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Endothall absorption and translocation by curly-leaved and sago pondweed

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ABSTRACT

Curly-leaved pondweed (*Potamogeton crispus* L.) (CLP) and sago pondweed [*Stuckenia pectinata* (L.) Börner] (SGP) are perennial, submersed aquatic species in the Potamogetonaceae family that produce perennating structures. CLP is an introduced species that infests water bodies across the United States, while SGP is a native species that becomes problematic in irrigation canals. These plant species are often managed using endothall (7-oxabicyclo[2.2.1]heptane-2,3-dicarxylic acid), but they respond differently to the herbicide even though they belong to the same plant family. The objective of this research was to determine if endothall behaved differently enough in these two species to explain the differential plant response. SGP plants were treated with a high endothall concentration (3 mg L^{-1}) and CLP plants with a high and a low endothall concentration, 3 and 0.75 mg L^{-1}, respectively. Endothall absorption and translocation was determined over a 192-h time course. Endothall absorption by CLP and SGP was slow; however, total accumulation was four to seven times higher than the concentration found in the water column. Endothall shoot-to-root translocation was limited in both species. CLP translocated 3.0% $\pm$ 0.23 and 3.6% $\pm$ 0.45 at 3 and 0.75 mg L^{-1} endothall, respectively, while SGP translocated 1.1% $\pm$ 0.02 when exposed to 3 mg L^{-1} endothall. Translocation to the mature tuber or turion that produced the plant was even more limited. The results of this study support the previously research that endothall can be translocated to the roots of aquatic plants; however, there was no evidence to explain differential response between SGP and CLP based on endothall behavior.

Key words: herbicide uptake, *Potamogeton crispus*, radiolabeled, *Stuckenia pectinate*.

INTRODUCTION

Invasive aquatic plants can adversely affect entire aquatic ecosystems and impact human activities such as water distribution, navigation, and recreation. Many invasive aquatic plants form extensive, undesirable surface canopies that negatively affect water quality and native plant communities by limiting light penetration, significantly lowering dissolved oxygen, and increasing water temperature, and they can also impact recreational uses of a water body such as swimming, fishing, and boating (Newroth 1985; Smith and Barko 1990; Madsen et al. 1991; Nikora et al. 2008).

Curly-leaved pondweed (*Potamogeton crispus* L.) (CLP) is a submersed aquatic macrophyte in the Potamogetonaceae family, native to Europe, Asia, Africa, and Australia, which was first identified in the United States in 1859 in Delaware (Stuckey 1979). Since then it has spread and established itself across the entire continental United States. It is an herbaceous perennial monocotyledonous plant with a life cycle that differs from most submerged species (Nichols and Shaw 1986). CLP is considered a cool water plant; however, it is found in a wide range of growing conditions, from very warm temperatures to ice-covered water with very low light intensities (Gettys et al. 2014). CLP is photosynthetically efficient even at low light intensities, which gives it a competitive advantage over most native species that rely on sexual reproduction and start growth from seeds or initiate growth under warmer water temperatures (Nichols and Shaw 1986). CLP reproduces primarily by producing turions, which are hardened modified reproductive buds that form at the shoot apex and leaf axils, but it also produces rhizomes and viable seeds (Barr and Ditomaso 2014). Plants achieve their maximum density in late spring, which is when they flower and produce turions. These turions remain dormant during the summer and sprout in the fall when daylength shortens and water temperatures drop (Netherland et al. 2000).

Sago pondweed [*Stuckenia pectinata* (L.) Börner] (SGP) is a native submersed macrophyte that is also in the family Potamogetonaceae (Kaplan 2008). It can be found worldwide but occurs most often in temperate regions. In these climates, SGP is one of the first species to initiate growth in the spring, providing an advantage compared to other native species that initiate growth later in the spring and summer (Kantrud 1990). Although it is native to the United States and an important source of food for wildlife and waterfowl, SGP can cause localized problems in lakes and is a major problem in flowing water, such as irrigation and drainage canals (Sisneros and Turner 1995; Bentivegna et al. 2004). Once established, SGP forms dense, monotypic stands that can clog irrigation canals and significantly reduce water flow (Bal et al. 2006). SGP spreads primarily through rhizomes but persists through the production of subterranean tubers (Spencer et al. 1989). A single plant can produce tens of thousands of tubers in one growing season, thus making it a very prolific colonizer (Yeo 1965).

Management in early spring can provide selective control of both CLP or SGP by interrupting the growth and

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reproductive cycle prior to the growth of other native species. There are a range of mechanical, cultural, physical, and biological methods available for invasive aquatic plant management; however, one of the most cost-effective methods for selective management of invasive aquatic plants is through the use herbicides labeled for that purpose. Endothall (7-oxabicyclo[2.2.1]heptane-2,3-dicarxylic acid) is a serine/threonine protein phosphatase inhibitor (Tresch et al. 2011; Bajsa et al. 2012) that controls a broad weed spectrum including monocotyledons, such as CLP and SGP, and dicotyledons (Westerdahl and Getsinger 1988; Madsen 1997). Although CLP and SGP are in the same plant family, they respond differently to endothall treatments. CLP appears to rapidly dissolve when treated with endothall, while SGP takes much longer to show symptoms, the first symptom being a general chlorosis.

Understanding the differential plant response to an herbicide is important, especially for long-term control of perennial species such as CLP and SGP. We hypothesized that herbicide accumulation and translocation from shoots to roots and subterraneous structures are different in these two plant species. Therefore, the objectives of this study were (1) to determine endothall absorption over a 192-h time course and (2) to determine translocation patterns of endothall in SGP and CLP.

MATERIALS AND METHODS

Plant material

CLP turions were collected in the fall of 2015 from Leggett Ditch, north of Boulder, CO (4013′N; 10508′W) and cultured under greenhouse conditions for two years. To produce uniform plant material for the research, turions of similar size were planted in 16 cm × 12 cm × 6 cm (1,152 cm^3) plastic pots filled with clay loam soil collected from Colorado State University's organic research farm and topped with 0.5 cm of play sand. Each pot was fertilized with 2 g of slow-release fertilizer[1] placed at the bottom of each pot. Six turions were planted uniformly spaced in each pot for a total of 10 pots. Plants were grown in dechlorinated tap water in 1.2 m × 1 m × 0.9 m (1,041 L) plastic tanks under greenhouse conditions. The photoperiod was 14:10 h day:night, with supplemental lighting using 400-watt sodium halide light bulbs (approximately 200 μmol m^{-2} s^{-1}), and temperatures 24 C day and 18 C night.

Four weeks after planting CLP turions, when shoots reached 15 cm in length, plants were removed from the pots, and the roots and turions were washed with tap water to remove soil residue. Those plants with the most developed roots and sprouted turions still attached were planted in 50-ml conical centrifuge tubes[2] filled with unwashed silica sand. Prior to transferring the plants, test tubes were cut to reduce the volume from 50 to 35 ml. This was done to ensure the aboveground plant material was fully exposed to the water column. After transferring the plants into test tubes, a low-melting-point eicosane wax[3] was used to seal the top of the tube to isolate the root system from the water column as previously described (Frank and Hodgson 1964; Ortiz et al. 2019). Plants were then moved to the laboratory and transferred to 4-L glass beakers (25 cm tall × 15 cm diam.) filled with 3.5 L of dechlorinated tap water and allowed to equilibrate for 24 h prior to treatment with ^{14}C-endothall.

Sago pondweed plants were propagated from tubers.[4] Tubers of similar size were planted into field soil, following the same methods as described for CLP, and when shoots reached 15 cm in length, they were transferred to test tubes following the same methods as described for CLP.

Herbicide exposure

Nine 4-L glass beakers (six containing CLP, three containing SGP plants) were filled with 3.5 L of dechlorinated tap water (pH 6.9). A total of 18 CLP and 18 SGP plants (six plants/beaker × three beakers for each species) were treated with formulated dipotassium salt of endothall[5] combined with ^{14}C-endothall (11.24 MBq mg^{-1} specific activity) to achieve a final concentration of 3 mg L^{-}1, and an additional 18 CLP plants (six plants/beaker × three beakers) were treated with a lower concentration of formulated dipotassium salt of endothall (0.75 mg L^{-1}). The low and high rates of endothall targeted 37 and 18.5 KBq L^{-1} of ^{14}C-endothall, respectively, and radioactivity present in each treatment was quantified by collecting 5 ml from each beaker and transferring it to 20 ml scintillation vial containing 10 ml of scintillation solution.[6] Radioactivity was quantified using a liquid scintillation spectroscopy (LSS)[7] before adding plants to the treatment solution. Six additional plastic test tubes without plants but with a toothpick simulating a plant stem were sealed with eicosane wax, randomly placed in treatment beakers, and harvested at 192 h after treatment (HAT). The purpose of these additional test tubes was to determine the efficiency of the eicosane wax to isolate plant roots from the treatment solution. This process was done at a different time.

Different plant species were kept in different beakers, and plants were held with a round test-tube rack[8] with a stir bar placed underneath each rack. During the experiment, plants were maintained in the laboratory, at 22 C, with 12:12 h day:night period, supplemented with two fluorescent grow lights (approximately 200 μmol m^{-2} s^{-1}), and beakers were stirred two times a day for 5 min each time. Plants were harvested at 6, 12, 24, 48, 96, and 192 HAT. Three replicates of each species were randomly harvested from a different tank at each time point, triple rinsed in nontreated dechlorinated tap water, and divided into shoots, roots, and tuber/turion. Five milliliters of water rinsate from the third rinse was quantified by LSS to confirm that non-absorbed radioactivity was removed from the plant surface. After separated plant parts were dried at 60 C for at least 48 h to achieve constant moisture, dry biomass data were recorded for each plant part. Plant tissues were combusted in a biological oxidizer[9] for 2 min, and absorbed ^{14}C was collected by a ^{14}C trapping cocktail.[10] The efficiency of the oxidizer was tested before oxidizing plant parts, and it was always greater than 92%. After oxidation, radioactivity was quantified by LSS. The study was repeated, and each species was replicated four times in run 2.

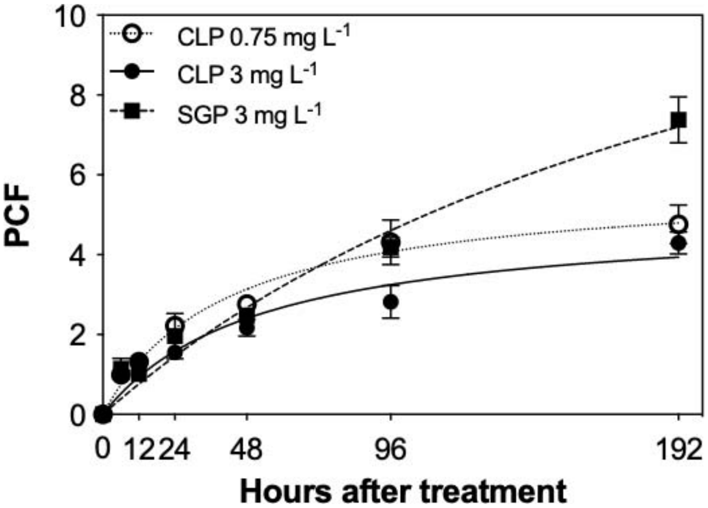

Figure 1. [14]C-endothall bioaccumulation in CLP and SGP over 192-h period expressed as plant concentration factor (PCF), divided into (i) CLP 0.75 mg L^{-1} ($y = 5.819x / 41.04{+}x$, $r^2 = 0.9580$); (ii) CLP 3 mg L^{-1} ($y = 5.004x / 51.91{+}x$, $r^2 = 0.9163$); and (iii) SGP 3 mg L^{-1} ($y = 16.54x / 248.7{+}x$, $r^2 = 0.9519$). Data presented are means and standard error of the mean ($n = 7$).

Statistical analysis

For each study, Levene's test for homogeneity of variance was performed using R,[11] and it was determined that studies could be combined ($\alpha = 0.05$ level of significance). Means and standard were calculated using MS Excel.[12] The plant concentration factor (PCF) was calculated to determine herbicide bioaccumulation, a metric often used in aquatic plants research to compare absorption across different herbicide concentrations and in different species. The equation used to calculate PCF was adapted from de Carvalho et al. (2007) and can be defined as

$$\mathrm{PCF} = \frac{\text{Herbicide concentration in plant (ng/g fresh biomass)}}{\text{Herbicide concentration in water (ng/mL)}}$$

GraphPad Prism 9[13] was used to plot the data and conduct nonlinear regression analyses to fit the hyperbolic function shown below (Kniss et al. 2011), where y is the predicted absorption at time x, and a and b are constants:

$$y = \frac{ax}{b + x}$$

Based on the predicted values resulting from the hyperbolic model, the distribution of herbicide, as a percentage of total absorbed, present in aboveground and belowground portions of the plant was calculated to determine shoot to root translocation and absorption at 192 HAT (A_{192}), and the predicted time to reach 90% of that absorption (t_{90}) was also calculated.

RESULTS AND DISCUSSION

Endothall absorption rate

Although the studies were conducted over a period typically longer than necessary to achieve control in a field setting, endothall absorption did not reach an A_{max}, or maximum asymptote, in either species; instead it fit the more typical asymptotic rise function (Figure 1). The ratio between [14]C-herbicide in the whole plant and in the water column at 3 mg L^{-1} 192 HAT (PCF_{192}) was 3.9 ± 0.11 and 7.2 ± 0.14 in CLP and SGP, respectively (Table 1). The accumulation of this herbicide in Eurasian watermilfoil, monoecious [*Hydrilla verticillata* L. f. (Royle)] hydrilla, and dioecious hydrilla at the same herbicide concentrations was 3.28 ± 0.43, 6.59 ± 0.74, and 11.00 ± 0.94, respectively (Ortiz et al. 2019). A_{max} was also not reached in these three species even though the asymptotic rise to max function is the most biologically relevant function to describe herbicide absorption (Kniss et al. 2011). CLP is very sensitive to endothall (Poovey et al. 2002; Skogerboe and Getsinger 2006; Skogerboe et al. 2008), and 3 mg L^{-1} is the highest recommended rate for CLP control. Therefore, we also examined endothall's behavior at 0.75 mg L^{-1} and found that endothall accumulation was not statistically different compared to its accumulation at 3 mg L^{-1} (Figure 1; Table 1).

Table 1. Predicted plant concentration factor 192 h after treatment (HAT) (PCF_{192}), endothall absorption (μg g^{-1}) at 192 HAT (A_{192}), and the time in hours required to reach 90% of A_{192} (t_{90}).

Species	Plant Part	PCF_{192}	A_{192} (μg g^{-1})	t_{90} (h)
CLP, 0.75 mg L^{-1}	Shoots	4.8 ± 0.10	44.32 ± 3.35	121
	Roots		0.94 ± 0.23	57
	Turion		0.38 ± 0.10	—
CLP, 3 mg L^{-1}	Shoots	3.9 ± 0.11	173.0 ± 50.3	132
	Roots		4.79 ± 1.29	45
	Turion		0.95 ± 0.25	—
SGP, 3 mg L^{-1}	Shoots	7.2 ± 0.14	169.4 ± 13.9	156
	Roots		1.40 ± 0.39	170
	Tuber		0.94 ± 0.14	—

Values represent the mean, and error terms represent the standard error of the mean ($n = 7$). Tuber/turion t_{90} could not be calculated due to extremely small concentration of herbicide in the plant part.

Based on its n-octanol/water partition coefficient (log K_{ow}), endothall, triclopyr, and penoxsulam accumulation should be very similar (–0.55, –0.45, and -0.35, respectively), but for both Eurasian watermilfoil and hydrilla herbicide PCF varied greatly (Vassios et al. 2017). Unlike terrestrial plants, log K_{ow} values less than 2 are not reliable predictors of herbicide accumulation in aquatic plants (de Carvalho et al. 2007), and increased herbicide accumulation does not necessarily correlate with better plant control.

Endothall's absorption (A_{192}) was similar for CLP and SGP at 3 mg L^{-1}; however, when the water column concentration was reduced to 0.75 mg L^{-1}, absorption by CLP was approximately four times less compared to 3 mg L^{-1} (Table 1). The relationship between water column concentration and plant absorption for herbicides with low log K_{ow} values has been previously described (Vassios et al. 2017). It appears that diffusion is a significant driver of absorption, meaning that increases in external concentration results in a stronger concentration gradient between the water column and the plant, leading to greater plant absorption (Vassios et al. 2017).

Although the total absorption (μg g^{-1}) was the same, the rate at which endothall absorption occurred differed by

Table 2. Predicted endothall distribution (% of total absorbed) in plant parts at 192 h ($Distribution_{192}$) and parameters.

Species	Plant Part	$Distribution_{192}$ (%)	a ± SE	b ± SE
CLP, 0.75 mg L^{-1}	Shoots	96.3 ± 10.03	118.8 ± 4.6	44.95 ± 4.7
	Roots	3.6 ± 0.45	3.828 ± 0.3	9.561 ± 3.2
	Turion	1.1 ± 0.12	1.077 ± 0.1	−1.001 ± 0.2
CLP, 3 mg L^{-1}	Shoots	88.7 ± 5.59	117.5 ± 8.0	62.39 ± 10.11
	Roots	3.0 ± 0.23	3.101 ± 0.3	6.732 ± 3.055
	Turion	0.6 ± 0.07	0.5767 ± 0.1	−3.340 ± 0.5
SGP, 3 mg L^{-1}	Shoots	96.0 ± 8.22	186.3 ± 20.3	180.7 ± 33.3
	Roots	1.1 ± 0.02	9.34 ± 4.8	1,453 ± 154
	Tuber	0.5 ± 0.03	0.682 ± 0.1	78.96 ± 21.36

Values represent the mean, and error terms represent the standard error of the mean ($n = 7$).

species. Total absorption by plant tissue based on predicted t_{90} values in the shoots was faster for CLP, with 90% occurring at 121 and 132 HAT for 0.75 and 3 mg L^{-1}, respectively, while t_{90} occurred by 156 HAT for SGP (Table 1). The reasons for greater endothall accumulation (PCF) in SGP and for both SGP and CLP not reaching a maximum asymptote are unknown, but it could be due to rapid endothall metabolism, maintaining a strong concentration gradient as endothall is irreversibly bonded to the herbicide's target sites. In this study it is especially important to consider that the experiment was conducted under laboratory conditions in a static system, and the herbicide exposures were maintained for the duration of the study. SGP is a major problem in flowing water environments, with high water exchange, so under field conditions the herbicide concentration would have decreased rapidly during the study.

Endothall translocation to belowground parts

The eicosane wax barrier was effective in isolating plant roots from the radiolabeled endothall treatment solutions. The ^{14}C-endothall concentration was 32.45 ± 0.71 Bq ml^{-1} in the treatment solution, while the amount found in the waxed test tubes with a toothpick 192 HAT was only 0.047 ± 0.021 Bq ml^{-1} or 0.14% ($n = 6$). This is the combination of all six samples, and there was no detected radioactivity in two of six test tubes. Based on these data, this insignificant amount of radioactivity did not impact the results.

Shoot-to-root translocation was limited in CLP and SGP. The maximum translocation 192 HAT at 3 mg L^{-1} was 3.0% ± 0.23 and 1.1% ± 0.02 of total absorbed radioactivity for CLP and SGP, respectively (Table 2). Endothall translocation to the roots of Eurasian watermilfoil and dioecious and monoecious hydrilla at the same concentration (7.94% ± 1.26, 16.40% ± 2.30, and 17.83% ± 5.07, respectively) was significantly higher than the translocation to the roots of these two pondweeds (Ortiz et al. 2019). Triclopyr, fluridone, and penoxsulam translocation to Eurasian watermilfoil roots 192 HAT was only 2.6% ± 0.3, 2.0% ± 0.4, and 1.3% ± 0.3 (Vassios et al. 2017), respectively, demonstrating the lack of translocation for herbicides assumed to be systemic based on research with terrestrial plants. In this study, endothall translocation to the roots of CLP was the same or higher than the three systemic herbicides applied to Eurasian watermilfoil, while SGP had the smallest amount of radioactivity in the roots.

Endothall translocation to turions/tubers was more limited than translocation to the roots. The maximum radioactivity found in CLP turions was 1.1% ± 0.12 at 0.75 mg L^{-1} and 0.6% ± 0.07 at 3 mg L^{-1} (Table 2). While this is a small percentage of the total absorbed radioactivity, there was a significant reduction in translocation to the mature turions at 3 mg L^{-1} compared to 0.75 mg L^{-1}. Since CLP disintegrates rapidly when exposed to 3 mg L^{-1} endothall, this rapid response may have limited translocation. For SGP, the amount of translocation to mature tubers was only 0.5% ± 0.03 of total absorbed radioactivity at 192 HAT (Table 2). It is not surprising that so little radioactivity was found in the SGP tubers, since these were mature tubers that the plants were established from and not new, developing tubers. Energy in the form of carbohydrates would be moving out of the mature tuber to establish new plants. If there was a system where herbicide accumulation could be monitored in developing tubers, we hypothesized that there would be greater herbicide accumulation in developing tubers. Controlling or suppressing turion and tuber formation is important because once they are formed, they are very resistant to management techniques (Poovey et al. 2002).

In conclusion, endothall absorption in SGP and CLP was slow; however, total accumulation was significantly higher than the concentration found in the water column. Endothall translocation to the roots of these two species was limited, and it does not explain the differential response between SGP and CLP. These data also support previously published data that endothall can be translocated to the roots of aquatic plants following shoot exposure (Ortiz 2019).

SOURCES OF MATERIALS

[1]Osmocote Classic 19-6-12, Everris NA, Inc., Dublin, OH 43017.
[2]Thermo Fisher Scientific, Waltham, MA 02451.
[3]Eicosane, 99%, ACROS Organics, Waltham, MA 02451.
[4]Sago pondweed tubers, Kester's Nursery, Omro, WI 54963.
[5]Cascade, United Phosphorus, Inc., King Of Prussia, PA 19406.
[6]Ecoscint XR, National Diagnostics, Atlanta, GA 30336.
[7]Packard 2500R, PerkinElmer, Waltham, MA 02451.
[8]No-Wire Round Rack, Bel-Art Scienceware, Wayne, NJ 07470.
[9]OX500, R. J. Harvey Instrument Co., Tappan, NY 10983.
[10]OX161, R. J. Harvey Instrument Co., Tappan, NY 10983.
[11]R, version 4.0.0, R Foundation, Vienna, Austria.
[12]Excel, MS Office 2016, Microsoft, Redmond, WA 98052.
[13]GraphPad Software, Inc., San Diego, CA 92108.

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