The Law of the Minimum and the Relation Between Pathogen, Weather, and Disease

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ABSTRACT

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To provide an alternative to multiple linear regression for estimating the effect of inoculum and environmental factors upon disease in the field, a method of fitting the Law of the Minimum was developed and tested with hop downy mildew and wheat leaf rust. The estimates of the effects of the factors by the Law varied less among samples of observations and resembled the effects measured in controlled experiments more closely than did the estimates of the parameters by multiple linear regression.

Additional key words: Pseudoperonospora humuli, Puccinia recondita, epidemiology.

It is easy to repeat the tenet of plant pathology that disease is determined by environment, pathogen, and host, but difficult to estimate the actual effect of each factor in the field. The effects of contributing factors often are estimated by measuring the factors and the subsequent disease in the field and then relating them statistically by multiple linear regression (MR). Since MR has recognized drawbacks (3), we have investigated whether the Law of the Minimum might be more applicable.

MR equations are standard linear combinations of factors, fit to observations by a well established statistical method, and produce estimates of the quantitative effect of each factor in, say, percent disease per degree temperature or per spore. The fit of MR equations to observations of disease, environment, and pathogen is respectable (4,16). Nevertheless, two problems with MR prompted a search for an alternative method for extracting estimates from observations. First, the interaction of environmental factors is notorious, and this causes erratic sample-to-sample fluctuation of the estimated effects of the parameters as one goes from sample to sample of observations (6). Second, adding the effects of factors can be illogical, as when an equation states that abundant rain will cause abundant disease in the absence of the pathogen.

Logically, an increase in disease is affected by changes in each antecedent stage of the cycle of the pathogen, as has been formulated in differential equations (8) and in flow charts of simulators (17). Thus, a 10% increase in spores or in favorability of temperature for germination can each increase lesions by 10%. This is inconsistent both with single factor limitation and with adding the effects of causal factors. Rather, it is consistent with their multiplication and hence, the "compensation" (14) of deficiency in one factor by favorability of another.

Superficially, coping with the multiplication of factors seems

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easy with MR by transformation to logarithms. Thus, disease y can be written as a product of factors $z_1, z_2, \ldots, z_j \ldots$ and their proportionality coefficients $b_1, b_2, \ldots, b_j \ldots$:

$$y = b_1 z_1 b_2 z_2 \ldots b_j z_j \ldots \quad (1)$$

and this equation transformed into

$$\log y = \log (b_1 b_2 \ldots b_j \ldots) + \log z_1 + \log z_2 + \ldots \log z_j + \ldots \quad (2)$$

But the effect of a factor (eg, b_j = disease per degree temperature) cannot be deciphered from the intercept $\log (b_1 b_2 \ldots b_j \ldots)$, and a regression coefficient estimated for $\log z_j$ should be 1 unless equation 1 is invalid. This difficulty, plus dealing with zeroes and worrying about the distribution of errors, suggests that transformation by logarithms is no answer.

Saying that a factor is "limiting" is common parlance. Thinking of the response of crops to fertilizer elements, Liebig (2) codified this concept in the Law of the Minimum (hereafter called "the Law"): If several factors affecting outcome are present in abundance and one factor is deficient, adding more of the deficient factor will likely change the outcome greatly whereas increasing the abundant ones will change the outcome little. Blackman (1) applied the same concept to the control of photosynthesis by light and carbon dioxide and called it the Law of Limiting Factors.

Rabinowitch (13) reviewed the shortcomings of these Laws and wrote that, although the Law of the Limit was a reasonable first approximation to the action of nutrients, it was not reasonable to mix temperature, the supply of energy, the concentration of carbon dioxide, and the amount of chlorophyll. Limitation *a la* Blackman (1) would occur only if the outcome were the product of successive steps and one step became a bottleneck, making the outcome independent of all factors not affecting the bottleneck.

Aside from extreme cases such as the exhaustion of the supply of healthy host, the success of all inoculum, or the prevention of a step (eg, no water, no germination), one must ask if plant disease is commonly limited at intermediate levels. Rotem (14) gave examples showing that one highly favorable factor can sometimes compensate for limitations imposed by a simultaneously unfavorable factor. Compensation is, of course, evident when one environment allows 10% germination, and a more favorable one allows 20%; clearly, doubling the number of spores could compensate for the less favorable environment.

Thus, we must be cautious as we try using the Law to estimate the effectiveness of factors that determine disease in the field. Like MR, the Law does not have a wholly logical foundation and the use of values of its parameters is circumscribed by the limits of the observations employed for their estimation. Nevertheless, we are justified in learning whether the parameters of the Law vary less among samples of observations and resemble the effects of factors in controlled experiments more than do the parameters of MR.

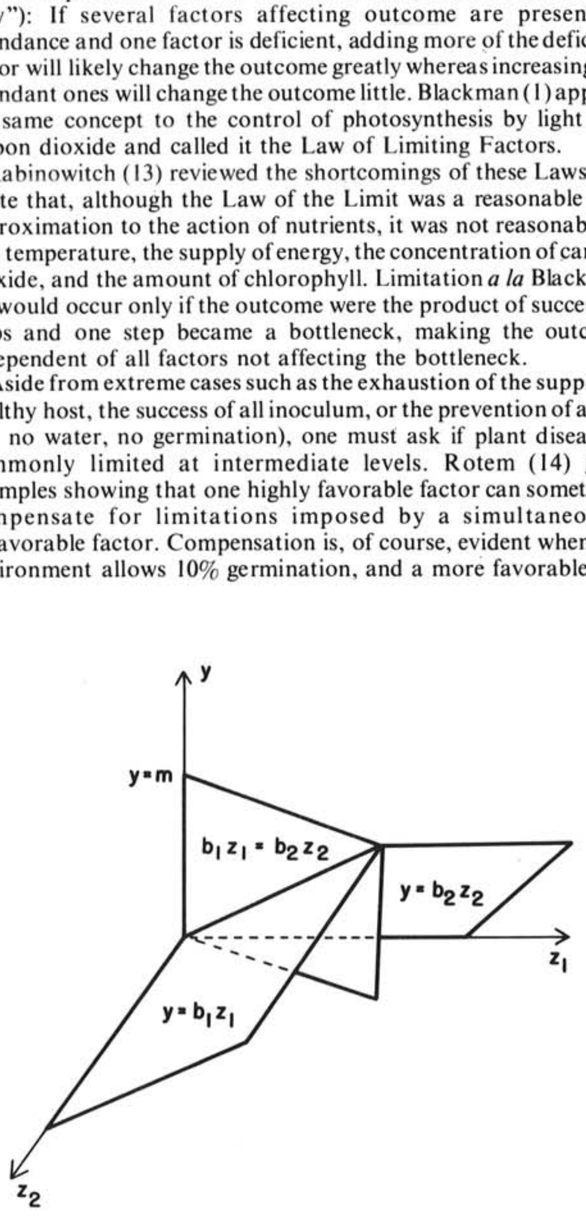

Fig. 1. Depiction of the Law of the Minimum for disease y and the factors represented by the variables z_1 and z_2. When $b_1 z_1 < b_2 z_2$ and m, y is in the plane $y = b_1 z_1$; when $b_2 z_2 < b_1 z_1$ and m, y is in the plane $y = b_2 z_2$; and when $m < b_1 z_1$ and $b_2 z_2$, y is in the plane y = m. For simplicity, the plane y = m is not drawn.

MATERIALS

Hop downy mildew (which is caused by *Pseudoperonospora humuli*) is encouraged by wetting of leaves, especially by rain. Royle (16) obtained independent measurements of infection by exposing successive groups of 10 healthy hop plants to the weather and natural sources of inoculum in a hop garden for 48 hr and then, after incubation in standard conditions, the percentage diseased among 150 to 290 leaves on each plant was observed.

Ten environmental variables based on airborne spores, moisture, temperature, and sunshine recorded during exposure were examined by MR in many combinations. RWD hr of leaf wetness with rain, RA mm of rain and AS spores per cubic meter of air combined in MR to explain about three-quarters of the variation in disease, y, on 27 occasions in 1969 and 24 occasions in 1970. We have employed the same three variables.

Wheat leaf rust (which is caused by *Puccinia recondita*) is encouraged by warmth and moisture. Eversmeyer and Burleigh (4) observed the rust in plots of Bison wheat at five locations at several times and made 68 observations in 1967 and 97 in 1968. Seven variables based on inoculum, temperature, and moisture were measured 8–14 days before disease severity was observed. The observations were generously sent to us by M. G. Eversmeyer (*unpublished*).

As a measure of disease, we chose to use the observed rust severity rather than an increment because severity was sometimes less at a later than at an earlier time. Culling the seven independent variables seemed practical. WSN or weekly accumulation of spores impacted on 10 rods rather than prior disease severity or accumulation of spores for a season seemed the most logical expression of inoculum. MIN (minimum temperature above −1C) rather than maximum was more frequently limiting when leaves were wet. Finally, FM (hours of free moisture) was logically and empirically a better predictor of disease than was days of precipitation. Consequently we have employed WSN, MIN, and FM as independent variables related to leaf rust.

METHODS

Our interest in the Law was awakened by R. B. Cate, and we have fit it to yields and fertilizer applications (18).

The Law can be expressed as

$$y = \text{AMIN} [f_1(z_1), f_2(z_2), f_3(z_3), m]$$

where the f_j are functions of the variables z_j (eg, Royle's duration of wetness, amount of rain, and number of spores). AMIN means choosing the least value within the brackets. The m is a limit upon y that is set by a factor not observed.

A simple yet logical function was employed to represent response of disease to each variable:

$$f_j(z_j) = b_j z_j$$

making the Law:

$$y = \text{AMIN} (b_1 z_1, b_2 z_2, b_3 z_3, m) \quad (3)$$

In this simple function b_j is the quantitative effect of the jth variable in units of disease y per hour of wetness or per millimeter of water or per spore per cubic meter of air. Although an intercept as in $a_1 + b_1z_1$ can be estimated (18), no intercept is included in the present functions because of the illogic of either negative or positive predictions of disease in the absence of causal factors.

The Law can be depicted in the three dimensions y, z_1 and z_2 (Fig. 1). When z_1 is small relative to z_2, the point (z_1, z_2) lies to the left of the plane $b_1z_1 = b_2z_2$. Here, z_1 is limiting and the plane $y = b_1z_1$ is the relation between the limiting variable z_1 and y. Similarly, when z_2 is small relative to z_1, the point (z_1, z_2) lies to the right of $b_1z_1 = b_2z_2$. Here z_2 is limiting and $y = b_2z_2$ is the relation between the limiting variable z_2 and y. When z_1 is limiting, the size of z_2 is inconsequential, and vice versa. Finally, some unmeasured factor will limit y to a maximum m when z_1 and z_2 are large. When a third variable z_3 is added, the boundaries between z_1 and other variables become

$$b_1z_1 = b_2z_2,\ b_1z_1 = b_3z_3,\ \text{or}\ b_1z_1 = m \qquad (4)$$

but the depiction of disease response to three variables simultaneously is not feasible.

Having decided upon the form of the boundaries between limiting variables, we finally establish a criterion for estimating the b_j for given data. We have chosen to minimize the sum of squares, S, of deviations of y_i around the Law, equation 3.

$$S = \Sigma_i(y_i - b_jz_{ji})^2 \qquad (5)$$

where y_i and z_{ji} are the ith observations of y and the limiting variable z_j.

Since the limiting variable is unknown for any i, boundaries between the variables are tried. At any boundary, equation 4 specifies

$$z_1 = \frac{b_2}{b_1}z_2,\ z_1 = \frac{b_3}{b_1}z_3,\ \text{or}\ z_1 = \frac{m}{b_1}$$

Accordingly values of b_2/b_1, b_3/b_1, and m/b_1 are assumed, and equation 5 becomes

$$S = \Sigma_i(y_i - b_1X_i)^2$$

where $X_i = z_{1i}$ when $z_{1i} < b_2z_{2i}/b_1, b_3z_{3i}/b_1$, and m/b_1; $X_i = b_2z_{2i}/b_1$ when $b_2z_{2i}/b_1 < z_{1i}, b_3z_{3i}/b_1$, and m/b_1; $X_i = b_3z_{3i}/b_1$ when $b_3z_{3i}/b_1 < z_{1i}, b_2z_{2i}/b_1$, and m/b_1; and $X_i = m/b_1$ when $m/b_1 < z_{1i}, b_2z_{2i}/b_1, b_3z_{3i}/b_1$. The proportionality b_1 is estimated as

$$\Sigma X_iy_i/\Sigma X_i^2$$

TABLE 1. Hop downy mildew and wheat leaf rust. Means and coefficients of determination[a] among observations of lesions per 100 leaves, inoculum,[b] and environment[c]

		Mean		Coefficient of Determination, r^2					
				RA		AS		Lesions y	
		1969	1970	1969	1970	1969	1970	1969	1970
Hop Downy Mildew	RWD, hr	15	2	.35	.77	.14	.02	.41	.57
	RA, mm	16	6			<.01	.04	.20	.36
	AS, spores/m³	5	1					.04	.03
	Lesions y	30	21						
				FM		WSN			
Wheat Leaf Rust	MIN	9	7	.02	.10	.06	.21	.23	.16
	FM, hr	5	8			.06	.04	.14	.05
	WSN spores on 10 rods	1,715	6,442					.38	.72
	Lesions y	11	9						

[a]These relations are not forced through the origin.
[b]AS = spores per cubic meter of air.
[c]RWD = hours of leaf wetness with rain; RA = rainfall (mm); MIN = minimum temperature above −1 C; FM = hr of free moisture per day; WSN = weekly catch of urediospores on traps.

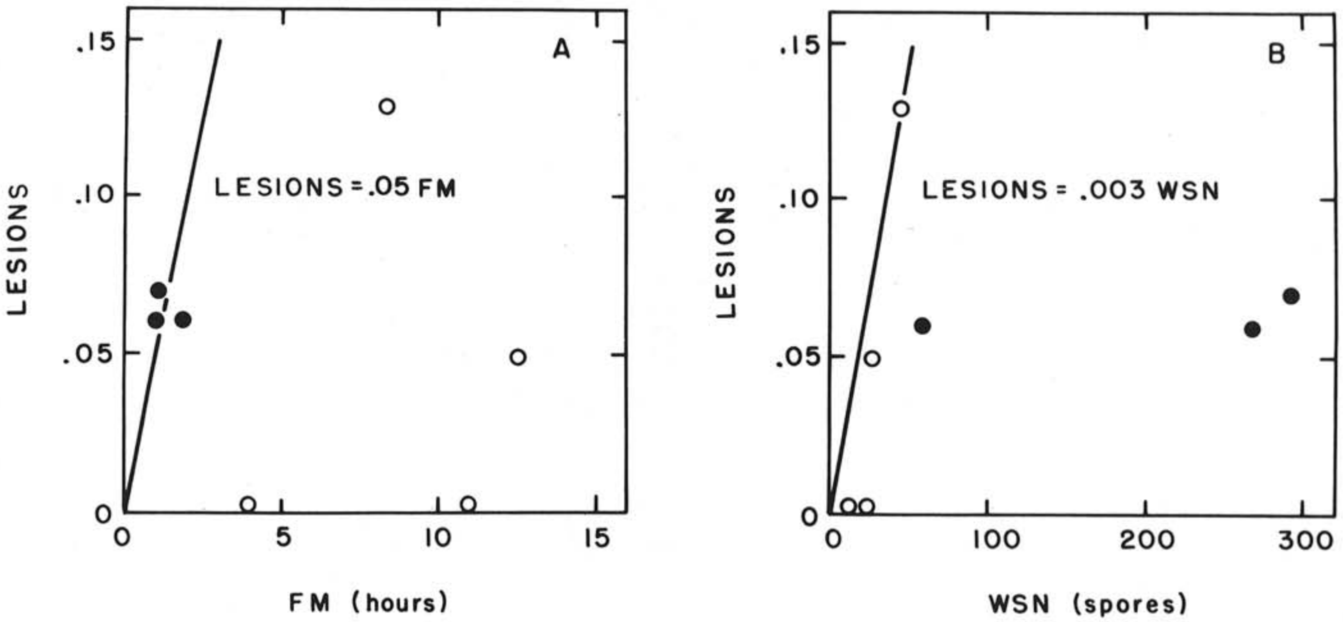

Fig. 2. The lesions of leaf rust per hundred wheat leaves observed at Colby in 1968 as functions of hours of free moisture on leaves, FM (left) and weekly accumulation of spores on traps, WSN (right). Numbers of lesions were limited by FM (•) or WSN (o).

We normalize the sum of squares, S, about the Law as R^2, the fraction explained by the Law of the total sum of squares of y_i about the mean. Repeated assignments of b_2/b_1, b_3/b_1, and m/b_1 generate surfaces of constant R^2, and at the core of the solids defined by these surfaces is found the maximum R^2. Since the sum of squares about the mean is constant, seeking maximum R^2 is the same as seeking minimum S. In the analyses that follow, disease appeared to be limited by the factors considered, hence a maximum $y = m$, set by an unknown factor, was not needed.

The significance of a variable in the Law can be calculated in a manner analagous to that used in MR. Since the relations of equation 3 pass through the origin, the sum of squares of y_i about zero is divided into that attributed to a single z_j, that attributed to the addition of a second and sometimes a third z_j, and the residual sum of squares. The variance-ratio test can then be used to test the significance of a variable.

The simple form of f_j (ie, $b_j z_j$) helps one decide upon transformation of disease observations by their relation to inoculum and environment. The decision is easiest if one thinks of spores. Logically a spore will cause a lesion and not a percentage of leaves diseased; therefore, the observed percentages were transformed into lesions per 100 leaves (5), giving b_j such reasonable dimensions as lesions per spore. Other b_j have such reasonable dimensions as the increment in lesions per degree Celsius of warming, per millimeter of rain, or per hour of wetness.

RESULTS

Hop downy mildew. The means and coefficients of determination (ie, r^2) among the variables are shown in Table 1. The 1969 season was wetter, more spores were in the air, and more mildew was observed than in 1970. The amount RA of rain and the hours RWD of wetness were correlated, as expected, but the spores AS per cubic meter of air were not closely correlated with moisture. RWD explained up to .57 of the variation in the number of lesions, RA explained up to .36, and AS explained little.

The estimates for MR and the Law are shown in Table 2. As expected from the close correlation of RWD and RA, the coefficients in the MR varied erratically. In contrast to MR, the parameters of the Law were never negative, and the R^2 for the Law was somewhat greater. RWD was limiting in 11 of the 27 cases in 1969 and in 3 of the 24 cases in 1970, and AS was limiting on only three occasions (in 1970); RA limited all other cases.

Wheat leaf rust. The means and r^2 are shown in Table 1. The year of 1967 was warmer and drier and fewer spores were trapped, but disease was about the same as in 1968. The correlations among moisture, temperature, and spores were not great. The portion, r^2, of variability in lesions explained by the independent factors was greatest for WSN spores trapped during a week.

The estimates for MR, Table 2, are shown for the 2 yr at the five locations. Despite the poor correlation among the variables, the parameters varied, occasionally becoming negative. The parameters of the Law were less erratic and never negative. When the Law was fit to all 1967 observations, 1 was limited to MIN, 20 by FM, and 47 by WSN. The numbers for 1968 were 2, 7, and 88. Again, the R^2 for the Law was usually greater than for MR.

The outcome of changes in the variables was tested by redefining MIN as temperature above 4.46 rather than −1C. Tested upon the 1967 observations, this change altered R^2 little, but it did increase the number limited by MIN. In another calculation, the disease index was changed from lesions to increase in lesions in 8–14 days. Although the number limited by MIN increased, the number limited by WSN spores remained large.

DISCUSSION

The operation of the Law can be seen in Fig. 2. In 1968, rust was observed at Colby on 7 days. MR of lesions on the three factors explained only a third of the variation in lesions. In Fig. 2 one sees that the Law explains .84 of the variation because the line "lesions equal .05 FM" closely fits the three cases limited by moisture, and the line "lesions = .003 WSN" closely fits the four cases limited by

TABLE 2. Estimates by multiple linear regression and the Law of the Minimum for hop downy mildew and wheat leaf rust

Disease	Location	Observations	Year	Basis for Estimation	R^2
				Multiple Linear Regression	
Wheat Leaf Rust[a]	Colby	11	1967	−.4 + .02 MIN + .05 FM + 10 × 10^{-4} WSN	.90
		7	1968	−0.1 + .02 MIN + <.01 FM − 2 × 10^{-4} WSN	.34
	Denton	10	1967	−4.1 + .80 MIN + .50 FM + 27 × 10^{-4} WSN	.80
		19	1968	−12.1 + 1.33 MIN + .66 FM + 6 × 10^{-4} WSN	.74
	Goodwell	12	1967	−8.8 + .32 MIN + 2.40 FM + 5 × 10^{-4} WSN	.57
		23	1968	−0.1 + .04 MIN − .14 FM + 211 × 10^{-4} WSN	.83
	Manhattan	18	1967	−24.0 + 2.34 MIN + 1.30 FM + 67 × 10^{-4} WSN	.86
		31	1968	3.7 + .40 MIN − .41 FM + 8 × 10^{-4} WSN	.82
	Stillwater	17	1967	.7 + .77 MIN − .38 FM +28× 10^{-4} WSN	.67
		17	1968	−3.9 + .04 MIN + .39 FM + 17 × 10^{-4} WSN	.81
Hop Downy Mildew[b]			1969	−3.3 + 1.05 RWD + .41 RA − .017 AS	.42
			1970	−.3 + .28 RWD + .42 RA +.023 AS	.61
				Law of the Minimum	
Wheat Leaf Rust[a]	Colby		1967	AMIN ([c] [c] 12 × 10^{-4} WSN)	.84
			1968	AMIN ([c] .05 FM, 30 × 10^{-4} WSN)	.84
	Denton		1967	AMIN (2.11 MIN, 7.05 FM, 247 × 10^{-4} WSN)	.78
			1968	AMIN (5.81 MIN, 2.91 FM, 32 × 10^{-4} WSN)	.78
	Goodwell		1967	AMIN (2.25 MIN, 2.81 FM, 78 × 10^{-4} WSN)	.84
			1968	AMIN (4.14 MIN, 3.17 FM, 158 × 10^{-4} WSN)	.82
	Manhattan		1967	AMIN (4.96 MIN, 12.24 FM, 626 × 10^{-4} WSN)	.92
			1968	AMIN (4.14 MIN, 7.97 FM, 10 × 10^{-4} WSN)	.78
	Stillwater		1967	AMIN (5.36 MIN, 5.82 FM, 276 × 10^{-4} WSN)	.89
			1968	AMIN (13.07 MIN, 9.44 FM, 22 × 10^{-4} WSN)	.91
Hop Downy Mildew[b]			1969	AMIN (1.34 RWD, 4.57 RA, 7.26 AS)	.49
			1970	AMIN (.61 RWD, 3.71 RA, 1.72 AS)	.74

[a] The parameters have dimensions of lesions per 100 leaves per degree temperature (MIN), hours with free moisture on leaves (FM), or spores trapped on 10 rods during 1 wk (WSN).

[b] The parameters have dimensions of lesions per 100 leaves per hour of leaf wetness (RWD), millimeters of rainfall (RA), or spores per cubic meter of air (AS).

[c] No observations limited by the variable.

inoculum.

The greater limitation of rust by spores than of mildew by spores is striking. One can only conjecture and suggest that this is caused by the greater requirement for water by hop downy mildew than by wheat rust. The frequent limitation by amount of water rather than duration of wetness for mildew is surprising and may be caused by RA indicating a thoroughness of wetting not reflected in RWD. It is not surprising that water more frequently limits *Puccinia* than does cool weather in Kansas.

The primary matter, however, is the weakness of the logical foundations of both MR and the Law, and we now examine whether the parameters of one model vary less than those of the other model among samples of data and which model has parameters more closely resembling observations in controlled experiments. These criteria will guide the choice between the two models because the fit to data was similar.

First, the more erratic behavior of the parameters of MR than of the Law is clear from Table 2. The negative parameters of MR embarrass us by estimating sometimes that mildew decreases with rain or with more spores or that rust decreases with the duration of free moisture on the foliage. As mentioned in the introductory section, the correlation among environmental factors commonly causes erratic fluctuations in the estimated parameters of MR as one goes from sample to sample of observations.

Second, Fig. 2 suggests that the parameters of the Law will resemble those of controlled experiments more closely than will those of MR. That is, the effect of a factor, say, duration of moisture, generally will be examined in the laboratory by making other factors, in this case temperature and inoculum, highly favorable or nonlimiting. As Fig. 2 shows, this is the way the Law is fit: the effect of FM is estimated from the three cases that have relatively abundant inoculum.

Finally, we compare the parameters of Table 2, which are from the field, with values observed in experiments in the laboratory. Two hr of moisture were required to produce any mildew on hop leaves inoculated in chambers, and 4 hr produced 25% angular leaf spot (15). The inoculum was a suspension of 5×10^4 sporangia per milliliter, or 10^4 spores per leaf if a leaf received 0.2 ml. Since about one lesion per hour RWD was estimated by both MR and the Law, both can be called accurate in the prediction of the result of 2 hr of moisture, but both failed to predict the great increase in disease after a second 2 hr.

To appraise the lesions produced per spore, we convert the AS spores per cubic meter into spores deposited per 100 leaves. In 48 hr air containing 1 spore per cubic meter will deposit about 1,000 spores that settle at 1 cm/sec on 100 leaves that are 50 cm^2 each. Thus, the estimate of .023 lesions per AS by MR corresponds to lesions per 1,000 spores (−.017 is, of course, nonsense). The 1.7 and 7.3 lesions per 1,000 spores estimated by the Law are several orders of magnitude larger, permitting a clear choice between models. A standard can be derived from Royle's (15) observations: If 25% angular leaf spot is produced by 10 lesions on a leaf and the leaf received 10^4 spores, the rate is one lesion per 1,000 spores. Discussing his field observations, Royle (15) pointed out a 50% leaf infection (ie, 70 lesions per 100 leaves) followed a period with 25 spores per cubic meter (ie, 25,000 spores per 100 leaves), providing an alternative estimate of three lesions per 1,000 spores. Similarly, spores of another fungus, *Botrytis*, produced one to two lesions per 1,000 spores (7). Thus, the 1.7–7.3 lesions estimated by the Law seem much closer to the outcome of other experiments than the .023 estimated by MR.

TABLE 3. Analysis of variance of hop downy mildew in 1970 according to the Law of the Minimum

Term[a]	Degrees of freedom	Mean square	Variance ratio
Test of AS	1	39	12.2
Test of RWD	1	59	18.5
Test of RA	1	143	44.7
Residual	21	3.20	...

[a]Abbreviations: AS = spores per cubic meter of air; RWD = hours of leaf wetness with rain; RA = rainfall (mm).

The test of the significance of variables is demonstrated by the analysis of variance of the 24 observations of mildew in 1970 (Table 3). All three variables make a highly significant contribution to the explanation of the variation in mildew.

To appraise the increase in rust per spore, we must convert the WSN to deposit per leaf. Since WSN was the weekly deposit on 10 rods, it is reasonable to say WSN equals the deposition on 10 leaves. In Table 2 the estimated coefficient for WSN has a median of .001 by MR and .005 by the Law. Since these estimates have dimensions "lesions/(100 leaves)/(spores on 10 leaves)", they must be divided by 10 to show lesions/spore, giving 0.1 lesion per 1,000 spores by MR and 0.5 lesions per 1,000 spores by the Law. In comparison, Manners (9) found about 5% of single-spore inoculations with *Puccinia glumarum* were successful, and Peterson (12) observed one infection focus per three spores of *Puccinia graminis* var. *tritici*. Thus, the 0.1 and 0.5 lesions per 1,000 spores estimated by MR and the Law are both much lower than the 50 to 300 found by Manners (9) and Peterson (12). However, the estimate of 0.5 by the Law is favored by a factor of five over the estimate by MR.

Below 25 C, warming increases rust. Melander (10) observed that the incubation period of *Puccinia graminis* was halved when the temperature increased from 10 to 20 C. Further, Peltier (11) found that when the temperature during 2 days after inoculation with *P. graminis* was increased from 15 to 20 and 25 C, the subsequent percentage of Marquis wheat leaves infected increased from 13 to 40 and 100%. Since the parameters for change in lesions per degree (Table 2) pertain to the entire disease process, a precise comparison with Melander's (10) and Peltier's (11) experiments is difficult. Nevertheless, their experiments certainly imply an increase of several lesions per 100 leaves per degree, favoring the values estimated by the Law (median 4.6) over those estimated by MR (median 0.4).

Neither the Law nor MR treat logically the multiplicative interactions and compensation among inoculum and environmental factors that affect plant disease development. However, the Law has important advantages over MR for description of plant disease. First, when fit to observations in the field to estimate the effect of the factors upon disease, the estimates by the Law vary less among samples of observations than estimates by MR. Second, because the estimates are made by the Law from only the cases in which other factors are relatively abundant, the estimates by the Law are larger and nearer the effects observed in controlled experiments where the experimenter attempts to remove limitations by extraneous factors. Thus, if the logical restraints upon the Law are remembered, it helps extract from field observations the effects of factors, it permits comparison of the estimates with controlled experiments, and it allows prediction of disease severity.

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