Can Venus flytraps be triggered to close by raindrops?

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Abstract: *Dionaea muscipula* traps, in a natural setting, are sometimes triggered to close without capturing prey. In the Florida panhandle, in dry weather, time-lapse photographs show the frequency of closure without capture to be 2.1 closures/% of active-traps/day. A sudden burst of intense rain can increase this by two to three orders of magnitude for a brief time. Frequencies of 15.5 closures/% of active-traps/hour and 148 closures/% of active-traps/hour have been measured. The large increase in closures occurs when rain first starts, because the most exposed and most sensitive traps are triggered early, leaving traps in a more sheltered position and those with a less sensitive response open. Only 6 to 12% of the traps in the field of view were closed by intense rain. Even rain so heavy that the traps were submerged in water left most of the traps open. Gentle rain can close traps, but this is not a common event. The necessity of two or more stimuli to close a trap accounts for traps general lack of responsiveness to raindrops in light rainfall. Traps observed to be closed by raindrops began reopening in an average of 4.5 hours and full reopening averaged 15.8 hours. Since partially open traps are capable of capturing prey, the average trap closed by rain is effective at trapping in about 12 hours. Rainfall is only a minor factor interfering with traps' ability to catch prey.

Introduction

Dionaea muscipula plants growing just inland from Cape Fear in the coastal savannas of the Carolinas are often subjected to torrential rain as well as more moderate storms. Can rain trigger trap closure? If so what intensity of rain is required to close traps?

In his book Insectivorous Plants (1875), Charles Darwin says of *Dionaea* traps that: "Drops of water, or a thin broken stream, falling from a height on the filaments [trigger hairs], did not cause the blades to close; though these filaments were afterwards proved to be highly sensitive. No doubt...the plant is indifferent to the heaviest shower of rain." By contrast, Williams and Pickard (1980), describing earlier measurements Williams made with Frank Lichtner, says 7.4% of 202 traps closed during a day of heavy rain during which no traps captured prey and that on a day with no rain 1.0% of 201 traps closed without capturing prey and 3.0% of traps captured prey. Williams and Lichtner conclude that there are fewer captures in rain, but that at least some traps were closed by raindrops during a day of heavy rain. Both Darwin's experiment, done under artificial conditions with cultivated plants, and Williams' single set of measurements, done with wild plants under natural conditions, in addition to contradicting each other, fail to convincingly answer the question: "Can a *Dionaea* trap be triggered by rain?"

Darwin, like many others who did early research on this topic, believed that a single contact with a trigger hair was adequate to trigger the closure of a trap (Brown & Sharp 1910). It was not until 1902 that Macfairlane (1902) demonstrated that under typical conditions two stimuli were required to close a trap. As early as 1876 Darwin's friend John Scott Burdon-Sanderson (Burdon-Sanderson & Page 1876) had shown that each touch of a trigger hair results in an action potential and that more than one action potential was required to close a trap, but for or over 30 years this requirement was

overlooked. In 1910 Brown and Sharp demonstrated that in ordinary conditions that two stimuli less than 20 seconds apart result in closure and that a few traps responded to two touches a minute apart. From these and many more recent repetitions of the same experiment (Williams & Pickard 1980; Böhm *et al*. 2016) it is clear that any stimulus that will bend a trigger hair sufficiently to produce an action potential, if delivered twice within 20 seconds, should trigger closure under ordinary conditions. It is unlikely that raindrops would be an exception.

It is the objective of this study to observe *Dionaea* traps, in the Florida panhandle coastal savannah during rain, and see if closure triggered by raindrops occurs, and to determine the number of traps closed per hour during heavy rain by comparing closures per hour in dry weather just before intense rain to closures per hour during intense rain. We also will measure the time required for traps closed by rain to reopen.

Methods

Plants in two stands of *Dionaea muscipula* established near Sumatra, Florida on private land within the Apalachicola National Forest on the coastal savannah were used in this study. One was the same as that used by Williams and Scholl (2021a). It is a wet site near a small stand of *Clitonia monophylla* trees that have covered the ground with leaf litter. *Sphagnum* is growing among the *Dionaea* plants. The second was the neighboring Florida population that originated from seed, descended from plants from the Carolinas broadcast 15 to 17 years ago, as described by Williams and Scholl (2021a). These are growing among scattered tall pines in a grassy area typical of a coastal savannah.

Photography and videography were done using the methods described by Williams and Scholl (2021b).

Figure 1: Traps that are not capable of closing are not active traps. These include Narrowed traps (Nar) digesting prey previously captured, Developing traps (Dev) not mature enough to be sensitive, Old traps (Old) no longer capable of responding, and Closed traps (Clo) temporarily closed with no capture.

Method of measuring frequency of trap closure

Definitions of terms used for measurements in this paper:

The terms "closure" and "narrowing" were used by Ashida (1934) for *Aldrovanda* traps. Their use was extended to *Dionaea* by Lloyd (1942).

Trap closure occurs in a fraction of a second and is the flipping of the trap from the open position to the position where the bristles along the edge of the leaf cross each other and only small gaps exist along the rim of the trap. See "Clo" in Figure 1. Closed traps that have not captured prey reopen from the closed position in hours (Fig. 2).

Trap narrowing occurs within minutes of the capture of prey. Mechanical stimulation from the struggling prey and later chemical stimulation from decomposing prey causes trap narrowing (Williams & Pickard 1980). Narrowed traps' lobes close tightly together, sealing along a smooth area just inside each trap lobe. The bristles along the edge of a narrowed trap are forced outward giving a narrowed trap a distinctive look. See "Nar" in Figure 1.

Active traps, as used in this study, refers to traps that are capable of closing. Since artificial triggering of trap closing would interfere with our observations, which were made continuously over long periods of time, estimates of the number of active traps were used in calculations.

Traps in Figure 1 that are not active traps include **Old traps** (Old) that no longer can close, **Developing traps** (Dev) not mature enough to close, **Narrowed traps** (Nar), and **Closed traps** (Clo).

Frequency of trap closure per day = closures/% of active-traps/day.

Frequency of capture per day = narrowed-traps/% of active-traps/day.

Frequency of closure without capture = (closures/% of active-traps/day) - (narrowed-traps/% of active-traps/day).

Method of measuring reopening time

Reopening time of a trap (Fig. 2) that has not narrowed was measured by subtracting the time when the trap was closed from the time when the trap was fully reopened. We also determined the time between trap closure and the time when the trap first began to move its lobes apart.

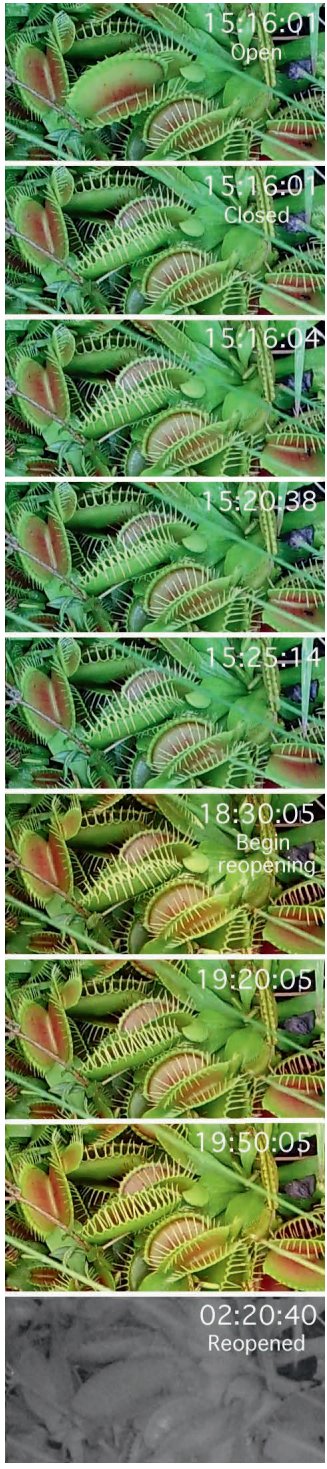

Figure 2: A trap closed by gentle rain. The top frame and second frame show an open trap that was closed a tenth second later. The frames are from a one-minute video in which raindrops were visible and audible with no other detectable stimulation. This was the only trap in the visual field that closed. The trap slowly tightened during the next 3.4 hours after which it began reopening. It was fully reopened after 11 hours. Partially opened traps, slightly more open than that in the second to last frame, have been observed to capture prey.

Table 1. Frequency of trap closure during 25-minute periods before, during, and after a period of intense rain.

	Before rain No rain	Intense Rain	After rain No rain
Active traps	155	155	145
Closed	0	10	0
Time (min)	25	25	25
Closure/% of active-traps/hr	0	15.5	0

Results and discussion

Closure triggered by rain: During gentle rain, closures caused by raindrops are infrequent enough that they are undetectable by statistical means. However, occasional instances of a trap closing in light rain, with no visible stimuli other than raindrops, have been recorded on video (Fig. 2). The response during heavy rain is a different matter. Table 1 shows the response of traps to a cloudburst that produced 25 minutes of intense rain. Of the 155 active traps in the camera's field, ten traps were triggered to close by the raindrops. Among active traps capable of closing, there were no closures that occurred during the 25-minute period before the cloudburst or the 25-minute period after the cloudburst. By contrast, during the cloudburst the traps closed at a frequency of 15.5 closures/% of active-traps/hour. Measurements of trap closures made over 10 days without rain show an average frequency of closures without capture on a dry day as 2.1 closures-without-capture/% of active-traps/day — the frequency of closure triggered by heavy rain was 177 times greater. Another very intense burst of rain closed 12% of the 65 active traps in less than 5 minutes (Fig. 3) and covered 1/3 of the *Dionaea* plants with water within 15 minutes. These traps closed at a frequency over a thousand times greater than closure frequency that would be expected on dry days. The traps were about half open 12 hours later (Fig. 3). Tropical storms are common in both the Florida panhandle and the coastal area of the Carolinas so rain of this magnitude is not unusual.

Raindrops in a heavy rain are capable of triggering closure at a frequency hundreds of times more frequently than they would normally in dry weather. Clearly *Dionaea* traps can be closed by a heavy shower of rain. Of course, this rapid frequency of closures cannot continue long for several reasons:

1. The active traps would be used up, lowering the frequency by reducing the number of active traps
2. The most sensitive traps would close first leaving the less sensitive traps
3. Traps oriented with their trigger hairs most exposed would be closed first leaving those less vulnerable to raindrops

Of the ten traps closed by raindrops, eight were positioned with the trap facing directly upwards, offering maximum exposure of the trigger hairs to raindrops.

Reopening of traps closed by rain: Traps closed by rain are never tightly closed (Fig. 2) because once the traps are closed the trigger hairs are protected from further stimulation by raindrops. Trigger hairs of traps closed by raindrops are likely to have only received two stimuli.

While very slow relative to the time required for closure, healthy traps are usually open before the next day. The average trap closed by rain began to open in 4.5 hours and was completely open in 15.8 hours (Table 2). The fastest opening of the ten traps timed, began opening in 2.5 hours and

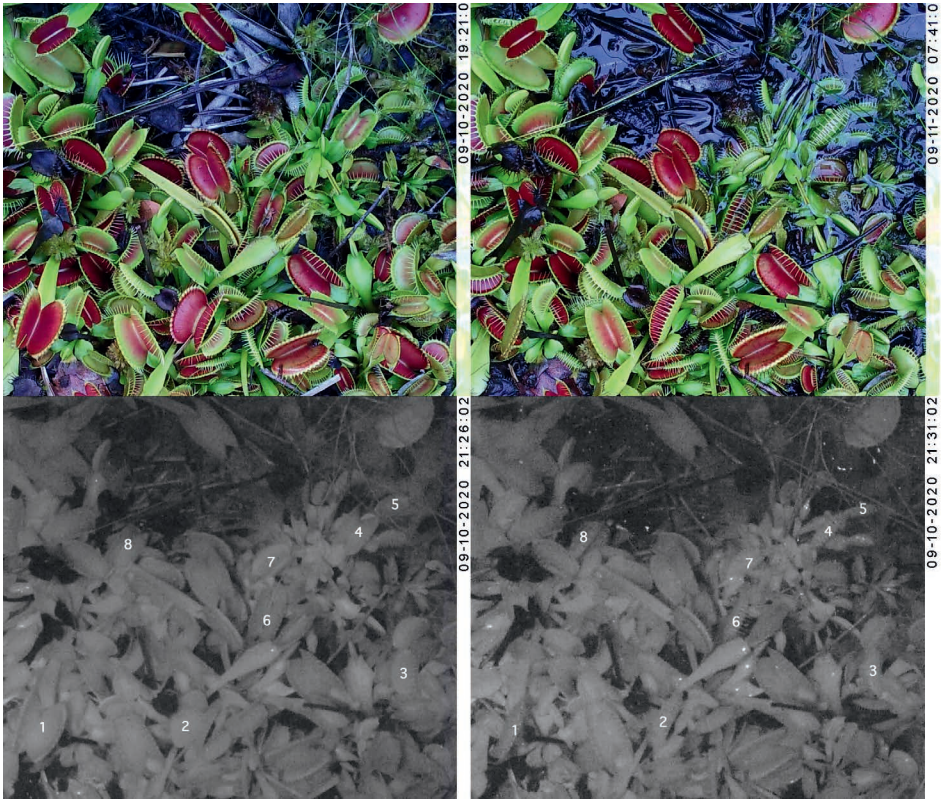

Figure 3: Trap closure caused by heavy rain. Upper left: The area before closure viewed in the light. There are 65 active traps. Upper right: The area the next morning, 10 hours after the trap closures. The closed traps are reopening. Lower left: Traps in the dark just before a burst of heavy rain closed them. Lower right: the traps just after closure. The numbered traps are the eight that closed during the 5 minutes between the two photographs.

was fully reopened in 8.5 hours. Traps do not need to be fully open to be functional. We have video showing traps that are partially open capturing prey.

Traps low responsiveness to rain: Raindrops from a gentle rain do not typically cause traps to close, although there are a small number that do. However, sudden heavy rain showers cause some of the more sensitive traps with exposed trigger hairs to close. After an initial burst of closing during a heavy rain shower, most of the traps remain open even when the rain is so heavy that they become submerged in water. In general, *Dionaea* traps are not highly sensitive to rain because only traps oriented such that drops would directly strike their trigger hairs would be affected. Of these, most would not have hairs struck by raindrops twice within the 20-60 seconds required for a response. In a very heavy rain shower only properly aligned traps are likely to receive two rapidly delivered stimuli and close.

While Darwin is incorrect when he says that *Dionaea* traps are "indifferent to the heaviest shower of rain", it is true that traps are not highly responsive to rain. Lighter rain showers result in very few trap closures and heavy showers close only the most exposed and sensitive traps. After closure,

Table 2. Time required for traps closed by raindrops to reopen.		
Trap number	Time for reopening to begin (hr)	Time of full reopening (hr)
1	4.5	13.5
2	2.5	16.3
3	5.2	7.8
4	2.0	8.5
5	4.0	8.9
6	6.1	15.1
7	3.5	23.5
8	5.4	14.0
9	7.0	27.5
10	5.2	23.3
Average +/- SEM	4.5 +/- 0.17	15.8 +/- 0.76

these traps reopen within about 16 hours. Even partially open traps are capable of capturing prey. It is unlikely that the closure of traps by rain greatly effects prey capture by *Dionaea muscipula*.

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