

# Thermal Stimulation and Thermal Adaptation of *Aldrovanda* Leaves, with a Note on Cold-Rigor

By

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*With 9 Text-figures*

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1) **Joji ASHIDA** will hereafter be re-spelled as above, in compliance with the system, lately adopted by the Government, of transcribing Japanese speech-sound into Roman letters.

### Introduction

A study of the stimulation of the *Aldrovanda* leaf by a sudden change of water temperature has already been reported (ASHIDA, '35). But research in this field is scarce, and the writer wished to fill in details, improving the method and extending the range of temperatures.

Furthermore, the velocity of adaptation to a new temperature was measured. This is important, since the measured velocity has a twofold meaning, namely, the velocity of the thermal adaptation in the usual sense, and the velocity of accommodation to a stimulus when the temperature change itself is considered as a stimulus.

Then a hypothesis is proposed concerning thermal stimulation and adaptation; and the relations of thermal excitation to the factors, namely, 1) the environmental temperature itself, and 2) the rate and extent of the temperature change, are explained.

Finally a trial to make the leaf insensible to stimulation by cooling is reported.

The experiments were made in the summers of 1936 and 1937.

Before going further, the author wishes to express his sincerest thanks to Professor Dr. K. KORIBA for his kind guidance for the studies. The author's gratitude is also due to Dr. T. SATO for the solution of the two differential equations in the paper. He also desires to acknowledge the assistance rendered this investigation by a grant from the Japan Society for the Promotion of Scientific Research.

### Thermal Stimulation

#### Method

In principle the method used is the same as before, but improvements are made in the following points:

1. Leaves to be observed are not allowed to float near the water surface, either a) in the water of the first temperature, or 2) in that of the second temperature after transfer.

a) When leaves are prepared for the thermal stimulation in small vessels which stand in a thermostat, the water in the former should not be stirred, although that of the latter is. So, near the water surface in the vessels, where leaves are floating, the water temperature is affected considerably by the air temperature. Hence whorls are isolated from one another by cutting the stem, and are put one by one in deep cylindrical glass vessels, the diameter of each of which is a little larger than that of the largest whorl. Each whorl is fixed horizontal by a heavy glass needle piercing the stem, with its leaves all at about 5 cms. beneath the water surface<sup>1)</sup>. The large variation, from leaf to leaf, of the threshold of the thermal stimulation can be somewhat reduced by this method of preparation. The water temperature in the cylindrical vessels is measured at the depth at which the whorl is fixed.

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1) In the natural floating position of *Aldrovanda*, as in the previous study, the stem is laid horizontal, so that the leaves are at different depths.

b) The water of the second temperature, too, should not be stirred after a leaf is transferred from the first temperature. Hence a glass ledge is made in the glass vessel used for the second temperature, to prevent the leaf from floating up to the water surface.

2. Very slow and gradual cooling is necessary to make the leaf temperature very low without stimulating the leaf (cf. p. 382). A thermostat to which a methylchloride refrigerating system is applied, fits the purpose.

3. Formerly, whether a leaf was stimulated or not was decided by an observation for 10 seconds, for this was considered to be long enough for the reaction time. But afterwards the reaction time was found to be as long as one minute, when a minimal stimulus of temperature change is given. Hence in the present experiment, the observation is continued for two minutes after the transference into the second temperature.

4. Leaves to be stimulated had been kept at the first temperature for a few hours, in the former experiment. But as the experiments proceeded, it became evident that this is insufficient (cf. p. 364). So in the present experiment, leaves are kept at the first temperature for more than 13 hours in case of moderate and higher temperatures, and more than 24 hours in case of low temperatures.

5. More attention than before is paid to the condition during cultivation, and to the morphological uniformity of the material.

Thus, the procedure of the experiment is as follows:—

Of the material cultured with *Zizania* in pots, the stem is cut at every internode to make each whorl free. Whorls are put in deep cylindrical glass vessels with weights for each. The water surface in the cylindrical vessel is made 1 cm. above the whorl. The vessels are put in a thermostat the temperature of which keeps the water around the whorls at the first temperature. In cases where the first temperature is lower than 20°, the vessels containing whorls are at first put in the thermostat of the room temperature, and the refrigerating mechanism is started after the leaves are quite open. In order to make the cooling velocity sufficiently slow not to stimulate the leaf by the decrease of temperature, the refrigerator is stopped automatically at intervals of ten minutes, or the cooling is cancelled by a weak electric heater working at the same time.

The experiment is commenced 13-24 hours after the water temperature has attained the intended first temperature. Before the experiment, water of the same temperature is added gently to the cylindrical vessels to make the water surface 5 cms. above the whorls.

The water of the second temperature is prepared in a small beaker covered with a thick layer of silk wool, by stirring with a thermometer. A leaf is cut off from the whorl at the petiole, and transferred with a small hemispherical glass spoon into the small beaker the temperature of which is exactly the second temperature. The opening of the leaf is directed downwards in the spoon, and when it is left at the bottom of the beaker it floats up with its petiole directed upwards and its opening downwards (for the buoyancy is maximum at the petiole). In floating up, the leaf is washed quickly by the water of the second temperature, without receiving mechanical agitation.

The leaf stops at the glass shelf in the beaker, and its reaction is watched there for two minutes. In cases where the second temperature is very high or very low, drops of hot water or cold water (or a small piece of ice) is added to the water surface and stirred gently by a thermometer in order to keep the temperature of the water above the shelf constant.

*Estimation of the threshold temperature.*—The reaction time, i. e. the time from the transference into the second temperature to the shutting reaction, of the leaves of an

individual plant was, in typical cases, as shown in Tables 1 and 2. Table 1 represents the result of transference of leaves adapted to 25° into lower temperatures, and Table 2, that of leaves adapted to 20° to higher temperatures. The threshold temperature of stimulation estimated for each whorl of an individual is shown in the lowest lines of the tables. The threshold values thus determined are averaged for about 10 individuals, with respect to whorls.

Table 1.

Reaction time in seconds. The first temperature is 25°. ∞ : the leaf did not react within 2 minutes.

2nd temp.	Whorl No.					
	I	II	III	IV	V	VI
21°	45'' ∞ ∞					
20°	30'' ∞	30'' 60'' ∞ ∞ ∞	∞			
19°	5'' 10''	30'' 35''	40'' ∞ ∞	∞		
18°		2''	15'' 25''	25'' 55'' ∞ ∞	50'' 55'' ∞ ∞	
17°				10'' 40''	40'' 50''	45'' 95'' ∞ ∞
16°						30'' 40''
Thresh. Temp.	20.5°	20°	19°	18°	18°	17°

Table 2.

Reaction time in seconds. The first temperature is 20°. ∞ : the leaf did not react within 2 minutes.

2nd temp.	Whorl No.					
	I	II	III	IV	V	VI
39°						10''
38°				30''	20'' 5''	35'' ∞
37°				10''	70''	∞
36°		15''	15''	100'' 20''	∞	
35°	20'' 5''	10'' 35''	10'' 15''	∞		
34°	10'' 20''	90'' ∞	∞ ∞			
33°	35'' ∞					
Thresh. Temp.	33°	34°	34.5°	35.5°	36.5°	38°

Result

The mean threshold difference, i.e. the difference between the first temperature and the mean threshold temperature, is shown in Tables 3 and 4, the former for temperature falls and the latter for temperature rises. The standard deviation,  $\sqrt{\frac{\sum(t_i - A)^2}{n}}$ , is about 10 p. c. of each of the average value.

Table 3.

Threshold differences in the case of stimulation by a sudden decrease of temperature. The marks of degree are omitted.

1st temp.	Whorl No.						
	I	II	III	IV	V	VI	IX-XII
40	7.7	8.3	9.5	9.8	10.3	10.9	12.3
35	6.5	7.4	8.6	9.5	9.7	10.0	11.4
30	5.8	6.8	7.3	8.1	8.5	9.0	9.9
25	4.7	5.3	6.0	6.7	7.3	7.5	8.1
20	4.1	4.3	4.6	5.2	5.5	5.5	6.9
15	3.1	3.4	3.9	4.2	4.5	4.4	5.5
10	2.6	2.8	3.1	3.6	3.7	4.0	4.5
5	2.0	2.0	2.3	2.5	2.8	2.7	3.4

Table 4.

Threshold differences in the case of stimulation by a sudden increase of temperature. The marks of degree are omitted.

1st temp.	Whorl No.						
	I	II	III	IV	V	VI	IX-XII
40	6.0	7.3	7.8	8.2	9.1	9.2	10.4
35	7.2	7.7	8.6	9.2	10.3	10.7	12.2
30	8.6	10.1	10.3	11.0	11.8	12.5	14.9
25	9.4	11.3	12.0	12.9	13.6	14.1	17.5
20	13.0	13.9	14.6	16.0	16.8	18.0	20.1
15	17.0	17.8	18.7	20.0	20.3	22.5	23.6
10	20.5	21.3	21.5	22.2	22.8	23.8	27.3
5	23.2	25.1	26.1	26.9	27.6	28.3	30.2
1	26.3	27.6	28.1	28.5	28.9	29.2	31.7

The values of threshold difference are smaller than those reported before. The chief reasons are two:

a) The duration of the observation is longer (3, p. 355):—Some small temperature differences which can not make leaves react within 10 seconds prove to be stimulative if each observation is continued for 2 minutes.

b) The leaves are put beneath the water surface (1, p. 354):—When a leaf is floating at the water surface, the larger the difference between the water (1st or 2nd) temperature and the air temperature, the greater the deviation of the thermometer reading from the actual leaf temperature. So the temperature changes measured in the previous study must have been larger than those the leaves actually underwent, whether it was a case of the rise or fall of temperature.

Table 5.  
The case of the sudden decrease of temperature.

1st temp.	Young (I-III)		Old (IX-XII)	
	Thresh. diff.	Thresh. temp.	Thresh. diff.	Thresh. temp.
40	8.5	31.5	12.3	27.7
35	7.5	27.5	11.4	23.6
30	6.6	23.4	9.9	20.1
25	5.3	19.7	8.1	16.9
20	4.3	15.7	6.9	13.1
15	3.5	11.5	5.5	9.5
10	2.8	7.2	4.5	5.5
5	2.1	2.9	3.4	1.6

Table 6.  
The case of the sudden increase of temperature.

1st temp.	Young (I-III)		Old (IX-XII)	
	Thresh. diff.	Thresh. temp.	Thresh. diff.	Thresh. temp.
40	7.0	47.0	10.4	50.4
35	7.8	42.8	12.2	47.7
30	9.7	39.7	14.9	44.9
25	10.9	35.9	17.5	42.5
20	13.8	33.8	20.1	40.1
15	17.8	32.8	23.6	38.6
10	21.1	31.1	27.3	37.3
5	24.8	29.8	30.2	35.2
1	27.0	28.0	31.7	32.7

In the following, the leaves of the whorls, I, II, and III, will be called *young leaves*, and those of IX, X, XI, and XII, *old leaves*. Average threshold differences and threshold temperatures of young and old leaves are shown in Tables 5 and 6, for temperature falls and rises, respectively. Their graphic representation is given in Fig. 1.

The three principles stated in the previous paper (p. 72) hold yet:—

- 1) *Cooling can stimulate leaves more easily than warming, below 35°.*
- 2) *The higher [lower] the initial temperature, the more sensitive the leaf tends to be to rises [falls], and the less to falls [rises].*

3) *The older the leaf, the less sensitive it is to a thermal shock, either a rise or a fall.*

If the leaf adapted to 1° is transferred into the water of 0°, it is not stimulated. The determination of the threshold temperature with super-cooled water is difficult, since it easily freezes, and the reaction time is too long to make the necessary observation at a constant temperature below 0°.

The threshold of thermal stimulation mentioned above concerns the case in which the leaf temperature is changed very rapidly. *If the change of temperature is made more and more gradual, the threshold difference becomes larger and larger.* And the leaf temperature can be changed without stimulating the leaf to any extent between 0.5° and 40°, if the rate of the temperature change is sufficiently slow.

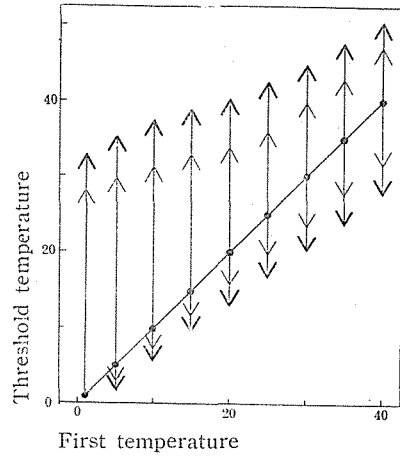


Fig. 1. Relation of the threshold temperature (tips of arrows) to the first temperature (dots). The thick arrows: old leaves; the thin arrows: young leaves. The lengths of the arrows represent the threshold differences.

#### Discussion

By improving the method of experiment, values of threshold difference are found to be smaller than those reported before. By the former experiments, it was ascertained that *a temperature decrease could be stimulative within the harmless range of temperature*, but this was not proved in the case of temperature increase. The chief source of error in the previous data was that the temperature of water near the surface was affected much by the air temperature. The greater the difference between the air and the water temperatures, the greater were the errors. But by the present experiment, it is proved that *an increase of temperature from a harmless to another harmless temperature may also be stimulative*. The leaf is stimulated by warming it even to 30°, if the first temperature is sufficiently low (cf. Table 6).

The higher the initial temperature, the smaller is the threshold difference of a temperature rise, and the larger that of a temperature fall. And the threshold differences of a rise and a fall are nearly equal at 35° (cf. Fig. 1). This may perhaps indicate that *Aldrovanda* is disposed to higher temperature than its habitat water in Japan which scarcely attains to 30° even in summer daytime.

The threshold for temperature discrimination of human skin is minimum near its own normal temperature (cf. GOLDSCHIEDER, p. 146). But in *Aldrovanda*, the threshold, either of a rise or of a fall, shows no speciality near the supposed optimum. It also seems that 0°C is not a special temperature

in the case of the thermal stimulation, for the leaf adapted to  $1^\circ$  is not stimulated by introducing it into  $0^\circ$ , a bit more cooling is needed for the stimulation.

Literatures concerning the stimulation by a sudden change of temperature were previously mentioned. Since then, FOX ('37), and KUZIRAI of our Institute (not yet published) have found that the growth rate of the root shows some abnormality after sudden changes of temperature. MARSH ('36) has ascertained that the changing of temperature brings about a change in potential across the protoplasmic layer of *Valonia*, temporarily opposite to that shown as it reaches its final steady level, and it occurs more frequently and with greater average magnitude of potential change as the temperature change becomes quicker. This tendency is quite similar to what has been observed in the case of *Aldrovanda*, if the change of potential in opposite direction in *Valonia* be considered to be due to stimulation. Cooling slower than  $0.15^\circ$  per minute, or warming slower than  $0.2-0.25^\circ$  per minute, fails to cause sensation of temperature in human skin, owing to "adaptation" (cf. GOLDSCHIEDER, p. 157). A slow change of temperature may introduce "adaptation," which makes the change less effective for stimulation, in *Aldrovanda* and in *Valonia*, as well as in the human skin.<sup>1)</sup> The relation of stimulation to adaptation will be discussed later.

### Thermal Adaptation

Let the threshold temperature of the leaf kept for many hours at a temperature,  $t_1$ , be  $s_1$ , and that of the leaf kept at another temperature,  $t_2$ , be  $s_2$ . Now if a leaf kept at  $t_1$  be transferred into the water of  $t_2$ , the threshold temperature must be shifted from  $s_1$  to  $s_2$ , sooner or later. In this case it may be said, in a sense, that the leaf which has been adapted to  $t_1$  becomes adapted to  $t_2$ . The aim of the present study is, in the first place, to see in what way the threshold temperature changes from  $s_1$  to  $s_2$ , namely to see how the thermal adaptation proceeds.

### Method

Leaves to be used in the experiment are adapted to the first temperature ( $t_1$ ) for a sufficiently long while, in the same manner as in the case of the thermal stimulation.

At first, the threshold of stimulation by a sudden decrease<sup>2)</sup> of temperature from  $t_1$  is determined with a few leaves from a whorl, the leaves of which are to be used for the experiment of adaptation. Let the threshold temperature now determined be  $s'_1$ . The mean threshold temperature (of young or old leaves) at  $t_1$  is known from Table 5. Let this value be  $s_1$ . The values of  $s_1$  and  $s'_1$  are not necessarily the same,

1) Not only the difference, but also the rate, of temperature change is important in causing the thermonastic movement of filaments of *Centaurea*, etc. (BÜNNING, '29a), and the shutting movement of the tulip flower (BÜNNING, '29b). According to JOST ('23, p. 364), the magnitude of the opening response of the tulip flower also depends on the rate of temperature change, though this BÜNNING denies.

2) The threshold for an increase of temperature is not used for the present experiment, since it is determined less definitely.



for  $s_1$  is the average of the whorls, I, II, and III, for "young leaves," and of IX to XII for "old leaves." The difference,  $s_1 - s'_1$ , represents how much the threshold of the leaves of a certain whorl differs from the average value of young or old leaves. Then, another leaf from the same whorl is transferred quickly into the water of the second temperature ( $t_2$ ), at which the adaptation velocity is to be measured.  $t_2$  may be either higher or lower than  $t_1$ . The difference  $t_2 - t_1$  or  $t_1 - t_2$  should here be less than the threshold difference, or else the leaf will be stimulated. The leaf is kept at  $t_2$  for a while. The duration of keeping leaves at  $t_2$  will be denoted with  $\tau$ . After a certain duration ( $\tau$ ), the leaf is suddenly carried, to stimulate it, into a third temperature ( $t_3$ ) which is always lower than  $t_2$ .<sup>1)</sup> And whether it is stimulated by this temperature change, or not, is observed. Similar determinations are made with other leaves of the same whorl, with respect to various values of  $\tau$  and  $t_3$ .

In order to put the results of whorls of different irritability together, the difference,  $s_1 - s'_1$ , of each whorl is added to  $t_3$ .<sup>2)</sup> And the results are shown in a diagram in which  $\tau$  and the corrected  $t_3$  are taken as the abscissa and the ordinate, respectively. There a stimulated leaf is represented with a solid circle, and that not stimulated, with a hollow circle. Fig. 2 is an example,  $t_1$  and  $t_2$  being 20° and 30°, respectively. The border-line between the areas occupied by solid and hollow circles may represent the change of the threshold temperature with time. Due to considerable variation of results, the border-line can not be clearly defined, the change of threshold being known only approximately. Similar diagrams to Fig. 2 are made for various combinations of  $t_1$  and  $t_2$ . In case  $t_2$  is lower than  $t_1$ , the graph takes a form like Fig. 2, inverted.

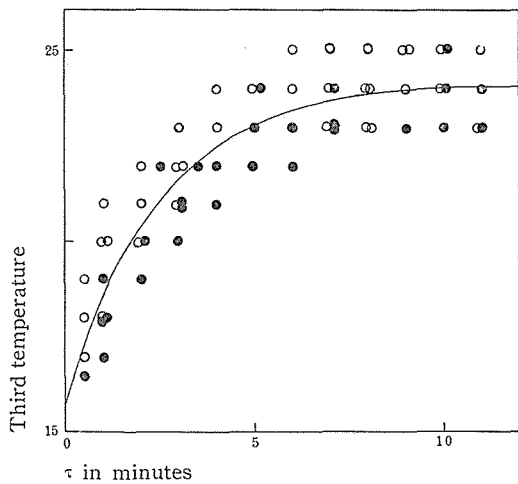


Fig. 2. The change of the threshold temperature after the transference from 20° into 30°. ○ : a leaf not reacted. ● : a leaf reacted.  $\tau$  : the time after the transference from  $t_1$  to  $t_2$ .

### Result

#### A. The case where $t_2$ is higher than $t_1$

The difference,  $t_2 - t_1$ , was chosen as 5°, 10° and 15°. The first temperatures were from 5° to 35°, and the second temperatures, from 20° to 40°.

The case of  $t_1 = 25^\circ$  and  $t_2 = 40^\circ$  was successful for old leaves, but not for young leaves, as these were stimulated by that temperature change. In the case of  $t_1 = 30^\circ$ ,

1) For the determination of threshold,  $t_2$  and  $t_3$  in the present chapter correspond to the first and the second temperature in preceding chapter, respectively.

2) This way of correction for irritability is rather rough. But the result is better than nothing.

and  $t_2=40^\circ$ , the leaf dipped into the water of  $t_2$  was not allowed to float out from the spoon at once, but was held in it for some seconds, to make the change of the leaf temperature a little slower than in ordinary cases, because  $t_2-t_1$  corresponded to the threshold difference in this case (cf. Table 5).

1. *The first stage of adaptation*

Immediately after the transference into  $t_2$ , the threshold of the leaf does not differ much from the value at  $t_1$ . For example, at half a minute after the transference from  $20^\circ$  to  $30^\circ$ , the leaf is not stimulated by a second transfer (from  $30^\circ$ ) into  $17^\circ$  (cf. Fig. 2). But the threshold goes up with time, and five minutes after the first transference ( $20^\circ \rightarrow 30^\circ$ ), the leaf is stimulated by decreasing its temperature (from  $30^\circ$ ) even to  $23^\circ$ . The threshold temperature seems, in Fig. 2, to shift with time exponentially.

In reality, if the threshold temperature at any moment be denoted by  $s$ , and the final value of  $s$  reached asymptotically, by  $s_m$ , then  $\log(s_m-s)$  plotted against  $\tau$  gives a straight line, in many cases. So the equation of  $s$  is

$$s = s_m - (s_m - s_1)e^{-k_s \tau}, \dots\dots\dots (1)$$

where  $k_s$  is a velocity constant ( $\text{min.}^{-1}$ ) of the change of threshold temperature, or that of the adaptation. ( $e$  is the base of the natural logarithm.)

The curve in Fig. 2, which is fitted for young leaves, is  $s=24.2-8.5 e^{-0.43\tau}$ . This value of  $s_m$  is not coincident with, but is a little higher than, the mean threshold temperature ( $s_2$ ) of young leaves adapted to  $30^\circ$  ( $t_2$ ), namely  $23.4^\circ$  (cf. Table 5). Why the two values differ from each other will be discussed later. In the first few minutes, the exponential curve seems to be above the true border-line.

Generally, when a body is exposed to a temperature different from its own, its temperature may change with time also exponentially. To test the temperature change of the leaf, the tip of thin thermo-junction was inserted in a closed leaf of *Aldrovanda*, and the leaf was transferred suddenly from the water of  $25^\circ$  into that of  $35^\circ$ . The temperature in the closed cavity of the leaf became about  $34^\circ$  in 10 seconds, and  $34.9^\circ$  in the following 10 seconds. Hence the velocity constant of the temperature change was about 14 ( $\text{min.}^{-1}$ ). There may have been many sources of error in that measurement. But the value of this velocity constant differs so much (35 times as large!) from that of the threshold temperature ( $k_s=0.40$ ), that there is no question that the change of the threshold temperature is not due merely to the physical change of the leaf temperature, but is of a physiological nature.

Values of  $k_s$  for various combinations of  $t_1$  and  $t_2$  are given in Table 7.  $\tau_1$  is the time when  $s_m-s=1^\circ$ , with possible ranges of variation. Possible ranges of  $k_s$ -values are also shown in brackets. For  $t_2=40^\circ$  and  $t_1=30^\circ$  or  $35^\circ$ ,  $\tau_1$  is too small to be determined by the present method.

With the same  $t_2$ , the lower the  $t_1$ , the smaller the  $k_s$ . And similarly for the same  $t_1$ , the lower the  $t_2$ , the smaller the  $k_s$ . In other words, *the lower the leaf temperature, the slower the adaptation.*

*Young leaves adapt faster than old ones.*

The temperature quotient,  $Q_{10}$ , of adaptation is shown in Table 8. The lower the temperature, the larger the  $Q_{10}$ .

Table 7.

$t_1$	$t_2$	Young leaves			Old leaves		
		$s_m - s_1$	$\tau_1(\text{min.})$	$k_s \times 10$	$s_m - s_1$	$\tau_1(\text{min.})$	$k_s \times 10$
35°	40°	5°	<2	>8	5°	<2	>8
30°	40°	9.9°	2~3	7~10	9.7°	2~3	7~10
25°	40°	—	—	—	14.0°	3.9±0.3	6.8(6.3~7.3)
25°	35°	8.9°	3.3±0.3	6.6(6.1~7.3)	8.7°	3.8±0.3	5.7(5.3~6.2)
25°	30°	4.8°	3.7±0.4	4.2(3.8~4.8)	4.8°	4.3±0.3	3.7(3.4~3.9)
20°	30°	8.5°	5.4±0.2	4.0(3.8~4.1)	8.0°	6.7±0.2	3.1(3.0~3.2)
15°	30°	12.9°	9.3±0.3	2.8(2.7~2.8)	12.1°	10.5±0.3	2.4(2.3~2.4)
15°	25°	6.9°	10.8±0.5	2.0(1.9~2.1)	8.0°	13.7±0.7	1.5(1.4~1.6)
15°	20°	5.0°	18.2±0.7	0.90(0.86~0.93)	4.9°	20.4±1.0	0.78(0.74~0.82)
10°	20°	9.5°	27.1±0.8	0.83(0.81~0.86)	9.5°	37.6±1.0	0.60(0.58~0.62)
5°	20°	14.1°	58.4±0.4	0.45±0.03	14.2°	68.4±0.5	0.39±0.00

Table 8.

$t_2 - t_1$	$t_1$	$t_2$	Young leaves		Old leaves			
			$k_s \times 10$	$Q_{10}$	$k_s \times 10$	$Q_{10}$		
5°	35°	40°	>8	} 4.7	>8	} 4.7		
	25°	30°	4.2		3.7			
	15°	20°	0.90		0.78			
10°	30°	40°	7~10	} 4.8	7~10	} 5.2		
	25°	35°	6.6		} 2.7		5.7	} 3.4
	20°	30°	4.0		} 4.0		3.1	} 4.2
	15°	25°	2.0		} 5.9		1.5	} 6.4
	10°	20°	0.83				0.60	
15°	25°	40°	—	} 6.1	6.8	} 2.9		
	15°	30°	2.8		2.4		} 6.1	
	5°	20°	4.5		0.39			

2. The second stage of adaptation

After the threshold temperature has reached the maximal value ( $s_m$ ), it goes down and very slowly approaches  $s_2$ .

In order to see the change of the threshold value in this stage, the values were determined at several time points and the average of them was made at each point taken. The results are plotted in Fig. 3.

Variation of the threshold temperature grows greater than in the first

stage. But nearly all the leaves show lower threshold values than  $s_m$ , with few exceptions. Hence the mean threshold temperature lowers. The number

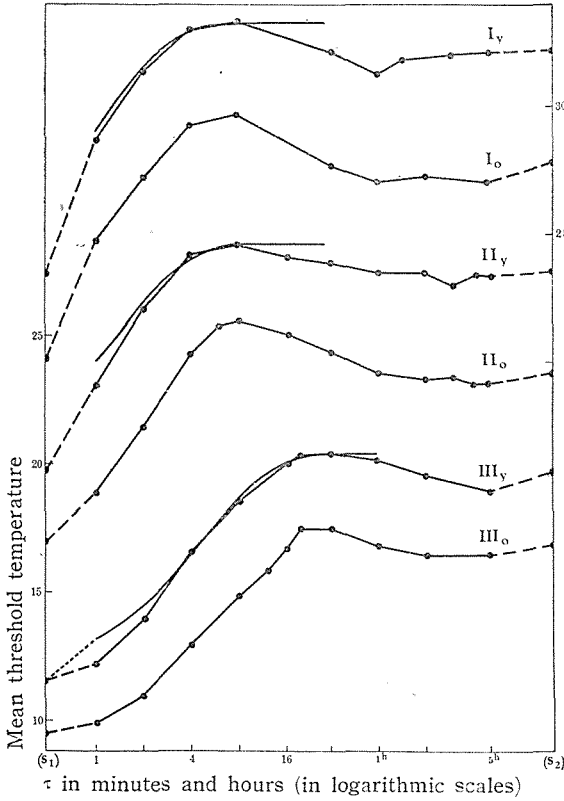


Fig. 3. The change of the mean threshold temperature after the transference from  $t_1$  to  $t_2$ , when  $t_1 < t_2$ . I:  $t_1 = 30^\circ$ ,  $t_2 = 40^\circ$ . II:  $t_1 = 25^\circ$ ,  $t_2 = 35^\circ$ . III:  $t_1 = 15^\circ$ ,  $t_2 = 25^\circ$ . The curves of young leaves are denoted by the suffix y, and those of old leaves by o. The curves begin from  $s_1$ -values and end at  $s_2$ -values. The smooth curves without dots are the exponential curves fitted for the first stage. The temperature scales of the ordinate for  $I_y$  and  $I_o$  are on the right above, and those of the other curves, on the left.

of leaves used for the present determination was less than in the case of determining  $s_1$  and  $s_2$  in Table 5, so the mean threshold temperature may deviate from  $s_2$ , even though the leaves might have been quite adapted to  $t_1$ . It is, however, certain that *at least a few hours are needed for leaves to react with the normal threshold of the new temperature*, in the cases shown in Fig. 3, namely when the leaf temperature is rapidly raised by  $10^\circ$ .

B. The case where  $t_2$  is lower than  $t_1$

Since the threshold differences are small in the case of lowering the temperature, the temperature decrease of  $5^\circ$  is possible only when  $t_1$  is above  $25^\circ$  (cf. Fig. 1).

When leaves were suddenly transferred from  $25^\circ$  to  $20^\circ$ , many young ones reacted. So they were held in the spoon for ten seconds

after the transference (to  $t_2$ ) to make the change of the leaf temperature slower. The changes of the threshold after the transference into  $t_2$  are shown in Fig. 4 A and B. In the present case, the changes in the first stage do not correspond to the exponential function so closely as in the preceding. Assuming, however, that analogous changes occur also in the present case, exponential curves are drawn, the velocity constant being roughly computed from Table 7. As seen in the figure, the observed values are at first below

the exponential curve, as in the case where  $t_2 > t_1$ . Then the two values approach each other, and again the former becomes lower, rather abruptly. Further, slowly rising, it seems to approach  $s_2$ . As in the preceding case where  $t_2 > t_1$ , at least a few hours are needed for the threshold to reach the normal value at  $t_2$ .

The lowering of threshold in the second stage is most conspicuous, and lasts for the longest time, in the case of  $t_1 = 25^\circ$  and  $t_2 = 20^\circ$ . The lower the temperature, the more stimulative is a temperature decrease. So the decrease of  $5^\circ$  must have greater influence in the case of  $t_1 = 25^\circ$ , than in the cases of  $t_1 = 30^\circ$  and  $35^\circ$ .

C. Slow change from  $t_1$  to  $t_2$

In the experiments mentioned above, the leaf temperature was changed from  $t_1$  to  $t_2$  very rapidly, in the same way as when the leaf was stimulated by the temperature change. For comparison, changes of threshold after a slow change of the leaf temperature were observed.

As before, whorls were sunk in deep cylindrical vessels, which stood in a thermostat. Leaves were kept at  $t_1$ . And then the water of the thermostat was warmed by an electric heater which was regulated with resistances. The temperature was raised roughly at a constant rate, and the heating was stopped when the leaf temperature reached  $t_2$ .

The threshold was determined *a*) when the water in the cylindrical vessels reached the new temperature ( $35^\circ$ ), *b*) 30 to 60 minutes after *a*, and *c*) 2 or 3 hours after *a*.

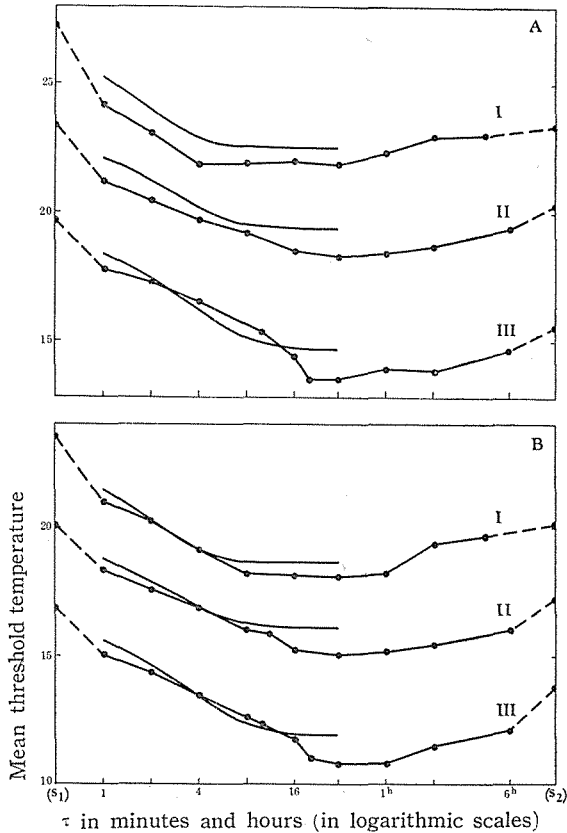


Fig. 4. The change of the mean threshold temperature after the transference from  $t_1$  to  $t_2$ , when  $t_1 > t_2$ . A: young leaves. B: old leaves. I:  $t_1 = 35^\circ$ ,  $t_2 = 30^\circ$ . II:  $t_1 = 30^\circ$ ,  $t_2 = 26^\circ$ . III:  $t_1 = 25^\circ$ ,  $t_2 = 20^\circ$ . The curves begin from  $s_1$ -values and end at  $s_2$ -values. The smooth curves without dots are the exponential curves fitted for the first stage.

When the temperature was raised  $10^\circ$  in 18 or 27 minutes, the threshold temperature at  $b$  was  $0.5^\circ$  to  $2^\circ$  lower than that at  $a$ , while at  $c$  it was very slightly higher than at  $b$ . The difference between the values of  $b$  and  $a$  gets small or hardly distinguishable if the temperature change is made slower, namely if elongated to 63 or 90 minutes. It should be noticed, however, that in these two cases the first time point,  $a$ , roughly corresponds to the time of minimum in the second stage of the rapid temperature change (cf. the curves  $\Pi_y$  and  $\Pi_o$ , Fig. 3).

If  $t_2 - t_1$  was smaller, namely if  $t_1 = 30^\circ$  and  $t_2 = 35^\circ$ , the value at  $b$  was nearly equal to that at  $a$ , even though the temperature was changed from  $t_1$  to  $t_2$  in 8 minutes.

In the case when  $t_2 < t_1$ , the temperature of the water of the thermostat was cooled by the refrigerator, the cooling velocity being controlled by a weak electric heater working at the same time. When the temperature was lowered from  $35^\circ$  to  $25^\circ$  in 30 minutes, the threshold temperature at  $c$  was higher than at  $a$ . The rise of the threshold temperature was observed even when the temperature change was finished in 110 minutes. In other words, a decrease of  $10^\circ$  should be made far more slowly than an increase of  $10^\circ$ , in order to avoid the abnormal changes of threshold in the second stage.

## Discussion

### 1. Terminology

Before discussing the experimental results, certain words should be defined, for the words, adaptation and accommodation, are used for various phenomena. Even relating to the present question, namely concerning temperature, three different categories of conception occur.

1. "Adaptation," "accommodation," and "acclimatization" mean, in some cases, the habituation of an organism to a climate different from that to which the individual in question or its ancestors have been habituated, phenomena taking days, years, or generations.

2. When HOPKINS ('37) observed that the rate of locomotion of *Amoeba* showed great fluctuation after a change of environmental temperature, it was said not to have "adapted" to the new temperature, until the rate of its locomotion took constant value, characteristic to the new temperature. Some hours are needed for the "adaptation" in this case.

3. The human skin feels a body of a certain temperature either warm or cold, according to whether it is "adapted" to cooler or warmer temperature. A conception of "accommodation" has been introduced to explain the facts that a slowly increasing electric current shows a higher threshold than a quickly increasing one, and that a nerve in which a current is flowing is excited when the current is cut off (cf. p. 372). "Adaptation" or "accommodation" is completed in minutes or even in a fraction of a second, in this case.

The thermal adaptation measured in the present experiment reminds us of the adaptation of temperature sensation of the skin. In plant physi-

ology, however, temperature is usually an environmental factor rather than a stimulating agent. So it is preferable to qualify the word, adaptation, so far as it is applied to the sensitivity to thermal stimulus.<sup>1)</sup>

By "tonus" or "tone" is meant the irritability or the activity effected and determined by an internal or external factor (RAWITSCHER, p. 12).<sup>2)</sup> So the adaptation in respect to irritability (perception and response) may be discriminated from adaptation in general by calling it *tonic adaptation*,<sup>3)</sup> or more accurately, *thermotonic adaptation*. The adaptation measured with changes of threshold is the tonic adaptation.<sup>4)</sup>

2. The case where  $t_2$  is higher than  $t_1$

When the leaf is transferred from  $20^\circ$  ( $t_1$ ) to  $30^\circ$  ( $t_2$ ), its temperature rapidly changes as indicated by the  $t$ -curve in Fig. 5 A. The shifting of the threshold for a temperature decrease was given by Fig. 2, and is represented again in Fig. 5 A as the  $s$ -curve, from  $s_1$  to  $s_m$ .<sup>5)</sup> The threshold of stimulation by a temperature increase was not measured, but it probably shifts in a way similar to the  $s$ -curve, only the initial and the final values being different. So it is shown in the same figure as the  $s'$ -curve, from  $s_1'$  to  $s_m'$ .

Shortly after the change of the leaf temperature from  $t_1$  to  $t_2$ , namely at  $\tau_p$ , for example, only a small temperature difference is sufficient to stimulate the leaf by a temperature increase (from  $t_2$  to  $s_p'$ ), while a great difference is needed to stimulate it by a decrease (from  $t_2$  to  $s_p$ ). Then the

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1) Adaptation to a stimulus is nothing but adaptation to the environment, for stimulus is a change in an environmental factor. But adaptation of inner conditions of cells concerning perception and response should be discriminated, if required, from adaptation of other characters of cells, or adaptation in general.

Generally the terms, adaptation and accommodation, are synonymous, and one or the other seems to be used conventionally. In this paper, however, the former term is used for the observable phenomena, while the latter is restricted to a hypothetical process assumed to explain the observed facts of adaptation (cf. p. 372).

2) By tonus ("Tonus" or "Stimmung" in German) is meant in some cases (cf. CZAPEK, p. 195, and MIEHE, p. 571), an excited condition due to a stimulus, and in some other cases (cf. SACHS, pp. 613 and 654, or PFEFFER, p. 78), a state in which the power of response is produced and maintained by some agency (in contrast to the state of rigor). But any change in the activity, especially that relating to stimuli (RAWITSCHER, p. 65), is also called a change in tone (PFEFFER, pp. 361, 611, etc.).

3) Even when phototropic sensitivity is lowered by preliminary exposure to light, the change of tone has been chiefly spoken of, the term, adaptation, being seldom used in plant physiology. Temperature, however, is the most fundamental and indispensable among environmental factors. So the conception of adaptation may better underlie the change of tone.

4) PRINGSHEIM ('09, pp. 274, 279) considers that the effect of tone ("Stimmung") is best known by the determination of threshold, presentation time, etc.

5) In human skin, too, the zero point of temperature feeling rises and falls corresponding to, but far more slowly than, changes in the skin temperature (cf. GOLDSCHNEIDER, p. 155).

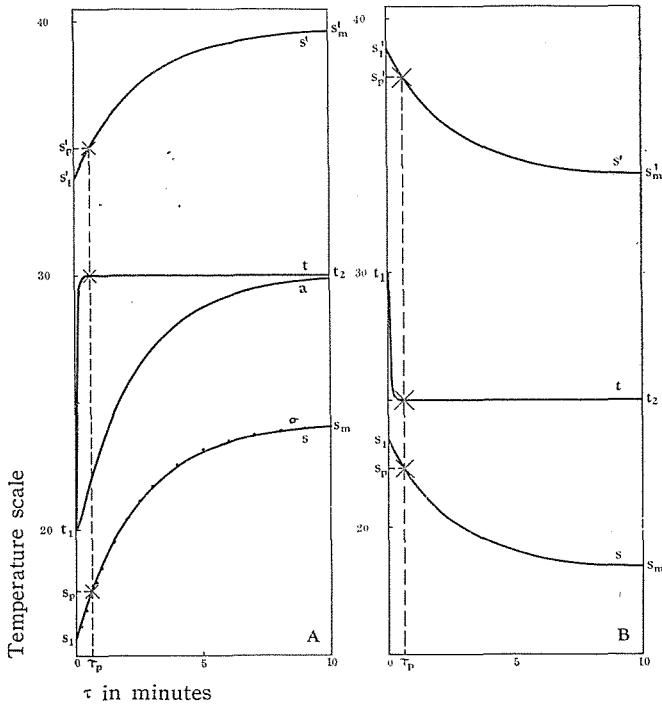


Fig. 5 A and B. Diagrams showing the relation between the change of leaf temperature ( $t$ ), and the change of the threshold of stimulation by a decrease ( $s$ ) or an increase ( $s'$ ) of temperature.  $s_p, s_p'$ : the values of  $s$  and  $s'$ , respectively, at  $\tau_p$ . A: The case of  $t_1=20^\circ$  and  $t_2=30^\circ$ .  $a$  is the curve of "accommodation" (after the equation, 6, p. 374), while  $\sigma$ , which is shown with dots unconnected, represents the same but with the threshold of stimulation by a temperature decrease (after the equation, 10, p. 377). B: The case of  $t_1=30^\circ$  and  $t_2=25^\circ$ .

threshold difference for the temperature increase grows larger and larger with time, until it reaches  $s_m' - t_2$  at  $\tau=10$  min., while that for the temperature decrease diminishes, until it reaches  $t_2 - s_m$ .

Let rise and fall of temperature be comparable to an increase and decrease in electric current, respectively. With the adaptation to an electric current, the threshold for the stimulation by a further increase in current may rise, while that by a decrease of current (e. g. by cutting it off) may lower.

How the tone for perception of thermal stimulus is shifted by a change of leaf temperature is suggested by the  $s$ -curve. Therefore, the constant,  $k_s$ , given in Table 7, is the *velocity constant* of change of tone, or, we may say, *of the tonic adaptation*.

But the tonic adaptation is not finished in the simple exponential curve, as  $s$ , but irregularity appears afterwards. In the first stage, the tone is



shifted to become roughly corresponding, somehow or other, to the new temperature. But still many regulation processes should go on to complete the adaptation, the threshold being affected in an irregular manner by such unusual processes in cells. Thus, the adaptation going on in the first stage may be called the *primary adaptation*, and that in the second stage, the *endonomous adaptation*. The primary adaptation may be regarded as induced directly by a change in an external factor (temperature), while the chief cause of the endonomous adaptation may be a fine disorder left behind the rough and gross regulation by the primary adaptation.

Locomotion of *Amoeba* (loc. cit.), growth of *Avena* coleoptiles (SILBERSCHMIDT, '25), CO<sub>2</sub>-production of *Phaseolus* (CROZIER and NAVEZ, '30-'31), and the potential of *Valonia* (MARSH, '36), also do not attain the steady normal rate (or value) at the new temperature within an hour after the temperature change. The length of the abnormal period in these cases is similar to that of *Aldrovanda*. The endonomous adaptation of *Aldrovanda* leaf mentioned above is a part of tonic adaptation, so far as it is determined with the threshold. Endonomous readjustment after a temperature change, however, may be performed by some abnormal metabolism, which may necessarily affect the threshold value, as well as the locomotion, growth, respiration, or potential.

Since variation of the threshold temperature is very large, it is supposed that the threshold temperature might fluctuate, just as the rate of locomotion of *Amoeba*, if the threshold of the self-same leaf could be traced. But in the case of *Aldrovanda* nothing is certain about the fluctuation, for only average threshold temperatures of different leaves can be examined. The abnormality (perhaps fluctuation) of the threshold temperature may be present also in the first stage, being observed merely as variations of the directional (exponential) change. In the second stage, the mean threshold values become lower, namely the average irritability lowers, and then gradually recovers.

NORTEN ('38) asserted that the fluidity in the cell changes without delay corresponding to the changing temperature, but the fluidity as measured by his method must be an incomparably rougher indication of the state of the cell than the irritability.

### 3. *The case where $t_2$ is lower than $t_1$*

In case  $t_2$  is lower than  $t_1$ , the relation between the leaf temperature and the threshold temperature is seen in Fig. 5 B. When the leaf is transferred from  $t_1$  to  $t_2$ , the leaf temperature lowers along the  $t$ -curve, and the threshold temperatures of stimulation by a fall and a rise of temperature become lower along the  $s$ - and the  $s'$ -curves, respectively. Thus, the threshold difference for stimulating with a temperature fall grows larger with time, from  $t_2 - s_p$  to  $t_2 - s_m$ , while that for a temperature rise becomes smaller, from  $s'_p - t_2$  to  $s'_m - t_2$ .

Successive lowering of temperature can be considered as summation of

stimuli. So, if a leaf is excited by transferring from  $t_2$  to  $s_p$ , shortly after the transference from  $t_1$  to  $t_2$ , it can be assumed that a small temperature difference,  $t_2 - s_p$ , can be stimulative owing to the after-effect of a stimulus of transferring from  $t_1$  to  $t_2$ , which has also been below the threshold. Then the divergence of the  $s$ -curve from the  $t$ -curve with time may mean the extinction of the after-effect of a foregoing stimulus.<sup>1)</sup>

The extinction of the effect of a stimulus has something in common with the adaptation to it. So it is not improper to consider that the earlier parts of the curves in Fig. 4 A and B roughly represent the courses of the primary adaptation.<sup>2)</sup> The difference in forms of the curves in this case from the case where  $t_2 > t_1$  may perhaps have some connection with the effect of summation of stimuli.

Before the primary adaptation reaches the final asymptote, the lowering of the mean threshold temperature appears. In the case where  $t_2 > t_1$ , the threshold temperature rises in the first stage and falls in the second stage, but in the present case, it falls in both of the stages. So the first and the second stages are separated from each other by the maximum of the curve in the former case, and by an abrupt lowering of the curve in the latter case.

The maximum of the curve, III<sub>y</sub> in Fig. 3, lies between 16 and 30 minutes, while the abrupt lowering of the curve, II in Fig. 4A, lies between 8 and 16 minutes. Though  $t_2$  is nearly the same in those two cases, the temperature range through which the leaf passes is lower in the former case ( $15^\circ \rightarrow 25^\circ$ ) than in the latter ( $30^\circ \rightarrow 26^\circ$ ). Therefore the second stage begins earlier in the latter case.

The duration of the endonomous adaptation, and the degree of abnormal lowering of threshold in that period, does not differ much in the present case ( $t_2 < t_1$ ) from the preceding ( $t_2 > t_1$ ), notwithstanding the fact that the temperature difference between  $t_1$  and  $t_2$  is  $5^\circ$  in the present case, while it is  $10^\circ$  in the preceding. This must have some connection with the fact that a temperature decrease stimulates the leaf with a smaller change than an increase.

#### 4. The case of slow change of temperature

By experiments, it is determined that the "abnormality" (temporary lowering of the average threshold temperature) in the second stage is less when the temperature change is slower ( $t_2 - t_1$  being the same), when  $t_2 - t_1$  is smaller, or when the leaf temperature is increased (namely when  $t_2 < t_1$ , than when  $t_2 > t_1$ ). The effect of these three conditions is the same as in the case of stimulation by a temperature change. The similar trend has been observed also by HOPKINS (the effect of extent of the temperature

1) For the extinction of the effect of the first stimulus in the case of summation of photo- or geotropic stimuli, see DU BUY and NUERNBERGK, III, p. 468, and RAWITSCHER, p. 46.

2) The curves are considered to represent the courses of thermal adaptation, for the reason that they show how the threshold values characteristic to  $t_1$ 's are shifted with time to those characteristic to  $t_2$ 's.

change), MARSH (the effect of rate of the temperature change) and KUZIRAI (do.).<sup>1)</sup> The "abnormality" in threshold, locomotion, respiration, growth, or potential, caused by a temperature change, may be a sort of response to a temperature change, as well as a manifestation of the endonomous readjustment. With *Aldrovanda* leaves, the shutting is considered the response to a stimulus. But even when the leaf does not shut, a temperature change affects the condition in cells, after the same rule concerning the rate, extent, and direction (i. e. plus or minus) of the temperature change.

The fluctuation of the threshold temperature in the second stage occurs even if the leaf temperature is changed more slowly than the primary adaptation (p. 366). Hence the cause of that "abnormality" may be a portion of the intracellular changes that is not readjusted during the period of the primary adaptation.

5. The cause of  $s_m \neq s_2$

The relation among cardinal threshold temperatures is shown in Fig. 6, viz.  $s_m > s_2$  ( $> s_1$ ) in the case where  $t_2 > t_1$  (A), and ( $s_1 > s_2 > s_m$  in the case where  $t_1 > t_2$  (B). A probable cause is as follows:—

Let  $d_1 = t_1 - s_1$ ,  $d_2 = t_2 - s_2$ , and  $d_m = t_2 - s_m$  (cf. Fig. 6A, B), then  $d_2 > d_m > d_1$  (case A) and  $d_2 < d_m < d_1$  (case B). Suppose that the character of the perception mechanism at  $t_1$  (such as to be stimulated by a temperature decrease of  $d_1$ ) changes only gradually towards the characteristic state at  $t_2$  (such as to be stimulated by a temperature decrease of  $d_2$ ). Then, in the course of such a change, the threshold difference may be intermediate. Therefore,  $d_m$  lies between  $d_1$  and  $d_2$ ,  $s_m$  being unequal to  $s_2$ .

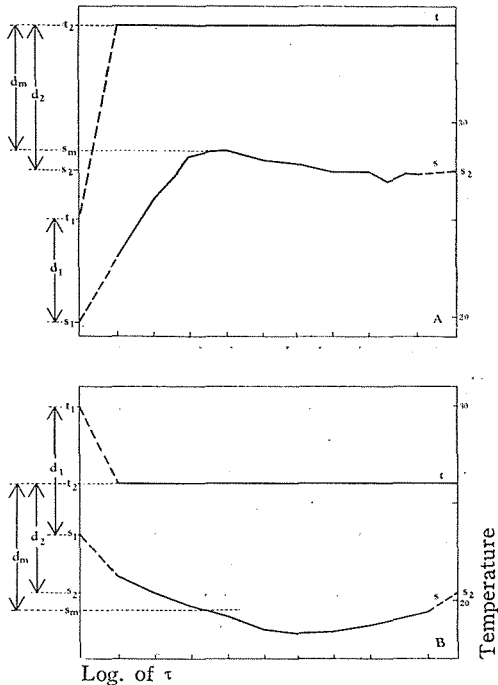


Fig. 6 A and B. Diagrams showing the cardinal threshold temperatures and differences. When the leaf temperature is changed as the  $t$ -curves, the mean threshold temperature changes as the  $s$ -curves.  $t_1$ : the first temperature;  $s_1$ : the mean threshold temperature at  $t_1$ ; and  $d_1 = t_1 - s_1$ .  $t_2$ : the second temperature;  $s_m$ : the final threshold temperature of tonic adaptation at  $t_2$ ;  $s_2$ : the mean threshold temperature at  $t_2$ ; and  $d_m = t_2 - s_m$ ,  $d_2 = t_2 - s_2$ .

1) A plant which has been in the dark shows abnormal rates of growth for a few hours after exposure to light—the light-growth response. In this case, too, a sudden increase of light intensity is the prime factor (cf. CHOLODNY, '31).

### A Hypothesis Concerning Thermal Stimulation and Adaptation

Even though the *Aldrovanda* leaf may be stimulated by a certain degree and speed of temperature change, it will not be stimulated by the same extent of the change if the rate of change is slower. The slower the temperature change, the greater must be the change, in order to stimulate the leaf. Similar facts have also been known concerning other types of stimulus. With respect to electrical stimulus, a sort of "accommodation" was assumed to explain the dependence of threshold upon the rate of change of the current (cf. NERNST, '08, and HILL, '36). In the following, too, the just-mentioned fact will be accounted for by introducing a conception of "accommodation." The idea of the hypothesis has already been suggested (ASHIDA, p. 74).

Two possibilities are conceivable concerning the way in which a change of environmental temperature acts on an irritable cell; namely, 1) the cell (or a part of it) is stimulated when its temperature is changed with a rate greater than a certain limit; and 2) a spacial temperature gradient caused in a cell makes a stimulus, when the gradient is over a certain value. (In this case the rate of change of the environmental temperature is an important factor for determining the steepness of the temperature gradient.) The present hypothesis is concerned with the first of the two possibilities.

Many physical and chemical forces may always be acting in a living cell. At a constant temperature, they may equilibrate one another.<sup>1)</sup> If the temperature is changed, their relations to one another may alter, for temperature coefficients are different for different forces. In other words, equilibria among forces and processes are disturbed by a temperature change. Let the cell be said to be put in a state of "*disturbance*" in that case. But if the second temperature be in the range of the biokinetic temperature, the equilibrium characteristic to the new temperature will be established sooner or later, and the normal life of the cell will then be continued. The attaining of the new equilibrium may be due to many physical and chemical changes in the cell, such as changes in distribution and quantity of substances, changes in dispersion of colloidal matters, etc., some duration of time being needed for those changes. Let the process of adjustment to establish the new equilibrium, obliterating the "disturbance," be called "*accommodation*."

Before attaining the new equilibrium, there is some residual "disturbance," to be obliterated by the "accommodation." Let such remaining portion be called "*net disturbance*." In a cell in the "disturbance," various features, such as pH, dispersion and hydration of colloidal particles, etc., may be more or less abnormal, the extent of the abnormality depending on the grade of "net disturbance." And when "net disturbance" amounts to a certain limit, a permeability change (or a contraction of plasma, or such)

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1) Living cells are in a state of non-equilibrium, or are said to be in a steady state. In the following, however, both of the states, of the equilibrium and of the steady state, are included in the term, equilibrium, in order to simplify the words.

may result, if the protoplasm is of a very sensitive type. In other words, irritable cells may be excited if sufficiently great "disturbance" be caused in them at a rate sufficiently quick not to be overtaken by the "accommodation." Such a condition may arise when an *Aldrovanda* leaf is transferred from the water of a certain temperature to the water of another very quickly, provided the difference between the two temperatures is greater than the threshold difference.

Such is the outline of the hypothesis. An example which makes the idea understood more easily is found in a BUNGENBERG DE JONG's observation on coacervates (cf. BUNGENBERG DE JONG, '32, p. 125). The solvate content of a certain coacervate is reduced by a temperature decrease. When the temperature is lowered gradually, coacervate drops are kept homogeneous, as there is enough time for surplus solvate to diffuse through, and out of, the drops. On the contrary, when the temperature is decreased rapidly, coacervate drops become vacuolated, since there is not sufficient time for the surplus solvate to be released from the drops.

According to the definition given above, the change of the capacity to hold the solvate is the "disturbance." And this "disturbance" causes diffusion of the surplus solvate, as the "accommodation" process. But if the increase of the "disturbance" is too rapid to be cancelled sufficiently by the "accommodation," the response (i. e. the vacuolization) takes place. It may be self-evident that the vacuolization does not occur if the temperature change is smaller than a certain degree, however rapidly the change may be made. So the rate and the degree of the temperature change are two important factors for the occurrence of vacuolization in certain coacervate drops, just as for the thermal stimulation of *Aldrovanda* leaves.

The hypothesis can be given explicitly in mathematical forms.

Let the leaf temperature at any moment be denoted by  $t$ , and the time by  $\tau$ . If a leaf which has been in water of a temperature,  $t_1$ , be transferred into water of another temperature,  $t_2$ , the rate of change of the leaf temperature may roughly be represented by an equation,

$$\frac{dt}{d\tau} = k_a(t_2 - t), \dots\dots\dots(2)$$

where  $k_a$  is a constant. Integrating this,

$$t = t_2 - (t_2 - t_1)e^{-k_a\tau}. \dots\dots\dots(3)$$

Since "disturbance" may be corresponding to the changing temperature,  $t$  may represent "disturbance," too, at the same time. And  $t_1$  and  $t_2$  mean no and maximum "disturbance," respectively. So  $k_a$  is the velocity constant of arising "disturbance," as well as of the change of leaf temperature.

"Accommodation" may also be represented with temperature scales, for it implies the decrease of "disturbance." Let "accommodation" at any moment, represented by the temperature scales, be denoted by  $a$ . (The initial and the final values of  $a$  are  $t_1$  and  $t_2$ , respectively.) Let it be assumed that the velocity of "accommodation" be proportional to the magnitude of the "net disturbance,"  $t - a$ , at any moment. Then

$$\frac{da}{d\tau} = k_a(t-a), \dots\dots\dots(4)$$

where  $k_a$  is the velocity constant of "accommodation," the value depending on temperature.

Substituting (3) into (4),

$$\frac{da}{d\tau} = k_a \{ t_2 - (t_2 - t_1)e^{-k_a\tau} - a \}. \dots\dots\dots(5)$$

By solving this,<sup>1)</sup> we have

$$a = t_2 - (t_2 - t_1) \frac{k_a}{k_a - k_u} e^{-k_a\tau} + (t_2 - t_1) \frac{k_u}{k_a - k_u} e^{-k_u\tau}. \dots\dots\dots(6)$$

Let "net disturbance" at any moment be represented by  $u$  (in the temperature scale). Then from (3) and (6),

$$u = t - a = (t_2 - t_1) \frac{k_u}{k_a - k_u} (e^{-k_a\tau} - e^{-k_u\tau}). \dots\dots\dots(7)$$

Let the time when  $u$  is maximum be denoted by  $\tau_m$ , then from  $\frac{du}{d\tau} = 0$ ,

$$\tau_m = \frac{\log k_u - \log k_a}{k_u - k_a}. \dots\dots\dots(8)$$

Hence the maximum value of  $u$ ,  $u_{max}$ , is

$$u_{max} = (t_2 - t_1) \left( \frac{k_u}{k_a} \right)^{1 - \frac{k_u}{k_a}}, \quad \dots\dots\dots(9)$$

1) Put  $\tau = x$   $a = y$   $k_a(t_2 - t_1) = A$   $k_u t_2 = B$ , (\*) then instead of (5), we have

$$y' + k_u y + A e^{-k_u x} - B = 0.$$

Since this is an equation of the BERNOULLI's type, we have

$$y = e^{-k_u x} [C - \{A e^{-k_u x} - B\} e^{k_u x} dx],$$

$C$  being an integral constant, which is determined by the initial condition ( $x=0, y=t_1$ ). Hence

$$y = \left( t_1 + \frac{A}{k_u - k_u} - \frac{B}{k_u} \right) e^{-k_u x} - \frac{A}{k_u - k_u} e^{-k_u x} + \frac{B}{k_u}.$$

By replacing  $x, y, A,$  and  $B$  into (\*),

$$a = \left( t_1 - \frac{k_u(t_2 - t_1)}{k_u - k_u} - t_2 \right) e^{-k_a\tau} + \frac{k_u(t_2 - t_1)}{k_u - k_u} e^{-k_u\tau} + t_2.$$

This is rearranged into (6).

2) From (7), 
$$u_{max} = (t_2 - t_1) \frac{k_u}{k_u - k_a} (e^{-k_a\tau_m} - e^{-k_u\tau_m}). \quad (**)$$

Since

$$e^{-k_a\tau_m} - e^{-k_u\tau_m} = e^{-k_a\tau_m} (1 - e^{(k_u - k_a)\tau_m}),$$

substituting (8) for  $\tau_m$ ,

$$\begin{aligned} e^{-k_a\tau_m} - e^{-k_u\tau_m} &= \left\{ 1 - e^{(k_u - k_a) \frac{\log k_u - \log k_a}{k_u - k_a}} \right\} e^{-k_a \frac{\log k_u - \log k_a}{k_u - k_a}} \\ &= \left( 1 - e^{\log \frac{k_u}{k_a}} \right) e^{-\frac{\log \frac{k_u}{k_a}}{k_u - k_a} - 1} = \left( 1 - \frac{k_u}{k_a} \right) \left( \frac{k_u}{k_a} \right)^{\frac{1}{1 - \frac{k_u}{k_a}}} = \frac{k_u - k_a}{k_u} \left( \frac{k_u}{k_a} \right)^{\frac{1}{1 - \frac{k_u}{k_a}}}. \end{aligned}$$

Substituting this into (\*\*), we have (9)

in the case of  $t_2 > t_1$ , and

$$u_{max} = (t_1 - t_2) \left( \frac{k_d}{k_a} \right) \frac{1}{1 - \frac{k_d}{k_a}}, \dots\dots\dots (9)$$

in the case of  $t_2 < t_1$ .

Let the cell be excited when  $u$  exceeds a certain critical value,  $U$ , namely when  $u_{max} > U$ , and be not excited when  $u_{max} < U$ .

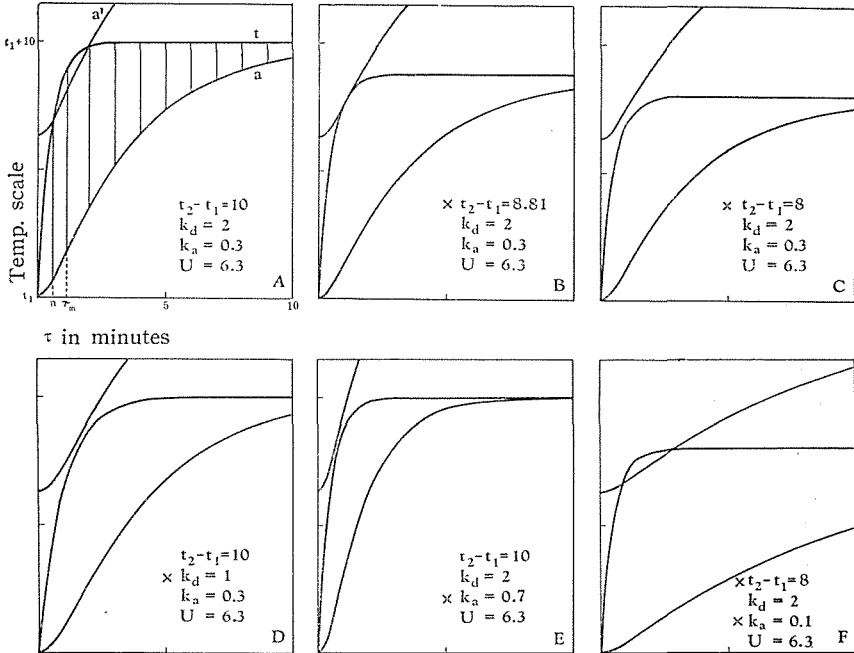


Fig. 7. Explanation in text. The condition different from those of A is noticed with  $\times$ .

The relations among “disturbance,” “accommodation,” “net disturbance,” and  $U$  are shown in Fig. 7 A. The values of  $t_2 - t_1$ ,  $k_d$ , and  $k_a$  are assumed to be 10, 2, and 0.3, respectively. ( $k_d$  is chosen much smaller than the value in the experiment in order to make the figure easier to understand.) The curves,  $t$  and  $a$ , represent “disturbance” and “accommodation,” respectively (after the equations 3 and 6, respectively). The vertical lines between these two curves represent the magnitudes of “net disturbance” at various time points. The value of  $u_{max}$  is 7.155,  $\tau_m$  being 2.116 min.

Now, if  $U=6.3$ , the value of  $u_{max}$  is larger than  $U$  in the present case; hence the excitation takes place. Whether excitation occurs or not is judged in the figure, whether the  $a'$ -curve, which is parallel to the  $a$ -curve, being  $a' = a + U$ , crosses the  $t$ -curve, or not. In Fig. 7 A, the curves,  $a'$  and  $t$ , intersect each other at  $\tau = 0.605$  min. (denoted by  $n$ ). The time,  $n$ , is the presentation time.

In the following, whether excitation occurs or not under various conditions will be discussed with respect to the equation (9), and figures.—

*i) Effect of the temperature difference*

In case both  $k_d$  and  $k_a$  are given,  $u_{max}$  is proportional to  $t_2 - t_1$ . Hence it becomes greater than  $U$  when  $t_2 - t_1$  exceeds a certain value. This means that if the mode of transference from  $t_2$  to  $t_1$  is constant ( $k_d$  given) and if at the same time the velocity of "accommodation" is constant ( $k_a$  given), the cell is excited if the temperature difference is sufficiently large.

If  $t_2 - t_1$  be decreased, other constants being the same as in Fig. 7 A, the portion of  $a'$ -curve included in the area of the "net disturbance" also decreases. And the two curves,  $a'$  and  $t$ , touch each other when  $t_2 - t_1$  becomes to be  $8.81^\circ$ . Fig. 7 B represents the case. If  $t_2 - t_1$  becomes still smaller,  $a'$  never intersects  $t$ , as shown in Fig. 7 C, for example. The threshold differences which were determined by the experiment and shown in Tables 3 and 4 are such critical values of  $t_2 - t_1$ , as  $8.81^\circ$  in the present case.

*ii) Effect of the rate of temperature change*

If  $t_1$  and  $t_2$  be given,  $k_a$  is also given, for  $k_a$  depends on both of  $t_1$  and  $t_2$ . In this case, the larger the  $k_d$ , the larger is the value of  $u_{max}$ , as is easily known from the equation (9). And inversely if  $k_d$  becomes smaller and smaller, other factors being the same as in the case of Fig. 7 A, the  $a'$ -curve becomes apart from the  $t$ -curve at last, as shown in Fig. 7 D. In other words, if the change of leaf temperature be slower than a certain limit, the leaf is not stimulated, as already described (p. 359).

*iii) Effect of the rate of accommodation*

In case  $k_d$  and  $t_2 - t_1$  are given, the larger the value of  $k_a$ , the smaller the value of  $u_{max}$ . How the  $a'$ -curve comes above the  $t$ -curve when  $k_a$  is large, is shown in Fig. 7 E.

The value of  $k_a$  depends on  $t_1$  and  $t_2$ . So it is often experienced at high temperatures, that when the change of temperature is made a little slower, for example if the floating up of a leaf out of the glass spoon is delayed a moment, the temperature change of a rather large  $t_2 - t_1$  fails to stimulate the leaf. On the contrary, the experiment is easier to conduct at low temperatures, for considerable variations of  $k_d$  do not make  $u_{max}$  less than  $U$ , owing to small values of  $k_a$ .

When the leaf is cooled down, even slow cooling often stimulates the leaf (cf. p. 381), for small values of  $k_a$  makes  $u_{max}$  sufficiently large even with small values of  $k_d$ . If  $k_d$  is constant, a smaller temperature change can be stimulative at low temperatures, owing to small values of  $k_a$ . The case is shown in Fig. 7 F. This case seems to be inconsistent with the fact that the threshold difference of the stimulation by a temperature rise is larger at low temperatures. But the account will be given later.—



In the above, it is shown how the experimental results can be explained by the hypothesis. All the figures used for the explanation (Fig. 7, A-F) concern the case when  $t_2 > t_1$ . For the reversed case when  $t_2 < t_1$ , the figures are inverted, the equation being (9').

It is not beyond question that the primary adaptation, determined by the experiment, corresponds to the "accommodation" discussed in the hypothesis. But it may be certain that there is a close connection between the two. Let it be assumed that the progression of the primary adaptation depends solely on the "accommodation." Then the equation of the former, denoted by  $\sigma$ , is

$$\sigma = s_m - \frac{s_m - s_1}{k_a - k_u} k_a e^{-k_a \tau} + \frac{s_m - s_1}{k_a - k_u} k_u e^{-k_u \tau}; \quad \dots\dots\dots(10)$$

because the initial and the final values of  $\sigma$  are  $s_1$  and  $s_m$ , respectively. The equations, (6) and (10), express the same fact in two different measures; namely in the former, the adaptation is expressed by the temperature to which the leaf is adapted, the initial and the final values being  $t_1$  and  $t_2$ , respectively, while in the latter equation, the adaptation is represented with the threshold temperature.

If  $k_a$  becomes infinitely large, the equation (10) is converted into the form of the equation (1) on p. 362. In most of the experiments made by the author,  $k_a$  is not less than 14 (cf. p. 362). Hence the curves by (1) and by (10), namely  $s$  and  $\sigma$  in Fig. 5 A, fit each other within the range of errors. In Fig. 5 A the  $\sigma$ -curve is shown with dots,  $k_a$  being chosen 0.42, so as to let this curve intersect the  $s$ -curve ( $k_s = 0.40$  by the experiment) at the middle between  $s_1$  and  $s_m$ . The "accommodation" curve,  $a$ , is given by the equation (6).

The excitation is assumed to occur when "net disturbance" reaches the value,  $U$ . Now if the leaf temperature were to change by  $U$  without any duration of time, the excitation would take place, because there is no time for "accommodation" to proceed.  $U$ , therefore, is the threshold difference in the ideal case, in which the leaf temperature is changed without time.  $U$  may then be called the ideal threshold difference.  $U$  can be calculated from the equation (9) (or (9')), for it equals  $u_{max}$  when  $t_2 - t_1$  (or  $t_1 - t_2$ ) is the experimental threshold difference, as in the case of Fig. 7 B.

Rough estimation of values of  $U$  for

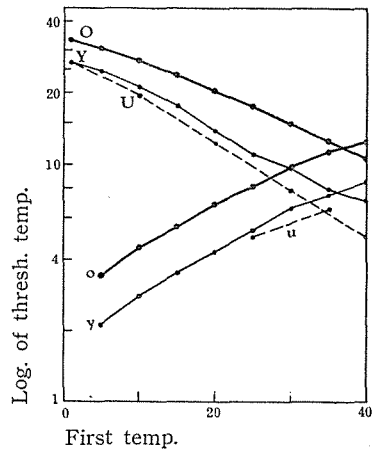


Fig. 8. Logarithm of the threshold difference plotted against the first temperature. O, o: experimental threshold difference of old leaves; Y, y: that of young leaves; U, u: the ideal threshold difference of young leaves. O, Y, and U: for the case of  $t_2 > t_1$ ; and o, y, and u: for the case of  $t_1 < t_2$ .

Table 9.

	$t_1$	Threshold differences		$Q_{10}$ of $U$
		Experimental	Ideal ( $U$ )	
Temp. increase	40°	7.0°	5.0°	} 0.64
	30°	9.7°	7.8°	
	20°	13.8°	12.3°	} 0.63
	10°	21.1°	19.6°	
	1°	27.0°	27.0°	} 0.70
Temp. decrease	35°	7.5°	6.5°	} 1.20
	25°	5.3°	5.0°	

young leaves are shown in Table 9. Logarithms of the experimental and the ideal threshold differences plotted against the first temperature are shown in Fig. 8. The plottings of  $U$  fall nearly in a straight line in the case of  $t_2 > t_1$ . (Temperature quotients,  $Q_{10}$ , of  $U$  are given in Table 9.)

The proposition on p. 376 that a smaller temperature change can be stimulative at low temperatures is shown by the fact that the differences between the experimental and the ideal threshold differences is smaller at low temperatures.

In the above, the case of the leaf temperature changing exponentially with time has been dealt with. Cases in which the leaf temperature changes in other ways may be discussed in similar manner. For example, in the

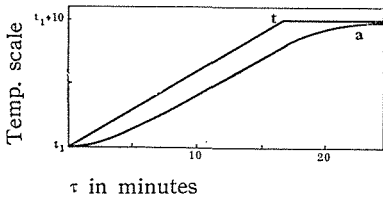


Fig. 9. Relation between the temperature change ( $t$ -curve) and accommodation ( $a$ -curve), when the temperature is changed with a uniform rate until the second constant temperature ( $t_2 = t_1 + 10$ ) is reached.

case of the linear change of temperature with time, as in the case of determining the effect of slow change of temperature upon the "abnormality" occurring in the second stage (cf. p. 365), equations of  $t$  and  $a$  are as follows:—

$$t = k_a \tau + t_1, \text{ and}$$

$$a = k_a \tau + t_1 - \frac{k_a}{k_a} (1 - e^{-k_a \tau}) \dots (11)$$

The relation between  $t$  and  $a$ , in this case, is seen in Fig. 9. Since the temperature change stops when  $t_2$  is reached, the  $t$ -curve breaks there; and the  $a$ -curve, which is given by the equation (11) until the break of the  $t$ -line, assumes a simple exponential curve thereafter. The value of  $u$  is maximum at the break of the  $t$ -line.

1) This is the solution of the differential equation,

$$\frac{da}{d\tau} = k_a(t-a) \text{ or } \frac{da}{d\tau} + k_a a - k_a(k_a \tau + t_1) = 0,$$

in case  $k_a \neq 0$ .

### General Discussion

When the temperature of a cell is changed, some disturbance must occur in the cell. Whether the cell will be excited by that temperature change or not, depends on whether the disturbance reaches a certain grade or not. Accordingly, disturbances caused by different amounts of temperature change do not radically differ from one another, whether they induce the excitation or not. This is the author's ground for discussing the adaptation process after the data of the temperature change below the threshold.

Readjustment, namely "accommodation," proceeds as a sequence of the arising disturbance to cancel this. When the net disturbance reaches the value of ideal threshold difference ( $U$ ), a secondary system of reactions may be released, which effect the response of the cell. Then, this system of reactions should be readjusted after the response, namely in the refractory period. But when the net disturbance fails to attain  $U$ , it is subdued by the "accommodation." Though the disturbance wanes markedly in a relatively short while (the first stage), a small portion of it needs far longer time to become completely readjusted (the second stage).

By the experiment, it is determined how the condition of cells shifts after a temperature change and reaches the normal adapted state at the new temperature. The adaptation in respect to the perception and response is a part of general adaptation of cells to the temperature change. Therefore, the cell is not yet completely adapted, before the threshold of thermal stimulation reaches the normal value at the new temperature. The duration needed for the endonomous adaptation depends on the modes (rate, extent, and direction) of the change of temperature, just as the thermal stimulation. This fact gives warning about the preparation of materials for various physiological researches, namely when they are brought to the experimental temperature which is different from the culture temperature. The smaller the temperature change, the more nearly normal they will behave. But if rate or degree of the change be over a certain limit, they may probably be in an abnormal state for a considerable while.

In most cases, leaves shut as soon as they are dipped in water of 45°, 50°, or higher. But if the temperature difference in that case is small, or if the change is slow enough, they shut after several seconds or even several minutes after the dipping in, even at such a high temperature. The response of the leaf in the former case may be due to the disturbance caused by the sudden change of temperature, as discussed before. But the cause must be different in the latter case, for the duration passed before the shutting is too long for the presentation time or the reaction time at high temperatures. The cause may be the injury of cells. The *Aldrovanda* leaf shuts when it is injured slightly, whatever kind of injury it may be. Beyond bio-kinetic temperatures, the new equilibrium may fail to be set up well, the cell being injured by the increasing disturbance. The leaf shuts from injury in several seconds to minutes at high temperatures, and in many hours near 0°.

The tonic adaptation in plants is best known with respect to light. The light-growth response occurs only after a sudden change of light

(CHOLODNY, '31). The stimulative action of light upon the respiration of roots is weak if this has previously been in light (MONTFORT and FÖCKLER, '38). Phototactic response of *Volvox*, some swarmspores, etc., is not the same, according to the rate of change of light intensity, or according to whether they have previously been in light or in darkness (cf. OLTMANN, pp. 323, etc.). The energy quantity of light necessary to cause the phototropism is greater with weak light than with intense light, the stimulus-quantity law not holding here on account of adaptation (DU BUY and NUERNBERGK, II, p. 259.)<sup>1)</sup>

In other words, "adaptation" to light is a change of tone such that the stimulating effect of light becomes less. This is also the common feature of "adaptation" in various receptors of animals. When the temperature of *Aldrovanda* leaf is raised (namely in case  $t_2 > t_1$ ), the threshold difference of stimulation by a temperature rise (to the third temperature) grows larger with "adaptation" (from  $s_p' - t_2$  to  $s_m' - t_2$  in Fig. 5A), and when lowered ( $t_2 < t_1$ ), that by a temperature fall also becomes larger with time (from  $t_2 - s_p$  to  $t_2 - s_m$  in Fig. 5B).

According to MAINX ('29), phototactic tone of *Volvox*, *Synura*, etc. is changed by external factors (as hydrogen-ion concentration), but the original tone is gradually recovered in some hours even in that changed condition. This case may also be the "adaptation" in respect to tone, though here it is returning to the original tone, while it is departing from the original tone in the above-mentioned cases. It is, however, not inappropriate to speak of "adaptation" in either of the cases, in spite of the apparent contradiction, the opposite effects depending on whether the factor affecting the phototactic tone is light or something else, namely whether the case concerns *heterogeneous induction* (NOLL, '92), or not.

The adaptability of organisms manifests itself in such different ways as have been mentioned, even considering photo-sensitivity alone. But on the other hand, in the case of *homogeneous induction* (namely when the tone with respect to a stimulus is induced by the same form of energy), the adaptation in sensitivity to temperature, light, etc., of various plants is quite similar to one another and to that of animals. It is beyond the scope of this paper, however, to discuss one of the fundamental characters of living matter, adaptation which reveals itself in innumerable ways, or to discuss the relation of tonic adaptation to adaptation in general.

In accordance with PFEFFER's idea ('04), many authors, as cited by SCHRÄMMECK ('34, p. 376 f.), consider that WEBER's law is an expression of dulling of sensitivity due to the existing stimulus, or in other words, due to the rise of tone ("Höherstimmung"). If the terms adopted above are

1) Or,  $J.t^p = \text{const.}$ ,  $p$  being smaller than 1 ( $J$ : intensity;  $t$ : time). In this case, even the possibility of adaptation of a primary photochemical process is discussed by them (III, p. 469). Yet the analyses are not advanced, even in phototropism which is studied most precisely, so far as to show at which part of the catenary reactions, from the primary process to the final (tropic) movement, the adaptation takes place.

used, the law may be attributed to the tonic adaptation in the case of homogeneous induction.

As summarized by STARK ('20), WEBER'S law holds true in taxis, tropisms, and nasties<sup>1)</sup> caused by various agencies such as chemical substances, light, gravitation, touching, etc., the tendency, that the stronger the stimulus, the greater the threshold for discrimination, being always evident, though numerical validity of the law is insufficient in some cases. But in the case of thermal stimulation of the *Aldrovanda* leaf, the higher the temperature at which the leaf is adapted, the smaller is the threshold of stimulation by a temperature rise, and *vice versa* (cf. Fig. 1). This means that the more the leaf temperature is raised, the more sensitive is the leaf to a further rise of temperature, and *vice versa*. This tendency is the reverse of what would be expected from WEBER'S law. Thermal stimulation of the *Aldrovanda* leaf agrees with other sorts of stimulation phenomena in the point that the effect of stimulation is weakened by the tonic adaptation (cf. p. 380). But when it is stimulated again after once becoming adapted, the relation of the additional stimulus to the existent one is different from other cases.

WEBER'S law indicates the relation of two stimuli given one after the other, or simultaneously on opposite sides. The organ in question is thus introduced to a state of tension,<sup>2)</sup> viz. the state of tonus in CZAPEK'S or MIEHE'S meaning (cf. F. N. p. 367). In the case of thermal stimulation of the *Aldrovanda* leaf, on the other hand, adaptation to a temperature (in the biokinetic range) does not put the leaf in the state of tension, though as in other cases the sensitivity is lessened while the adaptation is going on. Once adapted, no effect of stimulation due to the foregoing temperature change seems to remain, while in the case of other sorts of stimulus the dulling of sensitivity lasts, and affects the perception of the second stimulus, as long as the first stimulus (or its after-effect) persists. In other words, *temperature is no longer a stimulus if an organ is once adapted, while chemical substances, light, etc. still retain a character of stimulus even after the adaptation.*

The tendency toward the principle that the higher the temperature, the more easily the leaf is stimulated by raising temperature, and *vice versa*, may mean that the nearer the leaf temperature is drawn to the extremities of the biokinetic range, the more easily the disturbance in cells is caused.

Though adaptation to the first of the two successive stimuli is a necessary condition for WEBER'S law, it is self-evident that the law is not concerned if the organism be adapted to the second stimulus.

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1) Of these, some are subject to the all-or-nothing principle, while some others are not. But even in the latter case, definite magnitude of response is mostly taken as the criterion, the responses being treated as if of the former type.

2) "Ist also ein Organismus (Organ) durch Licht, chemische Agentien etc. bereits in einem Reizzustand versetzt, so ist ein absolut grössere Reizzuwachs nothwendig, um wiederum denselben Effekt . . . zu verursachen." (PFEFFER, II, p. 625).

### Cold-Rigor

Some tests were made to see whether or not *Aldrovanda* leaves become non-reactive to stimuli, at low temperatures.

Cylindrical glass vassels, in which whorls with open leaves were sunk 4 cms. below the water surface, were dipped in brine in the thermostat. The temperature of the thermostat was lowered very gradually by making the refrigerator work interruptedly, ten minutes' work after ten minutes' pause, the thermostat being covered to prevent heat conduction.

If the refrigerator was made to work continuously for a longer time, the number of leaves which shut during the cooling increased, even near 1°. This shows that leaves were stimulated by temperature falls even at such a low temperature. Many of the leaves were found shut when they were kept at 0.5° or 1° for one day and night. They are supposed to have shut gradually from injury by chilling.

Almost all the leaves that were left open after one day's stay at 0.5° or 1°, reacted to electrical, as well as to mechanical stimulation. The responsive movement was very slow, 2 or 3 seconds being needed for the conspicuous part of the shutting movement even in the quickest case, while in slower cases, the movement was not perceived, until the leaf was found shut after some minutes. If the observation be given up too early in this latter case, the leaf would falsely be considered to have fallen in the state of cold-rigor. When glass vessels containing whorls were put near the coolest part of the cooling coil (close to the expansion bulb), leaves were enclosed in ice, almost all leaves shut but a very few remained open. These latter ones may have been in cold-rigor, or the freezing may have been quicker than the shutting movement.

The threshold for the electrical stimulation was measured with leaves adapted at 5°, in comparison to those adapted at 26°, using Du Bois-REYMOND's coils and the key to produce single induction shocks (cf. ASHIDA, p. 62). Two platinum plates, 1 cm. square, were put 1 cm. apart from, and parallel to, each other. A leaf was put between them roughly in the dorsal position (cf. ASHIDA, p. 63). At first the coils were put 15 cms. apart. A single opening shock was sent to the leaf, and after a minute or more, another opening shock was applied, reversing the direction of the current. If the leaf was not stimulated by that, the coils were drawn 1 cm. nearer, and two shocks were given in the same way. The greatest coil-distance which served to stimulate the leaf was determined in this way. Table 10 shows the numbers of leaves which showed various maximal coil-distance. It is clearly recognized that *stronger shocks are needed at 5° than at 26°*. And out of 59 leaves tested at 5°, two, one from the whorl No. II and the other from IV, reacted neither to electrical shocks of the coil-distance of 0 cm., nor to mechanical agitation.

To conclude, *it is not easy to put Aldrovanda leaves in the state of cold-*

Table 10.

Number of leaves reacted, with threshold values represented by coil-distances in cms.

Whorl No.	Temp. Coil-dist.	26°						5°					Cold-rigor		
		7	8	9	10	11	12	Mean coil-dist.	5	6	7	8		9	Mean coil-dist.
I			1	3	14	1	1	9.9			5	1	1	7.4	
II			3	3	5	3		9.7		2	3	6		7.4	1
III			2	2	5	3		9.9		2	4	3		7.1	
IV	1	2	3	3	1			9.1	1	1	6	4		7.1	1
V		2	4	5	3			9.6	1	2	4	2		6.8	
VI	1	1	5	3	2			9.3		3	4	2		6.9	

*rigor*, though the sensitivity is somewhat lowered at low temperatures. It is reported that filaments of *Berberis* and *Mahonia* also react to stimulus even near 0°, although *Sparmannia* and *Mimosa* show no response below 11° (BÜNNING), and below 14° (WALLACE), respectively.

### Summary

1. Minimal temperature differences necessary to stimulate the leaf by a sudden change of temperature is determined, at various temperatures between 1° and 40°:—

a. In general, the threshold temperature differences are smaller in the case of sudden decrease of temperature than in the case of sudden increase.

b. The higher [lower] the initial temperature, to which the leaf has been adapted, the more sensitive is the leaf to an increase [a decrease] of temperature, and the less so to a decrease [an increase].

c. The older the leaf, the less sensitive it is to a temperature change.

2. A sudden temperature change, either an increase or a decrease, can be stimulative within the harmless temperature range.

3. The slower the change of leaf temperature, the greater change of temperature is necessary to stimulate the leaf.

4. In case the temperature of a leaf is changed rapidly from  $t_1$  to  $t_2$ , without stimulating it, the threshold of stimulation by a sudden change of temperature shifts from the value characteristic of  $t_1$  to the value characteristic of  $t_2$ . It is determined, in that case, that the threshold temperature is shifted with time roughly exponentially. This stage is called the first stage of adaptation. The higher the temperature, the quicker is the adaptation. Young leaves adapt more quickly than old ones.

5. The threshold temperature is not constant after the first stage, but fluctuates, to reach the value characteristic of  $t_2$  after several hours. This period is called the second stage of adaptation. Magnitude and duration of the abnormality in this stage depends on rate and degree of the temperature change the leaf has undergone.

6. A hypothesis is proposed to account for the observed relations of the thermal excitation to some factors. The hypothesis assumes that some "disturbance" is caused in cells of the leaf by the temperature change, and that this "disturbance" is at the same time repaired by the "accommodation" process, the excitation of the leaf depending on the relation between these two antagonistic processes.

7. A tendency quite reversed from WEBER's law exists in the relation between the adapted temperature and the threshold of thermal stimulation at it. The difference of the thermal adaptation from adaptation to other sorts of stimulus, as light, gravitation, chemical substances, etc., is discussed.

8. It is not easy to bring the leaf into the state of cold-rigor, even at temperatures near 0°.

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### Notation

- $a$ : "accommodation" expressed by temperature scale (a function of  $\tau$ ).  
 $a' = a + U$ .  
 $d_1 = t_1 - s_1$ ,  $d_2 = t_2 - s_2$ ,  $d_m = t_2 - s_m$ .  
 $k_a$ : velocity constant of "accommodation."  
 $k_u$ : velocity constant of change of leaf temperature, and of "disturbance" caused by the temperature change.  
 $k_s$ : velocity constant of primary (tonic) adaptation.  
 $s$ : threshold temperature (a function of  $\tau$ ).  
 $s_1$ ,  $s_2$ : mean threshold temperatures from  $t_1$  and  $t_2$ , respectively.  
 $s_m$ : mean threshold temperature finally reached asymptotically by the primary adaptation.  
 $\sigma$ : "accommodation" represented with threshold temperature.  
 $t$ : leaf temperature, and, at the same time, "disturbance" corresponding to the leaf temperature (a function of  $\tau$ ).  
 $t_1$ ,  $t_2$ ,  $t_3$ : the first, the second, and the third temperature. (When  $t$  represents "disturbance,"  $t_1$  and  $t_2$ , the initial and final value of "disturbance.")  
 $\tau$ : time from the transference (from  $t_1$ ) into  $t_2$ , until the stimulation of the leaf by changing the temperature from  $t_2$  to  $t_3$ .  
 $\tau_1$ : the value of  $\tau$  when  $s_m - s = 1^\circ$ .  
 $\tau_m$ : the value of  $\tau$  when  $u$  is maximum.  
 $u$ : net disturbance.  $u(\tau) = t(\tau) - a(\tau)$ .  
 $u_{max}$ : maximum value of  $u$ .  
 $U$ : critical value of  $u$ , over which the excitation takes place; and the ideal threshold difference (cf. p. 377).
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Lately E. GAUMANN (Ueber die experimentelle Auslösung der Guttation. Ber. deut. bot. Ges., **56**, 396. 1938) reported that the water absorbing activity of the roots of some plants was reduced by a rapid change of soil temperature, and that the effect of a temperature rise was recovered in a night at suitable temperatures, while that of a temperature fall was not at any of the temperatures of his experiment. It is interesting that a temperature fall has a stronger influence than a rise in the case of roots also. (cf. Tables 3~6 and Fig. 1.)