Special Topics

Computer Graphics Simulation of Growth and Sporulation of *Erysiphe polygoni*

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ABSTRACT

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Growth and sporulation of *Erysiphe polygoni* was observed and photographed for 7 days. The fungus was grown in a constant-temperature room with a 16-hr day at 22 C and 8-hr night at 19 C. Experimentally obtained values were the period between formation of a hyphal segment and branching of that segment (about 24 hr), mean hyphal length supporting one branch (162 μm, formed in 12 hr), the number of germ tubes formed over time (represented by a logarithmic expression or by experimental data), the period between formation of the hyphal segment and onset of sporulation (72 hr), the number of conidiophores per 162-μm segment after the 72-hr period (0.7), and the mean branching angle (44.8°). A computer graphics simulation of colony growth and sporulation was developed using these values as parameters. High correlations were obtained between the number of hyphae and conidia formed in vivo and in the graphics simulation. The graphics program appears to be a fairly realistic representation of colony formation of *E. polygoni*.

During the past 40 yr, scientists have investigated the mathematical relationships of networks of rivers (12), lungs (13), blood vessels (3,13), the nervous system (13), trees (1,10,13,14), and food chains (13). Recently, fungi have also been investigated (5,7,8,16,18,19). In this paper we used Quinn and Powell's model (21) of growth and sporulation of *Oidium begoniae* Puttemans as the basis for a computer graphics simulation of growth and sporulation of *Erysiphe polygoni* DeC & Mérat. We have added some stochastic features and some extra variables to the model that were necessary to depict fungal growth realistically. We believe this is the first computer graphics simulation of growth and sporulation of a fungus that uses numerous experimentally determined values to help generate the graphics. Computer simulations of trees (4,10,11) and lungs (13) have previously been described. The purpose of this study was, first, to determine to what extent the asexual life cycle of *E. polygoni* could be represented by computer graphics, and second, to provide a visual test of the concepts of the underlying mathematical model (21). An accurate graphics

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simulation will ultimately be more than just a way to draw pictures of fungi, and ways in which it can be expanded and used are discussed later.

E. polygoni, like *O. begoniae*, is a powdery mildew (*Erysiphaceae*) of the subgroup that forms one conidium per conidiophore per day (15,20,26,28). Other members of the group are *Uncinula* and *Microsphaera* spp. This simulation covers days 2–8 of colony development at optimum temperature (21 C) (27). During this time, the fungus grows at a fairly constant rate, begins to branch, and forms conidiophores and conidia. During the first

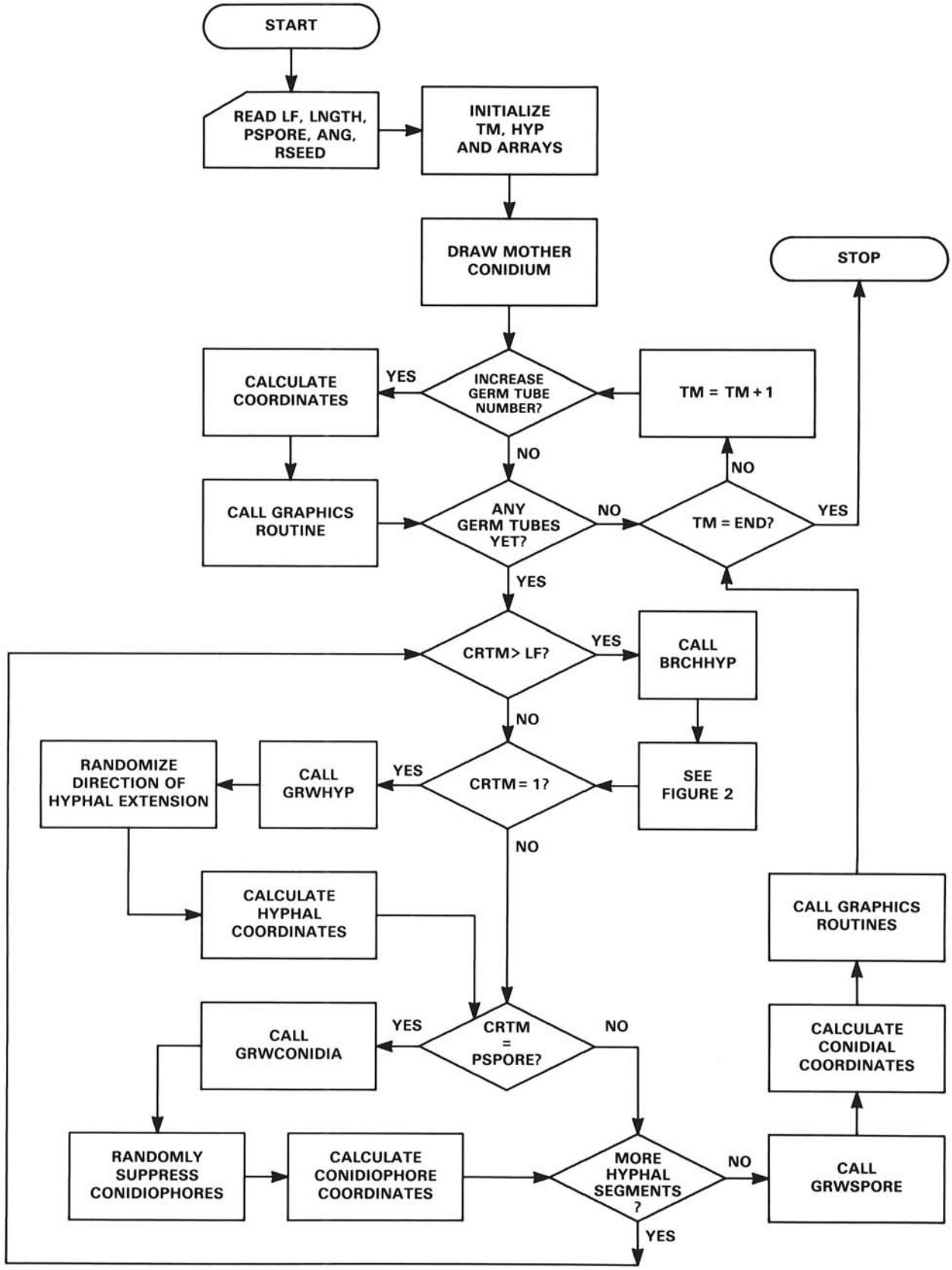


Fig. 1. Flow diagram of computer program for simulation of growth and sporulation of *Erysiphe polygoni*. TM = time after germination, LF = maturation period before a hyphal segment will branch, CRTM = creation time of a hyphal segment, PSPORE = maturation period before a hyphal segment will form a conidiophore.

day, before the primary haustorium is functioning, growth is slower. After 10–14 days of growth, colony growth and sporulation often slows (9,22), the colony may form perethecia (cleistothecia), and the colony will eventually kill the host cells and die. Simple patterns that can be incorporated into computer graphics simulations are not as evident at these later stages, and they are not considered at present. Thus, only young colonies are depicted in our simulation.

MATERIALS AND METHODS

Computer program. The computer program was written in FORTRAN 77 and was implemented on an Apollo computer. A flowchart of the program is presented in Figures 1 and 2. Table 1 lists the variables, parameters, constants, and arrays used in the program. The parts of the program follow.

The main program reads in the parameter values, initializes constants and arrays; draws the mother conidium; calculates when and where germ tubes are drawn; determines if the subroutines for branching, hyphal extension, or conidiophore formation are called; calls the graphics routines; and determines if the program will end.

Subroutine BRCHHYP (Fig. 2) calculates where branches are to be placed. The first branch on a primary hypha always forms in the simulation. Subsequent branches have a 50% chance of forming in each TM (time) segment until a maximum of two branches per hyphal segment (LNGTH) are formed. LNGTH is the mean length that a hypha grows during each TM segment. When two branches are formed on the same LNGTH, they are drawn on opposite sides from each other. The 50% branch suppression does not quite offset the LNGTH's forming two branches so that the number of branches formed is less than in the deterministic model, where exactly one branch forms on each HGU (the HGU is the mean length of hypha supporting one branch). LNGTH and the HGU are related but not quite equivalent terms. The stochastic method used in the simulation, using LNGTH, was considered sufficient, because formation of branches nearly opposite one another was common and the simulation was accurate in predicting the experimentally determined number of branches. Branching angles were randomly varied based on the standard deviation of branching in experimental observations.

Subroutine GRWHYP (Fig. 1) calculates where extensions of existing hyphae are drawn. Hyphal growth is assumed to occur at a linear rate typical of fungi in the logarithmic stage of colony growth (2). Simulated hyphae grow straight 34% of the time and are bent 9° right or left the remaining 66% (33% either direction). These values were arbitrarily selected to give the colony a realistic appearance. The direction of growth is determined randomly using the random number from subroutine RANDOM NUM.

Subroutine GRWCONIDIA (Fig. 1) calculates where conidiophores are drawn. Conidiophores are randomly suppressed 34% of the time. This number was chosen since only about 70% of LNGTH were experimentally found to produce conidiophores.

Subroutine GRWSPORE (Fig. 1) calculates the placement of conidia on the conidiophores after a maturation period (NSLAG).

Subroutine RANDOM NUM generates random numbers with a

TABLE 1. Constants, parameters, and variables used in the simulation of the growth and sporulation of *Erysiphe polygoni*

Term[a]	Definition and Units	Values used in the simulation
TM (*t*)	Time since germination minus 36 hr. Units are the time it took for one hyphal growth unit to form (12 hr)	0–16
(HGU)	Hyphal growth unit. The mean length of hyphae supporting one branch after maturation (in μm)	162 μm
LNGTH	A modification of the HGU term used in the simulation. LNGTH is the segment of a hypha that forms in one TM segment. This length was calculated in the same way as HGU. However, as time goes to infinity, LNGTH segments tend to have two branches	162 μm
HYP	The number of LNGTH units formed	
CRTM	Array of creation time of each LNGTH unit	
LF (*q*)	Period of maturation required before a LNGTH segment will branch	24 hr
BRCH	Array containing the number of branches formed on any one segment	0–2
HYPBR	Array containing direction of growth of the first branch (second branch will form on opposite side of mother hypha)	
ANG	Mean branching angle	45°
ANGDEV	Standard deviation of the branching angle	12.6°
PSPORE (*p*)	Period of maturation required before a LNGTH unit will form conidiophores minus one in TM units	5 (72 hr)
NSLAG	Lag time from conidiophore formation until a conidial formation in TM units	2 (24 hr)
NCNDA	Number of conidiophores formed during a a given TM unit	
CNDTM	Array containing formation time for each conidiophore	
SPTM	Array containing formation time for each conidium	
(*z*)	Number of conidiophores per HGU (This value was approximated with a random suppression of conidiophores in the simulation instead of use of a variable.)	0.7
XI,XJ	Arrays of x axis coordinates of every LNGTH unit. XI is the distal end, and XJ the proximal end	
YI,YJ	Arrays of y axis coordinates of every LNGTH unit	
XSX	Array containing X coordinates for conidia	
YSY	Array containing Y coordinates for conidia	
RSEED	Seed for Gaussian random number generator	0.9–1.05

[a] Variable names in parentheses are the approximate equivalents from (21).

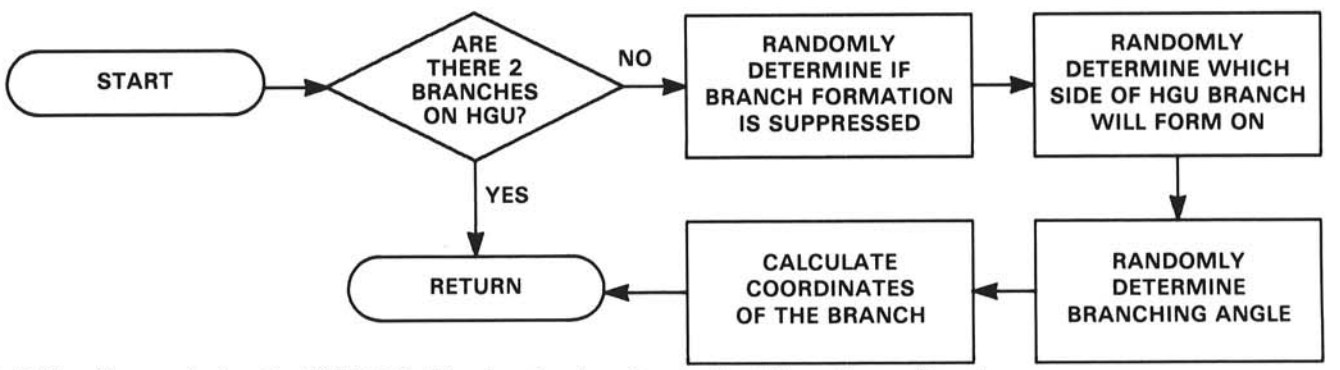


Fig. 2. Flow diagram of subroutine BRCHHYP. This subroutine determines the X and Y coordinates of branches.

Gaussian distribution (23). The numbers are used to randomly vary which side of a hypha a branch is formed on, suppression of branching, branching angle, direction of hyphal extension, and suppression of conidiophore formation.

Subroutine END GROWTH suppresses branches and hyphal extension based on hyphal density. The effect of this subroutine can be varied. In the example given here, it is set to no effect.

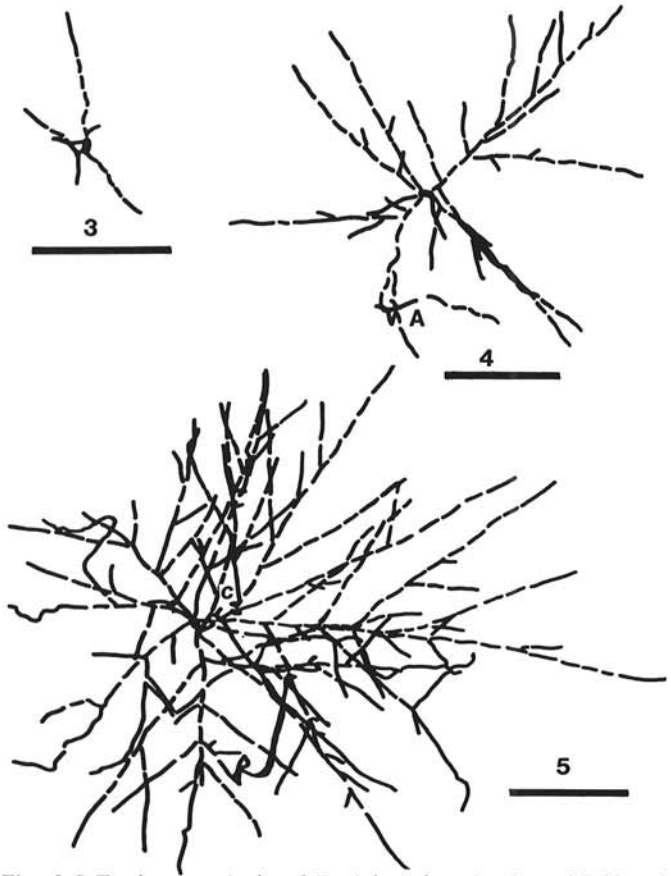
Several graphics subroutines drew lines, circles, boxes, or wedges.

Whenever a new LNGTH unit is formed, it is given a counter number (HYP) and its creation time (CRTM) is noted in an array. The number of conidiophores (NCNDA) and their creation time (CNDTM) is also noted. The FORTRAN program is available from the authors on request. Also available is a BASIC program that calculates number of hyphae, hyphal growth units, and conidia over time using the method of Quinn and Powell (21) and that does not have graphics routines.

Comparison of the program and mathematical model. Calculating the number of HGU will be given as an example. The number of HGU in the portion of a colony formed from a single germ tube was estimated to be (21):

$$HGU = (\Sigma_1^{t} 1) + (\Sigma_{i=1}^{t-q} \Sigma_1^{i} 1) + (\Sigma_{j=1}^{t-2q} \Sigma_{k=1}^{j} \Sigma_1^{k} 1) + \ldots (\Sigma_{m=1}^{t-rq} \ldots \Sigma_1^{n}) \quad (1)$$

in which t is the time (units is the mean time to form one HGU) since the germ tube formed (TM − CRTM), q (same units as t) is the hyphal maturation period LF. The first summation is the number of HGU formed on the hypha originating from the mother spore, the summations within the next set of parentheses are the number of HGU in the second-order hyphae that began as branches of the original hypha, the next set of summations is the HGU in "branches of branches," and so on until the maximum number of maturation periods (r) within time t have been accounted for ($t-rq$ must be greater or equal to 1). The final summation in each set of parentheses models increases due to hyphal extension, and the other summations model increases due to branching. The number of summations due to branching within each set of parentheses will equal the number of branching orders subtending the one under consideration.



Figs. 3–5. Tracings of colonies of *Erysiphe polygoni* on bean, 72, 96, and 120 hr after inoculation, respectively. **3,** Breaks in hyphae indicate positions of cell walls. **4,** Curvature in hyphae (A) is an artifact of the staining process. **5,** Just above three conidiophores is the letter c. Scale bars = 100 μm.

In the program, increase in number LNGTH (related to HGU but defined differently) was done as follows: An array was defined to keep track of the creation time of all LNGTH (CRTM). The germ tube was created in the main program, its CRTM was recorded, and it was given a designation number (HYP = 1). The main program was repeatedly run until the designated maximum TM was reached. After each run, TM was increased 1 unit. During each run, for each existing LNGTH, the following is considered. First, if LNGTH is 1 TM unit old (TM − CRTM = 1), subroutine GRWHYP is called. This subroutine will then increase the number of LNGTH by 1 every time it is called (HYP = HYP + 1). This is the increase due to hyphal extension. Second, if the LNGTH age is equal to the maturation period LF, then subroutine BRCHHYP is called. If the branch is not randomly suppressed, then BRCHHYP will increase the number of LNGTH by 1 (HYP = HYP + 1). This is the increase due to branching. The number of LNGTH at any given point in TM is equal to HYP. In concept, the model and the computer simulation calculate the number of HGU or LNGTH in the same way, repeatedly adding 1 as a function of time and the maturation period for branching. If the random number generators in the graphics simulation are not used and only one branch per LNGTH is allowed, the previously published model and the algorithm used in this graphics simulation are mathematically equivalent. The numbers are only manipulated in a different order. The simulation calculates the increase in LNGTH due to extension and branching separately, whereas the model calculates the increase in HGU due to discrete branching orders separately. This difference is needed since in the simulation, the age of each individual LNGTH unit must be known.

Application to *E. polygoni*. Conidia of *E. polygoni* were inoculated on 2-wk-old bean (*Phaseolus vulgaris* L.) cultivar dwarf horticultural Taylor from Meyer Seed Co. seedlings by lightly pressing infected leaves to the leaves of the test plants. The plants were set in subirrigation trays in a controlled temperature room with a 16-hr day (22 C) and 8-hr night (19 C). Relative humidity varied from 40–50% during the day to 75–90% at night. Two plants of similar size and coloration were chosen as subjects for the experiment; all the colonies observed formed on the primary leaves of these plants. At 24-hr periods, small leaf sections about 5 mm in diameter, peeled thin, so that mostly just upper epidermis was removed, were placed in lacto-glycerine cotton blue, were autoclaved for 10 sec at 1.05 kg/cm^2 (the sample was in the autoclave for about 5 min total heating and cooling time), were mounted on glass slides, and were microscopically examined. This method is rather harsh and can result in damage to colonies. Colonies were photographed with a Polaroid camera and parameters for use in the simulations were determined from the photographs. To improve quality and contrast, tracings of the photographs were made (Figs. 3–5). The experiment was discontinued after 7 days because colonies became too dense to identify individual hyphae. Ten colonies (different ones at each point in time) were examined at each time point, five from each plant.

The HGU (approximates LNGTH) was calculated by measuring about 100 96- and 120-hr-old hyphae, subtracting the unbranched length at the terminus, and dividing the remaining branched portion by the number of branches. ANG was measured by placing a protractor on the photographs of 72-, 96-, and 120-hr-old colonies and measuring a total of about 100 angles. TM, the time period for branching and the basic unit of time in this study, was determined by dividing the length of the branched portion of a hypha by the number of hyphae, by dividing the length of hyphae of known age by days to give a daily hyphal extension rate, and by dividing the first number by the second number to determine the basic unit of TM in days. LF, NSLAG, and PSPORE (the period of maturation required before a LNGTH unit will form

conidiophores minus 1 in TM units) were determined by simply observing when branches, conidia, and conidiophores first appeared on average (10 colonies observed at 24-hr intervals). LF can also be indirectly determined by measuring the length of unbranched hypha at the tips and determining the time it takes for the fungus to grow that distance.

RESULTS

Initially, growth of hyphae of *E. polygoni* was slow. The first hyphal segment 162 μm long (a hyphal growth unit or HGU in Trinci and coworkers' terminology [17]) did not form until 48 hr after inoculation. In the simulation, HGU was given the parameter name LNGTH. As the program evolved, LNGTH diverged from the HGU definition somewhat. The changes, random suppression of branching on any LNGTH segment 50% of the time, and the formation of two branches per LNGTH segment did not adversely affect the correlation of branch number between the simulation and observed results (Table 2) and depicted the fungus more realistically in the simulation, because branches originating from the same cell were fairly common in the observed colonies (Figs. 3–5). For purposes of the simulation, the first 36 hr was not counted as contributing to time (TM) and was ignored in the simulation. Germ tubes emerged as listed in Table 2. Few germ tubes emerged after 96 hr. In the computer simulation the emergence of the germ tubes was simulated two ways. At first we modeled it with equation 2, which was calculated using regression analysis:

$$w = (1n(TM) - 0.23)/0.31 \qquad (2)$$

where w is the number of germ tubes and TM is time in 12-hr increments (the mean time it takes to form one hyphal segment). The first 36 hr after inoculation were not included in the calculation of TM. This equation was obtained by regression and the r^2 of the regression was 0.99 with model standard deviation of 0.09. Later we used the experimental values for germ tube formation (Table 2) in the simulation. Using the experimental values instead of equation 2 resulted in an increase in the simulated variability that was more like the experimental variability. This difference is noted in Table 3.

Hyphae grew at a rate of about 325 μm/day and branches formed on hyphal segments an average of 24 hr after their formation (LF = 24 hr). The germ tube that first emerged has a somewhat longer period LF but has about the same length of unbranched hypha at its tip (i.e., it grows more slowly until the primary haustorium is functioning). There were two unbranched hyphal segments, totalling about 325 μm in length at the end of each hypha (Figs. 3–5). TM, the unit of time used in the simulation was approximately 12 hr as determined by measuring about 100 hyphae formed on days 4, 5, and 6. The mean branching angle of the experimentally observed colonies was 44.8 degrees with a standard deviation of 12.6 degrees. Setting TM units to 12 hr, LF to 24 hr, and the mean branching angle to 45 degrees, the number of hyphae in the computer simulation agreed closely with the experimental values (Table 2). The variation from colony to colony was also about the same when experimental values for germ tube

TABLE 2. Number of germ tubes, hyphae, and conidiophores of *Erysiphe polygoni* observed microscopically and calculated by computer simulation[a]

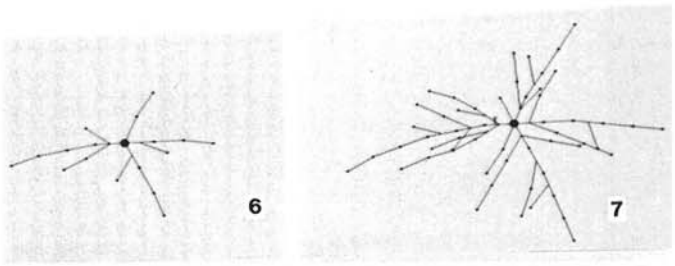
Days after inoculation	Experimentally observed (no.)			Computer simulation[b]	
	Germ tubes	Hyphae	Conidiophores	Hyphae	Conidiophores
2	3.3 ± 0.8	3 ± 0.8	0	3 ± 0.8	0
3	5.0 ± 0.8	8 ± 2	0	9 ± 1.1	0
4	6.5 ± 0.7	20 ± 5	1 ± 1.4	23 ± 4	1 ± 0.6
5	7.2 ± 0.6	68 ± 12	6 ± 4	62 ± 8	6 ± 1.8
6		138 ± 21	20 ± 9	137 ± 24	24 ± 4
7			67 ± 12		71 ± 13

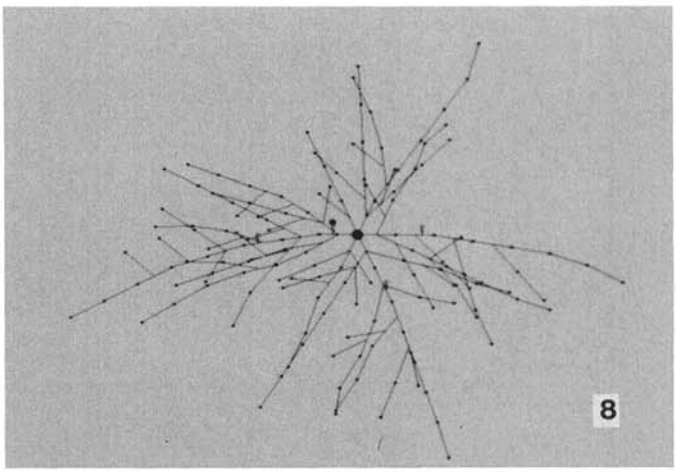
[a] Experimentally observed and computer simulation numbers are the means of 10 colonies followed by the standard deviation of the means.
[b] The experimentally determined germ tube number was used in the simulation. If time was greater than 5 days after inoculation, seven germ tubes were assumed.

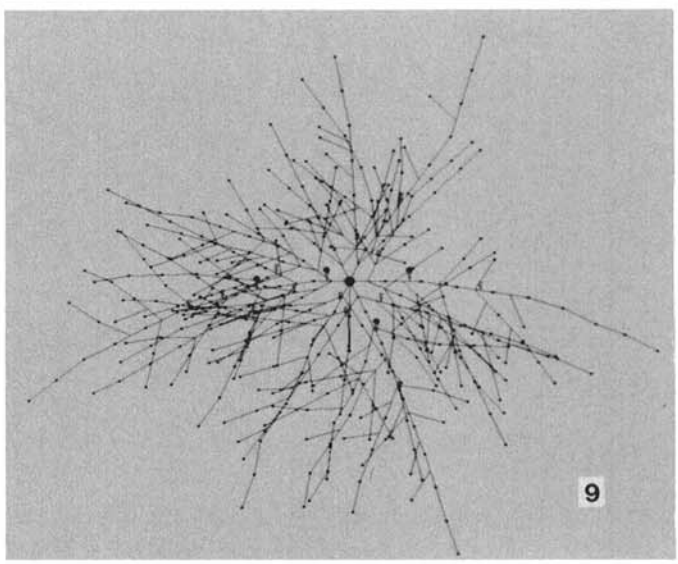
TABLE 3. Effect of variability in timing of germ tube formation (w)[a]

Days after inoculation	Experimental values of w in the simulation (no.)		Fixed values of w in the simulation (no.)[b]	
	Hyphae	Conidiophores	Hyphae	Conidiophores
2	3 ± 0.8	···	3 ± 0	···
3	9 ± 1.1	···	10 ± 0.7	···
4	23 ± 4	1 ± 0.6	22 ± 1.5	1 ± 0.4
5	62 ± 8	6 ± 1.8	59 ± 3.9	6 ± 1.3
6	137 ± 24	24 ± 4	134 ± 12	23 ± 2.1
7	···	71 ± 13	···	65 ± 4

[a] All numbers are the mean of 10 simulations followed by the standard deviation of the mean.
[b] Fixed values were obtained from equation 2.







Figs. 6–9. Computer simulation of colony of *Erysiphe polygoni* 72, 96, 120, and 144 hr after inoculation, respectively. Dots on the hyphae indicate beginnings and ends of LNGTH segments.

formation was used. Examples of the graphics simulation are given in Figures 6–9. Some distortion of hyphae was caused by the staining technique. Since this study we have found that fluorescence microscopy of living colonies is a better technique (24).

Conidiophores formed 72 hrs after hyphal segment formation (PSPORE = 5). On average, there were 0.7 conidiophores per hyphal segment ($z = 0.7$). The number of conidiophores observed and those drawn in the computer simulation using the above values is given in Table 2. Again they agree quite closely. Variation from colony to colony was greater in the experimental observations than in the simulation except 7 days after inoculation.

DISCUSSION

The mathematical model of colony growth and sporulation developed for *O. begoniae* can be used in a simulation of the early stages of logarithmic colony increase in *E. polygoni*. Hyphae and conidiophores appear at the same rate and frequency and at the same angles as the live ones. Because we used data from the experimentally observed colonies to generate the computer simulations, we do not claim that the simulation will hold for all colonies of *E. polygoni* on beans but merely that the simulation accurately depicted the colonies observed. The one deterministic feature that does not appear to be realistic is the placement of germ tubes. These should be randomized so as not to give the regular six-pointed star seen in Figure 9.

As a stochastic model, the simulation was successful in mimicking the colony-to-colony variability in hyphal number. It is possible that this is fortuitous, as the method of inducing variability in the model is partly due to a randomization process not based on biological data. The variability in conidiophore formation was less in the simulation during the early time periods, but similar 7 days after treatment. Variability is caused by a number of factors among which the most important are:

1. Physiological condition of the mother spore. This effect is indirectly measured by comparing simulations with and without variability in germ tube number (Table 3), since many of the germ tubes form before the first haustorium is established. In the early time periods this is the most important contributor to variability.
2. Interaction between genetic, biochemical, and physiological events. Random changes in the relative timing of some of these events may effect colony morphology.
3. Interaction between host, environment, and fungus. Sporulation may be more susceptible to suppression by host and environment interaction than hyphal extension and branching when the colony is young. This may underlie the poor prediction of early conidiophore variability by the simulation. If so, the program could be amended so that the random suppression of conidiophores and the number of conidiophores allowed per LNGTH segment are concurrently increased. The biological study justifying this change is yet to be done. It might be interesting to try and separate the effects of factors 2 and 3 above by growing the fungus on several different varieties of bean.

The present simulation, and computer simulations of fungal morphology in general, can be expanded and improved in many ways. Additional morphological features such as hyphal differentiation (e.g., in fungi where branches grow at different rates or have different diameters), sporulation in fruiting bodies, sclerotial formation, anastomosis, etc. can be simulated. Effects of density have been modeled elsewhere (5) and are included in our simulation but not implemented. When suitable biological data are acquired, density effects and later stages in colony development can be added. Environmental effects can be added. Temperature or other environmental factors could be indexed by time to describe their effects on the TM unit, LF, PSPORE, and other parameters, so that they can be included in the simulation. Some of this data exists for *E. polygoni* on *Trifolium pratense* (25). Physiological and biochemical interactions with morphology may be simulated too. For fungi capable of growing on defined media, the quantitative effects of varying nutrient levels or levels of inhibitors of specific synthetic pathways can be investigated. The use of the HGU is an attempt to base the simulation on units that have meaning at the physiological level (2,6).

As these expansions are added to the simulations, the model may become very complex. Possibly then, the simulations themselves will be "the only means of thoroughly testing a large and intricate theory" (17). The model would be the hypothesis, and the degree to which its answers, given in the simulation, approximate experimentally determined values would be the only way to test the theory. If the experimental results are not reproduced by the simulation, the model (theory) would be revised.

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