film reeled backward would present an equally accurate picture of a reverse process which is also occurring in the system and with equal frequency. Therefore in any system at equilibrium, time must lose the unidirectional character which plays so important a part in the development of the time concept. In a state of equilibrium there is no essential difference between backward and forward direction in time, or, in other words, there is complete symmetry with respect to past and future.

I believe that some of the ideas contained in this paper have been suggested by the work of Einstein, but he has not proposed this law of equilibrium. Indeed one of the first applications which I shall make, in a subsequent paper, will be to the interaction between matter and light, where I shall attempt to demonstrate the invalidity of Einstein's derivation of Planck's radiation formula. Another application will shortly appear in a paper by Dr. D. F. Smith and myself on the mechanism of chemical reactions.

[1] Wegscheider, *Z. physik. Chem.*, **39**, 273 (1901).

[2] See Lewis and Adams, *Physic. Rev.* **5**, 10 (1915).

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## *STUDIES ON DISEASE RESISTANCE IN THE ONION*

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The nature of resistance to disease in plants is a subject which has been of increasing interest to botanists in general and to plant pathologists in particular for several years past.[1] Earlier there was a tendency to assume that in various instances of disease resistance the causes were sufficiently similar to justify some single type or comparatively few types of explanation, as appears to be the case in certain cases of immunity in animals. Investigations indicate, however, that the causes of resistance in plants are widely varied and relatively complex, and that sound progress is dependent, for the present at least, upon critical study of specific examples wherever practicable. Some years ago it came to the writer's attention that the bulbs of the common onion show a wide range in susceptibility or resistance to certain fungous parasites and that this apparently is correlated with the occurrence of scale pigments. The studies summarized here are therefore presented as a contribution to the general subject of disease resistance in plants.

Horticultural varieties of the common onion (*Allium cepa*) are grouped into three classes with respect to the occurrence of pigment dissolved in the cell sap of the outer epidermal layer of the bulb. In one class, the white varieties, such pigment is absent or practically so. In another class, the yellow varieties, there is a light yellowish tinge to the fleshy scales and with the proper reagents the presence of flavone derivatives is readily demonstrated in the outer epidermis. The dry outer scales are of a deeper yellowish brown color, the intensity of which differs with the variety. In the third class, the red variety, the epidermal cells give positive micro-chemical tests for anthocyan and these tests indicate a certain amount of flavone derivatives also present. The dry outer scales are of a purplish red color.

The common names and causal fungi of the diseases considered are as follows: smudge (*Colletotrichum circinans* (Berk.) Vogl.),[2] neck rot (*Botrytis allii* Munn. and *Botrytis sp.*) and black mold (*Aspergillus niger* van Tieg.). All of these organisms subsist for a part of their life cycle saprophytically on dead organic material in or upon the soil. While they do not ordinarily invade the growing onion plant, they do often attack the dead outer scales before harvest. As soon as the plant is mature they infect the living fleshy storage tissues of the scales, causing gradual decay during storage. The smudge organism attacks the bulbs at any point on the outer scale, lives for a time saprophytically on this dead tissue, and as it reaches the fleshy scale penetrates the cuticle directly. The black-mold organism attacks in much the same manner. Both of these organisms penetrate the fleshy tissue very gradually as compared with the neck-rot fungi. The latter, though capable of living on the dead outer scales, do not ordinarily occur there except on the tissue at or above the neck of the bulb. As the tops die down, the neck-rot fungi invade those tissues and thereby gain entrance to the succulent scales whence they proceed downward rather rapidly. Considerable moisture is necessary to facilitate infection by these Botrytis species and as a rule a general epiphytotic of neck rot is experienced only when abundant rainy weather prevails at the harvest period.

Resistance of colored varieties of onion—both yellow and red—to smudge becomes evident some weeks before harvest. When they are grown on infested soil alongside white varieties, the disease becomes evident as black smudgy spots over the entire outer scales of the latter, even extending, under optimum conditions of moisture, to the sheath about the neck. Little or no infection is found on either red or yellow bulbs exposed to similar environment—except under optimum conditions when spots are found on the uncolored outer leaf tissue above the neck. This is strictly limited, however, to the region above the color. This tissue is largely removed at harvest and thus even under weather conditions extremely favorable to the disease the colored bulbs remain remarkably free from smudge throughout the remainder of the growing season and through storage. The disease advances steadily in the white variety from the time of initial infection.

The black mold disease is considered here by way of contrast. The fungus, attacking the plants a little later but in somewhat the same manner as smudge, is quite impartial to varieties as far as color is concerned. No consistent evidence of varietal resistance is to be noted.

In case of neck rot the white varieties are again always the more susceptible. The mode of attack is distinct from the other two organisms, in this case the succulent neck tissue being the one in question. Under moderately favorable conditions for infection, white varieties are often severely affected, while colored varieties remain quite free from the disease. Under the most favorable conditions for infection, however, the disease is often of consequence in the colored bulbs, but the degree of difference between them and the white bulbs remains essentially the same.

We thus have a distinct correlation between the flavone or anthocyan color in onion bulbs and their resistance to two common diseases, smudge and neck rot, while with a third disease under consideration, black mold, this difference from uncolored bulbs does not hold.

In an attempt to determine the inherent difference between colored and white varieties which contributes toward resistance in the former, attention was first given to the growth of the fungi in the expressed juice of succulent onion scales. It was found that although the undiluted extract retarded growth of all the organisms, no outstanding difference in this respect was to be found between that of colored and uncolored bulbs. The qualities of the succulent scales were therefore not to be expected to account for the greater resistance of colored bulbs. This conclusion was strengthened by the results of another experiment. The dry outer scales of yellow and red varieties were removed and inoculum containing spores of *Colletotrichum circinans* were placed directly on the succulent scales. Under such conditions, even the colored bulbs were readily infected. Similarly, when spores and mycelium of Botrytis were injected into wounds made in the necks of colored and white bulbs, they all decayed with about equal rapidity. Thus, when the infecting hyphae of either the smudge or the neck rot fungi once gain entrance to the succulent scales of colored bulbs, the resistance of the host no longer obtains.

It was therefore assumed that the resistant quality was to be found active in the dead outer scales which the parasite normally enters first before invading the living cells. The cells of the outer scales being dead, any water-soluble material present in the tissue would be expected to diffuse readily into drops of water which come into contact with them. Thus, spores or mycelium of either of these fungi, as they come in contact with the host, are exposed to any material which dissolves out of the outer scales. The study was therefore directed to a consideration of the effect of cold water extracts from dry outer scales of white, yellow and red bulbs upon the germination and growth of the fungi concerned.

Water extracts were made from the dry outer scales of red, yellow and white bulbs by adding approximately equivalent amounts of each to drops of water containing spores of the fungus concerned. The first and most extensive studies were made with the smudge organism. Normal germination and growth took place when white scale tissue was added to the germination drops. In drops to which either red or yellow tissue had been added, a decided toxic effect on the organism was noted. The abnormal response of the fungus became manifest in several forms. In some cases the spores were killed without any evidence of germination. Very often the spore enlarged perceptibly, often becoming septate, but producing

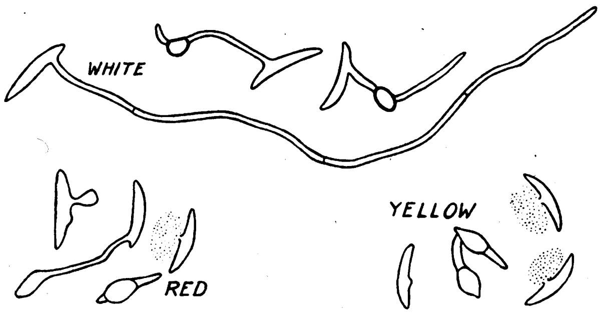


FIGURE 1

Effect of water extract of outer onion scales upon spore germination of the smudge fungus. Bits of dry scales of white, yellow and red onions were added to drops of spore suspension in distilled water. Note typical germ tubes and appressoria in the case of the white scale as compared with abnormal germination in the case of the colored scales. The abnormalities are of three types: (1) ruptured germ tubes, (2) short thick germ tubes, (3) swelling of spores without production of germ tubes.

no germ tube. Occasionally short, distinctly retarded germ tubes were formed. In the majority of cases the beginnings of germination were made but as soon as the germ tube had started to form, the wall at the growing tip disappeared while the cytoplasmic contents of the spore exuded through this opening into the liquid, thus precluding further functioning of the parasite. The results of a typical experiment showing the percentage of spores reacting in the various ways are given in table 1, and camera lucida sketches of spores after exposure to the various extracts are reproduced in figure 1. The presence in outer colored scales of a substance decidedly toxic to the smudge organism is clearly demonstrated, while in the white varieties this toxin is absent, or present in such small quantities as to be negligible. This substance dissolves readily in water and therefore functions when the organism comes into contact with colored scales, and when there is sufficient moisture present which, of course, would be necessary to infection.[3]

TABLE I

EFFECT OF DRY OUTER SCALE TISSUE OF RED, YELLOW AND WHITE VARIETIES OF ONION UPON THE GERMINATION OF COLLETOTRICHUM CIRCINANS

| COLOR OF TISSUE USED | SPORES GERMINATING NORMALLY (PER CENT) | SPORES NOT GERMINATING (PER CENT) | SWOLLEN SPORES (PER CENT) | SHORT ABNORMAL GERM TUBES (PER CENT) | SPORES EXUDING CATOPLASM (PER CENT) |
|---|---|---|---|---|---|
| Control | 91 | 9 | 0 | 0 | 0 |
| Red | 2 | 7 | 4 | 42 | 45 |
| Red | 0 | 12 | 0 | 0 | 88 |
| Yellow | 0 | 34 | 0 | 0 | 66 |
| Yellow | 0 | 24 | 0 | 0 | 76 |
| White | 92 | 8 | 0 | 0 | 0 |
| White | 87 | 13 | 0 | 0 | 0 |

The same type of experiment was conducted with the two neck-rot fungi and with the black-mold organism. The smudge organism was included for comparison. The data given in table 2 show the percentage of spores producing apparently normal germ tubes and the average length of those germ tubes after 24 hours. It will be seen that the results with *C. circinans* confirm those previously given in table 1. In the case of the two neck-rot organisms, germination and growth in white scale extract was equal to or better than the control. In the colored scale extract, with the exception of *Botrytis sp.* in yellow extract, the germination was very poor and growth very slight. In the exception just noted, although 47% of the spores germinated, the germ tubes grew very little. In contrast to the smudge and neck-rot organisms the germination of the black-rot organisms was greatly increased over the control in both colored and white scale extract and the rate of growth was infinitely better than the control in all three extracts.[4]

From these results it is concluded that the resistance of colored bulbs to smudge and neck rot is due to a readily soluble substance in the dry outer scales of colored varieties which is toxic to the causal organisms of the diseases concerned. The substance becomes functional by dissolving into the infection drop and inactivating the fungus before penetration can take place. The fact that this substance does not affect *Aspergillus niger* would seem to account in part at least for the lack of resistance in colored varieties to black mold.

The nature of this inhibitive substance constitutes a problem of exceeding interest. Its very close association with the scale pigment has already been shown while no evidence of its existence in uncolored tissue has been found. This is readily shown by adding to one germination drop portions of an outer scale taken from above the neck where the color does not develop and to another drop tissue of the same scale taken from just below the point where pigment is present. In the first, normal germination occurs; in the second, the typical toxic effects upon the organism result. It may be supposed that the coloring substance is actually the toxic substance. Although this is possible the final proof of the case is not easily attained.

TABLE 2

EFFECT OF DRY OUTER SCALE TISSUE OF RED, YELLOW AND WHITE VARIETIES OF ONION UPON THE GERMINATION AND GROWTH OF THE CAUSAL ORGANISMS OF SMUDGE (COLLETOTRICHUM CIRCINANS), NECK ROT (BOTRYTIS ALLII AND BOTRYTIS SP.), AND BLACK MOLD (ASPERGILLUS NIGER)

| ORGANISMS | GERMINATION (PER CENT) | | | | AVERAGE LENGTH OF GERM TUBES (MICRONS) | | | |
|---|---|---|---|---|---|---|---|---|
| | CONTROL | WHITE | YELLOW | RED | CONTROL | WHITE | YELLOW | RED |
| Colletotrichum circinans | 99 | 80 | 0 | 2 | 414 | 224 | 0 | 1— |
| Botrytis allii | 70 | 68 | 1 | 1 | 491 | 554 | 5 | 28 |
| Botrytis sp. | 72 | 99 | 47 | 3 | 24 | 146 | 8 | 1— |
| Aspergillus niger | 29 | 93 | 59 | 53 | 6 | 129 | 95 | 118 |

The fact that there is no constant difference between the amount of toxic material in red and yellow scales, together with the fact that flavones exist in both types of scale, would indicate the flavone derivatives rather than the anthocyan to be more probably the one concerned. The basic flavone derivative in colored onion scales is quercetin. This is found in the free state and combined with glucose in both the yellow and red scales. The nature of the anthocyan in the red scales is not known. Free quercetin, when extracted and purified, is only very slightly soluble in cold water and it has not been possible to duplicate the toxic effect upon the fungi with any solution of quercetin obtainable. Likewise, any glucoside of quercetin which has been isolated and chemically purified is very difficultly soluble in water.

It is possible that the toxic substance is a soluble derivative of quercetin, probably a glucoside, which is not readily isolated in its original form by ordinary chemical methods and which thus becomes less soluble in water due to loss of part of the glucose radicals. If this takes place in chemical extraction, the exact duplication of the results secured with crude water extract of colored scales becomes the more difficult.

[1] For accounts of other work on disease resistance in plants at the University of Wisconsin, see Jones, L. R.: "Disease Resistance in Cabbage," *Proc. Nat. Acad. Sci.*, **4,** 42–6(1918); Dickson, J. G., et al.: "The Nature of Resistance to Seedling Blight of Cereals," *Ibid.*, **9,** 434–9 (1923). For a general review of the literature on the subject see Walker, J. C.: "On the Nature of Disease Resistance in Plants," *Trans. Wis. Acad. Sci. Arts and Letters*, **21,** 225–247 (1924).

[2] For a detailed description of smudge see Walker, J. C.: "Onion Smudge," *J. Agr. Res.*, **20,** 685–722 (1921).

[3] For a more detailed account of studies of resistance to smudge see Walker, J. C., "Disease Resistance to Onion Smudge," *J. Agr. Res.*, **24,** 1019–40 (1923).

[4] See further, Walker, J. C., and Lindegren, C. C.: "Further Studies on the Relation of Onion Scale Pigmentation to Disease Resistance," *J. Agr. Res.*, **39**, 507–514(1924).

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# *NOTES ON STELLAR STATISTICS. IV. ON THE RELATION BETWEEN THE MEAN VALUES OF THE υ AND τ COMPONENTS OF PROPER MOTION.*

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In a previous paper[1] we have discussed the frequency function of velocities at right angles to the line of sight, under the assumption that the distribution of cosmic velocities can be represented by a single Maxwellian function with a drift superposed. It may sometimes be useful to consider also the distribution of the separate components of this tangential velocity and their arithmetic mean values.

Let the tangential velocity be resolved into two components, the $\upsilon$ component directed toward the apex of the drift, and the $\tau$ component at right angles to this direction. Consider a small area in the sky, situated at an angular distance $\lambda$ from the apex of the drift, and denote by $V$ the speed of the drift and by $h$ the constant of the Maxwell distribution. The frequency law of the $\tau$ components remains unchanged and the arithmetic mean value $\tau_a$ is equal to $\tau_a = 1/h\sqrt{\pi}$. The distribution of the $\upsilon$ velocities is given by:

$$f_\lambda(\upsilon)d\upsilon = \frac{h}{\sqrt{\pi}} \exp\ [-h^2(\upsilon - V \sin \lambda)^2]d\upsilon$$

and the arithmetic mean value $\upsilon_\lambda$ may be calculated from:

$$\upsilon_\lambda = V \sin \lambda \ \mathrm{erf}(hV \sin \lambda) + \frac{1}{h\sqrt{\pi}} \exp(-h^2 V^2 \sin^2\lambda)$$

The mean value $\upsilon_a$, of $\upsilon$ throughout, i.e., taken over the whole sphere, is subsequently determined by:

$$\upsilon_a = \int_0^{\pi/2} \upsilon_\lambda \sin \lambda d\lambda \ldots\ldots\ldots\ldots\ldots\ldots (1)$$

When dealing with giant and slow-moving stars, $hV$ is probably less than 1.7, and accordingly H. C. Plummer's[2] approximation to the error function

$$\mathrm{erf}\ (x) = \frac{6}{\sqrt{\pi}} \frac{x}{3 + x^2}$$