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Source: Weed Technology, 25(4):580-585. 2011.
Published By: Weed Science Society of America
DOI: http://dx.doi.org/10.1614/WT-D-10-00135.1
URL: http://www.bioone.org/doi/full/10.1614/WT-D-10-00135.1

Weed Technology 2011 25:580–585

Differential Response of Liverwort (*Marchantia polymorpha*) Tissue to POST-Applied Quinoclamine

James E. Altland, Glenn Wehtje, Jeff Sibley, Michael E. Miller, Charles H. Gilliam, and Charles Krause*

Quinoclamine is used in Europe, and was under evaluation in the Unites States for the control of liverwort in nursery crops. Liverwort is a nonvascular, chlorophyll-containing plant that can be problematic in greenhouse and nursery crops. POST-applied quinoclamine controls liverwort. However, liverwort structures vary in their sensitivity to POST-applied quinoclamine. Specifically, archegonial receptacles (female) are much more tolerant of quinoclamine than either antheridial receptacles (male) or thalli (leaflike structures). A series of studies were conducted to, first, document the degree of differential sensitivity between tissues to quinoclamine, and second, to determine the basis of this differential sensitivity. The dose that results in 50% of the population being controlled (I_{50}) of antheridial receptacles and juvenile thalli were estimated to be 1.60 and 1.27 kg·ha^{-1}, respectively. The I_{50} of archegonial receptacles could not be estimated, but exceeded 10.45 kg·ha^{-1}. Chlorophyll content varied between liverwort tissues, but the content did not correlate to quinoclamine sensitivity. Absorption of ^{14}C after application of radiolabeled quinoclamine was less in archegonial receptacles than in either antheridial receptacles or thalli. Scanning electron microscopy of the surface of the liverwort tissues revealed that archegonial receptacles had smaller pores (equivalent to stomata in higher plants) than either antheridial receptacles or thalli. The tolerance of archegonial receptacles to quinoclamine can be partially, but not exclusively, attributed to reduced absorption. This reduced absorption may be attributed to the limited pore size and less total pore area of the archegonial receptacles.
Nomenclature: Liverwort, *Marchantia polymorpha* L.; quinoclamine.
Key words: Chlorophyll, Bryophyta, herbicide absorption, nursery crops, ultrastructure.

La quinoclamina es usada en Europa y se estuvo evaluando en los Estados Unidos para el control de *Marchantia polymorpha* en cultivos en viveros. *M. polymorpha* es una planta no vascular, que contiene clorofila y que puede ser problemática en invernaderos y viveros. Las aplicaciones POST de quinoclamina controlan *M. polymorpha.* Sin embargo, las estructuras de esta planta varían en su sensibilidad a quinoclamina aplicada POST. Específicamente, los arquegonios (órgano reproductor femenino) son mucho más tolerantes a la quinoclamina que los anteridios (órgano reproductor masculino) o los talos (estructura compuesta con semejanza de hoja). Se realizaron una serie de estudios para poder primero, documentar el grado de sensibilidad diferencial entre tejidos al quinoclamina y segundo, para determinar las bases de esta sensibilidad diferencial. El I_{50} de los anteridios y talos jóvenes se estimaron en 1.60 y 1.27 kg ha^{-1} respectivamente. El I_{50} de los arquegonios no pudo ser estimado, pero excedió 10.45 kg ha^{-1}. El contenido de clorofila varió entre los tejidos de *M. polymorpha,* pero el contenido no tuvo correlación con la sensibilidad a la quinoclamina. La absorción de ^{14}C después de la aplicación de quinoclamina radioetiquetada fue menor en los arquegonios que en los anteridios o talos. El escaneo de la superficie de los tejidos de *M. polymorpha* con microscopio electrónico reveló que los arquegonios tuvieron poros (equivalentes a estomas en plantas superiores) más pequeños que los anteridios o talos. La tolerancia de los arquegonios a la quinoclamina, puede atribuirse parcial más no exclusivamente a una absorción reducida. Esta reducción en la absorción puede atribuirse al tamaño limitado de los poros y a una menor área total de poros en los arquegonios.

Liverwort is a nonvascular, chlorophyll-containing plant that is problematic in greenhouse and nursery crops. Liverworts are characterized by thalli, which are leaflike structures that grow prostrate over the soil or substrate surface. Liverwort can reproduce by sexual and asexual means. The sexual cycle results in airborne spores, which can also be disseminated by splashing of irrigation or rain (Svenson 1997). The sexual cycle utilizes archegonial and antheridial receptacles, which are two distinctly different structures borne on stalks that extend above thalli. The antheridial receptacle is male and produces sperm. Sperm are transferred by water to female archegonial receptacles. Upon fertilization and subsequent meiosis, spores are produced and released from the archegonia. Asexual propagation is by either asexually produced diaspores termed gemmae, or by thallus fragmentation.

Liverwort thrives in the low-light, high-humidity, and high-fertility conditions associated with plant nurseries (Svenson 1998). The herbicide quinoclamine is labeled for POST liverwort control as a broadcast application to nursery crops in some European countries. Excellent liverwort control combined with minimal phytotoxicity to a broad spectrum of ornamental species has been documented (Vea and Palmer 2006). Early research indicated that very high spray volumes (e.g., $>$ 100 gallons per acre) were required for quinoclamine to be effective (Vea and Palmer 2006). However, Altland et al. (2007) established that control was influenced only by quinoclamine application rate; neither spray volume nor spray pressure influenced quinoclamine efficacy. This research also established that ^{14}C absorption followed by ^{14}C-quinoclamine application into liverwort thalli approached 61% of the amount

DOI: 10.1614/WT-D-10-00135.1
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applied within 6 h after application. Although liverwort lacks vascular tissue, absorbed ^{14}C after ^{14}C-quinoclamine application was readily translocated away from the site of entry. In a subsequent study (Altland et al. 2008), quinoclamine was readily adsorbed by the media in which nursery crops are grown. The relatively small proportion that was not adsorbed and remained biologically active in solution was sufficient to provide PRE control of gemmae.

A frequent observation made by the authors during these aforementioned studies was that liverwort tissues varied in sensitivity to POST-applied quinoclamine. Specifically, archegonial receptacles were much more tolerant of quinoclamine than either antheridial receptacles or thalli. Generally in herbicide–plant interactions, flowering and fruiting structures are more sensitive to POST-applied herbicides than foliage. For example, application of dicamba or 2,4-D during vegetative growth resulted in less injury or yield reduction compared with applications during flowering or pegging of flax (Nalewaja 1969), soybean (Wax et al. 1969), wheat (Klingman 1953), and peanut (Keterchersid et al. 1978). However, in transgenic, glyphosate-tolerant cotton, tolerance is manifested largely in the foliage but not in the flowers (Pline et al. 2001).

Quinoclamine is a photosynthesis-inhibiting herbicide that removes electrons from photosystem I in a manner analogous to the bipyridinium herbicides, e.g., paraquat and diquat. However, all liverwort tissues, including archegonial receptacles, are green in appearance, indicating the presence of chlorophyll and a likely site for active photosynthesis. Thus the differential tolerance of these liverwort tissues to quinoclamine is puzzling. The first objective of this research was to confirm and measure the differential tolerance of selective liverwort tissues to quinoclamine. The second objective was to explore possible mechanisms for tolerance of archegonial receptacles, if any were observed. Three possible tolerance mechanisms examined were: differential absorption of quinoclamine, differential chlorophyll content, and differential anatomy or ultrastructure.

Materials and Methods

General Information. Test plants were grown and treated plants maintained in a double-layer polyethylene greenhouse located at Auburn University, Auburn, AL. The greenhouse was equipped with evaporative cooling that operated whenever the temperature within the greenhouse exceeded 23 C. Only natural lighting was received and day length ranged from a minimum of 10.9 h (midwinter) to 12.5 h November 2006 and March 2007.

Liverwort plants were grown in 10-cm^2 pots. Pots were filled with a pine-bark and sand (6 : 1 v/v) substrate that had been amended with a controlled-release granular fertilizer.[1] Media-filled pots were placed under mist irrigation and were interspersed with liverwort-infested pots. Juvenile liverwort plants typically established in the new pots within 1 mo. A 25% wettable powder formulation of quinoclamine was used. All experiments were repeated at least once. For all experiments data were pooled over all repetitions since no treatment-by-experimental repetition interactions were detected in the initial statistical analysis.

Differential Sensitivity of Liverwort Structures to Quinoclamine. Four liverwort tissue types were included: thalli from juvenile plants, thalli from mature plants, archegonial receptacles, and antheridial receptacles. To obtain these four tissues, two populations of liverworts were used. The first population, which supplied the juvenile thalli, was approximately 2 mo old at time of treatment. Thalli of the liverwort plants had not reached the pot edge and formation of antheridial or archegonial receptacles was minimal. The second population, which supplied the remaining three tissues, was approximately 6 mo old. Thalli extended over the pot edge, and in many cases new thalli were growing on top of older thalli. These very mature plants also had a very high number of both archegonial and antheridial receptacles.

Quinoclamine was applied at nine rates, from 0.17 to 10.45 $kg \cdot ha^{-1}$. Treatments were applied at 1,112 $L \cdot ha^{-1}$ at a pressure of 276 kPa within an enclosed-cabinet spray chamber with extended-range flat-fan spray nozzles.[2] Treatments were applied at approximately 9:00 A.M. and treated plants were not irrigated for 12 h. Control was rated 1 wk after treatment using a scale where 0 indicated no observable effect and 100 indicated complete death. Both liverwort populations were treated simultaneously, and each of the four aforementioned tissues was rated separately. A completely random design with four single pot replicates was used.

Nonlinear regression using SAS®[3] followed by a lack-of-fit test as described by Seefeldt et al. (1995) were used to compare quinoclamine response among liverwort tissue types. Briefly, assuming that the response of a particular structure to quinoclamine could be described by the log-logistic model, this procedure first determines whether the response to quinoclamine was equivalent or different between tissue types. If a significant difference is detected, this procedure can subsequently determine which of the four parameters (upper limit, lower limit, dose controlling 50% of the population [I_{50}], and slope) of the log-logistic model are equivalent or different between the two treatment series. SigmaPlot®[4] was used to summarize and graph data for presentation. If the data did not fit either a nonlinear or a linear response, treatment means and standard deviations are graphically presented.

Differential Absorption of ^{14}C-Quinoclamine by Liverwort Structures. The intent of this experiment was to determine quinoclamine absorption in three liverwort tissues or structures: i.e., archegonial and antheridial receptacles, and juvenile thalli. We hypothesized that the tolerance of archegonial receptacles to quinoclamine may be the result of minimal quinoclamine absorption. Representative samples of each of these three structures were selected from within pots covered with liverwort, and marked with colored pins. No more than four experimental units of each structure were selected from within a common pot, and the distance separating individual experimental units was at least 4 cm.

A portion of the spray suspension used in the previous experiment, mixed at 1.71 $kg \cdot ha^{-1}$ and 180 L ha^{-1}, was retained and supplemented with ring-labeled ^{14}C-quinoclamine so that the radioactivity concentration was 90 kBq μl^{-1}. A single 2-µl drop was then applied using a microapplicator to the selected liverwort tissues. The ^{14}C-quinoclamine was applied to archegonial and antheridial structures in the natural upright position and when tilted 90° from their upright position. The intent in treating receptacles held 90° from upright was to

Table 1. Results of nonlinear regression evaluating the relative sensitivity of selected liverwort structures to POST-applied quinoclamine.

Liverwort structure	Parameters for log-logistic equation[a]				r^2	Lack of fit
	Upper limit	Lower limit	I_{50}	Slope		
	%		kg ha^{-1}			probability
Thalli, juvenile	103	−6	1.27	1.9	0.95	NA
Thalli, mature plant	110	−1	3.36	1.9	0.93	< 0.01[b]
Antheridial receptacles (male)	102	−3	1.60	2.4	0.88	0.73[c]
Archegonial receptacles (female)	Regression analysis NA; see Figure 1.					NA

[a] The log-logistic equation is: $y = L + (U - L)/(1 + [x/I_{50}]^{slope})$, where L = lower limit, U = upper limit, and I_{50} = dose in which 50% of the population is controlled.

[b] Comparison between thalli of juvenile plant and thalli of mature plant.

[c] Comparison between thalli of juvenile plant and antheridial receptacles.

prevent the 2-µl droplet of ^{14}C-quinoclamine solution from falling from the upper surface of the archegonial receptacles and becoming encumbered in the spore-producing surfaces on the abaxial surfaces. Treated receptacles were discarded if droplet roll-off was observed during application. Treated tissues were harvested 6 h after treatment. Treated thalli were detached from the remainder of the plant using a scalpel. With juvenile thalli, the scalpel was used to sever the rhizoids that anchored the thalli to the media. Treated archegonial and antheridial receptacles were harvested by severing the supporting stalk at its base. Each tissue was added to a 20-ml scintillation vial containing 1 ml of a water : methanol solution [50 : 50 (v/v)] and agitated with a swirling motion for 30 s to remove any unabsorbed ^{14}C. After removing the structure, 10 ml of scintillation fluid was added into the vial in preparation for counting through liquid scintillation spectrometry.[5] The treated structure was dried at 45 C for 24 h, combusted in a biological tissue oxidizer,[6] and recovered radioactivity quantified through liquid scintillation spectrometry. In preliminary trials we recovered 93 to 105% of the amount applied. In light of the nearly complete recovery, data were normalized to 100% on the basis of the amount applied across all liverwort tissues evaluated. No attempt was made to determine whether recovered radioactivity represented unaltered parent quinoclamine or quinoclamine metabolite(s). For each experimental unit, radioactivity recovered in the wash and that recovered from within the liverwort structures (i.e., unabsorbed and absorbed, respectively) were summed. By expressing these two values as a percentage of the total radioactivity recovered, absorption as a percentage of the amount applied was calculated. An individual experimental unit consisted of a single treated liverwort tissue sample. A completely randomized experimental design was used with eight replications in the first experimental repetition and six replications in the second. Absorption data were subjected to ANOVA using the general linear model procedure in SAS and means between individual liverwort structures compared with Fisher's Protected LSD test at the 0.05 level.

Differential Chlorophyll Content of Liverwort Structures. Extraction of chlorophyll (CHL) from fresh foliage followed methods outlined by Inskeep and Bloom (1985) using *N*, *N*-dimethylformamide (DMF). Ten containers with liverwort populations were randomly selected from the aforementioned greenhouse. From each container, five thallus fragments, five antheridial receptacles, and five archegonial receptacles were removed, rinsed in deionized water, and air-dried for 5 min. A paper hole punch (0.31 cm^2) was used to remove thallus disks from each fragment. Archegonial and antheridial receptacles were severed from their stalks. Disks were weighed and placed in sealed test tubes containing 5 ml of DMF. Tubes were placed in a revolving rack at 4 C, in darkness, for 24 h to extract CHL. Extracts were assayed with a double-beam spectrophotometer[5] for differences in attenuances at 647 and 664.5 nm (Inskeep and Bloom 1985). Data were subjected to ANOVA using the general linear model procedure in SAS and means between individual liverwort structures compared with Fisher's Protected LSD test at the 0.05 level.

Differential Anatomy and Ultrastructure of Liverwort. Liverwort tissues were examined with a scanning electron microscope (SEM).[7] Ten samples for each tissue type, about 5 mm^2, were excised with a scalpel. All SEM specimens were fixed in 3% gluteraldehyde and 2% paraformaldehyde in a 0.1 M phosphate buffer. This was followed by dehydration in a series of ethanol and water mixtures. Samples were then critical-point dried in an Auto Samdri-814 drier,[8] mounted on aluminum stubs, and coated with gold palladium in a sputter coater.[9] Specimens were examined with a SEM operated with a 20-kV accelerating current and a 15-mm working distance. Four fields were examined within each sample. Within a field, pore number was recorded and pore diameter measured using the Quartz PCI v. 5[10] measuring tool synchronized with the SEM. Pore numbers were square-root-transformed before analysis, but back-transformed data are presented for clarity. Data were subjected to ANOVA using the general linear model procedure in SAS and means between individual liverwort structures compared with Fisher's Protected LSD test at the 0.05 level.

Examination of Quinoclamine in Solution. Quinoclamine solution was prepared with a concentration of 15 mg·ml^{-1}, which is the approximate concentration of quinoclamine at 1.71 kg·ha^{-1} in a spray volume of 1,112 L·ha^{-1}. A droplet of the suspension was placed on a SEM stub and allowed to air dry. Three droplets were placed on each stub. The 25% wettable powder of quinoclamine (dry formulated product) was sprinkled on a separate stub. All stubs were coated with platinum before placing in the SEM and viewed with 10-kV accelerating current. A droplet of the aforementioned quinoclamine solution, as well as the dry 25% wettable powder, was also applied to a glass slide and examined under a light microscope at ×20 magnification. A general description of the spray solution and particle sizes was recorded.

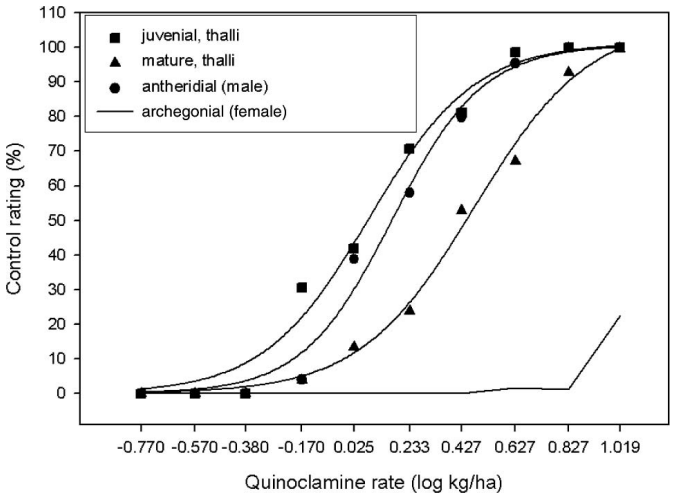

Figure 1. Regression analysis of quinoclamine sensitivity by selected liverwort tissues. Parameter estimates of regression analysis are presented in Table 1.

Results and Discussion

Differential Sensitivity of Liverwort Structures to Quinoclamine. The response of juvenile thalli, mature thalli, and antheridial tissues to quinoclamine could be described as a log-logistic response with r^2 values of ≥ 0.88 (Table 1 and Figure 1). As expected, juvenile thalli were most sensitive, with I_{50} value of 1.27 kg·ha^{-1}. Differences between juvenile and mature thalli were attributed solely to differing I_{50} values. A higher I_{50} for mature thalli indicates that a higher quinoclamine rate is required for control compared with juvenile thalli. Others have reported greater control of juvenile liverwort, compared with mature liverwort, with quinoclamine (Newby et al. 2006; Senesac 2005) and other herbicides (Newby et al. 2007). The response of antheridial receptacles to quinoclamine was equivalent to that of the juvenile thalli ($P = 0.730$; Table 1). In contrast, archegonial receptacles were only affected by the highest rate evaluated (10.45 kg·ha^{-1}), and only nominal injury was observed at this rate (Figure 1). As observed in preliminary studies, archegonial receptacles are more tolerant to quinoclamine than either thalli or antheridial receptacles.

Differential Absorption of ^{14}C-Quinoclamine by Liverwort Structures. Thalli absorbed 48.3% of applied radioactivity after application of ^{14}C-quinoclamine (Table 2). This is similar to previous research showing 61% absorption in thalli (Altland et al. 2007). Archegonial receptacles absorbed less ^{14}C than either thalli or antheridial receptacles. Although this difference was significant, it was not sufficient to explain the lack of response in archegonial receptacles. We speculated that ^{14}C droplets could have been shed from the upright receptacles and thus artificially depress the amount of recovered ^{14}C in those structures. However, application of a 2-µl droplet to receptacles held 90° from their upright position resulted in relatively similar amounts of recovered ^{14}C compared with those in the upright position (Table 2). Similar ^{14}C absorption in both upright and tilted receptacles led us to reject our hypothesis that spray droplets were shed from the receptacle. These data suggest that approximately 40% less herbicide is absorbed into archegonial tissue compared with thallus and antheridial tissue. However, Figure 1 shows that control of archegonial tissue was far less than what one would predict with just 40% less active ingredient. Thus some other mechanism, alone or in combination with the amount absorbed into tissue, is responsible for reduced control.

Differential Chlorophyll Content of Liverwort Structures. Chlorophyll content varied between the liverwort tissues (Table 2). Across all three tissue types, chlorophyll content was low compared with that in higher plants (Sibley et al. 1996). This was expected considering that thalloid liverworts have a relatively thin layer of photosynthetic tissue on the dorsal surface, covering the much thicker layer of nonphotosynthetic parenchyma tissue (Hill et al. 1960). Chlorophyll content of the liverwort tissues did not reflect their respective quinoclamine sensitivity. Chlorophyll content was highest in the thalli (1.09 µg·g^{-1}) and lowest in the antheridal receptacles (0.29 µg·g^{-1}), both of which are sensitive to quinoclamine (Table 2). The archegonial receptacles, which display no response to quinoclamine at proposed labeled rates, had a chlorophyll content that was intermediate to that of the thalli and antheridal receptacles, i.e., 0.72 µg·g^{-1}.

Differential Anatomy and Ultrastructure of Liverwort Tissues. Pore size varied among liverwort tissues (Table 2, Figure 2). Pore sizes of thalli and antheridial tissues were

Table 2. Parameters that were investigated as possible explanations for the differential sensitivity between liverwort tissues to POST-applied quinoclamine.

	^{14}C-Quinoclamine absorption[a]			Pore characteristics			
Liverwort tissue	Plants vertical	Plants horizontal[b]	Chlorophyll content	Pore number	Pore diameter	Area per pore	Total pore area
	% of applied		µg g^{-1} tissue	# mm^{-2}	µm	µm^2	µm^2 mm^{-2}
Archegonial receptacles (female)	29.3 b[c]	22.2 b	0.72b	140 a	16 b	203 b	28,420
Antheridial receptacles (male)	48.0 a	55.3 a	0.29c	86 ab	33 b	852 b	73,272
Thalli, juvenile	48.2 a	—	1.09a	60 b	37 a	1,076 a	64,560

[a] Quinoclamine suspension that had been prepared to deliver a 1.71 kg ha^{-1} and 180 L ha^{-1} rate was supplemented with ^{14}C-quinoclamine. Single, 2-µl drops were applied.

[b] Plants were tilted 90° from their normal vertical position. Intent was to preclude the possibility of the 2-µl droplet of ^{14}C-quinoclamine solution from falling from the upper surface of the archegonial receptacles and becoming encumbered in the spore-producing surfaces on the abaxial surfaces.

[c] Means followed by different letters are significantly different by Fisher's Protected LSD test at the 0.05 level.

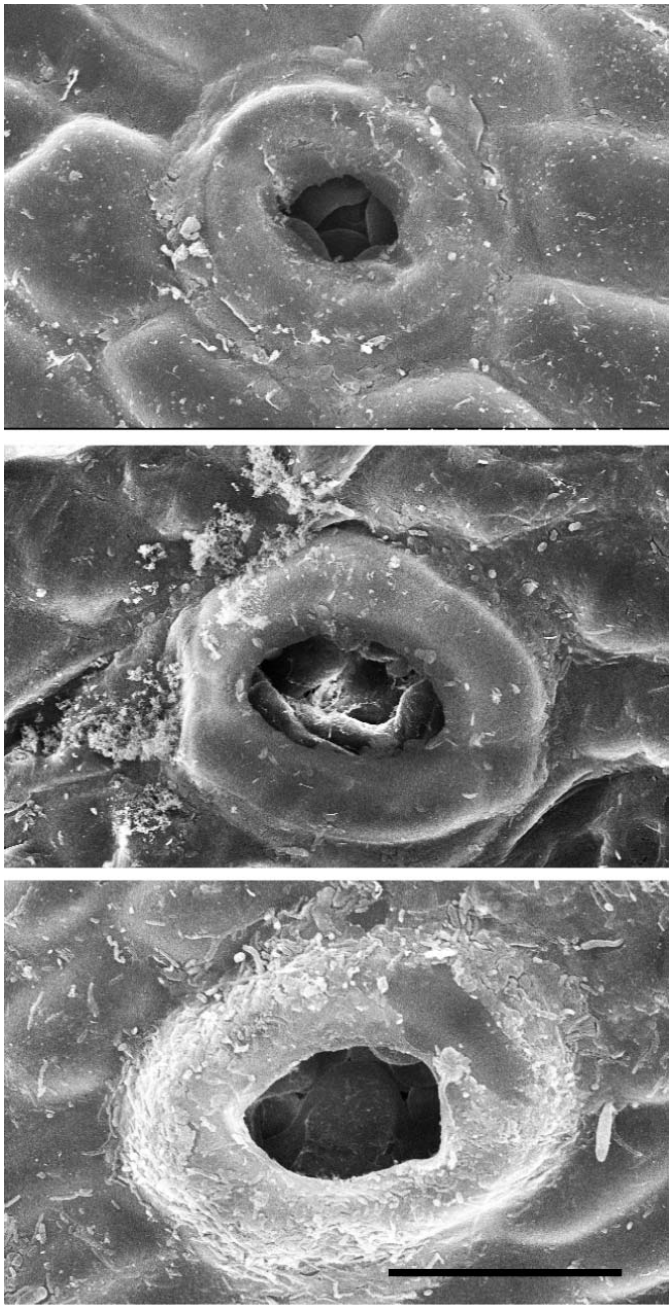

Figure 2. Relative pore size of representative archegonial (top), antheridial (middle), and thallus (bottom) tissues. All photos are at ×1,500 magnification. The solid black bar represents 30 μm.

similar at 37- and 33-μm diam, respectively, and were similar to those in images presented by Schönherr and Ziegler (1975). Pore size of archegonial pores were smaller, about 16 μm in diameter. Average dimensions of elliptical-shaped stomata in higher plants is about 18 μm long and 6 μm wide, with the area of the opening in 37 species of cultivated plants averaging 92 μm^2 (Hill et al. 1960). By comparison, liverwort pores of all tissue types are more circular in shape and have greater surface area than those found in higher plants (Table 2). Characteristics of the surface pores of the liverwort tissues provide partial agreement with their respective quinoclamine sensitivity. Radioactivity absorbed by the archegonial receptacles was only 29.3% of the applied amount (Table 2). Absorption by antheridial receptacles and thalli was 48.0 and 48.3%, respectively. Examination of the liverwort surface tissues with SEM revealed that individual pores in the archegonial receptacles were at least 50% smaller in diameter, and thus about 75% smaller in open area than the pores in antheridial receptacles or thalli (Table 2). Although archegonial receptacles had a greater number of pores per surface area than antheridial receptacles or thalli, the total amount of pore area was calculated to be about 56% less in the archegonial receptacles than in either antheridial receptacles or thalli.

The relatively large pore openings of liverwort thalli and antheridial tissue compared with the archegonial tissue could explain the apparent dichotomy in control vs. no control in these liverwort tissues. A broad spectrum of higher plants is reported to have no negative response to quinoclamine applications (Vea and Palmer 2006). Stomatal opening size varies by plant species, but the aforementioned average of 92 μm^2 for higher plants (Hill et al. 1960) fits with the notion that pore/stomata size opening governs the uptake of quinoclamine and subsequent herbicidal activity.

Examination of Quinoclamine in Solution. Examination and comparison of a quinoclamine suspension and dry particles under light microscopy confirmed that the particles of the wettable powder formulation of quinoclamine are largely unaffected when mixed with water. The particles remain intact, and are neither appreciably dissolved nor reduced in size. SEM of a quinoclamine suspension showed a range of particle sizes from 2.1 to 46.1 μm in width (data not shown) with irregular shapes, although most particles were approximately 3 to 5 μm in width. When mixed at the proposed labeled rate in a spray volume of 1,112 $L \cdot ha^{-1}$, the concentration of quinoclamine in water is 15 $mg \cdot ml^{-1}$. Solubility of quinoclamine is only 0.0207 $mg \cdot ml^{-1}$ at 20 C. Thus, less than 0.5% of the quinoclamine suspended in a spray droplet would be in solution. It is unlikely that quinoclamine in solution accounts for all the herbicidal activity in thalli or antheridial tissue. It is likely that mass movement of the spray droplets with suspended quinoclamine particles through open pores is necessary for complete control. Although quinoclamine particle sizes are generally smaller than all liverwort pore types, the relatively large pore size of thalli and antheridial tissues likely facilitates movement of a quinoclamine suspension into the inner cavities where chloroplasts are present. Conversely, the smaller size of pores in archegonial tissue and stomata in higher plants restricts mass movement of quinoclamine suspensions; thus relatively little or no control is realized.

As a 25% wettable powder, the manufactured product leaves a dense coating of residue on plant foliage at the recommended rates (3.8 to 7.6 $kg \cdot ha^{-1}$ ai) for several days (personal observation). Some injury on ornamental crops at the recommended rates was speculated to be merely from high residue levels that blocked light or otherwise interfered with normal functioning of the leaf surface, and not from any sort of herbicide activity within the plant. Thus injury to antheridial structures at the highest rate (10.45 $kg \cdot ha^{-1}$) may not have been the result of herbicide activity on photosystem I, but instead indirect injury from high herbicide residue levels.

In conclusion, the archegonial receptacles absorbed less radioactivity after application of ^{14}C-quinoclamine than either antheridial receptacles or thalli. This differential absorption can likely be attributed to different pore characteristics. However, in the opinion of the authors, the differential absorption resulting from differential pore characteristics provided only a partial explanation for the differential quinoclamine sensitivity. As previously mentioned, both antheridial receptacles and thalli are sensitive, whereas archegonial receptacles are not affected by quinoclamine applied at the proposed labeled rates. Thus we conclude that other factors beyond those that we evaluated here are likely involved.

Sources of Materials

[1] Granular, slow-release fertilizer, Polyon® 17N-6P-12K, available from Harrell's Fertilizer, Inc., 203 West 4th Street, Sylacauga, AL 35105.

[2] XR TeeJet®, available from Spraying Systems, P.O. Box 7900 Wheaton, IL 60189-7900.

[3] SAS ® Statistical Analysis System Software. Release 8.3, SAS Institute, Inc., Box 8000, SAS Circle, Cary, NC 27513.

[4] SigmaPlot® 2000 for Windows® Version 6.00, Systat Software Inc., 501 Canal Boulevard, Suite E, Point Richmond, CA 94804-2058.

[5] Spectrophotometer model 25, Beckman Instruments, Irvine, CA 92620.

[6] OX 700, R. J. Harvey Instruments, 11 Jane St., Tappen, NY 10983.

[7] Hitachi S4700 scanning electron microscope, Hitachi High Technologies America Inc., 5201 Great America Parkway, Pleasanton, CA 94588.

[8] Auto Samdri-814 Drier, Tousimis Research Corp., P.O. Box 2189, Rockville, MD 20852.

[9] Hummer 6.2, Anatech, 2947 Whipple Rd., Hayward, CA 94540.

[10] Quartz PCI v. 5, Quartz Imaging Corp., 403-6190 Agronomy Road, Vancouver, BC V6T 1Z3, Canada.

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Received October 6, 2010, and approved May 10, 2011.