THE BEHAVIOUR OF *DROSERA ROTUNDIFOLIA* L. (DROSERACEAE)

TRAPPING LEAVES IN NATURAL HABITATS

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Introduction

The role of carnivory in plants can vary in different plant communities and also from the availability of different nutrients in the soil (Kraft & Handel, 1991). According to Dore & Maham (1969) and Small *et al.* (1977), carnivory is more or less facultative for *Drosera* species. Furthermore, the influence of carnivory is weak for plants in the natural habitat (Stewart & Nilsen, 1992).

The behaviour of trapping leaves of *Drosera* species was first studied in artificial conditions more than a hundred years ago (Darwin, 1875; also Hooker, 1916). The leaves of most *Drosera* species have short tentacles in the central part of the leaf blade and long marginal tentacles on its periphery. In particularly active species such as *Drosera rotundifolia*, when future prey provide sufficient stimulation to the leaf blade, all tentacles bend inwards and cover the prey with an enzyme-containing slime. Upon stimulation by the prey, there is a (1) rapid movement of tentacles in the first 10-30 seconds after touching and (2) slow movement by tentacles that were not at first in contact with prey. This slow movement is observed within several hours after initial contact (Hooker, 1916; Bopp & Weber, 1981). Juniper *et al.* (1989) state that sundews secrete slime just as the prey is captured. The most intensive slime secretion in *D. rotundifolia* occurs on the second day after prey capture (Muravnik, 2002). After slime secretion, the edge of the leaf blade slowly bends and covers the captured prey. When the digestion process has ended, the leaf blade unwraps, the tentacles straighten and the slime dries (Hooker, 1916).

Secretion activity of the tentacles of *Drosera* is highest when the relative air humidity is high and light intensity is low (Gomez, 1998; Volkova *et al.*, 2001; Volkova, 2002b; Vokova *et al.*, 2003), showing that the behaviour of at least these carnivorous plant traps depends not only on the number and condition of the captured animals. Ostashova (2002) found that the leaves of *D. rotundifolia* move rhythmically independent of prey trapping. In the north of Karelia plants were observed in which the period of such movement was equal to 15 hours and in Vologda region (Middle Russia) plants exhibited a movement period of 12 hours.

Unfortunately, most observations on *Drosera* leaf-trapping behaviour were made in laboratories. This fact does not allow for the natural fluctuations in the number of available prey and the influence of weather factors on the leaf-trapping behaviour to be taken into account. Previously we investigated different aspects of *D. rotundifolia* biology in natural habitats (Volkova *et al.*, 2001; Volkova, 2002a; Volkova, 2002b; Volkova & Shipunov, 2002; Volkova *et al.*, 2002; Volkova *et al.*, 2003). The main goal of the current paper is to investigate the influence of weather conditions and captured prey on the leaf-trapping behaviour of *D. rotundifolia* in the natural habitat.

Materials and Methods

We observed two *D. rotundifolia* plants in Loukhi district of North Karelia, cape Ivanov Navolok (66° 20'N, 33° 20'E) on 25-27 of July 2000 (referred to hereafter as "series 1" data), and two *D. rotundifolia* plants in Vyshnevolotsk district of Tver' region (middle Russia), on the western shore of the Ol'shevo lake (58° 15' N, 34° 30'E) on 20-23 of June 2002 (referred to here-

after as "series 2" data). The daylight duration on 29 July for the series 1 data was lasted 19 h 17 min, and on 29 June for series 2 it was 18 h 17 min (these data are from astronomical software "XEphem", Downey, 2000).

The plants were selected randomly from a typical population that occurred in a typical habitat (wet *Sphagnum* bogs). Continuous, non-manipulative observations on each pair of investigated plants lasted 72 hours in natural, undisturbed conditions. The two plants in the series 1 data had 5 and 4 leaves, while the two plants in the series 2 data had 3 and 4 leaves. For each set of observations we estimated (a) the shape of the leaf blade, (b) the degree of slime secretion, (c) bending percentage, i.e. percentage of curved margin tentacles (see Table 1) and (d) the number of captured prey for each of sixteen leaves chosen for the study. The observations were made every 40 minutes in series 1, and every 30 minutes in series 2, during the entire observation period. In the series 2 data we also measured atmospheric pressure every two hours, air temperature and relative air humidity using Assman's aspiration psychrometer.

Table 1. Criteria of visual estimation of the leaf blade's conditions.

Points	Degree of Leaf Secretion ("wet")	Leaf Blade Shape ("shape")	Degree of Tentacle Bending ("tent")
0	poor (the leaf blade is almost dry)	—not used—	No or few bent tentacles
1	medium	almost flat	The minority of tentacles are bent
2	high (droplets well formed)	flexed	Approximately half the tentacles are bent
3	—not used—	bent	The majority of tentacles are bent
4	—not used—	—not used—	Almost all tentacles are bent

Leaf behaviour for each plant was similar (see below), so for each plant in the study, the "average leaf shape," "average degree of secretion," and "average bending percentage" were calculated as the average of the characteristics for all leaves of each plant during one observation. We calculated non-parametric Spearman correlation coefficients to demonstrate a connection between investigated leaf characteristics, weather conditions and number of captured animals (see Table 2, 4). For calculations we used STATISTICA (tm) software (StatSoft, Inc., 1999).

Table 2. Spearman correlation coefficients between averaged characteristics of each series 1 plant's leaves (N=81, all significant correlation coefficients are included, "wetN av" — average ("av") on all leaves of plant number N degree of secretion).

Correlating Characteristics	Correlation Coefficient
tent1 av & tent2 av	0.59
wet2 av & tent2 av	-0.54
tent1 av & wet2 av	-0.33
wet2 av & shape2 av	-0.25

The Behaviour of Trapping Leaves

In the series 1 observations, reactions in the bending percentage of the leaf blades were not observed in the first hour after capture, but did become evident after 2-3 hours (Table 3). No changes were noticed in the degree of secretion in response to the caught prey. Leaf shape was significantly changed after capture in only two leaves (~22% of the sample).

The condition of leaf blades changed frequently whether or not prey were present. Leaf blades periodically dried when the prey on them had not yet been digested. Tentacles at the margin of 50% of the leaf blades containing prey that was freshly caught, but that had not yet been digested, were not bent; at the same time 25% of these leaf blades remained uncurved. Hence, there was no significant relationship between the different leaf blade characteristics (Figures 1-3, Table 2). For all the leaves of each plant the degree of secretion, the leaf shape and the per-

Table 3. The leaf behaviour in series 1: the percentage of leaves with noticed changes.						
Leaf Blade Characteristic	Change after prey came to the leaf blade			Change with no prey	Change with constant number of animals	Previously undocumented leaf behaviour
	< 1 h	1-2 h	3 h			
Secretion	0%	0%	17%	67%	63%	88%
Shape	0%	17%	17%	83%	100%	25%
Bending	0%	50%	50%	100%	75%	50%

centage of bending were related (R=0.4-0.7; $p<0.05$) to averaged leaf characteristics. Consequently, the average characteristics of the leaf blade can be used to describe the common tendencies of the leaf behaviour of any given plant. Moreover, the changes of different characteristics of the leaf blade in different plants were also correlated.

In the series 2 observations, approximately half of the investigated leaves reacted to captured animals less than one hour after its capturing (Table 5). In this time period, 40% of leaves moistened their leaf blades, 50% curved their leaf blades, and 70% increased the degree of tentacle bending. Of the comparatively few plants that did not change their leaf conditions less than one hour after prey capture, almost all did so after 2-3 hours. The degree of secretion and the shape of leaf of 60-70% of the leaves depended directly on the number of caught prey, whereas all leaves without captured prey changed their characteristics in a way that did not have a clear period. Such behaviour was noticed for the majority (70-80%) of investigated leaves when a constant number of recently caught, as-yet undigested prey was observed. Very often completely different behaviour of leaves with fresh animals was observed than is discussed in the literature. Nearly all investigated leaves did not secrete slime while capturing prey and tentacles at margin in 70% of investigated leaves containing undigested animals were not bent (Table 5).

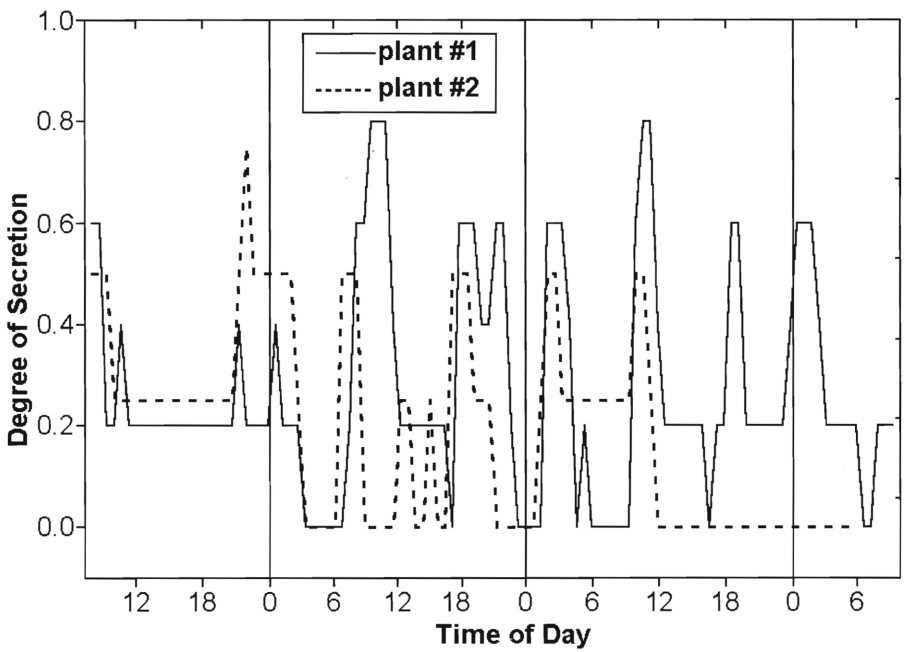

Figure 1: Changes in the degree of secretion for series 1 data. The indices for degree of leaf secretion are described in Table 1. Vertical lines indicate midnight during the series 1 data observations.

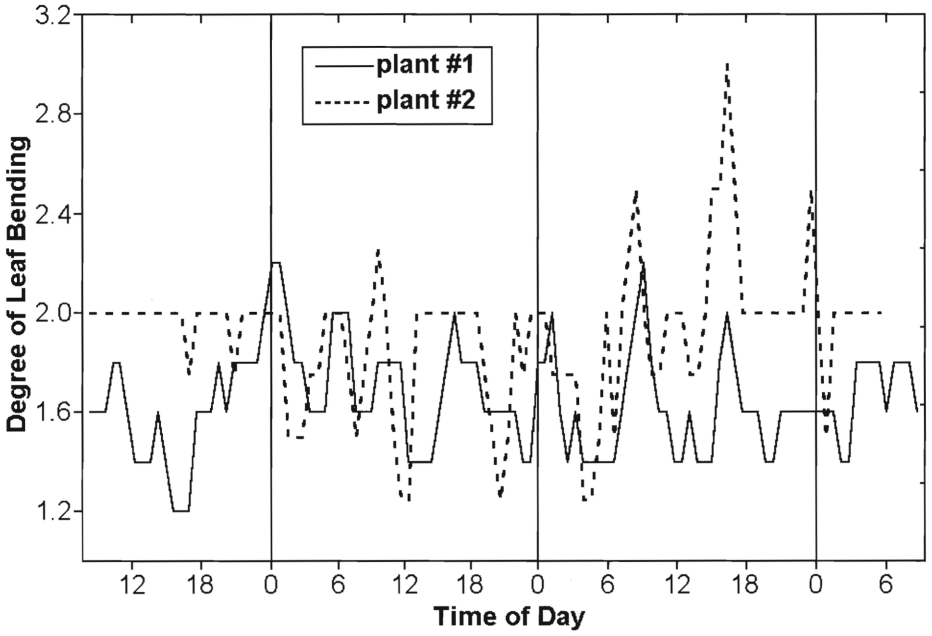

Figure 2: Changes in the shape of the leaf blade for series 1 data. The indices for degree of leaf bending are described in Table 1. Vertical lines indicate midnight during the series 1 data observations.

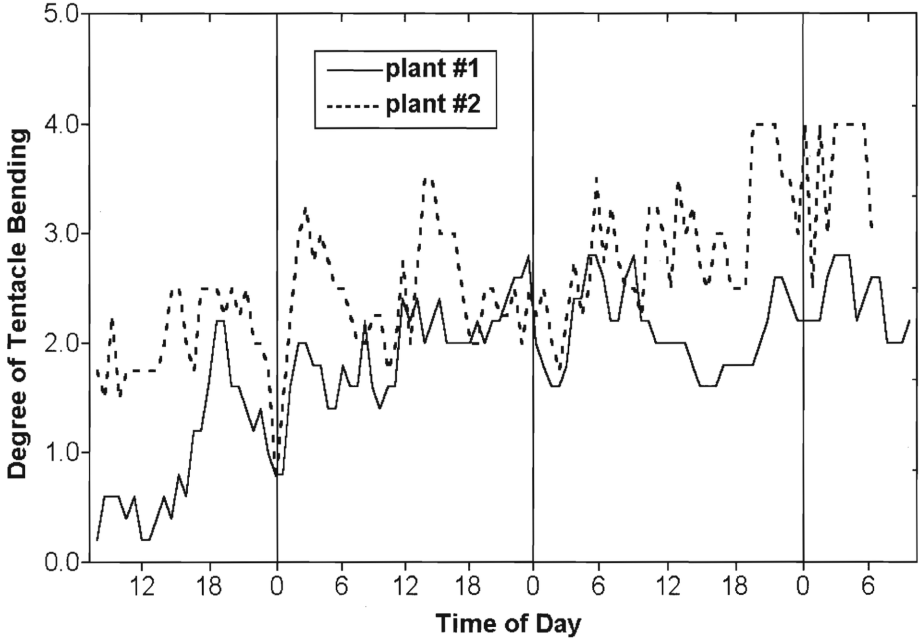

Figure 3: Changes in degree of tentacle bending for series 1 data. The indices for degree of tentacle bending are described in Table 1. Vertical lines indicate midnight during the series 1 data observations.

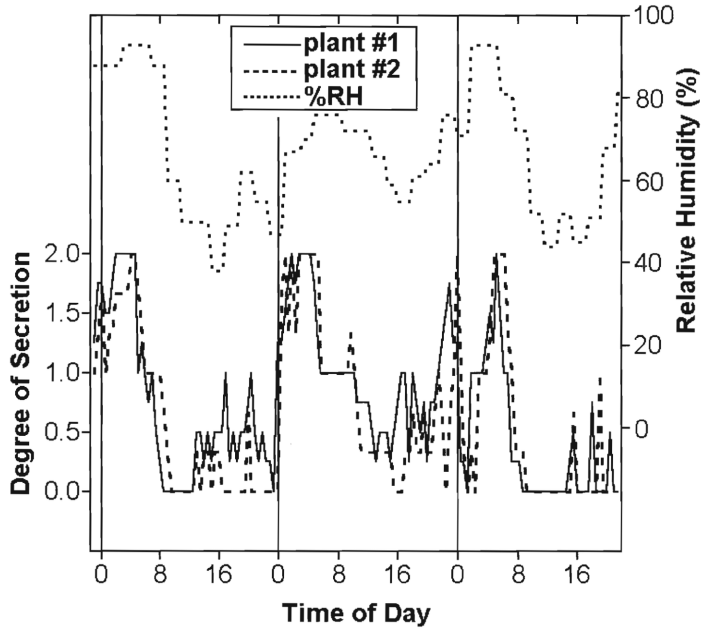

Figure 4: Changes in the degree of secretion for series 2 data. The indices for degree of leaf secretion, measured on the left y-axis, are described in Table 1. The relative air humidity (%RH) is measured on the right y-axis. Vertical lines indicate midnight during the series 2 data observations.

The leaf blade shapes were related to the bending percentage (R=0.4-0.6, p<0.001; Table 4). No significant relationship between the degree of secretion, leaf shape and bending was observed (Figure 4-6, Table 4). As in the series 1 data, the degree of secretion, leaf shape and bending for each leaf in series 2 was correlated with averaged characteristics (R=0.7-0.9, p<0.05; Table 4). An interesting observation is the coincidence in leaf behaviour for all of investigated leaves (Figure 4-6, Table 4).

The degree of secretion for all investigated leaves directly depended on the relative air

Table 4. Spearman correlation coefficients between averaged characteristics in series 2 data. (N=144, all significant correlation coefficients are included, abbreviations as in Table 2, including P for atmospheric pressure, RH for relative humidity, and T for ambient air temperature.)

Correlating Characteristics	Correlation Coefficient	Correlating Characteristics	Correlation Coefficient
wet2 av & wet1 av	0.78	RH & wet2 av	0.61
tent2 av & tent1 av	0.65	T & wet1 av	-0.61
shape2 av & shape1 av	0.64	P & tent1 av	0.56
shape1 av & tent1 av	0.61	P & shape1 av	0.48
tent2 av & shape1 av	0.41	T & wet2 av	-0.46
shape2 av & tent1 av	0.36	P & tent2 av	0.41
shape2 av & tent2 av	0.34	T & shape1 av	0.23
wet2 av & shape2 av	0.24	P & wet2 av	-0.23
shape2 av & wet1 av	0.24	RH & tent2 av	0.20
RH & wet1 av	0.68	P & shape2 av	0.20

Table 5. Leaf behaviour in series 2 data: the percentage of leaves with noticed changes.						
Leaf Blade Characteristic	Change after prey came to the leaf blade			Change with no prey	Change with constant number of animals	Previously undocumented leaf behaviour
	< 1 h	1-2 h	3 h			
Secretion	43%	0%	70%	100%	83%	86%
Shape	57%	43%	29%	100%	67%	29%
Bending	71%	29%	29%	100%	83%	71%

humidity (R=0.5-0.7, p=0; Figure 4, Table 4). In all investigated leaves it was noticed that there was a less positive dependence between bending degree and leaf shape and between leaf shape and the atmospheric pressure (R=0.2-0.5, $p<0.05$; Figure 5, 6, Table 4) from another. However, dependence of the captured prey number on the weather conditions was not observed.

The daily average air temperature (17°C) in the observation period remained constant. The air temperature fluctuations daily existed from minimum of 9°C (at 5-6 a.m.) to a maximum of 26°C (2-3 p.m.). No significant influence of air temperature on of the leaf blade characteristics was observed. Weak dependence of characteristics of the leaf blade on air temperature, observed for some leaves, are definitely caused by the clear negative relationship between the air temperature and relative humidity.

Discussion

Our observations show that in both our study sites for *Drosera rotundifolia*, different characteristics of the leaf blades that we studied exhibited changes that were independent both from each other, and from the presence of prey. However, the different leaf changes were more correlated in the plants from middle Russia than in those from the arctic region. Moreover, the leaf

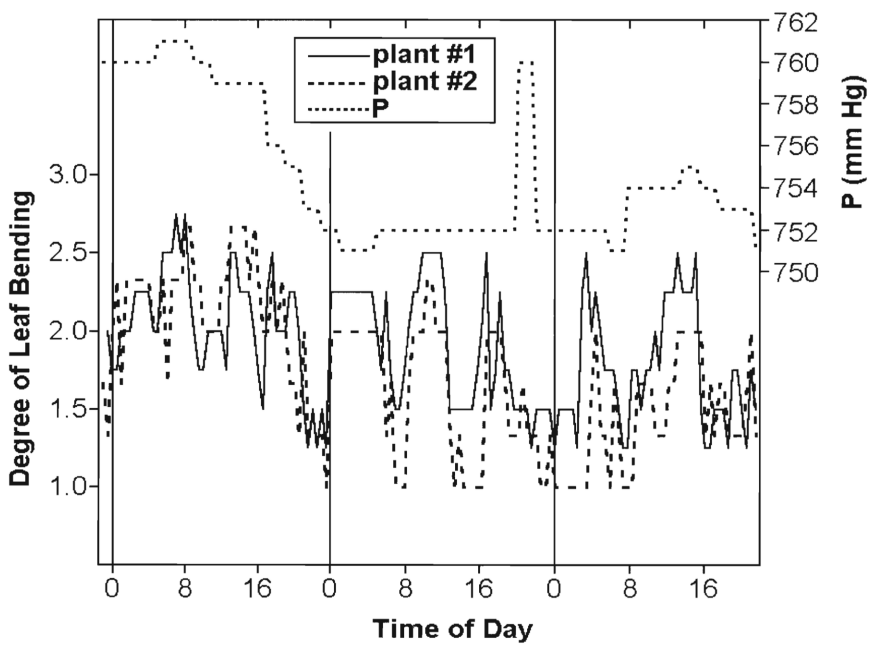

Figure 5: Changes in the shape of the leaf blade for series 2 data. The indices for degree of leaf bending, measured on the left y-axis, are described in Table 1. The atmospheric pressure (in mm Mercury) is measured on the right y-axis. Vertical lines indicate midnight during the series 2 data observations.

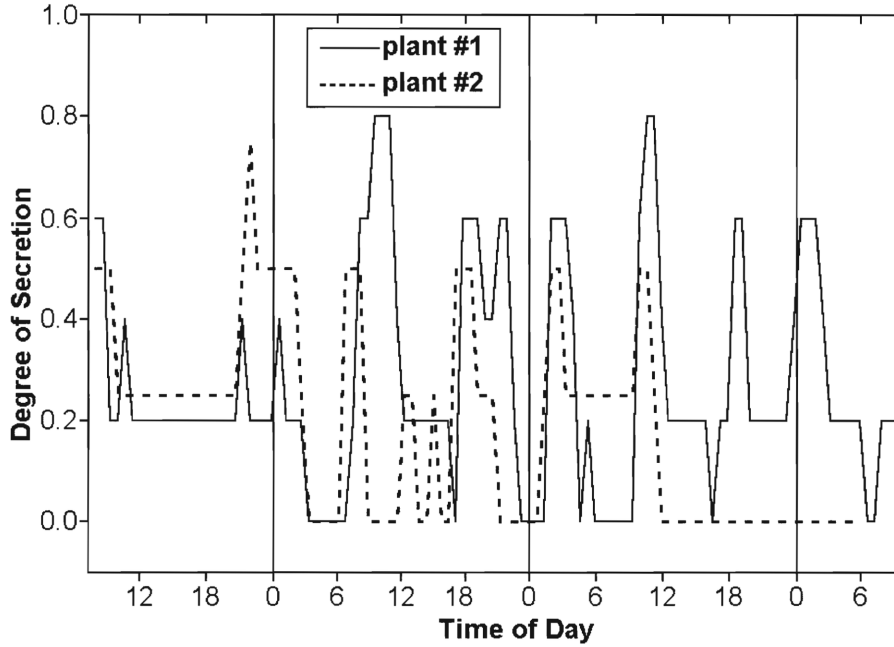

Figure 6: Changes in degree of tentacle bending for series 2 data. The indices for degree of tentacle bending, measured on the left y-axis, are described in Table 1. The atmospheric pressure (in mm Mercury) is measured on the right y-axis. Vertical lines indicate midnight during the series 2 data observations.

reactions to the capturing of prey were more dramatic in the plants from middle Russia. Such differences are probably related to harder habitat conditions expected by *D. rotundifolia* in the Arctic region in comparison with temperate Middle Russia, which could influence negatively the co-ordination of feeding behaviour.

The degree of moistening in the leaf blades for carnivorous plants is at least partially dependent on the relative air humidity. This behavior is not, however, related to cost-benefit models of plant carnivory (Ellison & Gotelli, 2001); while plant carnivory is well-known to be more important in wet habitats than in dry ones (Gomez, 1998; Ellison & Gotelli, 2001; Volkova, *et al.*, 2003), our investigations of the changes in secretion intensity occurred *in situ*, where the humidity and moisture levels were relatively constant.[1] The chemical composition of slime changes in prey capture (Muravnik, 2002) while the amount of the slime produced is practically constant. The relation of leaf-blade shape and tentacle bending to atmospheric pressure was probably caused by the dependence of leaf characteristics on the internal cellular pressure. The laboratory observations on the trapping-leaf behaviour (Darwin, 1875; Hooker, 1916; Muravnik, 2002) could not take into account the influence of weather conditions on the leaf blade conditions, which can exceed the effect of captured prey in natural conditions.

The correlated behaviour of leaf blades from different plants also indirectly shows the absence of dependence between trapping leaves behaviour and prey. This fact was also investigated by field observations of Ostashova (2002).

We propose that the changes of the leaf blade characteristics of *D. rotundifolia* are probably casual and are augmented only by the external factors such as relative air humidity, atmosphere pressure and presence of the prey on the leaf blade. No rhythmic, diurnal motions of the

[1]In August 2003 we manually applied prey to leaves of plants in north Karelia. We observed the same leaf reaction under conditions of both very high relative air humidity (frequent rains), and low relative air humidity (dry weather). This observation shows the absence of influence the relative air humidity on interactions between prey and leaf.

leaf blades were observed, contrary to the observations of Ostashova (2002). Thus we can consider that secretion, leaf blade curving and tentacle bending at some time after prey capturing in most cases is a coincidence. This situation is not unique, because the active reaction of traps on the captured animal is not an obligatory attribute of the carnivorous plants. Some *Drosera* species, e.g. *D. binata*, have large leaves that simply cannot change their shape relatively fast. Phylogenetically close *Nepenthes* (Nepenthaceae) species have pitcher-traps that do not capture the prey actively (Ellison & Gotelli, 2001). It is possible that only in *Aldrovanda* and *Dionaea* (Droseraceae) prey capturing and changes in leaf-trapping characteristics are strongly related.

Our data on the absence of clear linkage of leaf-trapping behaviour and presence of captured animals for *D. rotundifolia* support the recent hypothesis on the facultative role of carnivory in the carnivorous plants (Dore & Maham, 1969; Small *et al.*, 1977; Stewart & Nilsen, 1992; Ellison & Gotelli, 2001).

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Looking Back: CPN 25 years ago

This issue's "Looking Back" selection is not a fragment of text, but is instead a photograph. If you have a copy of the now twenty-five year old issue 8:1, treat yourself by looking at the photograph on page 23. Compliments of Longwood Gardens, the photograph appears to be of a girl pouring herself a glass of orange juice, perhaps for breakfast. What is the connection to carnivorous plants? Look at the photo yourself, and ask yourself if you would want pulp in your juice!