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ENVIRONMENTAL INFLUENCES ON NECTAR SECRETION

BY LESLIE ALVA KENOYER

AGRICULTURAL EXPERIMENT STATION
IOWA STATE COLLEGE OF AGRICULTURE
AND MECHANIC ARTS

BOTANY AND CHEMISTRY SECTIONS



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ENVIRONMENTAL INFLUENCES ON NECTAR SECRETION

By Leslie Alva Kenoyer

This study was undertaken to summarize and supplement existing knowledge of the factors which stimulate or retard the secretion of nectar. The work was carried out under the direction of the botany section of the Iowa Agricultural State Experiment Station in cooperation with the chemistry section, being done mostly at Ames, Iowa, from June, 1914, to June, 1916.

HISTORICAL

One of the most complete treatises on nectar, with quite an extensive account of some of the environmental factors in its secretion, was given us by Bonnier (1). The subject of secretion has been debated from a physical standpoint. Godlewski (9) attributes it to a fluctuation in the concentration of the cell sap due to alternate splitting and recombination of complex molecules. Pfeffer (19) advances three possible causes for secretion: First, an unequal permeability of the membrane of the absorbing and excreting portion of the cell; second, an unequal distribution of solutes in the absorbing and excreting portions of the cell; third, the transformation into sugar of the outer portion of the cell wall, and the osmotic action of this sugar upon the liquid contents of the cell. Lepeschkin (14) in a study of the coenocytic plant, *Pilobolus*, finds evidence that the first of Pfeffer's theories is the correct one for the excretion of water drops. Wilson (29) gives evidence in support of Pfeffer's third theory, showing that the thoro washing of a nectary stops the secretion if the nectary is past the stage of metamorphosis of the cell wall, but that secretion is resumed on the addition of sugar to the surface of the nectary. The validity of his results are called in question by Lepeschkin (14) and Büsgen (5).

Haupt (10) in a study of extrafloral nectaries finds that after washing, some nectaries become inactive, while others, as those of the leaves of *Impatiens parviflora* continue excretion of water but not that of sugar, thus becoming equivalent to hydathodes.

Livingston (16) likens nectar secretion to guttation, accounting for the latter by decrease in the permeability of the plasma membrane induced by an increased turgidity, for the former by hypothetical rapid increase in the solute content and thereby of

the osmotic pressure in the cell,—a change which induces a like decrease in the permeability of the membrane.

Comparatively little work has been done on the chemistry of nectar. Wilson (28), Von Planta (27) and Bonnier (1) have analyzed a few sorts of nectar finding that in some cases it contains no sucrose while in others it is almost wholly this kind of sugar. In some cases fructose and in others glucose is the dominating reducing sugar. The sucrose of nectar is almost wholly digested in honey, Browne (4) finding as the average composition of 138 honey samples from widely separated localities 38.65% fructose, 34.48% glucose and 1.76% sucrose.

EXPERIMENTAL

I. Methods

Nectar, when secreted in sufficient quantities, was measured by means of a graduated capillary pipette, or weighed after absorption on strips of filter paper which had been previously weighed in small vials. Many of the most important honey plants secrete such small amounts of nectar to the individual flower that neither of these methods is practicable. In these the amount of sugar external to the nectaries was approximately determined by adding to a counted or weighed quantity of the flowers a definite volume of water, shaking frequently for a half hour, then decanting. A similar method was employed by Von Planta (27) and Bonnier (2). In some of the flowers investigated, this treatment extracts some sugar from the floral tissues, as shown by the appearance in the solution of colors from the floral envelopes. Hence it is of value mainly for the comparison of flowers of the same species. Buckwheat, because of its rapid maturing and its value as a honey producing crop as well as its comparative freedom the above noted source of error, was employed in many of the experiments.

Sugar determinations were made by reduction of Fehling's solution. The method found most practicable, and employed for the greater part of the work, was based on that described by Schoorl (24). A carefully measured amount (1 cc. and for minute quantities of sugar, 10 cc.) of the material to be analyzed was placed in a 150 cc. Erlenmeyer flask, heated on an asbestos gauze over a flame so adjusted that the liquid began to boil in just two minutes, then boiled two minutes longer. To the contents of the flask, after cooling to 60° C., were added sulphuric acid and potassium iodide. The liberated iodine, which corresponds to the unused copper sulphate, was titrated against sodium thiosulphate. Sugar values were obtained by the careful analysis of known quantities of sugar. This method has the advantage of being both rapid and delicate enough to

determine minute quantities of sugar with a probable error of not over .04 mg.

Floral tissues, when not too bulky, can be analyzed by the same method, the reagents being added directly to the tissues after covering them with water. When tissues were more bulky or when greater accuracy was required, extractions were made with alcohol or water, and were purified by treatment with neutral lead acetate.

II. Humidity

It is well known that any watery exudation from plants accumulates when atmospheric humidity is high and evaporation thereby is retarded. This can easily be demonstrated in connection with bleeding from several tissues, or with guttation thru water stomata. Bonnier (1) states that nectar secretion corresponds to guttation and that it varies inversely with the transpiration. So far as the volume of nectar is concerned this was found to be true in all the plants experimented upon with this end in view. But, as shown by Pfeffer (20), two factors are involved in nectar secretion, the exudation of water and that of sugar. Haupt (10) has found that extrafloral nectaries begin secreting only when humidity is relatively high, an observation which confirms the theory that secretion is due to a decreased permeability caused by increased turgor, but that after secretion begins, increased air moisture increases water secretion, the secretion of sugar remaining constant. It is probable that this applies to nectaries in general. Nectar is more dilute when humidity is high, and honey that is stored at such times is likely to be high in water content.

At Ames the seasons of 1914 and 1915 represented extremes of humidity, the summer months of the former year being excessively dry and warm, while those of the latter were excessively wet and cool. Hence the comparisons in table I of nectar washed from flowers are of interest.

TABLE I—COMPARISONS OF NECTAR WASHED FROM FLOWERS IN SEASONS OF DIFFERENT HUMIDITY.

	1914 (Dry and warm)		1915 (Wet and cool)	
	No. of samples analyzed	Ave. mg. sugar per gm.	No. of samples analyzed	Ave. mg. sugar per gm.
<i>Melilotus alba</i> , flowers.....	6	2.13	3	.65
<i>Medicago sativa</i> , flowers.....	4	1.15	3	.80
<i>Trifolium pratense</i> , corollas.....	4	3.64	13	3.90

It is seen that the wet season yielded scarcely as much sugar as the dry. It may be stated further that bee visitors to *Melilotus* were several times as abundant in 1914 as in 1915. The author found by experiment that flowers of alfalfa grown in dry soil contain about 60% more sugar than those grown in wet soil.

Buckwheat flowers kept humid under a bell jar secreted much more liquid than flowers exposed to the rather dry greenhouse air. However, 12 comparative analyses of the nectar of each showed in the humid, 1.04 mg. sugar per 10 blossoms; in the dry, .98 mg. sugar per 10 blossoms. Analysis of the flower after removal of the nectar, in 6 of the above pairs of cases showed .74 mg. per 10 blossoms in the humid, and .98 mg. per 10 blossoms in the dry. More sugar accumulated in a dry atmosphere and practically the same amount is excreted.

The accumulation of sugar under low moisture conditions is in line with the discovery by Lundegardh (17) that increase of moisture favors the accumulation of starch, decrease of moisture its digestion.

Six plants of *Impatiens Sultani* in saturated air accumulated in a day 3.26 mg. sugar each from the extrafloral nectaries, the basal teeth of the leaves, while 6 plants in greenhouse air accumulated 5.42 mg. sugar each. The excess of the latter is very likely due in part to the running away of drops under the humid conditions. The nectar averaged 23.4% sugar in the former and 45.3% of the latter.

III. Rainfall

The author has shown in a statistical study (12) that heavy rainfall just prior to the secreting season is advantageous as it gives the plants greater vigor. But during the season of greatest secretion, good years are somewhat drier than poor. Also, a rainy day shows a lighter honey yield than a day before or after the rain.

The deterrent effect of the rain on the honey flow is twofold: It hinders the activities of bees and it washes away the nectar. To illustrate the latter point, in 1915 on the morning following a day of continual rainfall, red clover corollas were found to contain .02 mg. sugar per gm., whereas a day earlier they contained 3.8 mg.; a day later, .6 mg., and two days later 4.4 mg. Buckwheat blossoms were subjected to an experiment to determine the extent to which rains wash away the nectar. Flowers subjected before gathering to a spray for 20 minutes, 15 mm. of water falling were found to contain .12 mg. per 10 as against 1.28 mg. per 10 untreated flowers. A 30 minute rain of 35 mm. reduced the nectar of red clover blossoms from .48 to .19 mg. per 10 and that of white clover blossoms from .27 to .07 per 10.

IV. Temperature

Wilson (29) states that temperature has not a marked effect upon the rate of secretion of nectaries that have commenced secreting. He finds, however, that *Prunus Laurocerasus* will not

begin secretion unless the temperature is 12° C. or over. Haupt (10) also finds that a minimum temperature is necessary to induce secretion. Lepeschkin (14) finds in the hyphae of *Pilobolus* a secretion steadily increasing with, and much more rapidly than, the absolute temperature. In other cases he finds an optimum above which secretion diminishes. In the case of secreting hairs of the bean leaf this optimum is 20° C., in the *Abutilon* nectary it is 26° C.

Experiments were carried out in uniform temperature incubators. For much of the work, to avoid light exclusion which is detrimental to secretion, incubators were employed which were especially constructed for the purpose, being covered with two glass plates separated by an air space.

The optimum temperature for amount of secretion lies between 20° C. and 25° C. for *Cucurbita pepo*, *Lilium speciosum*, *Canna indica*, *Euphorbia pulcherrima*, and extra floral nectaries of *Impatiens Sultani*. For *Salvia splendens* and most of the *Leguminosae* tested it is about 15° C. As a rule the sugar concentration of the nectar does not differ materially for the different temperatures. Table II gives typical sugar determinations obtained from the flower of *Abutilon striatum*, the blossoms being quartered and one piece of each placed in each incubator, thereby eliminating any error due to individual variations.

TABLE II—TYPICAL SUGAR DETERMINATIONS FOR
ABUTILON STRIATUM.

Degrees temperature	Mg. invert sugar per flower.			
	10°c	16°c	23°c	30°c
After 36 hours.....	10.20	12.00	16.00	10.32
After 16 hours (another set).	3.07	6.57	12.97	10.87

Here the optimum is clearly not far from 23° C.

Bonnier and Flahault 91.30 call attention to the fact that nectar secretion is greater in the same species at high latitudes and altitudes than at low when the species grows normally in both latitudes of altitudes compared, and furthermore that species which do not secrete in France are nectariferous in Norway and in the Alps. He suggests that this fact may be due to the greater range between maximum and minimum daily temperatures which prevails at high altitudes and latitudes, or to the greater range in the humidity of the air.

Phillips (21) observes that alfalfa is, as a rule, valuable as a honey plant in the great prairie region of the west and not in the eastern states, that buckwheat is of more value in New York, Pennsylvania and Michigan than in Indiana and Illinois, and that white clover is of greater importance in the north than in the south. Basswood is said to secrete better in the more northerly portions of its range. It therefore seems desirable to investigate the hypothesis of Bonnier.

As already shown by the author, (12), the study of a 30-year weight record of a hive at Clarinda, Iowa, lends strong support to this assumption. Thirty-eight periods of continual and fairly rapid gain in weight were selected, and the days of each divided about equally between days of high gain and days of low gain. In 32 cases the average diurnal temperature range for the days of high gain is greater than that for the days of low gain. In all of the six exceptional cases the difference between the average is small.

Sladen (14) states that the heaviest single day's increase in hive weight noted for two seasons in England in a record kept by Dr. Moore Ede was on a day that began with a heavy early morning frost, the honey coming from the heather, *Calluna vulgaris*.

Table III represents the amount of reducing sugar in mgs. found after keeping the plants or flowering branches for a time in the incubators.

TABLE III—AMOUNT OF REDUCING SUGAR IN VARIOUS PLANTS AFTER INCUBATION.

Trifolium incarnatum, 10 corollas 2 da.....	.56	.63	.43	.38
Trifolium repens, 10 fs. 2 da.....		1.12	.94	.70
Nectar washed from same.....		.07	.02	.01
Trifolium repens. 10 fs. 2 da.....	.93	.63	.4756
Nectar washed from same	0	0	008
Medicago sativa 10 fs. 4 da.	3.44	2.08	.52
Caragana frutescens 10 fs.	37.55	22.22	11.95	24.33
Nectar washed from same	.64	4.80	2.00	2.88
Fagopyrum esculentum 10 fs. 4 da.....	.69	.73	.58
Nectar washed from same	1.36	.80	.0
Salvia splendens 10 corollas 4 da.....		25.7	13.8	12.9
Coleus blumei 10 corollas 4 da.....		.86	.78	.62
Taraxacum officinale per gm. fs. 1 day.....	38.7	45.0	19.3	13.9
Taraxacum officinale per gm. fs. 1 day.....	15.6	17.1	11.9		not developing

In field conditions it can readily be shown that lower temperatures increase the sugar content in dandelion and the clovers.

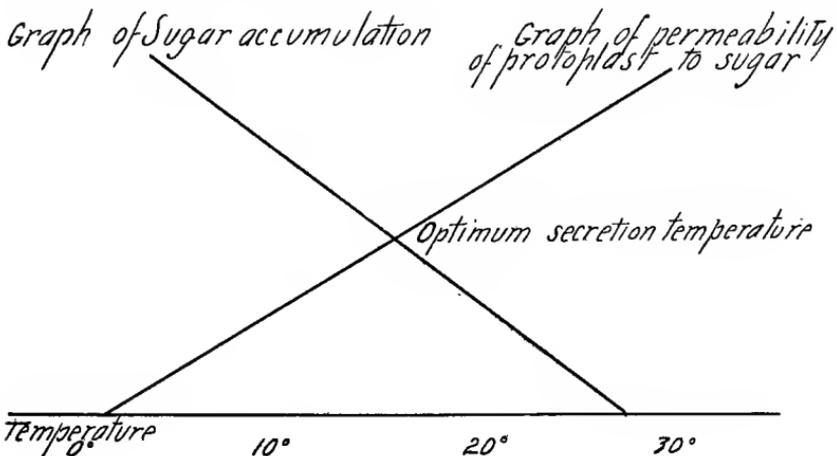
VanRysselberghe (26) determined that with increase in temperature the permeability of the protoplast to water and solutes rapidly increases,—that of *Tradescantia* epidermal cells for

water being eight times as great at 30° as at 0° C., and that for solutes seeming to follow the same proportional rule. To demonstrate whether this holds for nectary cells, the lowest sucrose concentration necessary to plasmolyze the multicellular secreting hairs which cover the nectary of *Abutilon* was determined. After four days at 10° C. a .6 molecular solution was found sufficient, while for another portion of the same flower after four days at 25° C. a 1.1 molecular solution was necessary.

In a study of the influence of low temperature Müller-Thurgau (18) found that sugar accumulates in potatoes when surrounding temperature is below 10° C., and the same thing is true of hemp seedlings and various other plant organs. He advanced the theory that the accumulation comes from the digestion of starch or oil more rapidly than the resulting sugar can be utilized,—its respiratory destruction being retarded by the low temperature.

The accumulation of stored sugar from starch in low temperature is a well-known phenomenon in the twigs of woody plants which is amply discussed by Fisher (8). Indeed, this accumulation seems to be rather in its occurrence among plant tissues. Besides being applicable to floral tissues, as table III so clearly shows, it affects the leaves and the peduncles of white clover, the former after two days treatment having 30% more sugar, and the latter 58% more, at 10° C. than at 25° C.

The evidence points to the conclusion that at a uniform temperature the secretion of nectar is a balance between two factors,—the accumulation of sugar in and near the flower under the influence of low temperatures and increasing permeability of the plasma membrane under the influence of high temperature. The position of the optimum, then, might be represented somewhat as in the figure below.



The two graphs are limiting factors to nectar secretion and the intersection, i. e., the point where the effective limit stands highest, is the optimum secretion temperature. If the fact discovered by Eckerson (7) for root cells, that above a certain point (25° - 35°) the permeability again decreases, applies also to nectary cells, the situation may be somewhat complicated thereby.

Better than any uniform temperature for secretion is a change from a lower to a higher temperature,—as the table indicates. The influence of such a change might be graphically indicated by folding the above diagram so that two temperatures,—say 10° C. and 30° C.,—are brought together. Both limiting factors are raised; the sugar which has accumulated at the lower temperature is secreted at the higher.

V. Atmospheric Pressure

In the author's study previously cited (6) it was shown that of 18 periods of continual honey production, 16 have a lower barometric pressure on the days of heavier yield than on the days of lighter yield, the two exceptional cases having very slight differences. The increased secretion already credited to high altitudes might be attributed to the diminished pressure, but this explanation would of course not account for the similar increase at high latitudes.

In investigating experimentally the influence of pressure, the plant under experiment was covered with a tabulated bell jar waxed to fit tightly to a ground glass plate and connected by means of a stop cock with the water aspirator. A similar plant was placed under a control bell jar. In some of the experiments air was daily renewed in both low pressure and control jar; in others its continual renewal was provided for by admitting a current of air which bubbled thru water and in the case of the low pressure jar, entered by means of a capillary tube with a very small aperture. This latter method is similar to one employed by Schaible (22). By the use of an aneroid barometer the pressure was maintained at about 50 cm. or two-thirds atmospheric pressure, the prevailing condition at altitudes of about ten thousand feet. Repeated investigations were made with the following plants:

For guttation—*Tropaeolum majus* and *Avena sativa*.

For nectar secretion—*Tropaeolum majus*, *Impatiens Sultani*, *Abutilon striatum*, *Euphorbia pulcherrima*, *Canna indica*, *Fagopyrum esculentum*, *Salvia splendens*, *Coleus Blumei*, *Antirrhinum majus* and *Prunus americana*.

There were no constant differences in secretion which could be detected by either physical or chemical means. It is very doubtful therefore whether the much smaller variations in pressure

which occur in nature could measurably affect nectar secretion.

It is a matter of common knowledge among beekeepers that bees are more active when the barometer is low, the warmth and stillness of such periods favoring activity. Hence it seems very probable that any relation between atmospheric pressure and honey flow is to be attributed to the bees and not to the plants.

VI. Light

Darwin (6), Wilson (2)⁹ and Haupt (10) note the fact that the extrafloral nectaries of several species of *Vicia* are stimulated to activity by light. The first author adds *Lobelia erinus* and the last, the *Euphorbiaceae*, as plants that require the light stimulus for secretion. The two latter authors, however, state that in the greater majority of cases, secretion is only indirectly related to light. Haupt found that in most extrafloral nectaries even disturbances in photosynthesis by darkness show their influence on secretion only very slowly. Light in *Vicia* doubtless increases the permeability of the protoplast, as Lepeschkin (15) has found that it does in the pulvini of Leguminosae in general.

Schimper (23) found that extrafloral nectaries on the leaves of *Cassia neglecta* cease their activity in a few days when the plant is kept in darkness or in an atmosphere deprived of carbon dioxide, but that secretion continues when the leaf is in the light and only the nectaries are darkened.

The author experimented upon both the floral and the extrafloral nectaries of *Impatiens Sultani*, and it seems clear that the withdrawal of light makes its influence fairly rapidly and very decidedly felt. Table IV gives a typical study of floral nectaries, the measurements being millimeters in length of the part of the spur which contains nectar. The table includes average increases over last measurement of the spur in those flowers which were open when the last record was taken, and the average measurement for those flowers which have opened since the last record. One plant was covered with a bell jar, the other was an opaque jar of about the same size.

TABLE IV—NECTAR SECRETION IN DARK AND LIGHT.

Days	Light		Dark	
	Gains	New flowers	Gains	New flowers
2	4.4	21.6	1.2	16.1
3	4.8	22	1.1	13.6
4	2.	23	1.1	15.7
6	3.5	29	-1.2	17.3
7	5	20	.1	16
8	4.1	21.7	.5	14
9	3.3	19	-.4	13
10	3.2	22	-.5	

At this time the dark plant had taken on an etiolated appearance and new flowers were scarcely developing. Secretion from extrafloral nectaries had practically stopped after 3 days in the dark.

Half the leaves of a plant were covered with black tissue paper which was fastened by means of small brass paper clips, the basal or nectar-secreting teeth only being left uncovered. These leaves secreted very little after the third day, whereas the uncovered leaves of the same plant were uninterrupted in their secretion.

Buckwheat flowers were gathered at the same time from under light and dark jars and it was found that after two days in the dark, altho the total amount of liquid secretion was not in the least diminished, the proportion of sugar began to decrease, the secretion not tasting sweet nor giving a very positive sugar test. An average of eleven such analyses of the nectar of flowers that had been covered for from two to eight days gives per 10 blossoms 1.20 mg. invert sugar in the light and .41 mg. in the dark. Sugar contained in the flowers does not differ greatly, however, in the two cases, there being .79 mg. to 10 flowers from the light and .73 mg. to 10 flowers from the dark. Plants which had been left in the dark for some time continued to secrete less than normal quantities of nectar for a week or more after the removal of the cover.

That the diminution of sugar is due to the interference with photosynthesis may be shown by removing all the leaf blades from a number of plants. Eleven analyses averaged in mg. invert sugar in the nectar of ten flowers, .36 from plants with leaves removed from 3 to 10 days, .85 from the normal plants serving as checks. Seven of the above pairs of cases give for the entire invert sugar content of the flowers, .59 mg. from the mutilated and .92 mg. from the check.

The same result may be gained by covering all the leaves of the plant with black tissue paper, and comparing nectar with that of normal plants. Here we find as an average of six analyses of 10 flowers .23 and .69 mg. invert sugar, respectively, in the nectar, and .83 and 1.40 in the whole flowers. After four days in the dark there is approximately one-fourth as much sugar secreted per flower.

When the flowers only are covered from the light, they secrete fully as much sugar as those not covered. So the extrusion of sugar is clearly dependent upon the food reserves of the plant.

The same relation was found to exist in the *Canna* blossom. Darkening of the entire plant materially diminished the nectar secretion, while darkening the flower cluster alone had no influence upon it.

Other flowers analyzed, among them being *Antirrhinum majus*, *Cucumis sativus*, *Salvia splendens* and *Coleus Blumei*, both contained less sugar and also secreted less sugar when kept in the dark. Furthermore, the nectar was usually less in volume. *Euphorbia pulcherrima* did not begin secretion in a dark chamber, and *Abutilon striatum* secreted only very slowly and very

scantly. Even plum branches, which contain supplies of stored food, when developed in the dark have scarcely over half as much sugar in the tissues and about a fourth as much nectar as when developed in the light.

VII. *Fertility of Soil and Vigor of Plant*

Hunter (11) states that alfalfa yields the greatest amount of nectar under conditions that tend to give it the most vigorous growth, proper heat and moisture upon suitable soil. All of the observations and experiments in this work tend to confirm this for the various plants investigated. Red clovers grown on fertilized plots were found to contain slightly more sugar and to secrete slightly more as nectar than those on the unfertilized control plots adjoining.

Bonnier (2) experimented on the secretion of several plants as influenced by different soils. He found that *Sinapis alba*, *Isatis tinctoria* and *Medicago sativa* yield most nectar on limy soil, while *Phacelia tanacetifolia* does better on clay, and *Fagopyrum esculentum* on sand. It is probable that soils which are conducive to greater vigor and more surplus food in the plant are on the whole more favorable for nectar yield.

White clover, the leading honey plant in Iowa, collected the same day in the same part of the city gives the following tests:

	Sugar per gm. flowers in	
	<i>Nectar</i>	<i>Flowers</i>
Stunted by rank growth of weeds.....	.2	15.9
Stunted by close mowing.....	.6	20.8
Vigorous	3.7	21.6

Vigorous plants of buckwheat yield about twice as much nectar as did weak ones in the same bed. The flowers were found on analysis to contain from 20% to 50% more sugar. Plants which had been allowed to dry to the wilting point several times in the course of their growth, and were consequently stunted to about one-half normal height, yielded less nectar, the average of six comparisons being .44 mg. per 10 flowers of the stunted and 1.39 mg. per 10 of the normal. Plants grown in a greenhouse in which the temperature was low and which consequently were stunted to about one-third normal height, blooming not until twice the age of normal blooming plants, secreted practically no nectar.

It was further noticed that a salvia deeply rooted in the soil secreted better than one that was hampered by a small pot, and that of the former plant young vigorous branches yielded more nectar than old stunted ones.

VIII. Portion of Flowering Period and Age of Flower

Table V illustrates the relation of nectar secretion to the part of the flowering season in which the flower in question appears. In all cases the compared flowers were collected on the same day, but from patches varying in stage development.

TABLE V—RELATION OF NECTAR SECRETION TO FLOWERING SEASON.

	Early in Blooming Season		Late in Blooming Season	
	Sugar in Nectar	Sugar in Flowers	Sugar in Nectar	Sugar in Flowers
Red Clover (<i>Trifolium pratense</i>)...	9.3	20.7	4.6	18.6
Alfalfa (<i>Medicago sativa</i>) per gm. flowers.....	1.5	38.9	.3	26.8
Buckwheat 10 fs. (ave. 4 tests).....	1.62	.72	1.09	.60

As a rule the younger plant is undergoing more active photosynthesis and has greater reserves of food to be secreted by the nectaries.

Kurr (13) makes the statement that secretion of nectar commences very rarely before the dehiscence of the anthers; it is generally most rapid during the pollination period; and it ceases as soon as the fruit begins to develop. Bonnier (1) agrees to this proposition and insists that nectar is simply a manifestation of the surplus food stored in the nectariferous part corresponding to an arrest in the development of the organ. In the case of floral nectaries, then, it is most pronounced after the ovary has attained maximum development and before the fruit

TABLE VI—SECRETION OF NECTAR AND MATURING OF FLOWERS.

	Buds		Mature flowers		Declining flowers	
	Invert Sugar	Sucrose	Invert Sugar	Sucrose	Invert Sugar	Sucrose
<i>Medicago sativa</i> (Alfalfa) per gm...	32.5	2.8	56.4	0	26.1	0
<i>Melilotus alba</i> (White sweet clover) per gm.....	22.2	2.6	31.1	trace
<i>Melilotus officinalis</i> (Yellow sweet clover) per gm.....	16.0	0	28.8	0
<i>Trifolium repens</i> (White clover) per gm.....	8.1	.1	8.3	1.8	7.5	0
<i>Trifolium hybridum</i> (Alsike clover) per gm.....	*13.8	*	*8.6	*	*	*
<i>Taraxacum officinale</i> (Dandelion) per gm.....	17.8	27.2
<i>Impatiens Sultani</i> per 100 fs.....	47.5	0	248.4	0	190.0	48.9
<i>Lilium speciosum</i> rubrum per flower..	119.5	26.7	179.3	10.9	76.0	1.0
<i>Lilium longiflorum</i> per flower						
Younger	51.4	14.9
Older	95.9	21.3	95.2	11.3	22.2	0

*Including sucrose.

has commenced to develop. He finds a maximum proportion of sucrose in the floral organs corresponding to this time of greatest secretion. Chemical analyses of the floral tissues show that the climax of sugar accumulation is about the time of the dehiscence of the stamens, and that as the flower withers there is a very rapid decrease in the amount of sugar. Table VI gives some examples from my work, the tissues having been extracted and purified.

It seems that in most cases the excess of sucrose, the storage form of sugar is rather before the flower opens and nectar secretion begins.

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Summary

1. By increasing humidity, the secretion of water, but not that of sugar, from nectaries is increased.
2. Excessive water supply lessens the sugar surplus in the parts of the flower.
3. Dilution and washing by rain causes much of the sugar of nectar to be lost.
4. Rate of secretion for both sugar and water increases with temperature up to a certain optimum.
5. Accumulation of sugar in the flower and its vicinity varies inversely as the temperature.
6. The optimum condition for sugar secretion is an alternation of low and high temperatures.
7. Variation of atmospheric pressure has no marked influence on secretion.
8. Sugar excretion is markedly diminished in darkness on account of limitation of the food reserves of the plant. Water excretion may or may not continue, depending on the species. Removal of the leaves has the same deterrent effect.
9. The more favorable all conditions for growth and the more vigorous the plant, the greater is the amount of sugar secreted.
10. Nectar is most abundant early in the blooming season, other things being equal.
11. Accumulation and secretion of sugar is most pronounced near the time of the opening of the flower.

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