L4 exposed, and (G) L5 exposed. (a = assimilate source-leaf)

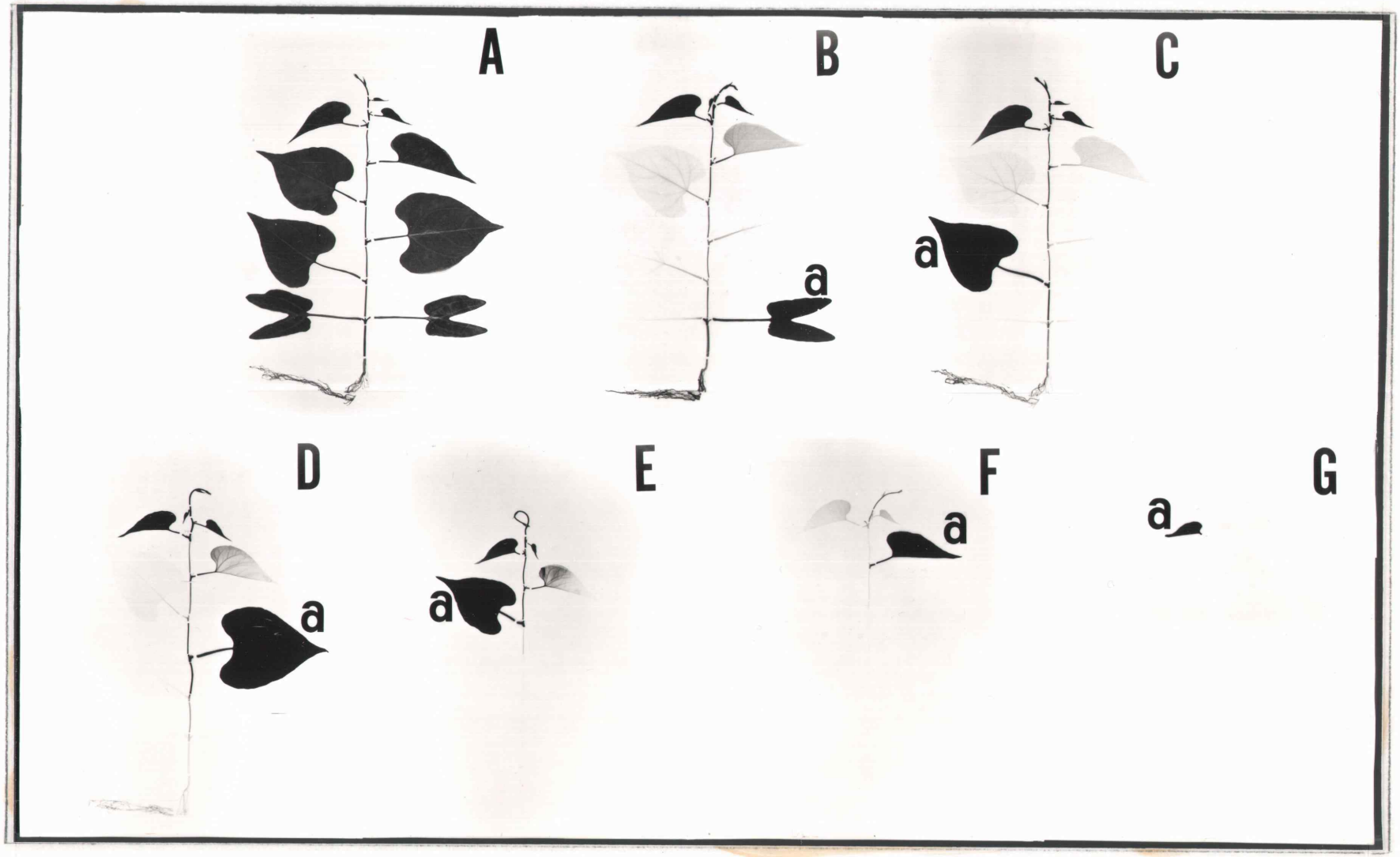

Figure 2.

Mature leaves showed indications of very limited ^{14}C-import. This was especially evident in leaves above a treated leaf. Autoradiographs of treated and untreated plants grown together in the same chamber demonstrated that label in mature untreated leaves was not just the result of $^{14}CO_2$ contamination. Neither was it an artifact of direct plant-film contact. Whether this translocation of ^{14}C occurred via the xylem, phloem, or both was not discernable at this point. However, it is known that limited amounts of assimilate are normally translocated in the xylem (5,62), and could account for the observed movement of ^{14}C into mature leaves.

The two basic methods of altering assimilate flow are: (1) To prevent movement into natural sink regions, and (2) to promote transport towards artificially created sinks. Girdling was an effective means of reducing or preventing assimilate transport (Figure 3). A girdle placed on the stem below a $^{14}CO_2$ treated leaf stopped essentially all basipetal movement (3B,D), indicating such transport is via the phloem. When single or double girdles were placed on the stem above a treated leaf (3C,D), reduction of acropetal transport was dramatic, but not complete. Trace amounts of ^{14}C were translocated apoplastically through the girdles and distributed throughout old and new leaves above the girdle. Though ^{14}C must have passed apoplastically through the girdle, some repartitioning from the transpiration stream back into the phloem is likely. Petiole girdles

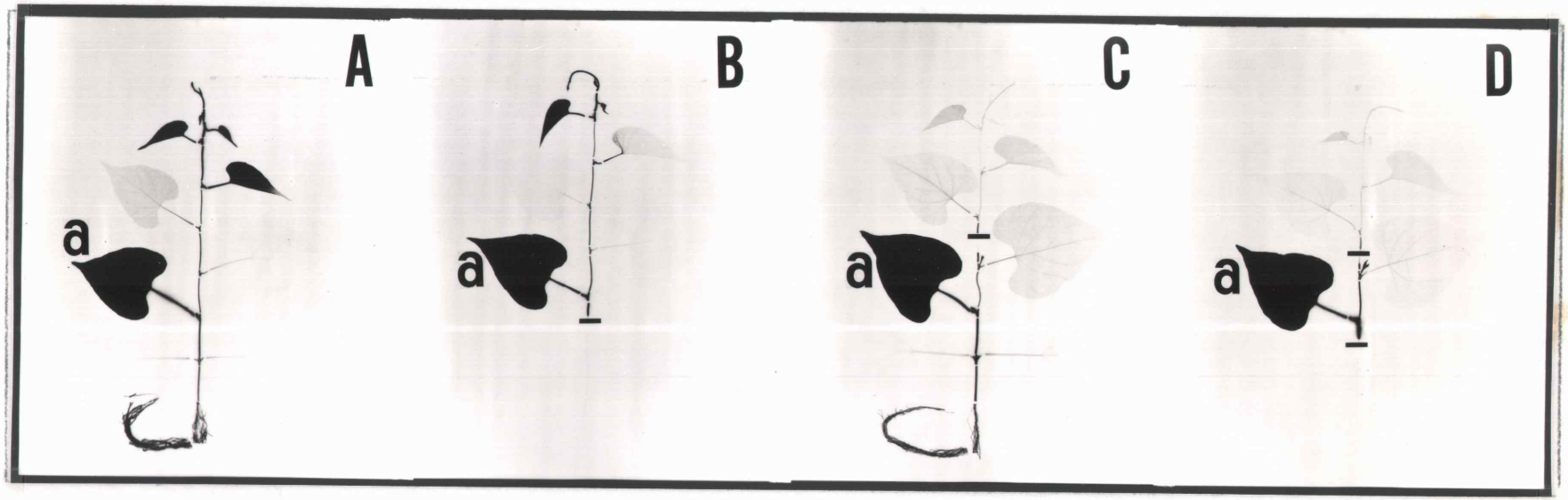

Figure 3. The effect of stem girdling on ^{14}C-assimilate translocation patterns from L1; (A) no girdles, (B) girdle below L1, (C) girdle above L2, and (D) girdle both above L2 and below L1. (a = assimilate source-leaf, — = girdle)

(Figure 4) gave further evidence that at least a portion of the ^{14}C normally observed in mature leaves enters via the xylem. Figure 4B demonstrates the effect of petiole girdles on two mature leaves above L1. Both managed to take up appreciable amounts of ^{14}C in spite of girdles. The effect of a petiole girdle on the treated leaf (Figure 4C) suggests that ^{14}C-assimilate is exported from a treated leaf exclusively via the phloem.

Creation of artificial sinks was a major objective of this study. By definition, the technique would involve the conversion of an exporting tissue into a strong importer of assimilate. It was concluded through additional experiments that girdling alone would not create assimilate sinks in mature leaves (Figure 5). A series of treatments were then applied to assess the sink-creating potential of leaf darkening and cytokinin used singly (Figure 6) and in various combinations with girdling (Figures 7 and 8). L2 was targeted as the potential artificial sink.

Neither leaf darkening nor cytokinin alone were of any measurable influence as sink promoters (Figure 6). Darkening alone actually appeared to reduce the amount of ^{14}C normally present in the mature target leaf (6B). The foil envelope probably reduced transpiration enough to prevent the limited import of label via the xylem.

Two-way combinations of girdling, leaf darkening, and benzyladenine also failed to produce adequate results (Figure 7). Only the

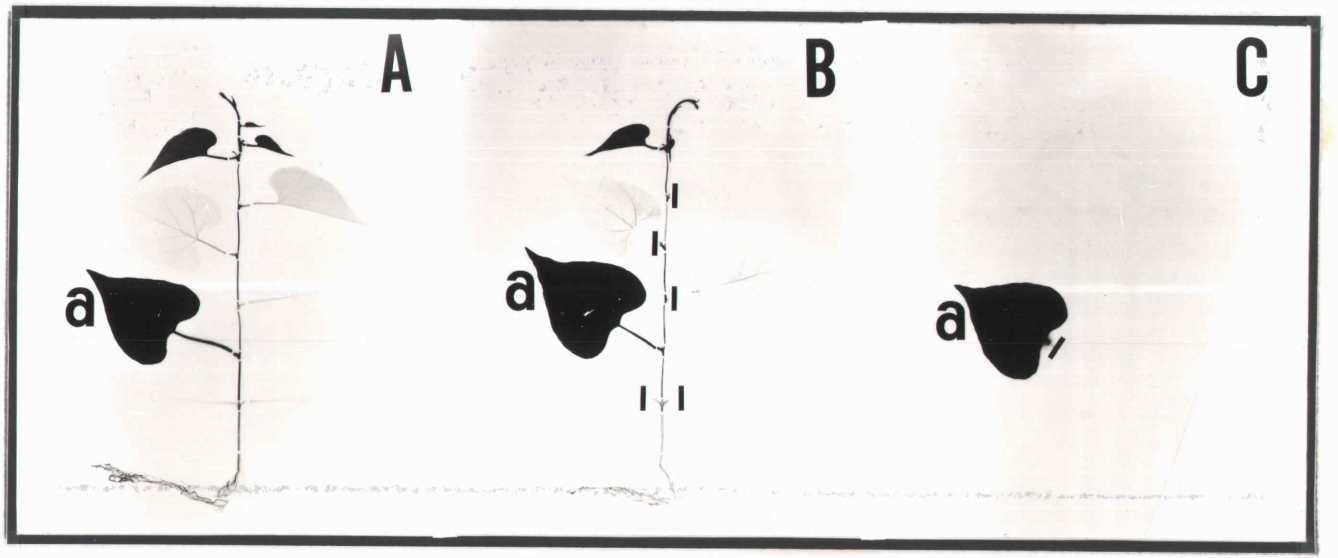

Figure 4. The effect of petiole girdling on ^{14}C-assimilate translocation patterns; (A) no girdles, (B) girdle on petioles of CR, CL, L2, L3, L4, and (C) girdle on petiole of L1. (a = assimilate source-leaf, — = girdle)

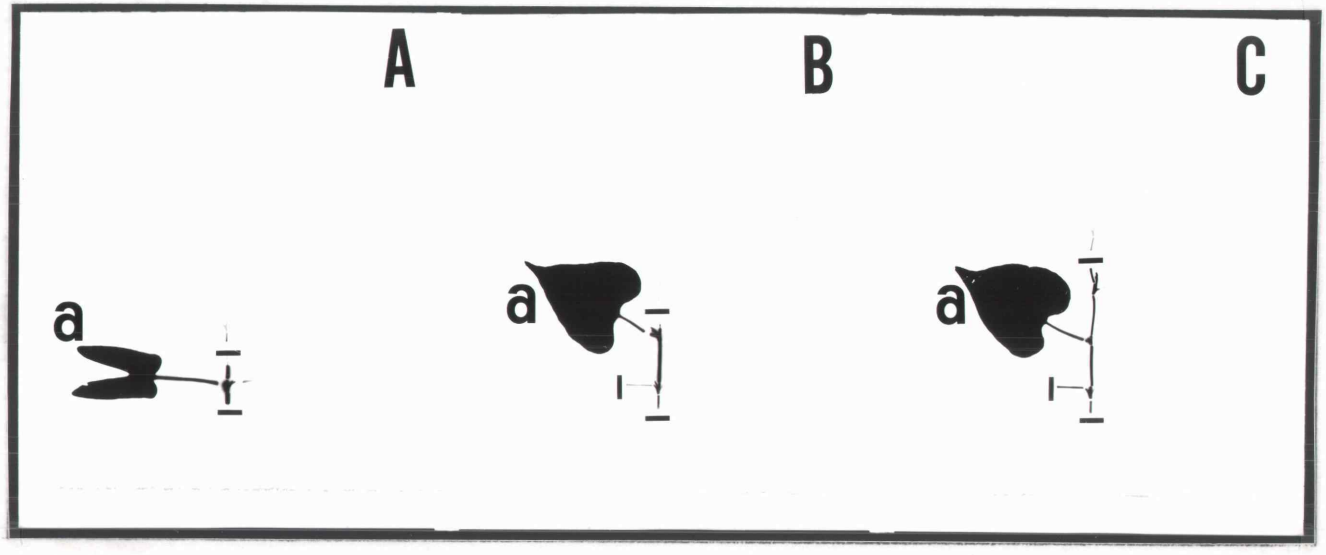

Figure 5. Various girdling combinations used frequently in this study. (a = assimilate source-leaf, — = girdle)

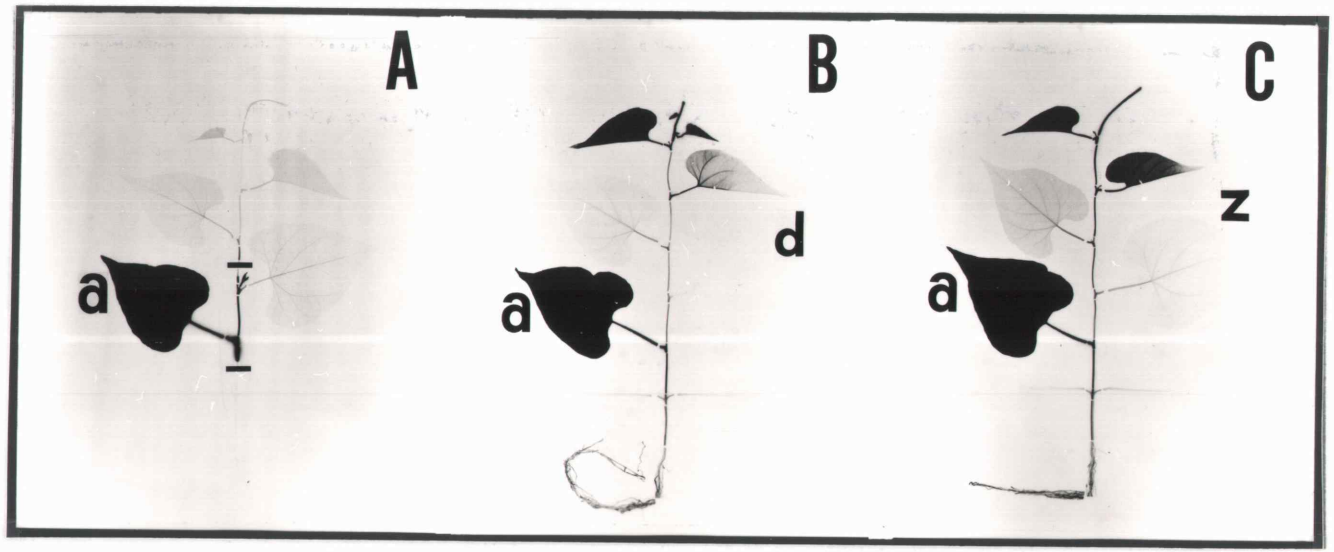

Figure 6. The effectiveness of girdling, leaf darkening, and localized benzyladenine applications in creating an artificial assimilate sink in L2; (A) girdling, (B) L2 darkened, and (C) benzyladenine application to L2. (a = assimilate source-leaf, — = girdle, d = darkened, z = benzyladenine)

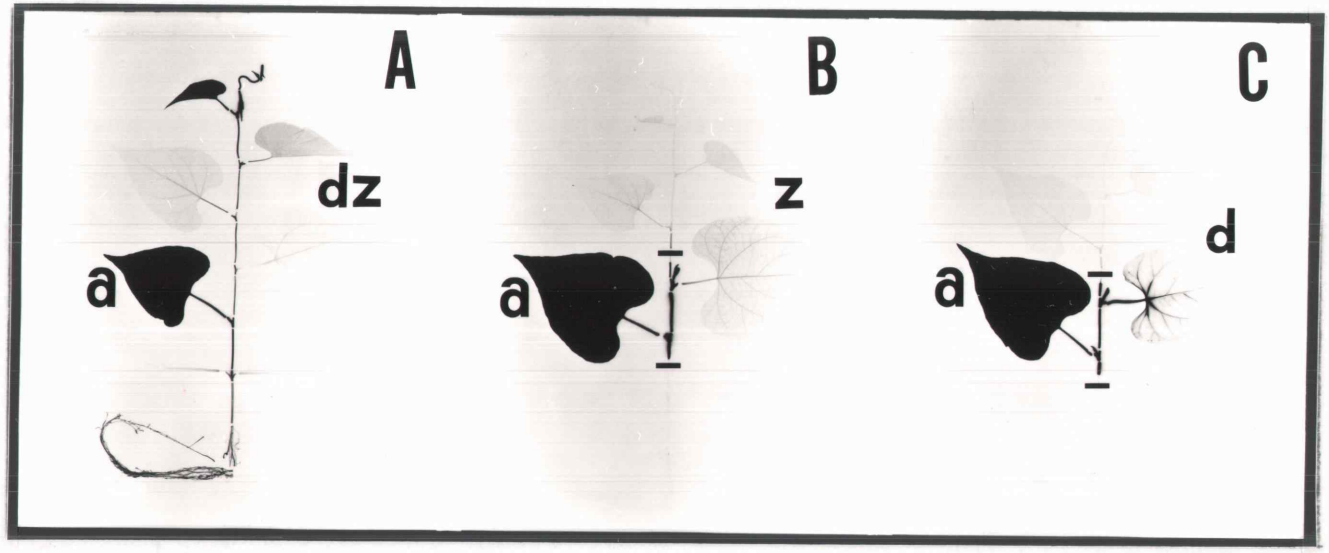

Figure 7. The effectiveness of 2-way combinations of girdling, leaf darkening, and benzyladenine applications in creating an artificial assimilate sink in L2; (A) darkening + benzyladenine, (B) girdling + benzyladenine, and (C) girdling + darkening. (a = assimilate source-leaf, — = girdle, d = darkened, z = benzyladenine)

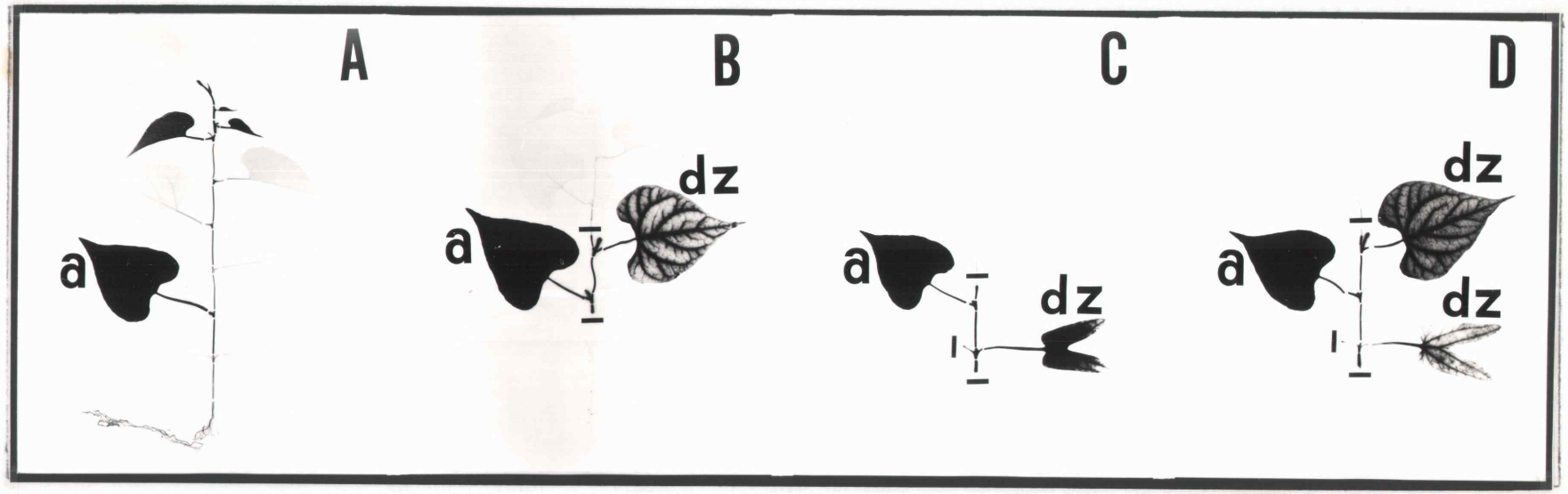

Figure 8. The effectiveness of a 3-way combination of girdling, leaf darkening, and benzyladenine as a method of creating artificial assimilate sinks; (A) normal translocation, (B) sink in L2, (C) sink in CR, and (D) sinks in L2 and CR. (a = assimilate source-leaf, — = girdle, d = darkened, z = benzyladenine)

girdle + shading combinations (7C) showed definite evidence of some sink activity.

Not until all three variables were combined was it possible to consistently create strong artificial sinks in mature leaves. Figure 8 allows the comparison of ^{14}C import into L2 under normal conditions (8A) and after the combined influence of girdling, leaf darkening, and benzyladenine (8B). Figure 8 also demonstrates the fact that ^{14}C could be moved to an artificial sink above and/or below the source leaf.

Label could be transported up or down between leaves separated by several internodes. Figure 9 demonstrates basipetal translocation to a cotyledonary sink from L1, L2, or L3. The ability of an artificial sink to import ^{14}C was, however, influenced by the number of source leaves contributing to its assimilate demand, especially by leaves located between the ^{14}C-source and sink. In Figure 10, translocation of ^{14}C from L2 to CR is improved by eliminating the assimilate contribution of L1. In Figure 11A it is apparent that the sink demands of CR are completely satisfied by L1 and L2. When they are eliminated as potential assimilate sources by girdling (11B), much of the demand in CR is met by L3.

Girdling, creation of artificial sinks, and changing the site of $^{14}CO_2$ application, all proved to be effective means of characterizing assimilate translocation in tall morningglory. We anticipate that

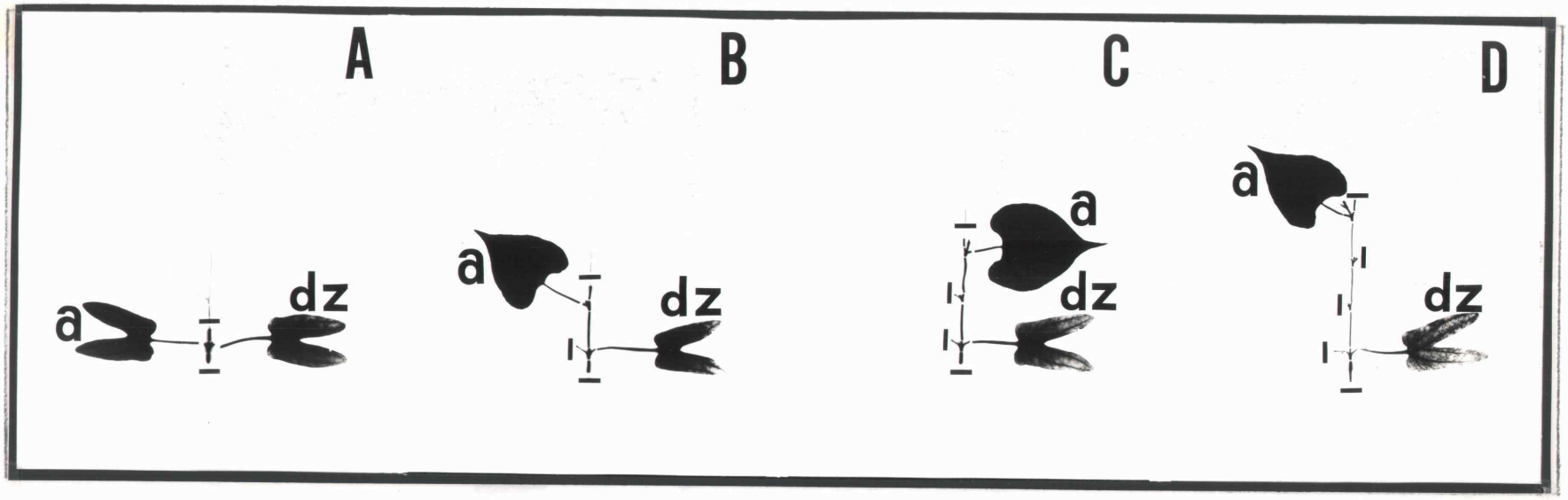

Figure 9. The effect of distance between ^{14}C-assimilate source and artificial sink; (A) same node, (B) 1 internode, (C) 2 internodes, and (D) 3 internodes. (a = assimilate source-leaf, — = girdle, d = darkened, z = benzyladenine)

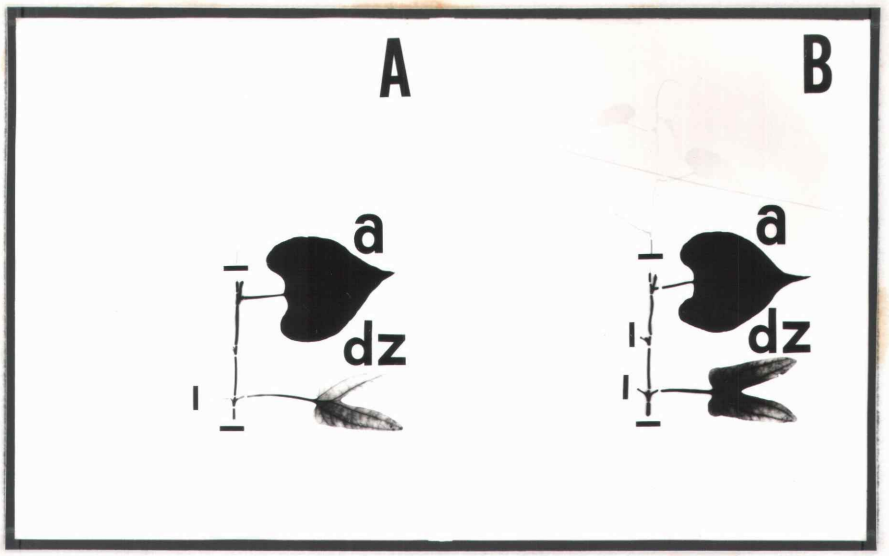

Figure 10. The effect of one source-leaf between the ^{14}C source and sink; (A) L1 normal and (B) L1 girdled. (a = assimilate source-leaf, — = girdle, d = darkened, z = benzyladenine)

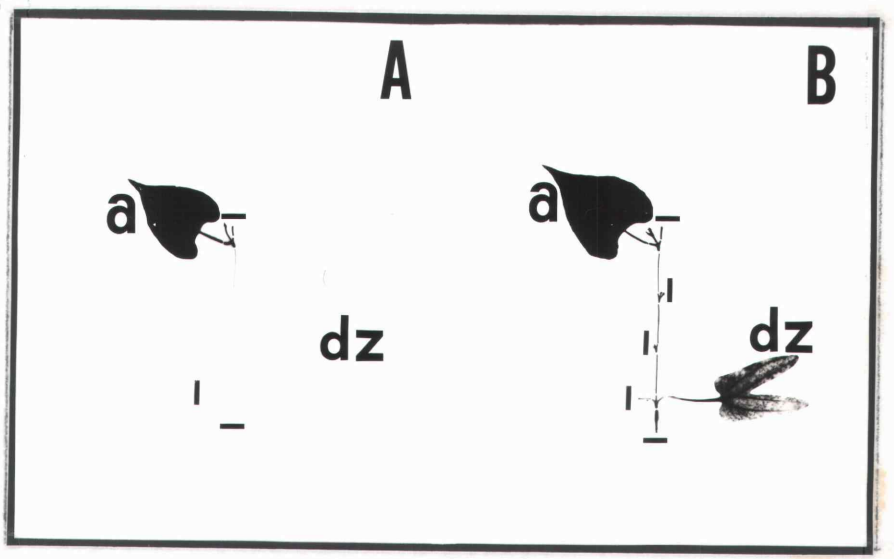

Figure 11. The effect of two source-leaves between the ^{14}C source and sink; (A) L1 and L2 normal and (B) L1 and L2 girdled. (a = assimilate source-leaf, — = girdle, d = darkened, z = benzyladenine)

the information obtained will aid in interpreting results from herbicide translocation studies in this species.

CHAPTER 2

The Effect of Girdling and Artificial Assimilate Sinks on the Translocation of a Xylem-Mobile Herbicide in Tall Morningglory [Ipomoea purpurea (L.) Roth]

INTRODUCTION

Translocation properties of assimilates have been studied using numerous experimental techniques which alter normal flow in some way (32,41,45,46). One of the most commonly used techniques involves the disruption of phloem tissue along a limited length of stem or petiole (15,37,60). This girdling process is an effective means of preventing the passage of phloem-carried solutes, while allowing the transpirational flow of water to continue (42,44).

It was the objective of this research to determine whether transport of a xylem-borne solute would continue normally in young morningglory plants after stems or petioles had been heat-girdled. The influence of artificial assimilate sinks on xylem transport also was tested.

MATERIALS AND METHODS

Simazine [2-chloro-4,6-bis(ethylamino)-s-triazine], a xylem-translocated herbicide (14,15), was applied as the ^{14}C-labeled isotope to 16-day-old morningglory plants. The plants had been

grown from seed in growth chambers maintained at 26 C constant temperature, 14-h photoperiod, photosynthetic photon flux density (PPFD) of 215 uE $s^{-1}m^{-2}$, and 60-65% RH. Twenty-four hours prior to simazine treatment, selected plants were girdled and a mature cotyledonary leaf on each plant received a treatment known to induce assimilate import (an artificial sink). The treatment consisted of painting both surfaces of the leaf with a 1 x 10^{-3} M solution of N^6-benzyladenine (1% Tween 20 added, v/v), allowing it to dry, and then enclosing the leaf in an aluminum foil envelope. Girdling was accomplished by passing a heated copper wire loop along a 2-cm section of stem or petiole, until internal tissue damage was evident (30-60 s).

^{14}C-simazine had been formulated in methanol (1 uCi/ml) for storage. Prior to treatment 0.2-ml units were placed in 10-ml test tubes, and the methanol was evaporated. Seven ml of water were then added to each test tube. The roots of plants were washed free of the pearlite-peat mixture in which they had been growing, and were placed in the test tubes. Parafilm was placed over the mouth of the tube to reduce evaporation, and the entire test tube was wrapped in aluminum foil. Plants were supported on bamboo stakes. When simazine was leaf applied, 0.2 ml of the methanol formulation was evaporated down and the simazine was taken back up in 0.15 ml of ethanol. That volume was applied to the adaxial surface of a

leaf as multiple small droplets and allowed to dry. The leaf was enclosed in a polyethylene bag after the ethanol had evaporated.

Twenty-four hours after treatment, plants were harvested and dissected into 24 parts (two cotyledonary leaves, six true leaves, seven nodes, seven internodes, root, and shoot tip). A clean blade was used for each cut to minimize contamination between plant parts. Plants were then pressed and dried with forced air (45 C). Those to be autoradiographed were mounted and exposed to Kodak X-Omat R film for 21 days. All plants were arranged for mounting as depicted in Figure 12. Actual internode lengths were greater than depicted in the mounts. Plants to be oxidized and counted were weighed and then combusted on a Packard model 306 sample oxidizer. The label recovered from each sample was counted on a liquid scintillation counter, and corrected for quench and background. Treatments were replicated three times. The study was repeated using ^{32}P rather than ^{14}C-simazine, with similar results (data not included).

RESULTS AND DISCUSSION

Root-applied simazine was translocated as expected, from roots to transpiring tissues (Table 1). In all plants studied, movement of simazine into the shoot-tip region was negligible (Figure 13), probably due to low transpirational demand in that region.

Autoradiographs indicated that girdling had little effect on

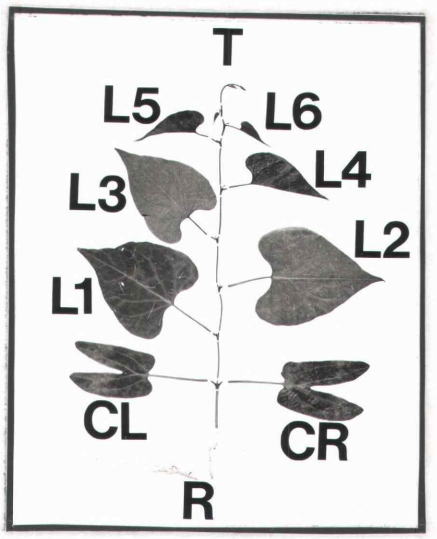

Figure 12. Mounting arrangement of all plants used in autoradiographs; root (R), left cotyledon (CL), right cotyledon (CR), first leaf (L1), second leaf (L2), third leaf (L3), fourth leaf (L4), fifth leaf (L5), sixth leaf (L6), and shoot tip (T).

Table 1. Distribution of ^{14}C in above-ground plant parts following root application of ^{14}C-simazine.

Plant part	dpm	dpm/mg	% of total translocated
Tip	271	16	.2
L6	1945	57	1.1
L5	11161	423	6.1
L4	15864	466	8.7
L3	19586	398	10.7
L2	27103	417	14.8
L1	15645	276	8.4
CR	12255	268	6.7
CL	10375	233	5.6
Stem	69552	381	37.9
Root	--	--	--

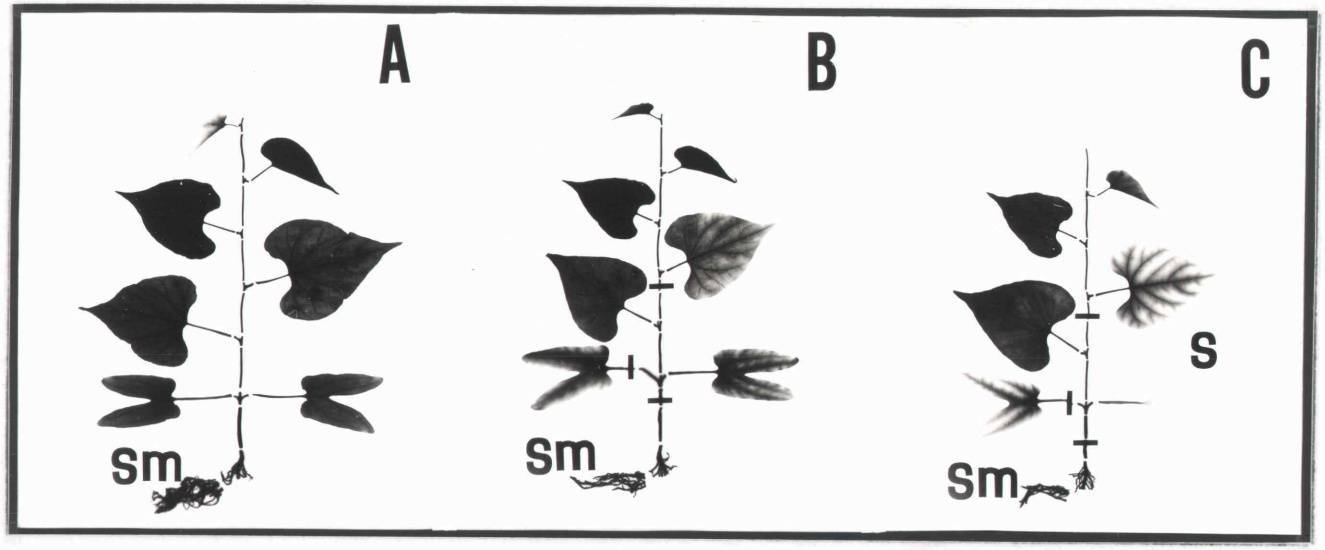

Figure 13. Translocation patterns from root-applied ^{14}C-simazine; (A) normal, (B) girdled, and (C) girdles + artificial sink. (sm = simazine application site, — = girdle, s = artificial sink)

simazine uptake and distribution (Figure 13B,C). The artificial sink treatment seemed to greatly reduce simazine movement into CR (Figure 13C). This effect was presumed to have been the result of the foil envelope minimizing transpiration in that cotyledonary leaf.

The effects of girdling and artificial sinks on foliar-applied simazine were studied autoradiographically (Figure 14). Simazine failed to export from the treated leaf in either the normal or girdle + sink treatment.

Plants similar to those in Figure 13A and C were combusted and the ^{14}C-label was counted. The data appear in Table 2. Total uptake of ^{14}C-simazine was essentially the same in girdled and non-girdled plants (2.9% difference) even though the latter group of plants had been stem-girdled at ground level and above L2. However, girdling and artificial sinks did cause differences in the distribution of label within plants. The stem girdle above L2 significantly reduced apoplastic transport upward, while leaves below that girdle showed a corresponding increase in simazine uptake. ^{14}C movement into the foil-covered cotyledon (CR) was significantly reduced. CL showed no effects from having received a petiole girdle.

The results of this study demonstrate that girdling and the artificial sink treatment can influence the movement of xylem-mobile solutes. However, translocation patterns resulting from such

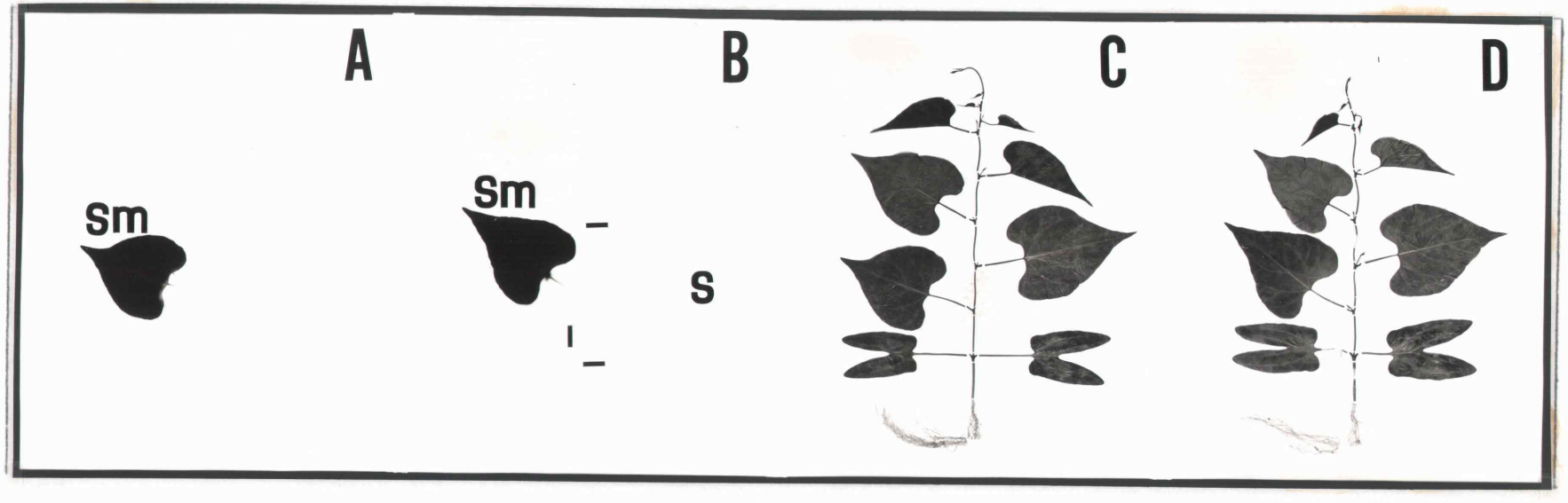

Figure 14. Translocation patterns from leaf-applied ^{14}C-simazine; (A) normal, (B) girdles + artificial sink, and (C, D) corresponding plant mounts. (sm = simazine application site, — = girdle, s = artificial sink)

Table 2. The effect of girdling and artificial sinks on the translocation of root-applied ^{14}C-simazine.

	dpm		Change from normal pattern
	Normal	Girdles[a] + sink[b]	
Tip	271	155	
L6	1945	1795	
L5	11161	6381	-19.6%*
L4	15864	16486	
L3	19568	14417	
L2	27103	26170	+11.3%
L1	15645	21413	
CR	12255	4468	-63.5%**
CL	10375	11397	+9.9%
Stem	69552	75691	+8.8%
Root	--	--	
Total	183739	178373	-2.9%

a/Girdles placed on stem above the root, below L3, and on petiole of CL

b/Artificial sink created in CR

* Means differ significantly (P.05)

**Means differ significantly (P.01)

manipulations are characteristically different from those of phloem-borne solutes.

CHAPTER 3

Glyphosate Translocation in Tall Morningglory [Ipomoea purpurea (L.) Roth] as Influenced by Stem Girdling, Leaf Darkening, and Localized Cytokinin Application

INTRODUCTION

Glyphosate translocation has been studied extensively in numerous plant species, and under a variety of environmental influences. The herbicide is generally assumed to move via the phloem, from assimilate sources to sinks. Less clear, however, is the amount of apoplastic translocation which may also occur.

Glyphosate can be transported in the xylem, as evidenced by studies where it is taken up through cut stems and distributed in large quantities throughout all transpiring tissues (47,53). In spite of that fact, reports commonly indicate little or no apoplastic translocation occurring in intact plants (1,31,48,49,50,56,68). When appreciable movement is observed in the transpiration stream of intact plants, it generally occurs only within the treated leaf (23, 36,52,66). However, there are studies which indicate more widespread apoplastic distribution of significant glyphosate quantities (29,67,70).

The objective of this research was to characterize glyphosate translocation in tall morningglory, using some of the techniques

proven useful in assimilate transport studies. We anticipated that these methods would help to clarify both the symplastic and apoplastic translocation capabilities of the herbicide.

MATERIALS AND METHODS

Tall morningglory [Ipomoea purpurea (L.) Roth, 'Heavenly Blue'] was grown from seed to a height of approximately 1 m (16 days) in 10-cm plastic pots containing a 3:1 (v/v) mixture of pearlite and a peat-based commercial potting medium (Jiffy Mix Plus). Plants were maintained under growth chamber conditions of 60 to 65% RH, 26 C constant temperature, 14-h photoperiod, and a photosynthetic photon flux density of 215 uE $s^{-1}m^{-2}$. Prior to treatment, plants were selected for uniformity based on plant height, mature leaf sizes, internode lengths, and expansion stage of the newest leaves.

Forty-eight hours before harvest, plants were paired, and pairs were subjected to one of several treatments designed to produce a specific assimilate translocation pattern. Treatments consisted of various combinations of girdling, leaf darkening, and localized application of benzyladenine. N^6-benzyladenine was brush-applied as a 1×10^{-3} M solution with 0.1% Tween 20 (v/v) to a single leaf until both abaxial and adaxial surfaces were completely wetted. The leaf was allowed to dry, and then enclosed in an 18- by 28-cm aluminum foil envelope. Girdling was accomplished by slowly passing

an electrically heated 24-guage copper wire loop along a 2-cm length of stem or petiole (Appendix Figures 1 and 2) until a loss of cellular integrity was evident (30-60 s). The 4-mm diameter wire loop was not allowed to contact plant tissue directly during the girdling process. In all cases stem girdling above a ^{14}C-exporting leaf consisted of two girdles placed approximately 5 cm apart.

Twenty-four hours prior to harvest, one plant of each pair was exposed to $^{14}CO_2$ and the other was treated with ^{14}C-methyl-labeled glyphosate. Labeled CO_2 was generated in a collapsing polyethylene reservoir of known volume, by the addition of perchloric acid to ^{14}C-labeled barium carbonate. A single leaf on each plant was enclosed and sealed in a polyethylene bag. A known quantity of $^{14}CO_2$ (.75 uCi or 1.95 uCi) in 5 or 10 cc of air was extracted from the reservoir and then injected into the bag using a hypodermic syringe. Glyphosate (specific activity 2.01 mCi/mM, 97.5% purity) was prepared as an isopropylamine salt in aqueous solution by adding 2.0 mg of the acid to 0.6 ml water, 0.7 mg isopropylamine, and 2.4 mg Mon 0818 surfactant. Leaves were wiped with a moistened cotton swab and allowed to dry prior to glyphosate application. The herbicide (4 or 5 ul, 0.04 uCi/ul) was applied to a single leaf on each plant, using a 10-ul syringe. Application was made as multiple small droplets scattered over the entire adaxial leaf surface. Droplets were allowed to dry, after which the treated leaf was enclosed

and minimal $^{14}CO_2$ contamination in the growth chamber. Recovery

in a polyethylene bag like those used for $^{14}CO_2$ exposure. When glyphosate was applied to a stem, that section of stem (5 cm) was covered with either polyethylene or parafilm. Localized bagging was shown in preliminary studies to significantly increase glyphosate absorption (37.1 vs 84.5% of applied) while having a minimal effect on overall translocation patterns (Appendix Figure 3, Appendix Tables 1 and 2).

At harvest, bags were evacuated and all plants were immediately dissected into 21 parts (two cotyledonary leaves, five true leaves, six nodes, six internodes, root, and shoot tip). A clean blade was used for each cut. Plants to be autoradiographed were pressed, dried with forced air (45 C), mounted, and exposed to Kodak X-Omat R film for 24 days. Plant parts in all mounts were arranged as shown and labeled in Figure 15. Actual internode lengths were greater than depicted in the mounts (Appendix Table 3). Plants to be used in quantitative determination of label distribution were pressed and dried with forced air following dissection. Glyphosate-treated leaves were washed for 5 min by gentle agitation in 5 ml of water prior to pressing. Following drying, plant parts were weighed and then oxidized in a Packard model 306 sample oxidizer. The samples were counted for 10 min on a Beckman Model LS7500 liquid scintillation counter. Counts were corrected for quench, background, and minimal $^{14}CO_2$ contamination in the growth chamber. Recovery

of applied ^{14}C-glyphosate was 93.3%.

Autoradiographic studies were repeated twice with treatments occurring only once in each study. Quantitative studies were conducted twice with treatments being replicated a total of three times.

Data are presented as percent of the total translocated ^{14}C. Translocated ^{14}C was considered to be the total amount of label recovered from a plant, minus that remaining in the treated leaf.

RESULTS AND DISCUSSION

Normal Translocation. Autoradiographic comparisons of ^{14}C-glyphosate and ^{14}C-assimilate movement in normally-translocating plants failed to indicate distribution pattern differences. As indicated in Figure 16, glyphosate and assimilate label moved from source (L1) to sink (roots, new leaves, and shoot tip), essentially bypassing other mature leaves. If pursued no further, this autoradiographic evidence would suggest that glyphosate moves exclusively via the phloem in the same pattern as assimilates.

When a more quantitative evaluation of the same translocation patterns was made using liquid scintillation techniques, some evidence of possible distribution differences appeared (Table 3). The basic pattern for both materials was still from source to sink, bypassing mature leaves. However, roots and stem appeared to be the stronger sinks for assimilate. The shoot tip imported a greater

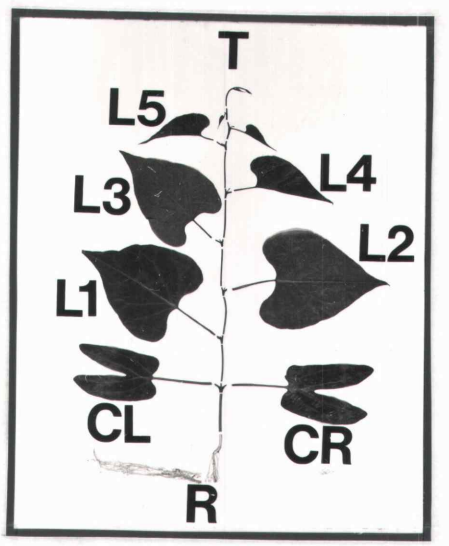

Figure 15. Mounting arrangement of all plants used in autoradiographs; root (R), left cotyledon (CL), right cotyledon (CR), first leaf (L1), second leaf (L2), third leaf (L3), fourth leaf (L4), fifth leaf (L5), and shoot tip (T).

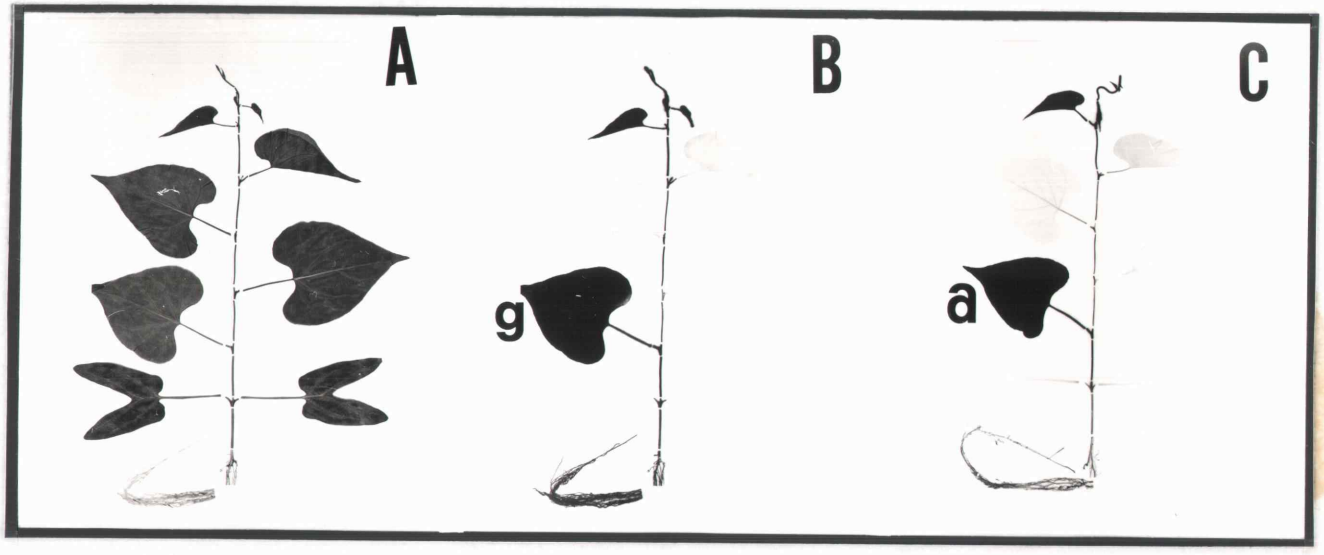

Figure 16. A comparison between normal ^{14}C-glyphosate and ^{14}C-assimilate translocation patterns; (A) representative plant mount, (B) L1 treated with ^{14}C-glyphosate, and (C) L1 exposed to $^{14}CO_2$. (g = glyphosate source-leaf, a = assimilate source-leaf)

Table 3. ^{14}C distribution in plants exposed to $^{14}CO_2$ or ^{14}C-glyphosate.

Plant part	Translocated ^{14}C (% or total)		Dry weight (% of total)	
	Glyphosate	Assimilate	Glyphosate	Assimilate
Tip	47.2 ± 4.32[a]	25.6 ± 1.40	3.9	4.9
L5	10.4 ± 3.10	13.1 ± 3.97	2.9	4.3
L4	2.4 ± 2.30	3.3 ± 1.95	7.7	8.0
L3	.5 ± .10	1.0 ± .32	11.5	11.1
L2	1.0 ± .12	.7 ± .06	14.1	13.5
L1*	--	--	8.9	9.9
CR	.1 ± .06	.1 ± .06	7.2	6.9
CL	.2 ± .15	.1 ± .06	7.5	7.5
Root	1.7 ± .56	6.3 ± 3.57	8.0	7.6
Stem	36.7 ± 4.67	50.2 ± 2.57	28.3	26.4

* Leaf receiving original ^{14}C application

a/ Standard deviation (three replications per mean)

portion of the translocated glyphosate.

Girdling. Basipetal translocation of ^{14}C-glyphosate appeared completely arrested when a stem girdle was positioned below a treated leaf (Figure 17A,B,C). Girdling the petiole of a treated leaf prevented all export of the herbicide (Figure 17C). Stem girdles placed above a treated leaf greatly reduced acropetal movement, but did not eliminate it. Though both ^{14}C-assimilates and ^{14}C-glyphosate were shown to move up through a girdle, the leakage was noticeably greater in the case of glyphosate. This relationship was also demonstrated when the distribution of label in girdled plants was determined numerically (Table 4). In this representative girdling pattern, an average of 1.0 percent of the translocated ^{14}C-assimilate was found to have passed through the upper girdle, compared with 3.7 percent of the translocated glyphosate.

It often appeared that girdling resulted in slightly more apoplastic movement of ^{14}C-glyphosate into all mature leaves above the lowest girdle. Leakage into the apoplast may have been increased by confining higher than normal ^{14}C-glyphosate concentrations between two girdles.

Artificial Sinks. ^{14}C-assimilates were strongly imported by artificial sinks (Figure 18D,E,F). Labeled glyphosate responded in much the same manner (Figure 18A,B,C). As was the case with

Figure 17. The effect of girdling on translocation patterns of ^{14}C-glyphosate (A,B,C,D) and ^{14}C-assimilate (E,F,G,H). (g - glyphosate source-leaf, a = assimilate source-leaf, — = girdle)

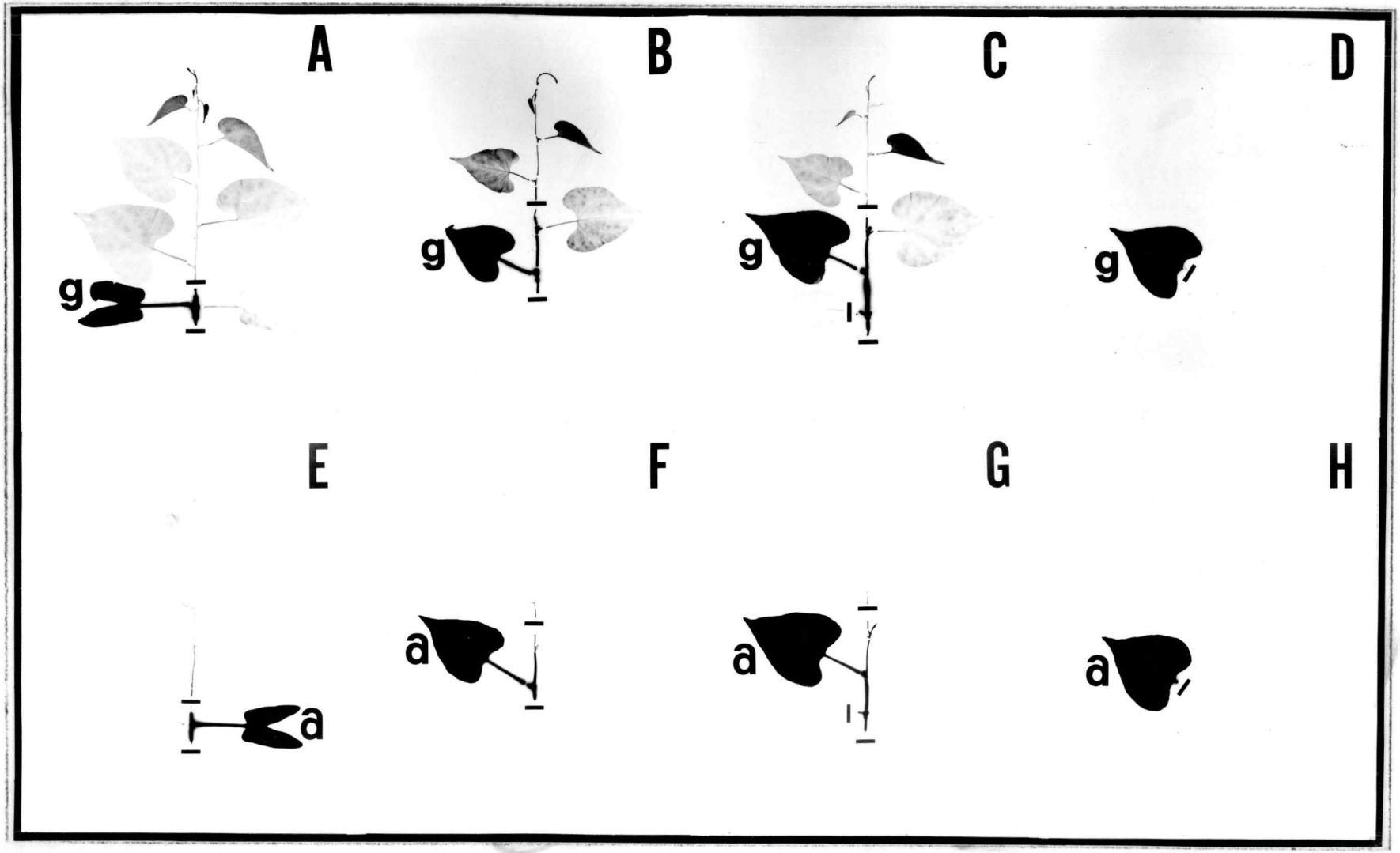

Figure 17.

Table 4. The effect of girdling[a] on ^{14}C-glyphosate and ^{14}C-assimilate translocation patterns.

Plant part	Translocated ^{14}C (% of total)		Dry weight (% of total)	
	Glyphosate	Assimilate	Glyphosate	Assimilate
Tip	.5 ± .06[b]	.2 ± .10	2.2	1.9
L5	.7 ± .25	.2 ± .12	1.9	1.4
L4	1.1 ± .49	.3 ± .15	5.1	4.4
L3	1.4 ± .17	.3 ± .10	8.4	7.8
L2	1.9 ± .17	.8 ± .71	17.6	16.8
L1*	--	--	10.7	10.4
CR	.5 ± .06	.3 ± .06	8.9	9.8
CL	.6 ± .20	.2 ± .15	9.0	9.1
Root	.6 ± .21	.7 ± .12	6.3	6.3
Stem	92.6 ± .35	97.0 ± .74	30.1	32.0

* Leaf receiving original ^{14}C application

a/ Girdles located on stem above the root, below L3, and on petiole of CL

b/ Standard deviation (three replications per mean)

Figure 18. The effect of girdling and artificial sinks on ^{14}C-glyphosate (A,B,C) and ^{14}C-assimilate (D,E,F) translocation patterns. (g = glyphosate source-leaf, a = assimilate source-leaf, — = girdle, s = artificial sink)

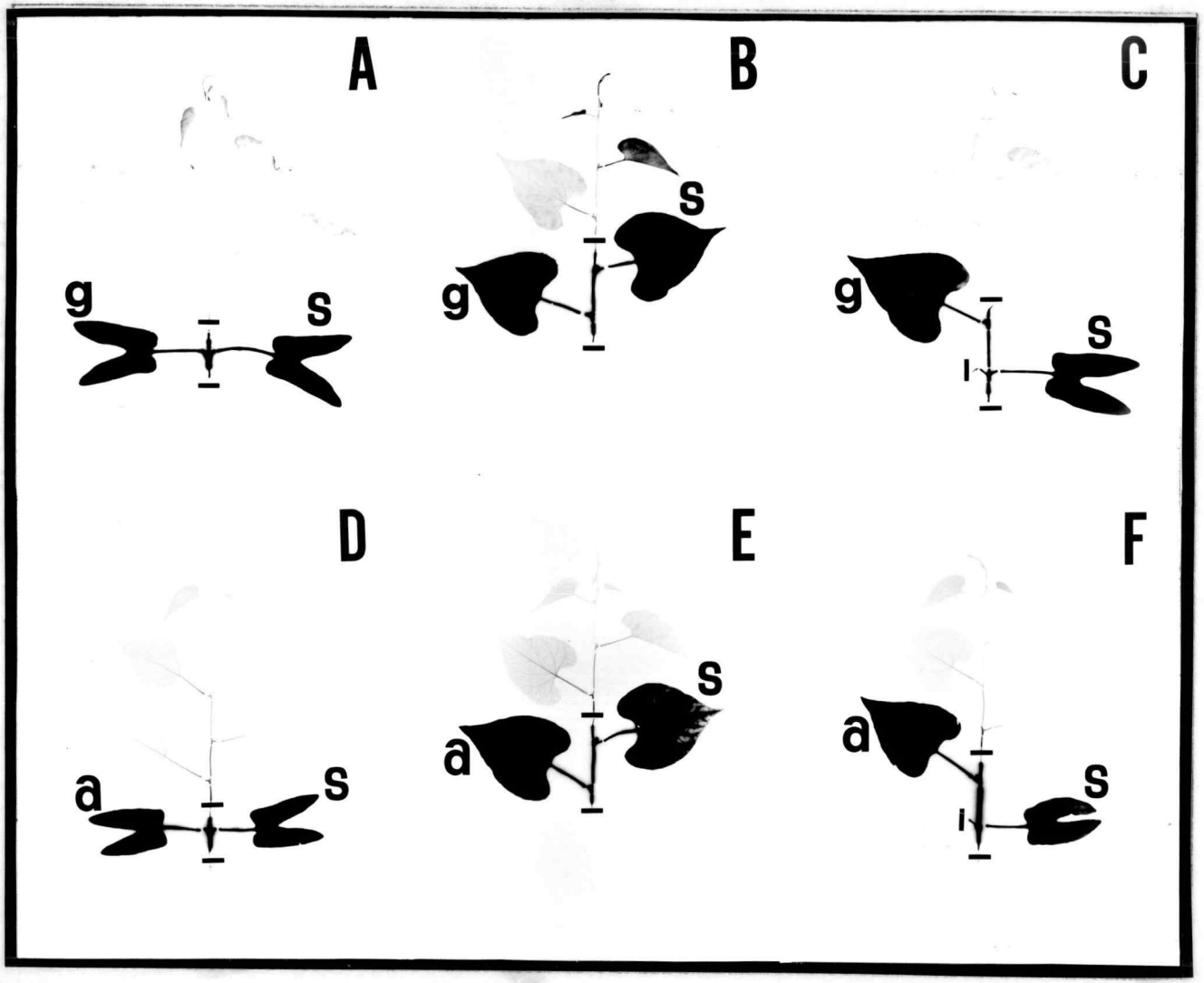

Figure 18.

^{14}C-assimilate, herbicide could be moved from any mature leaf to another by using the appropriate combination of girdles and sinks. The pattern differences which became evident were associated primarily with apoplastic movement, rather than the specific response to an artificial sink. As was noticed in the girdling treatments, glyphosate appeared more capable of leaking through an upper girdle. Glyphosate also appeared to enter mature leaves below an upper girdle in greater amounts than did ^{14}C-assimilates. Evidence of greater apoplastic mobility was most noticeable when glyphosate was being transported acropetally from a source to an artificial sink (Figure 19). Why acropetal and basipetal movement along an equivalent section of stem should produce different amounts of apoplastic leakage, is unclear. However, the same phenomenon was observed repeatedly throughout the study. It was also noted for assimilates, but to a lesser degree.

Artificial sinks above a ^{14}C source leaf were usually less effective at importing label than were sinks located below a source, especially when a second source-leaf was allowed to contribute to the assimilate demand of the sink. This, again, was most noticeable in the case of glyphosate (Figure 19). Greater leakage into the transpiration stream when ^{14}C is moving acropetally, and hence, less ^{14}C available for symplastic import by the upper artificial sink may be a part of the explanation. But, it is still not clear why less

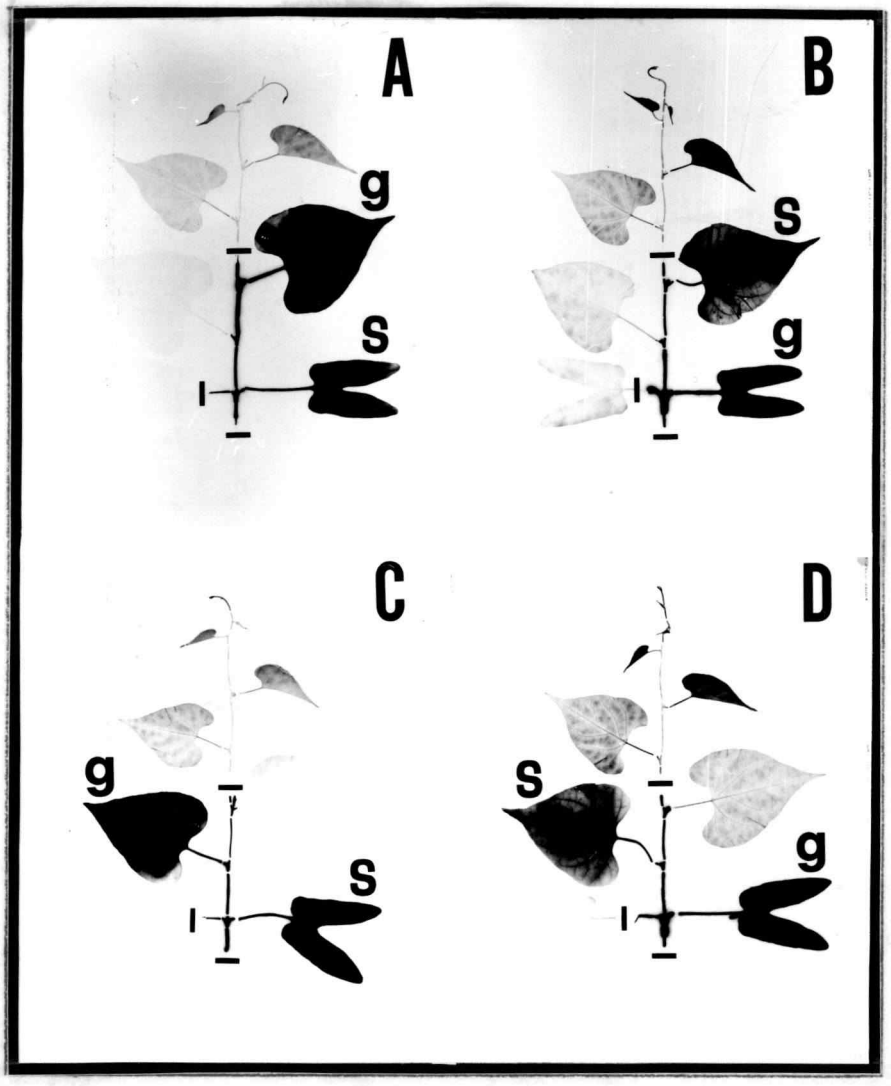

Figure 19. The effect of sink position on apoplastic translocation patterns of ^{14}C-glyphosate; (A,C) sink below source, and (B,D) sink above source. (g = glyphosate source-leaf, — = girdle, s = artificial sink)

leakage should occur from symplast to apoplast when label is moving basipetally along the same section of stem.

The two translocation patterns shown in Figure 19C and D are represented quantitatively in Tables 5 and 6. Both demonstrate glyphosate leakage past the upper girdle in greater proportions that occurred for assimilates. As noted in the autoradiographs, the greater amount of glyphosate leakage occurred when the artificial sink was above the source (3.4 vs 2.1%) (Table 6). Data in Tables 5 and 6 also confirm that sink strength with respect to glyphosate was significantly reduced when the sink was located above the source.

Site of Application. Changing the site of ^{14}C-glyphosate application from the leaf to the stem, in conjunction with the use of girdles and artificial sinks, provided additional information about glyphosate translocation capabilities. Figure 20 contrasts "normal" glyphosate translocation patterns resulting from leaf and stem applications. An autoradiograph of a root-applied, xylem-mobile herbicide (^{14}C-simazine) is provided as a reference. Applied to the stem, glyphosate moved readily into all tissues above the treated area. There was still strong basipetal movement into the roots, with the fully-expanded cotyledons being bypassed. Figure 21 demonstrates the effect of girdling on stem-applied glyphosate. Girdles did not visibly reduce acropetal movement of the labeled herbicide in the

Table 5. The effect of girdling[a] and artificial sinks[b] on ^{14}C-glyphosate and ^{14}C-assimilate translocation patterns: CR sink.

Plant part	Translocated ^{14}C (% of total)		Dry weight (% of total)	
	Glyphosate	Assimilate	Glyphosate	Assimilate
Tip	.3 ± .06[c]	.1 ± .06	2.2	2.0
L5	.4 ± .23	.1 ± .00	2.2	1.6
L4	.8 ± .20	.2 ± .00	4.9	5.2
L3	.6 ± .10	.3 ± .15	7.5	7.2
L2	.9 ± .15	.6 ± .40	15.6	17.1
L1*	--	--	10.7	10.4
CR	54.0 ± 7.22	32.8 ± 11.70	9.6	9.3
CL	.7 ± .26	.2 ± .06	9.6	9.4
Root	.2 ± .06	.4 ± .06	7.1	7.4
Stem	42.0 ± 6.97	65.4 ± 12.01	30.3	30.2

* Leaf receiving original ^{14}C application

a/ Girdles located on stem above the root, below L3, and on petiole of CL

b/ Artificial sink created in CR

c/ Standard deviation (three replications per mean)

Table 6. The effect of girdling[a] and artificial sinks[b] on ^{14}C-glyphosate and ^{14}C-assimilate translocation patterns: L1 sink.

Plant part	Translocated ^{14}C (% of total)		Dry weight (% of total)	
	Glyphosate	Assimilate	Glyphosate	Assimilate
Tip	.8 ± .46[c]	.1 ± .00	2.5	3.0
L5	.7 ± .29	.1 ± .06	2.1	2.6
L4	.9 ± .26	.2 ± .00	5.3	5.5
L3	1.0 ± .55	.4 ± .06	8.2	8.2
L2	1.3 ± .17	.9 ± .58	16.0	15.0
L1	12.0 ± 5.60	28.3 ± 6.59	12.9	13.5
CR*	--	--	6.7	7.2
CL	.9 ± .35	.2 ± .10	9.7	9.7
Root	.3 ± .15	.6 ± .21	6.0	5.5
Stem	82.2 ± 6.41	69.2 ± 7.30	30.6	29.7

* Leaf receiving original ^{14}C application

a/ Girdles located on stem above the root, below L3, and on petiole of CL

b/ Artificial sink created in L1

c/ Standard deviation (three replications per mean)

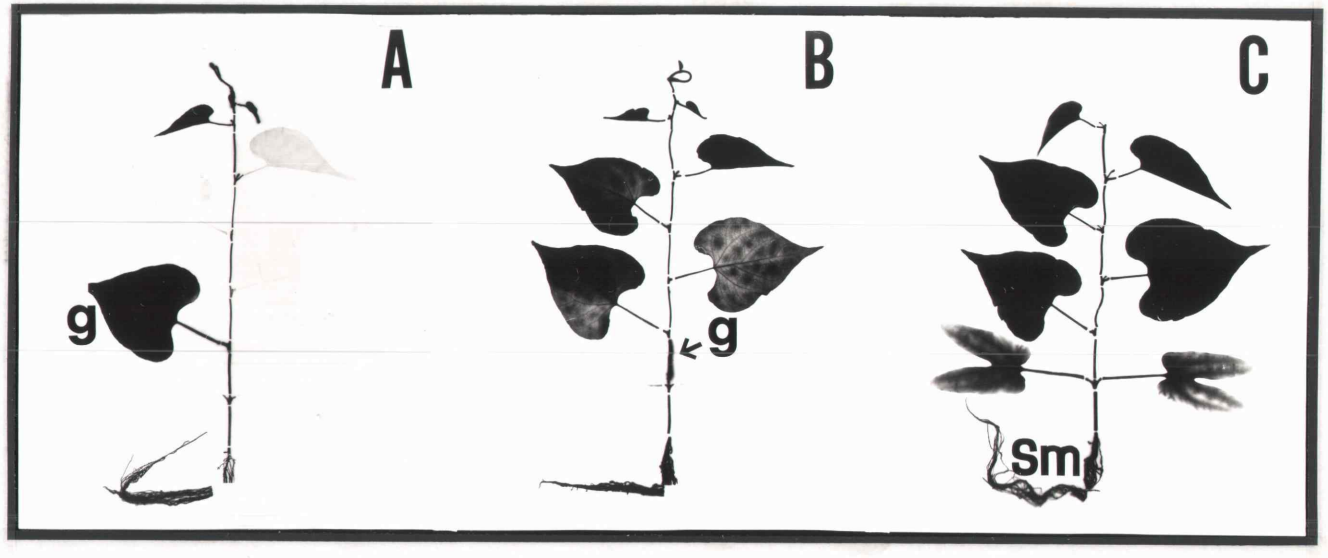

Figure 20. A comparison between translocation patterns of stem-applied and leaf-applied ^{14}C-glyphosate; (A) glyphosate applied to L1, (B) glyphosate stem-applied below L1, and (C) ^{14}C-simazine applied to roots. (g = glyphosate source, sm = simazine source)

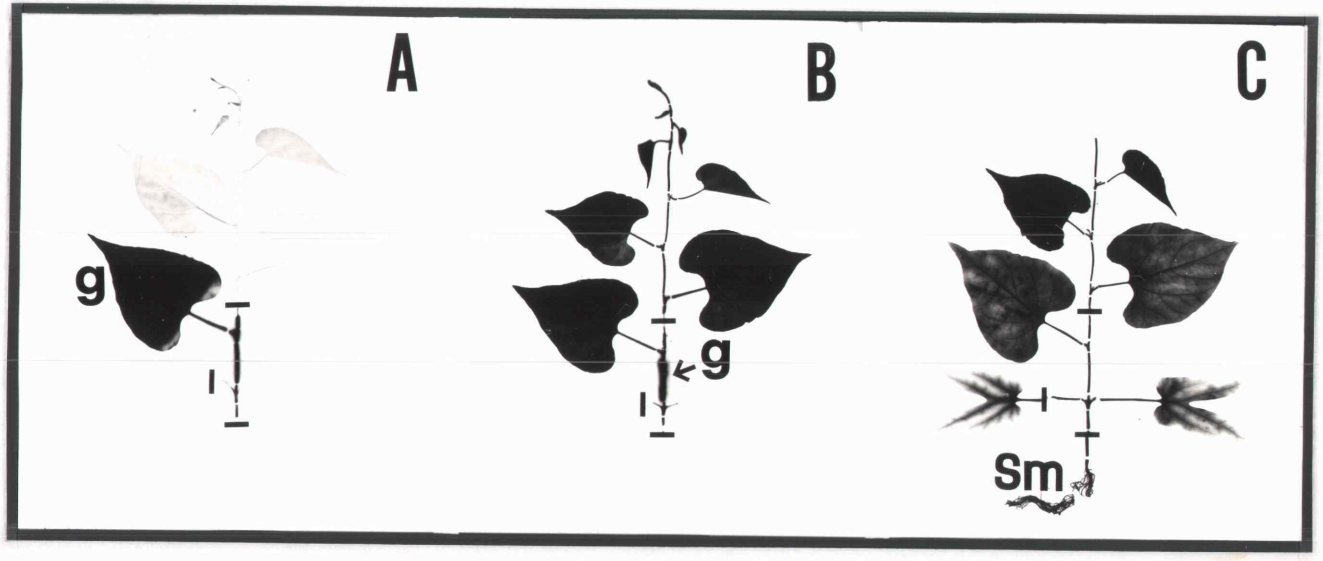

Figure 21. Translocation patterns of stem-applied ^{14}C-glyphosate as influenced by girdling; (A) glyphosate applied to L1, (B) glyphosate stem-applied below L1, and (C) ^{14}C-simazine applied to roots. (g = glyphosate source, sm = simazine source, — = girdle)

autoradiographs, but were effective in preventing basipetal transport. The fact that stem-applied glyphosate strongly labeled the shoot tip and new leaves (where transpiration is expected to be minimal) demonstrates its capacity to partition from xylem to phloem, once past the girdle. Stem-applied glyphosate also responded readily to artificial sinks (Figure 22). A comparison similar to that in Figure 22 is made quantitatively in Table 7. The site of application in Table 7 is above rather than below L1. Some 13.3-times more glyphosate (actual dpm's) moved past the upper girdle in the stem-applied treatment, even though the total amount of ^{14}C translocated in each case was nearly equal (10% difference).

The results of this study suggest that glyphosate translocation patterns in tall morningglory result from the sum of at least four basic characteristics. First, glyphosate moves readily via the symplast from source to sink following the same routes established for assimilate transport. A change in assimilate distribution results in a corresponding change in glyphosate translocation. Second, the herbicide moves in large quantities through the transpiration stream from the site of application to all transpiring areas "downstream" from that point. This was most obvious when glyphosate was stem applied, but has been reported to occur within glyphosate-treated leaves (23,36,67). Third, glyphosate transfers from the apoplast into the phloem with apparent ease, as evidenced by its

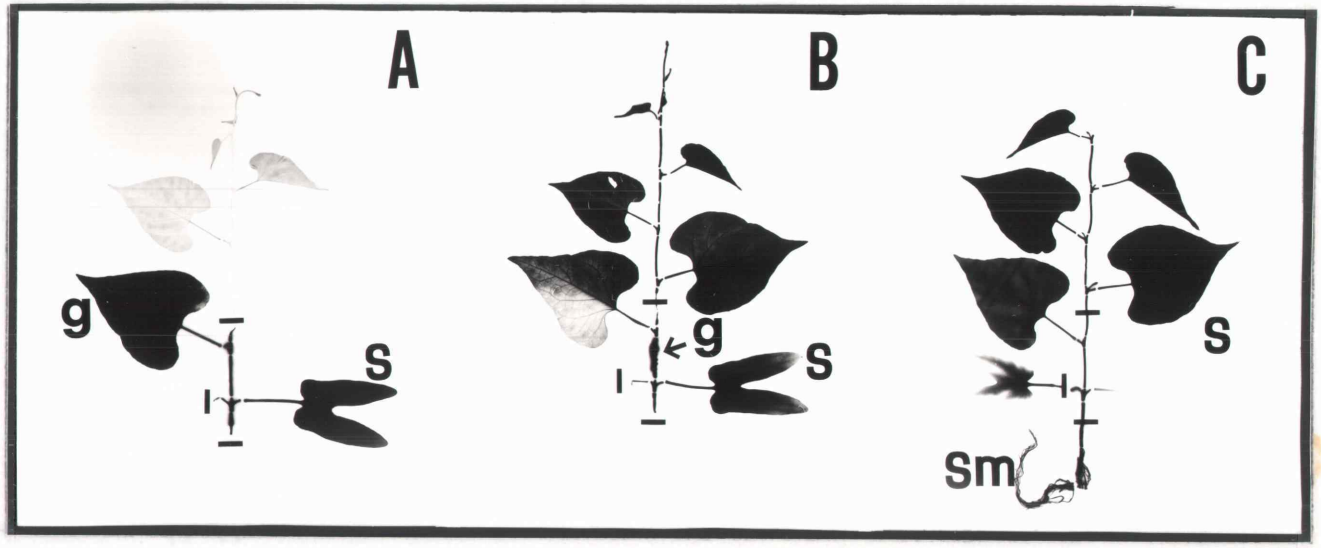

Figure 22. Translocation patterns of stem-applied ^{14}C-glyphosate as influenced by artificial sinks; (A) glyphosate applied to L1, (B) glyphosate stem-applied below L1, and (C) ^{14}C-simazine applied to roots. (g = glyphosate source, sm = simazine source, — = girdle, s = artificial sink)

Table 7. A comparison between translocation patterns of stem-applied[a] and leaf-applied[b] ^{14}C-glyphosate, when plants were subjected to girdling[c] and artificial sinks[d].

Plant part	Translocated ^{14}C-glyphosate (% of total)		Dry weight (% of total)	
	Stem applied	Leaf applied	Stem applied	Leaf applied
Tip	7.0 ± 1.87[e]	.3 ± .06	1.7	2.2
L5	5.2 ± 2.76	.4 ± .23	1.4	2.2
L4	9.2 ± 2.15	.8 ± .20	4.6	4.9
L3	5.0 ± .38	.6 ± .10	6.8	7.5
L2	32.1 ± .70	.9 ± .15	16.6	15.6
L1	.3 ± .20	--	14.4	10.7
CR	11.8 ± 1.31	54.0 ± 7.22	8.9	9.6
CL	.1 ± .06	.7 ± .26	10.6	9.6
Root	.2 ± .00	.2 ± .06	6.1	7.1
Stem	29.1 ± 1.92	42.0 ± 6.97	26.3	30.3

a/ ^{14}C-glyphosate applied to stem between L1 and L2

b/ ^{14}C-glyphosate applied to L1

c/ Girdles located on stem above the root, below L3, and on petiole of CL

d/ Artificial sink created in CR

e/ Standard deviation (three replications per mean)

presence in shoot tips of girdled plants. Fourth, though strongly retained once in the phloem, glyphosate has a tendency to leak back into the apoplast; more so than is normally noted for assimilates.

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APPENDIX

Preliminary Study: Labeling Assimilates with ^{14}C-urea

^{14}C-labeled urea is reported to hydrolize rapidly when applied to a leaf surface, and the liberated $^{14}CO_2$ is incorporated through photosynthesis into sucrose and other assimilates (14,15). Urea has been substituted for CO_2 as the ^{14}C-label source in several assimilate translocation studies because it is considerably more convenient to work with (14,15). Crafts and Yamaguchi (15) concluded that labeled products translocated from a ^{14}C-urea treated leaf were very similar, if not identical, to those from normal photosynthesis.

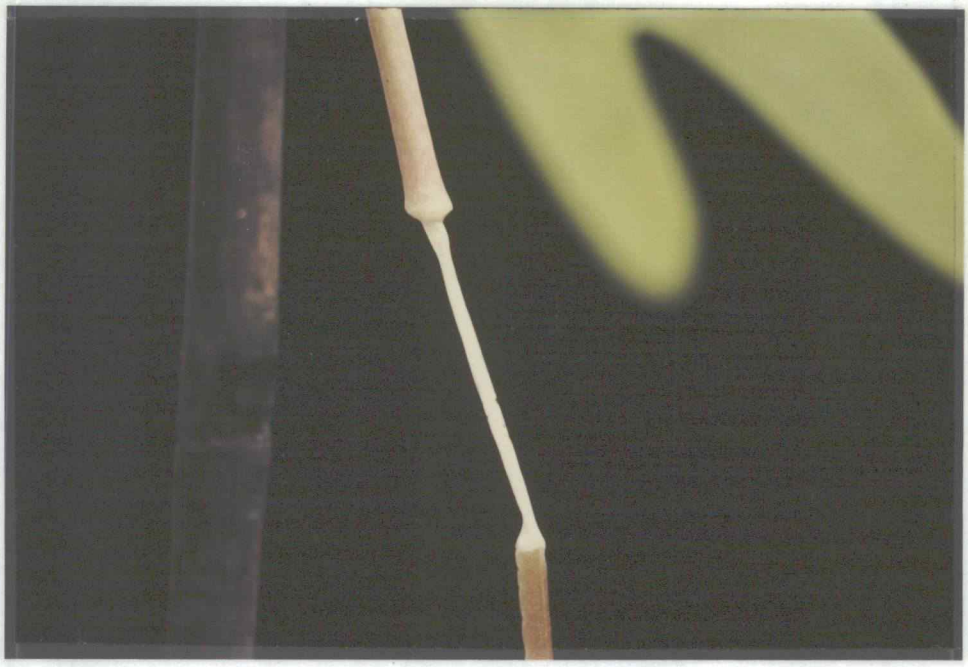
^{14}C urea was used to label assimilates during some of our preliminary autoradiographic translocation studies. Translocation patterns from urea-treated leaves closely resembled expected assimilate transport patterns, but there was slightly more apoplastic movement of label than had been anticipated. Label from stem-applied urea moved readily via the transpiration stream up through stem girdles. Direct comparisons with $^{14}CO_2$-treated plants also demonstrated translocation differences (usually minor); again, regarding primarily apoplastic movement. Based on these observations urea was judged unacceptable for use in our assimilate translocation studies. We felt that ^{14}C-urea gave a close approximation of assimilate translocation patterns, but it was not identical. The translocation of small amounts of intact ^{14}C-urea may account for

some of the overall pattern dissimilarities, even though Crafts and Yamaguchi were not able to detect urea in plant parts other than a treated leaf (15).

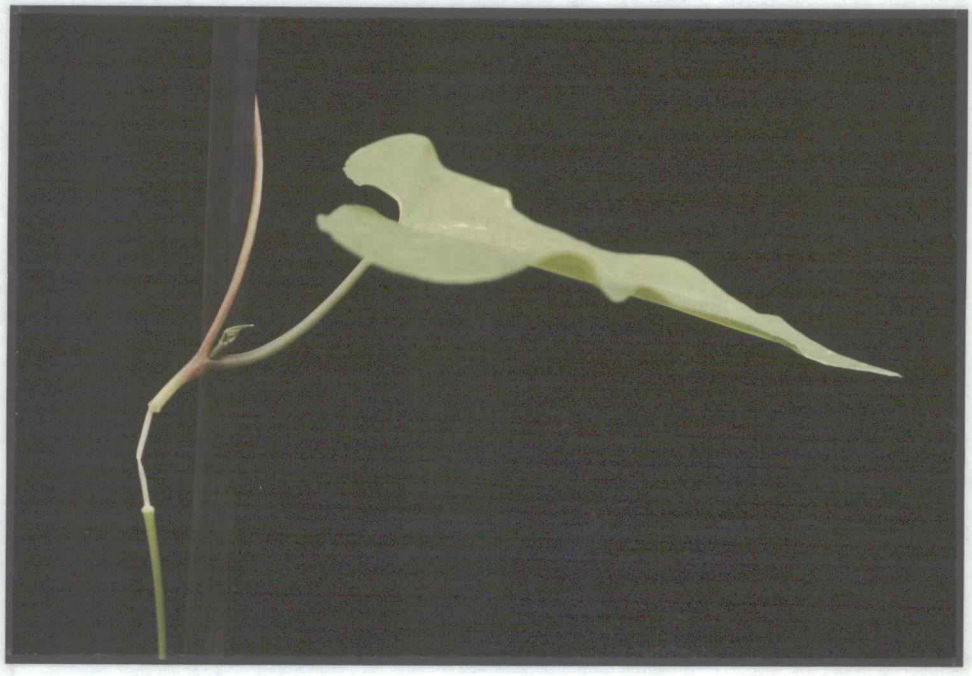
A

B

Appendix Figure 1. Petiole girdle on CL; (A) immediately prior to girdling and (B) 24 hours after girdling.



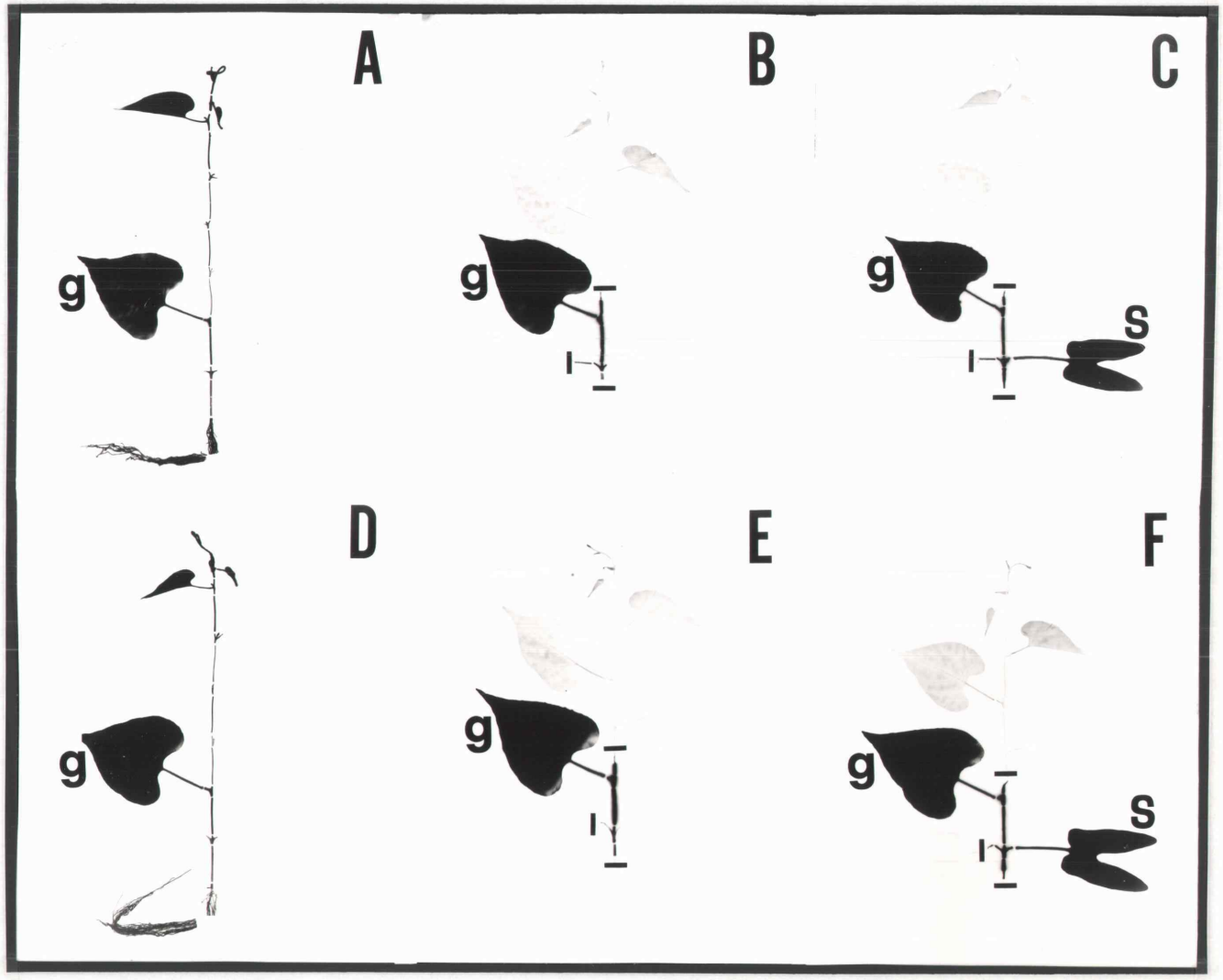
A



B

Appendix Figure 2. Stem girdles; (A) below cotyledonary node and (B) below L3.

Appendix Figure 3. A comparison between glyphosate translocation patterns from bagged and unbagged source-leaves; (A,B,C) L1 unbagged and (D,E,F) L1 enclosed in polyethylene bag after treatment. (g = glyphosate source-leaf, — = girdle, s = artificial sink)



Appendix Figure 3.

Appendix Table 1. The effect of bagging on total ^{14}C-glyphosate absorption per plant[a].

^{14}C (dpm)	Bagged[b]	Unbagged
Applied	373954	347243
Recovered	368508 ± 34114[c]	334368 ± 85091
Absorbed	316115 ± 26519	128999 ± 36569
Translocated	201189 ± 23365	55327 ± 30315

a/ ^{14}C applied to L1; stem girdles below cotyledons and above L2; petiole girdle on CL; artificial sink in CR

b/ Treated leaf (L1) enclosed in polyethylene bag after ^{14}C-glyphosate application

c/ Standard deviation (three replications per mean)

Appendix Table 2. The effect of bagging on ^{14}C-glyphosate translocation patterns.

Plant part	Translocated ^{14}C-glyphosate (% of total)		Dry weight (% of total)	
	Bagged[a]	Unbagged	Bagged	Unbagged
Tip	.3 ± .06[b]	.3 ± .15	2.2	1.6
L5	.4 ± .23	.3 ± .17	2.2	1.3
L4	.8 ± .20	.9 ± .25	4.9	5.2
L3	.6 ± .10	.6 ± .26	7.5	7.8
L2	.9 ± .15	2.3 ± .91	15.6	16.3
L1*	--	--	10.7	13.4
CR	54.0 ± 7.22	38.1 ± 7.88	9.6	8.8
CL	.7 ± .26	.6 ± .26	9.6	10.0
Root	.2 ± .06	.5 ± .06	7.1	5.8
Stem	42.0 ± 6.97	56.5 ± 7.05	30.3	29.8

* Leaf receiving original ^{14}C-glyphosate application

a/ L1 enclosed in polyethylene bag following treatment

b/ Standard deviation (three replications per mean)

Appendix Table 3. Typical internode lengths (cm) of normal and girdled plants used in Chapter 3.

Internode	Normal							Girdled						
	R_1	R_2	R_3	R_4	R_5	R_6	$\bar{x}$	R_1	R_2	R_3	R_4	R_5	R_6	$\bar{x}$
Soil to cotyledons	14.0	14.3	14.1	15.6	14.1	14.6	14.5	13.3	14.4	15.8	12.2	13.0	15.0	14.0
Cotyledons to L1	5.4	8.7	6.2	10.2	5.3	8.2	7.3	5.9	6.7	6.9	8.7	6.2	8.5	7.2
L1 to L2	6.6	7.6	10.1	8.2	9.7	7.3	8.3	8.3	6.4	9.7	7.0	9.3	7.4	8.0
L2 to L3	13.3	17.2	16.5	17.3	17.5	16.8	16.4	19.7	17.4	17.1	19.9	16.4	16.7	17.9
L3 to L4	14.1	17.5	14.2	18.2	17.1	16.9	16.3	15.9	16.5	15.1	15.6	16.8	16.7	16.1
L4 to L5	14.2	13.9	13.1	17.5	16.4	15.8	15.2	15.9	13.9	13.7	13.0	14.6	12.2	13.9
L5 to tip	25.5	27.2	28.1	25.6	24.8	24.4	25.9	22.5	14.8	11.7	25.6	17.5	14.2	17.7
Overall height	93.1	106.4	102.3	112.6	104.9	104.0	103.9	101.5	90.1	90.0	102.0	93.8	90.7	94.7

Appendix Table 4. Actual dpm values[a] for ^{14}C-glyphosate treated plants: normal[b] pattern.

	Tip	L5	L4	L3	L2	L1	CR	CL
R_1	70756	18553	812	485	1476	145290	63	240
R_2	54951	11865	1863	597	1032	150511	121	409
R_3	40859	6983	4777	553	896	125779	49	111
$\bar{x}$	55522	12467	2484	545	1135	140527	78	253

	Root	Untreated stem	Leaf-wash	Total applied[c]	Total recovered	Total absorbed	Total trans-located
R_1	1647	43791	20128	(320532)	303060	282932	137642
R_2	1732	42717	43376	(320532)	309172	265796	115285
R_3	2247	39337	36516	(320532)	258107	221591	95812
$\bar{x}$	1874	41948	33340	(320532)	290113	256773	116247

a/ All values in Appendix Tables 4 thru 13 have been corrected for quench, background (51.2 dpm/sample), and growth chamber contamination (0.52 dpm/mg tissue)

b/ ^{14}C applied to L1; no girdles or artificial sinks

c/ An average value

Appendix Table 5. Actual dpm values for ^{14}C-glyphosate treated plants: girdled[a].

	Tip	L5	L4	L3	L2	L1	CR	CL
R_1	893	1386	1235	1679	2649	212703	795	825
R_2	627	823	1032	1859	2235	158777	664	998
R_3	666	624	2128	1924	2629	140198	601	545
$\bar{x}$	729	944	1465	1821	2504	170559	687	789'

	Root	Untreated stem	Leaf-wash	Total applied[b]	Total recovered	Total absorbed	Total trans-located
R_1	1134	133212	50252	(400665)	406763	356511	143808
R_2	554	115021	39160	(320532)	321748	282588	123811
R_3	668	115266	42888	(320532)	308136	265248	125050
$\bar{x}$	785	121153	44100	(347243)	345549	301449	130890

a/ ^{14}C applied to L1; stem girdles below cotyledons and above L2; petiole girdle on CL

b/ An average value

Appendix Table 6. Actual dpm values for ^{14}C-glyphosate treated plants: L1 sink[a].

	Tip	L5	L4	L3	L2	L1	CR	CL
R_1	1086	1166	2688	1619	2733	36323	128211	2927
R_2	940	873	1236	1114	2703	10243	105155	1180
R_3	2288	1812	1378	2883	2135	25401	88197	1569
$\bar{x}$	1438	1284	1767	1872	2524	23989	321563	1892

	Root	Untreated stem	Leaf-wash	Total applied[b]	Total recovered	Total absorbed	Total translocated
R_1	792	177520	35740	(400665)	390804	355064	226853
R_2	832	163621	21940	(320532)	309836	287896	182742
R_3	382	137844	33486	(320532)	297374	263888	175691
$\bar{x}$	669	159662	30389	(347243)	332671	302283	195095

a/ ^{14}C applied to CR; stem girdles below cotyledons and above L2; petiole girdle on CL; artificial sink in L1

b/ An average value

Appendix Table 7. Actual dpm values for ^{14}C-glyphosate treated plants: CR sink[a].

	Tip	L5	L4	L3	L2	L1	CR	CL
R_1	698	538	1543	1351	1428	153340	114025	988
R_2	689	1566	1463	1260	2517	98251	111959	2181
R_3	605	637	1944	1029	1695	93187	97511	1171
$\bar{x}$	664	914	1650	1213	1880	114926	197832	1147

	Root	Untreated stem	Leaf-wash	Total applied[b]	Total recovered	Total absorbed	Total trans-located
R_1	352	62157	43886	(400665)	380305	336419	183079
R_2	394	105535	69343	(400665)	395158	325815	227564
R_3	258	88076	43948	(320532)	330061	286113	192926
$\bar{x}$	335	85256	52392	(373954)	368508	316116	201190

a/ ^{14}C applied to L1; stem girdles below cotyledons and above L2; petiole girdle on CL; artificial sink in CR

b/ An average value

Appendix Table 8. Actual dpm values for ^{14}C-glyphosate treated plants: stem applied[a].

	Tip	L5	L4	L3	L2	L1	CR	CL
R_1	9901	15869	13951	9495	64110	1025	20198	454
R_2	21548	12223	22381	11570	77682	270	30238	369
R_3	16403	5889	15760	12318	72952	660	28799	319
$\bar{x}$	11327	11327	20697	11128	71581	652	26412	381

	Root	Untreated stem	Treated stem	Leaf-wash	Total applied[b]	Total recovered	Total absorbed	Total translocated
R_1	485	61424	19255	113474	(400665)	329640	216166	196911
R_2	574	71559	14487	21254	(320532)	284155	262901	248415
R_3	469	61689	19192	18158	(320532)	262607	244449	225257
$\bar{x}$	509	64891	17645	50962	(347243)	292134	241172	223528

a/ ^{14}C-glyphosate applied to stem below L1; stem girdles below cotyledons and above L2; petiole girdle on CL; artificial sink in CR

b/ An average value

Appendix Table 9. Actual dpm values for ^{14}C-glyphosate treated plants: unbagged[a].

	Tip	L5	L4	L3	L2	L1	CR	CL
R_1	260	197	788	638	1134	75536	41990	625
R_2	201	182	231	118	1224	53030	12260	320
R_3	85	56	379	272	867	92451	13271	107
$\bar{x}$	182	145	466	343	1075	73672	22507	351

	Root	Untreated stem	Leaf-wash	Total applied[b]	Total recovered	Total absorbed	Total translocated
R_1	471	44169	24669	(400665)	412476	165807	90271
R_2	201	24907	200084	(320532)	292758	92674	39644
R_3	132	20898	119352	(320532)	247868	128516	36066
$\bar{x}$	268	29991	114702	(347243)	317701	128999	55327

a/ ^{14}C applied to L1, but leaf not bagged with polyethylene; stem girdles below cotyledons and above L2; petiole girdle on CL; artificial sink in CR

b/ An average value

Appendix Table 10. Actual dpm values for $^{14}CO_2$-treated plants: normal[a] pattern.

	Tip	L5	L4	L3	L2	L1	CR
R_1	48488	31671	2606	1874	1417	81811	475
R_2	48912	28664	5385	1470	1350	86669	234
R_3	51656	16323	9922	2691	1198	109501	192
$\bar{x}$	49685	25553	6304	2012	1322	92660	300

	CL	Root	Stem	Total applied	Total recovered	Total translocated
R_1	390	19981	93139	(1.95 uCi)	279451	197640
R_2	206	6791	99974	(1.95 uCi)	280656	193987
R_3	237	9480	98420	(1.95 uCi)	299619	190118
$\bar{x}$	278	12084	97178	(1.95 uCi)	286575	193915

a/ ^{14}C applied to L1; no girdles or artificial sinks

Appendix Table 11. Actual dpm values for $^{14}CO_2$-treated plants: girdled[a].

	Tip	L5	L4	L3	L2	L1	CR
R_1	153	171	297	251	125	59101	152
R_2	295	149	603	454	1295	165798	293
R_3	90	127	353	507	2268	129120	452
$\bar{x}$	179	149	418	404	1229	118006	229

	CL	Root	Stem	Total applied	Total recovered	Total translocated
R_1	124	356	58618	(0.75 uCi)	119346	60245
R_2	243	1123	183718	(1.95 uCi)	353970	188172
R_3	550	1183	139436	(1.95 uCi)	274086	144966
$\bar{x}$	306	887	127257	(1.55 uCi)	249134	131128

a/ ^{14}C applied to L1; stem girdles below cotyledons and above L2; petiole girdle on CL

Appendix Table 12. Actual dpm values for $^{14}CO_2$-treated plants: L1 sink[a].

	Tip	L5	L4	L3	L2	L1	CR
R_1	224	200	299	485	2244	43860	65857
R_2	116	92	336	703	1352	45691	56849
R_3	283	250	326	763	1253	64576	54345
$\bar{x}$	208	181	357	650	1616	51377	59017

	CL	Root	Stem	Total applied	Total recovered	Total translocated
R_1	415	648	89613	(1.95 uCi)	203845	137988
R_2	262	980	171679	(1.95 uCi)	278061	221211
R_3	492	1163	129456	(1.95 uCi)	253515	199170
$\bar{x}$	390	1097	130249	(1.95 uCi)	245140	186123

a/ ^{14}C applied to CR; stem girdles below cotyledons and above L2; petiole girdle on CL; artificial sink in L1

Appendix Table 13. Actual dpm values for $^{14}CO_2$-treated plants: CR sink[a].

	Tip	L5	L4	L3	L2	L1	CR
R_1	99	80	116	34	78	46248	11894
R_2	253	134	347	496	1492	146229	86438
R_3	260	196	447	764	1522	121208	64074
$\bar{x}$	204	137	303	431	1031	104560	54135

	CL	Root	Stem	Total applied	Total recovered	Total translocated
R_1	98	228	43633	(0.75 uCi)	102507	56257
R_2	237	629	104081	(1.95 uCi)	340344	194105
R_3	398	692	126110	(1.95 uCi)	315669	194461
$\bar{x}$	244	516	91275	(1.55 uCi)	252840	148275

a/ ^{14}C applied to L1; stem girdles below cotyledons and above L2; petiole girdle on CL; artificial sink in CR

Appendix Table 14. Harvest dry weight values (mg) for ^{14}C-glyphosate treated plants: normal[a] pattern.

	Tip	L5	L4	L3	L2	L1
R_1	16.6	10.2	29.3	45.1	50.9	32.4
R_2	13.7	12.6	29.4	42.0	51.2	33.4
R_3	10.0	7.8	21.2	32.5	44.3	27.1
$\bar{x}$	13.4	10.2	26.6	39.9	48.8	31.0

	CR	CL	Root	Stem	Total weight
R_1	25.4	29.1	31.9	126.4	397.3
R_2	24.4	24.9	26.7	103.6	361.9
R_3	25.1	23.9	25.0	64.8	281.7
$\bar{x}$	25.0	26.0	27.9	98.3	347.0

a/ ^{14}C applied to L1; no girdles or artificial sinks

Appendix Table 15. Harvest dry weight values (mg) for ^{14}C-glyphosate treated plants: girdled[a].

	Tip	L5	L4	L3	L2	L1
R_1	8.3	6.6	16.4	23.3	55.7	36.7
R_2	6.2	5.8	13.2	25.3	54.6	34.4
R_3	5.4	4.7	16.5	27.0	48.1	25.2
$\bar{x}$	6.6	5.7	15.4	25.2	52.8	32.1

	CR	CL	Root	Stem	Total weight
R_1	25.6	27.9	17.1	92.9	310.5
R_2	29.9	27.3	23.4	92.8	312.9
R_3	24.3	25.4	15.8	85.8	278.2
$\bar{x}$	26.6	26.9	18.8	90.5	300.5

a/ ^{14}C applied to L1; stem girdles below cotyledons and above L2; petiole girdle on CL

Appendix Table 16. Harvest dry weight values (mg) for ^{14}C-glyphosate treated plants: L1 sink[a].

	Tip	L5	L4	L3	L2	L1
R_1	8.4	7.2	17.5	28.6	60.7	50.8
R_2	6.0	4.6	12.5	21.5	37.6	35.5
R_3	9.0	8.1	19.6	26.2	51.1	34.2
$\bar{x}$	7.8	6.6	16.5	25.4	49.8	40.2

	CR	CL	Root	Stem	Total weight
R_1	24.4	38.3	19.9	113.8	369.6
R_2	20.0	21.5	17.5	84.6	261.3
R_3	18.0	30.8	18.0	86.5	301.5
$\bar{x}$	20.8	30.2	18.5	95.0	310.8

a/ ^{14}C applied to CR; stem girdles below cotyledons and above L2; petiole girdle on CL; artificial sink in L1

Appendix Table 17. Harvest dry weight values (mg) for ^{14}C-glyphosate treated plants: CR sink[a].

	Tip	L5	L4	L3	L2	L1
R_1	3.4	2.5	9.5	19.8	41.1	28.4
R_2	7.2	9.1	15.3	21.5	44.6	32.0
R_3	6.8	6.0	14.8	20.7	40.0	25.9
$\bar{x}$	5.8	5.9	13.2	20.1	41.9	28.8

	CR	CL	Root	Stem	Total weight
R_1	26.6	20.3	18.5	68.3	238.4
R_2	27.1	26.6	20.6	90.1	294.1
R_3	23.8	30.4	18.2	85.0	271.6
$\bar{x}$	25.8	25.8	19.1	81.1	268.0

a/ ^{14}C applied to L1; stem girdles below cotyledons and above L2; petiole girdle on CL; artificial sink in CR

Appendix Table 18. Harvest dry weight values (mg) for ^{14}C-glyphosate treated plants: stem-applied[a].

	Tip	L5	L4	L3	L2	L1
R_1	6.0	5.7	15.2	21.3	62.3	58.2
R_2	5.0	4.6	15.1	23.1	45.2	50.6
R_3	5.2	3.5	14.8	22.6	55.1	32.3
$\bar{x}$	5.4	4.6	15.0	22.3	54.21	47.0

	CR	CL	Root	Untreated stem	Treated stem	Total weight
R_1	29.2	37.3	19.5	88.6	9.4	352.7
R_2	26.1	28.3	23.3	80.3	6.9	308.5
R_3	32.4	38.6	17.1	88.6	7.7	317.9
$\bar{x}$	29.2	34.7	20.0	85.8	8.0	326.4

a/ ^{14}C-glyphosate applied to stem below L1; stem girdles below cotyledons and above L2; petiole girdle on CL; artificial sink in CR

Appendix Table 19. Harvest dry weight values (mg) for ^{14}C-glyphosate treated plants: unbagged[a].

	Tip	L5	L4	L3	L2	L1
R_1	2.6	2.7	12.6	21.4	53.0	49.0
R_2	6.3	5.4	15.7	24.1	45.6	32.6
R_3	5.2	3.3	17.4	23.4	45.6	36.7
$\bar{x}$	4.7	3.8	15.2	23.0	48.1	39.4

	CR	CL	Root	Stem	Total weight
R_1	26.5	30.7	15.7	78.8	293.0
R_2	25.6	26.0	16.0	88.8	286.1
R_3	25.7	31.1	20.0	95.7	304.1
$\bar{x}$	25.9	29.3	17.2	87.8	294.4

a/ ^{14}C applied to L1, but leaf not bagged with polyethylene; stem girdles below cotyledons and above L2; petiole girdle on CL; artificial sink in CR

Appendix Table 20. Harvest dry weight values (mg) for $^{14}CO_2$-treated plants: normal[a] pattern.

	Tip	L5	L4	L3	L2	L1
R_1	11.7	11.5	17.5	27.3	29.2	25.3
R_2	16.8	11.9	28.8	36.6	50.4	34.1
R_3	15.0	14.8	24.8	53.1	40.6	28.8
$\bar{x}$	14.5	12.7	23.7	33.0	40.1	29.4

	CR	CL	Root	Stem	Total weight
R_1	16.0	18.3	21.2	69.2	247.2
R_2	26.7	25.4	25.3	102.7	358.7
R_3	19.1	23.1	21.5	63.8	286.6
$\bar{x}$	20.6	22.3	22.7	78.6	297.5

a/ ^{14}C applied to L1; no girdles or artificial sinks

Appendix Table 21. Harvest dry weight values (mg) for $^{14}CO_2$-treated plants: girdled[a].

	Tip	L5	L4	L3	L2	L1
R_1	7.7	5.7	16.6	27.9	57.5	33.4
R_2	6.6	5.0	14.5	25.4	54.4	31.6
R_3	3.5	2.6	10.7	20.6	46.3	32.8
$\bar{x}$	5.9	4.4	13.9	24.6	52.7	32.6

	CR	CL	Root	Stem	Total weight
R_1	37.3	31.2	23.6	107.0	347.9
R_2	26.6	26.5	15.9	97.2	303.7
R_3	28.3	27.9	20.2	96.7	289.6
$\bar{x}$	30.7	28.5	19.9	100.3	313.7

a/ ^{14}C applied to L1; stem girdles below cotyledons and above L2; petiole girdle on CL

Appendix Table 22. Harvest dry weight values (mg) for $^{14}CO_2$-treated plants: L1 sink[a].

	Tip	L5	L4	L3	L2	L1
R_1	11.3	8.1	13.3	21.8	54.6	41.1
R_2	6.6	4.9	15.2	26.1	42.6	44.4
R_3	8.4	10.4	20.3	25.0	35.5	34.3
$\bar{x}$	8.8	7.8	16.3	24.3	44.2	39.9

	CR	CL	Root	Stem	Total weight
R_1	23.5	27.9	20.8	100.5	322.9
R_2	23.0	33.0	14.6	89.4	299.8
R_3	17.0	25.0	13.6	73.1	262.6
$\bar{x}$	21.2	28.6	16.3	87.7	295.1

a/ ^{14}C applied to CR; stem girdles below cotyledons and above L2; petiole girdle on CL; artificial sink in L1

Appendix Table 23. Harvest dry weight values (mg) for $^{14}CO_2$-treated plants: CR sink[a].

	Tip	L6	L5	L4	L3	L2
R_1	5.8	4.5	15.6	20.9	53.2	33.6
R_2	6.6	5.3	18.1	23.4	51.8	32.2
R_3	6.4	5.4	14.6	22.3	53.5	31.0
$\bar{x}$	6.3	5.1	16.1	22.2	52.8	32.3

	CR	CL	Root	Stem	Total weight
R_1	28.2	25.4	22.8	90.4	300.9
R_2	30.7	31.9	22.8	94.1	316.9
R_3	27.5	30.2	23.3	96.1	310.3
$\bar{x}$	28.8	29.2	23.0	93.5	309.4

a/ ^{14}C applied to L1; stem girdles below cotyledons and above L2; petiole girdle on CL; artificial sink in CR

Appendix Table 24. Actual dpm values[a] for ^{14}C-simazine treated plants: normal[b] pattern.

	Tip	L6	L5	L4	L3	L2
R_1	149	479	14214	17564	21308	24172
R_2	321	2820	10751	13710	19123	26943
R_3	343	2535	8519	17317	18274	30195
$\bar{x}$	271	1945	11161	15864	19568	27103

	L1	CR	CL	Stem	Total
R_1	22432	12779	13118	60385	186600
R_2	15283	12743	12457	79067	193218
R_3	9221	11244	5549	69203	171400
$\bar{x}$	15645	12255	10375	69552	183739

a/ Counts corrected for quench and background

b/ ^{14}C-simazine applied to roots; no girdles or artificial sinks

Appendix Table 25. Actual dpm values[a] for ^{14}C-simazine treated plants: CR sink[b].

	Tip	L6	L5	L4	L3	L2
R_1	74	2773	6902	16344	10458	19529
R_2	114	317	5115	18904	16965	30405
R_3	278	2294	7126	14211	15827	28576
$\bar{x}$	155	1795	6381	16486	14417	26170

	L1	CR	CL	Stem	Total
R_1	18918	4043	11482	76505	167028
R_2	23083	4239	11658	67346	178146
R_3	22237	5122	11052	83221	189944
$\bar{x}$	21413	4468	11397	75691	178373

a/ Counts corrected for quench and background

b/ ^{14}C-simazine applied to roots; stem girdles below cotyledons and above L2; petiole girdle on CL; artificial sink in CR

Appendix Table 26. Harvest dry-weight values (mg) for ^{14}C-simazine treated plants: normal[a] pattern.

	Tip	L6	L5	L4	L3	L2
R_1	7.1	11.3	13.0	16.6	24.1	29.5
R_2	7.9	17.1	11.0	14.2	21.1	28.3
R_3	7.6	13.9	10.9	14.6	20.4	28.9
$\bar{x}$	7.5	14.1	11.6	15.1	21.9	28.9

	L1	CR	CL	Stem	Total
R_1	29.0	20.8	21.9	82.9	256.2
R_2	22.2	20.9	18.6	84.5	245.8
R_3	23.1	19.2	17.9	75.7	232.2
$\bar{x}$	24.8	20.3	19.5	81.0	244.7

a/ ^{14}C-simazine applied to roots; no girdles or artificial sinks

Appendix Table 27. Harvest dry-weight values (mg) for ^{14}C-simazine treated plants: CR sink[a].

	Tip	L6	L5	L4	L3	L2
R_1	6.6	12.2	11.2	15.7	22.6	40.6
R_2	3.7	5.7	7.1	14.1	17.9	30.3
R_3	4.7	7.2	7.0	12.5	18.8	32.9
$\bar{x}$	5.0	8.4	8.4	14.1	19.8	34.6

	L1	CR	CL	Stem	Total
R_1	37.3	25.6	27.5	94.4	293.7
R_2	33.3	26.5	24.2	81.0	243.8
R_3	27.6	28.1	31.9	90.5	261.2
$\bar{x}$	32.7	26.7	27.9	88.6	266.2

a/ ^{14}C-simazine applied to roots; stem girdles below cotyledons and above L2; petiole girdle on CL; artificial sink in CR