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Glyphosate effects on Canada thistle (*Cirsium arvense*) roots, root buds, and shoots

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Summary: Résumé: Zusammenfassung

Glyphosate† was sprayed at 0·009–1·12 kg a.i. ha^{-1} on the foliage of large potted glasshouse-grown Canada thistle [*Cirsium arvense* (L.) Scop.], which had extensive, well-developed roots. Increasing the glyphosate rate progressively reduced the total number of visible adventitious root buds plus emerged secondary shoots per plant proportionately more than root biomass, 10 days after treatment. Cortical tissue of thickened propagative roots became soft, water-soaked, darkened, and some regions decomposed, exposing strands of vascular tissue. Lateral roots completely decomposed. When thickened roots were segmented to stimulate secondary shoot emergence from root buds 10 days after foliar treatment, fewer secondary shoots emerged than expected from the number of visible adventitious root buds present on both control and herbicide-treated plants. Increasing the rate of glyphosate also reduced the regrowth potential of root buds proportionately more than root biomass. Regrowth potential was measured as the number of emerged secondary shoots 35 days after segmenting unearthed roots from plants that had been sprayed 10 days earlier. When foliar-applied at 0·28 kg ha^{-1}, glyphosate decreased the regrowth potential of root buds to zero in 2 and 3 days, as measured by secondary shoot dry weight and number, respectively, even though root fresh weight was unchanged 3 days after foliar treatment. These dose–response and time-course experiments demonstrate that glyphosate did not reduce root biomass as much as it decreased root bud numbers and secondary shoot regrowth potential from root buds.

Les effets du glyphosate sur les racines, les bourgeons radiculaires et le développement des tiges du chardon des champs (Cirsium arvense *L.*)

Le glyphosate a été appliqué à la dose de 9 à 1 120 g de m.a. ha^{-1} sur le feuillage de plants de serre largement développés de chardons des champs dotés d'un système radiculaire important. Des doses croissantes de glyphosate réduisent progressivement le nombre total des bourgeons adventifs radiculaires ainsi que l'émergence de brins secondaires plus qu'elles ne réduisent proportionnellement la biomasse des racines 10 jours après le traitement. Le tissu cortical des racines principales devient tendre, spongieux, noirâtre et par endroits décomposé laissant apparaître le tissu vasculaire. Les racines latérales sont complètement décomposées. Lorsque les racines principales ont été sectionneés pour stimuler une ramification à partir des bourgeons radiculaires 10 jours après le traitement foliaire, le nombre de pousses secondaires fut très inférieur à ce que l'on était en droit d'attendre en raison du nombre de bourgeons radiculaires visibles, présents au moment du traitement. L'augmentation des doses de glyphosate a également réduit le

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potentiel de reprise de bourgeons radiculaires davantage que la biomasse des racines. Ce potentiel de reprise a été mesuré par les pousses secondaires dénombrées 35 jours après la segmentation de racines isolées des plants traités 10 jours plus tôt. Lorsqu'il a été appliqué à 280 g ha^{-1}, le glyphosate a provoqué une inhibition du potentiel de repousses des bourgeons radiculaires dans les 2 à 3 jours. Cette inhibition a été mesurée par le poids sec des pousses secondaires ainsi que leur nombre, tandis que le poids frais des racines restait inchangé 3 jours après le traitement foliaire. Ces études montrent que le glyphosate ne réduit pas la biomasse radiculaire autant qu'il inhibe le nombre de bourgeons radiculaires et leur potentiel de reprise.

Wirkung von Glyphosat auf Wurzel, Wurzelknospen und Spross der Acker-Kratzdistel (Cirsium arvense)

Pflanzen der Acker-Kratzdistel (*Cirsium arvense* (L.) Scop.), die im Gewächshaus in grossen Töpfen angezogen worden waren und ein kräftiges Wurzelsystem entwickelt hatten, wurden mit 0,009 bis 1,12 kg AS ha^{-1} Glyphosat behandelt. Die Zahl der sichtbaren Knospen an den Wurzeln zusammen mit den ausgetriebenen Wurzelsprossen pro Pflanze war 10 Tage nach der Behandlung proportional zur steigenden Aufwandmenge des Glyphosats stärker als die Wurzelmasse herabgesetzt. Die Rinde der verdickten Wurzelausläufer wurde weich, schwammig, verfärbte sich dunkel und begann stellenweise zu faulen. Seitenwurzeln zerfielen gänzlich. Wenn die verdickten Wurzeln 10 Tage nach der Behandlung zerteilt wurden, um die Bildung von Wurzelsprossen zu induzieren, entwickelten sich weniger Sprosse, als nach der Zahl der sichtbaren Knospen zu erwarten gewesen war. Mit steigender Aufwandmenge an Gylphosat sank das Potential zur Bildung von Wurzelsprossen, das als die Zahl der innerhalb von 35 Tagen nach der Zerteilung von Wurzeln gebildeter Wurzelsprosse gemessen wurde. Innerhalb von 2 bis 3 Tagen nach einer Blattbehandlung mit 0,28 kg AS ha^{-1} wurden keine Knospen mehr an den Wurzeln angelegt, wenn auch die Frischmasse der Wurzeln 3 Tage nach der Behandlung noch unverändert war. Es zeigte sich, dass Glyphosat nicht so sehr die Wurzelmasse, sondern vor allem die Anlage von Knospen an den Wurzeln und die Entwicklung von Wurzelsprossen herabsetzt.

Introduction

Cirsium arvense is a perennial weed with an extensive, spreading root system (Rogers, 1928; Hayden, 1934; Hodgson, 1971; Amor & Harris, 1975). Adventitious root buds arise from its roots to form new secondary shoots (Hayden, 1934; Hamdoun, 1970, 1972). This is the major method of vegetative propagation for the plant after seedling establishment.

Glyphosate is a non-selective, foliar-applied herbicide, which has been shown to translocate from the shoot to the roots of small *C. arvense* plants with fibrous roots, and other plants (Penner, 1975; Gottrup *et al.*, 1976; Kells & Rieck, 1979; Sandberg, Meggitt & Penner, 1980; Schultz & Burnside, 1980; Dewey & Appleby, 1983). The extent and pattern of ^{14}C-glyphosate translocation is unknown for well-established, mature *C. arvense* with extensive roots, many root buds, and secondary shoots. Glyphosate at low doses controls seedling *C. arvense*, but higher rates are needed for control of established plants in the field. Despite higher application rates, control in the field often is short-lived and erratic.

These experiments were started to quantify the effect of foliar-applied glyphosate on root biomass, adventitious root buds and secondary shoot regrowth potential of glasshouse-grown *C. arvense*, which had well-developed roots and root buds, in preparation for studies of ^{14}C-translocation in such plants. While ^{14}C-glyphosate translocation has been studied in small *C. arvense*, with undeveloped fibrous roots having few or no root buds (Sprankle *et al.*, 1975; Gottrup *et al.*, 1976; Sandberg *et al.*, 1980), ^{14}C-glyphosate transport has not been related to the biological response of *C. arvense* to the herbicide. Our experiments characterize the dose–response and time-course of glyphosate damage to well-rooted *C. arvense*, and establish that glyphosate reduced root biomass less than either root bud numbers or regrowth potential of secondary shoots from root buds. An attempt is made to describe the statistical variability of root growth parameters because so few precedents exist in the literature for experimenting with large potted well-rooted plants in the glasshouse; most studies employed seedlings or small plants of this perennial weed.

Materials and methods

General methods

Experiments were conducted in a glasshouse during winter, from October to April. *Cirsium arvense* plants (var. *integrifolium* Wimm. and Grab.) (Moore & Frankton, 1974) were grown from 4–8-cm long root cuttings (Donald, 1984). Root cuttings were placed in 21 × 30 × 8 cm trays, containing fine vermiculite, for 1·5–2 months. The vermiculite was watered with one-third strength nutrient solution (Blankendaal *et al.*, 1972) or tap water. Uniform plants with five to seven leaves were transplanted to 1 l pots (16·5-cm diameter × 18-cm height), containing glasshouse potting soil (73% sand, 19% silt, 8% clay and 3·6% organic matter) at pH 7·9. A slow-release fertilizer, which contained $N:P_2O_5:K_2O$, 18:6:12, was added to the potting soil at 20 g pot^{-1} at the time of potting. Plants were grown for 2–2·5 additional months before spray treatment. Plants were selected for uniformity in each experiment based on plant height, leaf node number and flowering stage. Leaves less than 3–4 mm in length were not counted. Morphological characteristics, rather than chronological age, were used to determine stage of development because plants develop at different rates at different times of the year. In order to give a 14-h day length, sunlight was supplemented with fluorescent lights, which provided 85–140 $\mu E\ m^{-2}\ s^{-1}$ at the canopy height, 42–60 cm below the fluorescent bulbs. Relative humidity ranged between 30% and 85%. The glasshouse was normally maintained at 25°C in the day and 20°C at night. Occasionally the temperature fluctuated between extremes of 20°C and 32°C in the day, and 16°C and 23°C at night.

Glyphosate was sprayed on the *C. arvense* shoots in one pass with a movable nozzle hooded sprayer, travelling at 0·77 km h^{-1}. A #800067 flat-fan Teejet nozzle supplied 234 l ha^{-1} at 179 kPa. Glyphosate was diluted to volume in distilled tap water with 5 ml l^{-1} surfactant. The surfactant was Ortho X-77 Spreader (Principal agent: alkylaryl-polyoxyethylene glycols, free fatty acids, and isopropanol; 90%). The soil surface was covered with 3 cm of vermiculite before spraying to prevent herbicide contact with the potting soil. The vermiculite was removed after the spray had dried.

Plants were harvested 10 days after spray treatment, except in the translocation-time experiment. Treated shoots were severed at the soil surface and discarded. Roots were unearthed, washed free of soil with tap water and cut into 10-cm lengths. The root system was stored in darkness at 0–5°C for 1–4 days during harvest. The root segements were replanted 1 cm deep in trays (12 × 16 × 5·5 cm, 1 l) filled with fine vermiculite. The root system was segmented to break apical dominance, and promote secondary shoot formation from elongating adventitious root buds. Secondary shoots above the vermiculite surface were counted 45 days after spray treatment, which was 35 days after root segmentation. Secondary shoots were allowed to grow for 35 days, although few secondary shoots emerged between 28 days and 35 days after harvest. Secondary shoots were severed at the junction between the secondary shoot and the original root segment, washed free of vermiculite, and dried at 70°C for 3 days before shoot dry weight was recorded. Secondary shoots arise from adventitious root buds on the root system. Measurements of secondary shoot number and dry weight indicate plant vigour, but underestimate total adventitious root bud number.

All experiments were arranged as a completely randomized design with four to eight replicate pots per treatment. Data were analysed by regression analysis and analysis of variance (ANOVA), and treatment means were separated with Fisher's protected least significance difference (l.s.d.) where appropriate ($P = 0·05$) (Steel & Torrie, 1980). ANOVA probability values are expressed as a fraction of 1·0, the area under an F distribution. Each set of data analysed by regression analysis includes the individual data points, the regression curve, the 95% confidence interval, the regression equation, and the coefficient of determination (R^2). The 95% confidence interval contains 95% of the data values, but is not a treatment mean separation test. The coefficient of determination is the ratio of the regression sum of squares to the total sum of squares, and indicates the per cent ($R^2 \cdot 100\%$) of variation in the dependent variable due to the independent variable in the regression model. All experiments were conducted twice and results combined where no experiment by treatment interaction occurred.

Glyphosate rate

The increase in *C. arvense* shoot height was recorded 2, 4, and 10 days after glyphosate application. Increase in shoot height was used, rather than shoot height, to minimize the innate variability among shoots. Visible glyphosate injury symptoms and their time of occurrence were noted. Root fresh weight and adventitious root bud number were recorded 10 and 45 days after glyphosate application. Adventitious root buds were classified as unemerged, 0–1 mm, 2–5 mm, 6–10 mm, longer than 10 mm, or secondary shoots. Bud lengths were measured with an eyepiece micrometer, which was accurate to 0·1 mm. Glyphosate was applied at 0, 0·0088, 0·018, 0·035, 0·070, 0·11, 0·14, 0·18, 0·21, 0·25, 0·28, 0·32, 0·35, 0·39, 0·56, and 1·12 kg a.i. ha^{-1} plus 5 ml l^{-1} X-77 surfactant. Sixteen rates of glyphosate were used over a short range to ensure that the regression curve would accurately fit the data. Canada thistle shoots were $89·7 \pm 9·6$ cm tall, had $47·1 \pm 4·2$ cm diameter foliar canopy, with $30·1 \pm 6·0$ leaf nodes and $0·39 \pm 0·35$ flower buds (all means $\pm$ s.d.) at the time of glyphosate treatment.

A completely randomized design was used with four replications per treatment, and the experiment was conducted twice. Because many glyphosate rates were used over a narrow range, fewer replicates per rate were required relative to previous research (Donald, 1984) to attain adequate precision in the regression curve modelling.

Translocation time

Plants that were $83·1 \pm 10·8$ cm tall with a $41·8 \pm 3·5$ cm diameter foliar display, $31·6 \pm 3·7$ leaf nodes, and $0·03 \pm 0·11$ flower buds were sprayed with 0·28 kg ha^{-1} glyphosate, or were not sprayed. Primary shoots were removed after 6, 12, 24, 48 or 96 h, and the roots were harvested as described previously. Secondary shoot number and dry weight were recorded 35 days after removal of the primary shoots. A completely randomized design was used with five replications in the first trial and six in the second.

Results and discussion

Glyphosate rate

In the United States the recommended field application rate of glyphosate is from 0·84 to 2·25 kg ha^{-1} for control of *C. arvense* shoots (Monsanto Company, St Louis, MO 63167). Some residual suppression of secondary shoot regrowth

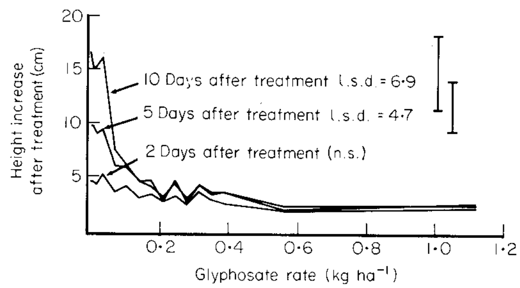

Fig. 1 Effect of glyphosate at various rates plus 0·5% (v/v) X-77 surfactant on the primary shoot height increase of *C. arvense* 2, 5, and 10 days after foliar treatment.

is expected for at least a year after treatment. In our experiments, glyphosate at much lower rates stopped shoot growth in the glasshouse, even though plants were large (89·7 cm tall) at the time of treatment (ANOVA, $P < 0·0001$) (Fig. 1). Primary shoot growth stopped between 2 days and 5 days after glyphosate application, when glyphosate was applied at $\geqslant 0·07$ kg ha^{-1}. Growth was not reduced further at rates above 0·018 kg ha^{-1}, although shoots had died at $\geqslant 0·39$ kg ha^{-1}, 10 days after treatment. Visual injury symptoms were due to glyphosate and not X-77 surfactant, because surfactant applied alone did not induce these symptoms.

Root fresh weight decreased linearly as glyphosate rate increaed 10 days after foliar treatment (ANOVA, $P < 0·0013$) (Fig. 2a). Glyphosate at 1·12 kg ha^{-1} reduced root biomass by 67%. Roots were soft, water-soaked, and darkened after shoot treatment with glyphosate. Small lateral roots and root tips of thickened storage roots decomposed at glyphosate rates $\geqslant 0·07$ kg ha^{-1}. Large storage roots partially decomposed at 0·14 kg ha^{-1} glyphosate leaving portions of the exposed vascular strand intact. Approximately half of the root system decomposed at 0·35 kg ha^{-1} glyphosate, leaving only the vascular strand. Such uneven root decomposition suggests that glyphosate is distributed unevenly throughout large well-established roots.

There was a further dose–dependent decrease in root fresh weight 45 days after foliar treatment, when roots were unearthed 10 days after glyphosate treatment, segmented and placed in vermiculite for 35 days to allow secondary shoots to grow from root buds ($P < 0·033$) (Fig. 2b and c). Root fresh weight was reduced more by lower rates of glyphosate 45 days after treatment (Fig. 2b and c) than 10 days after treatment (Fig. 2a). The root

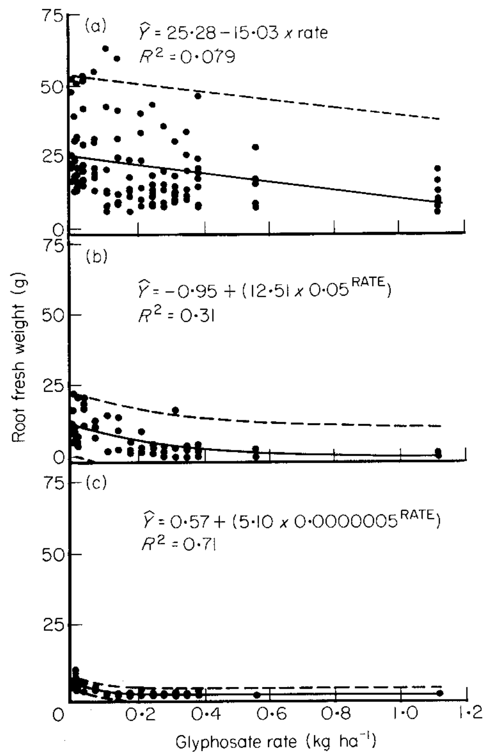

Fig. 2 Effect of glyphosate at various rates plus 0·5% (v/v) X-77 surfactant on *C. arvense* root fresh weight 10 days after treatment (a) and 45 days after treatment (b and c for trials 1 and 2). The best fitting regression curve (——) and regression equation, the 95% confidence interval (– – –), data points (·) and the coefficient of determination (R^2) are presented.

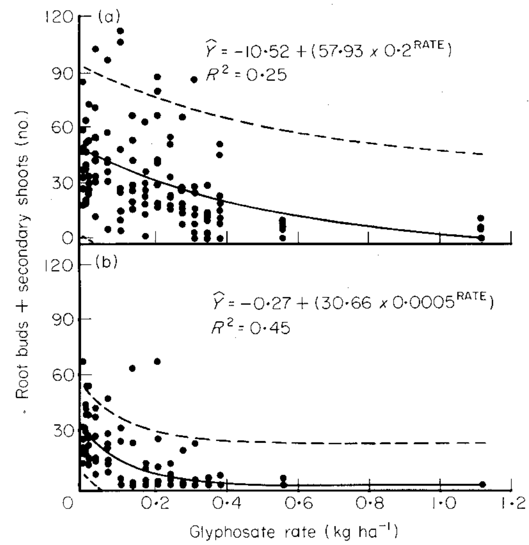

Fig. 3 Effect of glyphosate at several rates plus 0·5% (v/v) X-77 surfactant on visible *C. arvense* root bud number 10 days after treatment (a) and 45 days after treatment (b).

fresh weight of controls decreased by 54% between 10 days and 45 days after the start (Fig. 2). The decrease in control roots was due to decomposition of small lateral roots; thickened storage roots remained firm, white, and healthy. Thickened cortical tissue did not decompose as it did following foliar glyphosate application. These results suggest that 10 days after foliar treatment, when roots were unearthed and segmented, they had received sufficient glyphosate at sites of action to kill root buds and to prevent further secondary shoot emergence 35 days later. Glyphosate-induced decreases in root fresh weight do not represent remobilization of root storage reserves into growing secondary shoots (Figs 2 and 3), because secondary shoot growth was reduced relatively more at lower glyphosate rates than was root biomass.

Unemerged root buds were identified by external morphological characteristics. Broad bulges near bends in the thickened storage roots associated with a lateral root were the characteristics used to identify unemerged root buds; identification was verified by electron microscopy of cryofractured buds. Unemerged root buds have been identified previously by both distinctive external characteristics and lactic acid root clearing (McIntyre & Hunter, 1979; McAllister & Haderlie, 1985a).

Control roots had fewer visible adventitious root buds plus secondary shoots 45 days after the start than at 10 days when the roots were unearthed (Fig. 3), mirroring decreases in root fresh weight (Fig. 2). The number of control root buds plus secondary shoots after 45 days was 53% of that at 10 days, whereas the root fresh weight at 45 days was 20% and 49% of that at 10 days in the first and second trials, respectively.

Glyphosate seems to act on sensitive tissue over an extended period, rather than acting only upon initial exposure. The number of root buds plus secondary shoots continued to decrease in glyphosate-treated plants between the time when roots were unearthed and segmented 10 days after treatment, and 35 days later ($P < 0{\cdot}0001$) (Fig. 3a and b). Higher glyphosate rates were also needed to reduce bud numbers 10 days after treatment than after 45 days. When roots were segmented 10 days after treatment, glyphosate may have been mobilized and transported from root cortical tissue into root buds that were beginning to grow, thus increasing the severity of glyphosate

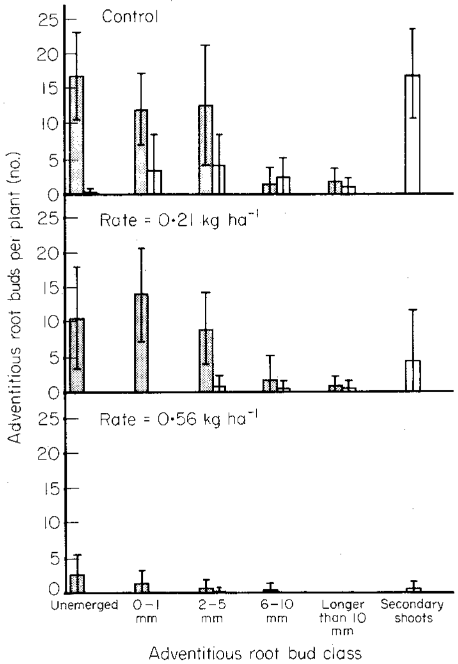

Fig. 4 Effect of glyphosate at 0·21 and 0·56 kg ha^{-1} plus 0·5% (v/v) X-77 surfactant on adventitious root bud number per plant in different size classes 10 (▨) and 45 (□) days after glyphosate application. Means and standard deviations are presented.

damage. Alternatively, the same quantity of glyphosate may have been in secondary shoots after initial entry into root buds, but root bud decomposition may have required more than 10 days to occur. Adventitious root buds were not stimulated to form or elongate in this dose–response experiment, as has been observed when other species were sprayed with glyphosate (Baur, Bovey & Veech, 1977; Baur, 1979; Lutman, 1979; Lee, 1984; Villanueva, Muniz & Tames, 1985; Waldecker & Wyse, 1985).

In addition to reducing numbers of root buds plus secondary shoots, glyphosate altered the proportion of root buds in different size classes (Fig. 4). Between 10 days and 45 days after foliar treatment with 0·21 kg ha^{-1} glyphosate, the number of buds less than 5 mm in length decreased by 97% ($P<0{\cdot}0001$). This dramatic decrease in the number of small root buds was not matched by increases in the number of root buds in larger size classes. Still fewer root buds remained on roots when glyphosate was applied at 0·56 kg ha^{-1}.

Ninety-one per cent of the root buds were less than 6 mm long on control root systems, 10 days after glyphosate application (Fig. 4), but no secondary shoots were present. Thirty-five days later, 26% of the root buds were less than 6 mm long, but 60% of the buds had emerged as secondary shoots. The number of buds longer than 10 mm remained relatively unchanged. Secondary shoots may have been derived directly from shorter root buds, or there may have been a transition of buds from shorter length classes to intermediate length classes, which then formed secondary shoots. These data do not eliminate the possibility of formation of new buds after the roots were segmented, as has been suggested previously (McAllister & Haderlie, 1985b). Individual buds must be identified to determine the formation and transition of root buds into shoots.

Newly emerged secondary shoots had narrow chlorotic leaves and suppressed growth at 0·07 kg ha^{-1} glyphosate or greater (data not presented). However, not all secondary shoots on the same root system were affected to the same degree. This observation, in addition to those on cortical decay, suggests that either glyphosate was unevenly distributed throughout the large *C. arvense* root system, or that there was uneven movement of glyphosate into growing secondary shoots from where glyphosate was translocated in the roots. Most later-emerging leaves on secondary shoots grew normally, but slowly. Eighty-three per cent of secondary shoots had narrow chlorotic leaves 24 days after treatment with 0·07 kg ha^{-1} glyphosate, but only 0·9% of secondary shoots were unable to produce normal leaves after 45 days. Perhaps glyphosate is not remobilized, from where it is stored in the roots to the developing shoot apex, in quantities high enough to inhibit subsequent leaf growth of secondary shoots, even though the first-formed leaves were malformed. In earlier research, glyphosate reportedly caused emerging secondary shoots to become chlorotic and form strap-shaped leaves (Saidak & Marriage, 1976; Beuerman, Hensley & Carpenter, 1984), but damage was not observed over a long enough period to detect normal regrowth after initial restricted growth.

When thickened roots were segmented to stimulate secondary shoot emergence from root buds 10 days after foliar treatment, fewer secondary shoots emerged (Fig. 5) than expected from the number of visible root buds present (Fig. 3) on roots of both control and herbicide-treated plants. Emerged secondary shoot dry weight (Fig.

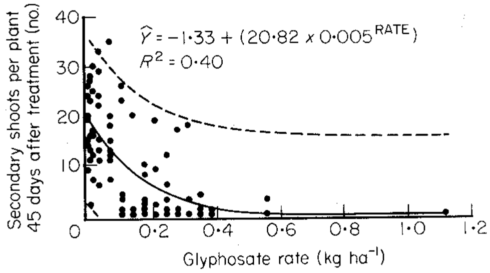

Fig. 5 Effect of glyphosate at various rates plus 0·5% (v/v) X-77 surfactant on *C. arvense* secondary shoot number per plant 45 days after treatment.

6) decreased more rapidly than the secondary shoot number (Fig. 5) with increasing glyphosate rate ($P < 0{\cdot}0001$). For example, numbers of secondary shoots per plant decreased by 72% at 0·21 kg ha^{-1} glyphosate, compared with the control 45 days after initial glyphosate treatment ($P < 0{\cdot}0001$) (Fig. 5). However, secondary shoot dry weight decreased by at least 93% at 0·21 kg ha^{-1} glyphosate, compared with the control (Fig. 6). Some secondary shoots stopped growing after emerging from the vermiculite, but did not die. Many of these secondary shoots were separated from the initial root segment because the base of the secondary shoot or the root cortical tissue decomposed. Secondary shoots were growing under nearly optimum conditions in moist vermiculite, and thus were able to absorb enough water and nutrients to remain alive even though growth

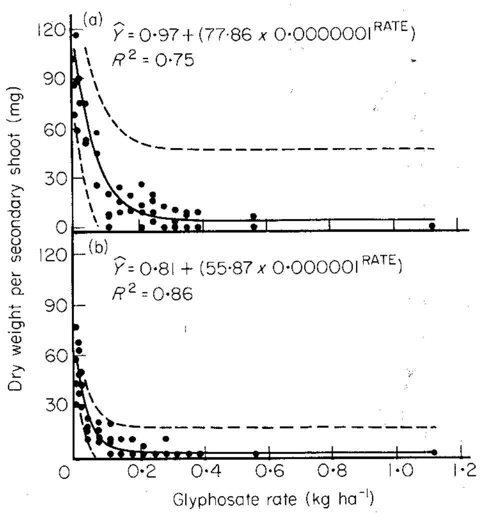

Fig. 6 Effect of glyphosate at several rates plus 0·5% (v/v) X-77 surfactant on *C. arvense* dry weight per secondary shoot 45 days after treatment for trial 1 (a) and trial 2 (b).

had ceased. New roots on some of these secondary shoots were beginning to form at the base of the stem. However, under more competitive conditions, such as in the field, many of these secondary shoots probably would not have survived to establish new plants.

Secondary shoot number and dry weight were decreased by 90% over a very narrow range of glyphosate rates in the glasshouse (Figs 5 and 6). In a previous field study, glyphosate at 1 kg ha^{-1} was required to reduce *C. arvense* shoot number by 51–75%, and 3 kg ha^{-1} glyphosate was needed for a 97–98% reduction, depending upon *C. arvense* variety (subspecies) (Saidak & Marriage, 1976). Secondary shoot number and dry weight were reduced in the present study at much lower rates of glyphosate than recommended for the field. This sensitivity may have been due to more complete spray coverage and greater uptake into the relatively succulent leaves of glasshouse-grown plants, compared with field-grown plants. This sensitivity also may have been due to the variety used in the present study.

Translocation time

When glyphosate at 0·28 kg ha^{-1} was applied to well-established *C. arvense* with extensive roots, enough herbicide translocated to roots between 2 days and 3 days after treatment to inhibit subsequent secondary shoot emergence 45 days later (Fig. 7). Root fresh weight was unchanged in herbicide-treated plants 3 days after foliar treatment (data not presented). The secondary shoot number was reduced almost to zero when glyphosate was allowed to translocate to the root system for 3 days (Fig. 7), but the number of secondary shoots of controls increased linearly over the same 3-day period. Secondary shoot dry weight decreased earlier than secondary shoot number after foliar treatment, and was reduced to zero after approximately 2 days (data not presented). Secondary shoot dry weight of control plants remained unchanged over the same time period. A period of 3 days is recommended between glyphosate application to *C. arvense* and tillage in the field. Three hours were adequate for glyphosate to translocate from sprayed to untreated shoot in an untilled field, as measured by chlorosis and stunting of neighbouring untreated plants (Beuerman, *et al.*, 1984). However, unsprayed, herbicide-stunted shoots were not controlled

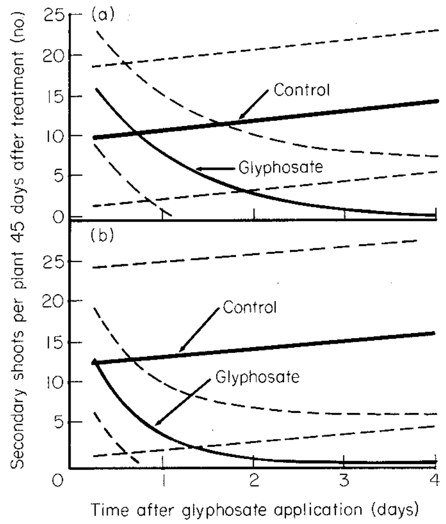

Fig. 7 Effect of time after glyphosate application (0·28 kg ha^{-1} plus 0·5% (v/v) X-77 surfactant) until removal of the primary shoots on the later formation of secondary shoots 45 days after treatment. The regression equations and coefficients of determination (R^2) were: glyphosate A: $\hat{Y}=-0{\cdot}40+(20{\cdot}45\times0{\cdot}4^{\mathrm{TAGA}})$, $R^2=0{\cdot}72$, $P=0{\cdot}0001$; control A: $\hat{Y}=9{\cdot}71+1{\cdot}14\times\mathrm{TAGA}$, $R^2=0{\cdot}11$, $P=0{\cdot}0001$, glyphosate B: $\hat{Y}=-0{\cdot}41+(19{\cdot}45\times0{\cdot}2^{\mathrm{TAGA}})$, $R^2=0{\cdot}70$, $P=0{\cdot}0001$, control B: $\hat{Y}=12{\cdot}26+0{\cdot}97\times\mathrm{TAGA}$, $R^2=0{\cdot}048$, $P=0{\cdot}0003$. TAGA = time after glyphosate application until shoot removal. The best fitting regression curves (——) and 95% confidence intervals (– – –) are presented for the first (a) and second (b) trials of this experiment.

when glyphosate was allowed to translocate for 3 days.

Our data demonstrate that sufficient foliar-applied glyphosate was absorbed and translocated to roots of *C. arvense* to prevent secondary shoot emergence totally, 45 days after roots were unearthed, segmented, and placed in vermiculate to resprout (Fig. 7). While further foliar uptake of glyphosate may occur after 3 days if treated plants are not disturbed, it is unlikely to enhance the herbicide's effectiveness in preventing secondary shoot growth from root buds. Sandberg *et al.* (1980) observed that small glasshouse-grown *C. arvense* absorbed most foliar-applied ^{14}C-glyphosate in 3 days, but continued to translocate the herbicide to untreated secondary shoots between 3 days and 14 days after treatment. Our data suggest that such an extended period of translocation is unimportant for control of emerging secondary shoots (Fig. 7). However, one must question the significance of experiments using ^{14}C-herbicides applied to foliage in microdrops to study herbicide absorption and translocation when most foliage is not sprayed with unlabelled herbicide (e.g. Sandberg *et al.*, 1980). Glyphosate may inhibit its own translocation in *C. arvense*; a 'cold' pretreatment may prevent further ^{14}C-glyphosate translocation after 3 days.

Glyphosate damage to annual and perennial plant shoots is well documented, but there are few reports quantifying effects on root systems. This is the first report to document quantitative effects of glyphosate at various rates on root bud numbers and secondary shoot emergence of well-established, glasshouse-grown *C. arvense* with extensive roots. It is also the first report to characterize herbicide effects on different size classes of root buds, and monitor quantitative changes in these classes over time.

Fewer plants per treatment ($n=4$) were needed in these experiments with glyphosate than with earlier research with chlorsulfuron ($n=8$ or 9) to observe treatment differences (Donald, 1984). Research with large perennial *C. arvense* is reproducible within limits if care is taken (see Materials and methods section). This greenhouse research complements field observation in that data are expressed per plant rather than on a per hectare basis. Gathering such data in the field would be technically difficult.

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