Should seeds fly or not?

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Abstract

This paper describes some results of our computer simulation concerning ecological competition on the target area of seed dispersal. It is better for any kinds of plants to disperse their seeds as far as possible because it might spread in new frontier earlier than the others. But, it would be better to put the seeds down just at the neighbor position when the environmental condition is stable. From drawing a fitness landscape for distance and area of dispersal through a computer simulation, it was revealed that both of these strategies are locally optimal to gain more reproductive success, and neighboring strategy is the best when the environment is unchanged and uniform. We examined a type of evolutionary process to investigate the effects of three kinds of environmental parameters, scale of disturbance, death-sprout ratio, and geographical granularity of fertility. The population initialized by random parameters converged into either or both of two types of species, far and broad dispersal and neighboring reproduction. For all of three parameters, the experimental results showed that the probability to converge into dispersal of longer distance becomes greater corresponding to the degree of environmental change in time and space.

Introduction

Known as *seed dispersal*, some types of plants are facilitated to distribute their seeds efficiently using animals, birds, wind, stream of river, and so on (Howe 82; Ueda 99). Burrs cling to animals' fur. Birds and monkeys eat fruits but the seeds are excreted at the other place. Seeds of dandelion fly in the wind. Walnuts and coconuts drift with the stream and the current. A lot of biologists have investigated many types of dispersal strategies from view points of seed morphology, symbiosis between plants and animals, and evolutionary ecology.

As summarized in (Howe 82), it seems reasonable that the further and broader area seeds can reach the more adaptive against environmental changes, because it provides advantage to be able to occupy new frontier faster. On the other hand, it is also the fact that the other types of strategies for plant propagation use bulbs, stolons, rootstocks, and so on. These are to propagate new plants near around the old one rather than far away. It is also explainable by the probability of good environmental condition for sprout and growth at the position where a seed reaches. It is unreliable in the other place far away from the ancestor. The fact that both strategies exist in plants *as-we-know* suggests both of them are the candidates of the optimal solutions for efficient propagation. If we accept this hypothesis, it would be an interesting issue to illustrate the fitness landscape of seed dispersal region under some conditions. Some models of seed dispersal have already been proposed in such as (Chambers 94). They are based on the field observation to build a diagram of the effects among seed production, dispersal, germination, and death from the view point of ecology, but are not used to draw the fitness landscape from the view point of evolutionary theory. This paper provides a hint to consider the selective forces that produces sophisticated morphology for seed dispersal.

The following part of this paper describes our design of the model of plant propagation, drawing of the fitness landscape via competitions between two species that disperse seeds into the areas of different distance and width, and then results of our simulation of evolutionary process concerning the effects of three kinds of environmental parameters, scale of disturbance, death-sprout ratio, and geographical granularity of fertility.

Model of propagation

Our design of the model of propagation is as follows. A plant occupies a circle of constant diameter d on the ground, two dimensional plane of continuous Euclidean space. In the initial state, a number of plants are placed in random positions so as not to collide each other. In each simulation step, each of plants produces one seed with probability P_s and dies out with probability P_d. The position of seed is determined from two parameters associated with the ancestor plant. The seed sprouts and grows in diameter d if there is no other plant within the distance d. The order of execution among plants is randomly shuffled in each step. The region of seed

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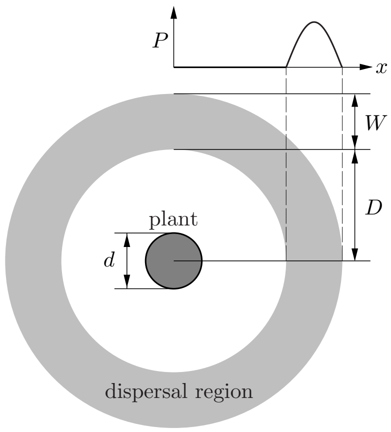


Figure 1: Dispersal region of seeds from a plant in our model.

dispersal for a plant is shaped as shown in Figure 1. It is represented by shortest distance D and the width W. The probability $P(x)$ to select a distance x is defined by the following equation.

$$P(x) \;=\; \begin{cases} \dfrac{\pi}{2W}\sin\dfrac{x-D}{W}\pi & \text{if } D < x < D+W \\ 0 & \text{otherwise.} \end{cases} \qquad (1)$$

The above probability is practically realized in our simulator by calculating the value of x using following expression.

$$x \;:=\; \frac{\arccos(2u-1)}{\pi} \qquad (2)$$

where u is a random number of uniform distribution within $[0, 1)$. The orientation is determined using a random number of uniform distribution.

Both of D and W are inherited from a mother plant to daughter seeds. Each of our experiments starts with 3,000 plants at random positions. We assume the field of propagation is a square space of which length of the edge is 100 times of plant's diameter d, and is formed as a torus to prohibit the effects of the boundaries, that is, the upper and lower edges and the left and right edges are connected respectively.

Drawing a fitness landscape

To investigate the shape of the fitness landscape on dispersal region, we examined competitions between two species of different D and W exhaustively for $D = 1, 2, \ldots, 7$[1] and $W = 0, 1, \ldots, 6$, totally $(7\times7)\times(7\times7-1)/2 = 1176$ matches. The other parameters are set up as $P_s = 1$ and $P_d = 0.1$. We stop each of matches when either species is extinguished or 1,000 steps passed. Figure 2 summarizes the result of matches, which indicates

[1] Practically, we used 1.01 instead of 1 for the value of D to avoid erroneous collision among plants caused by error of numerical computation.

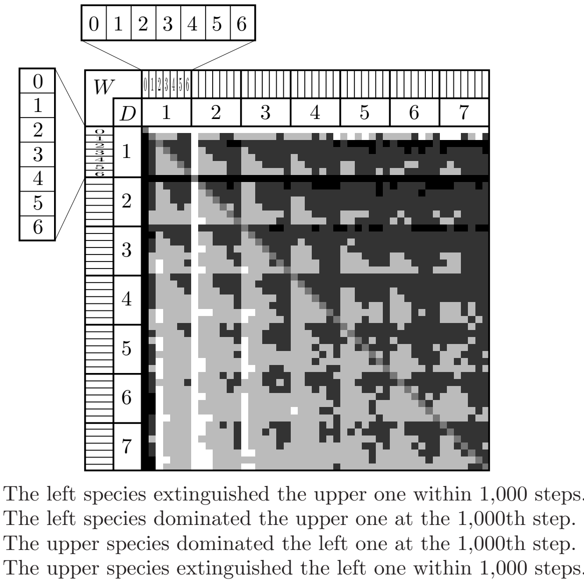


Figure 2: Result of matches between species of different parameters for dispersal region.

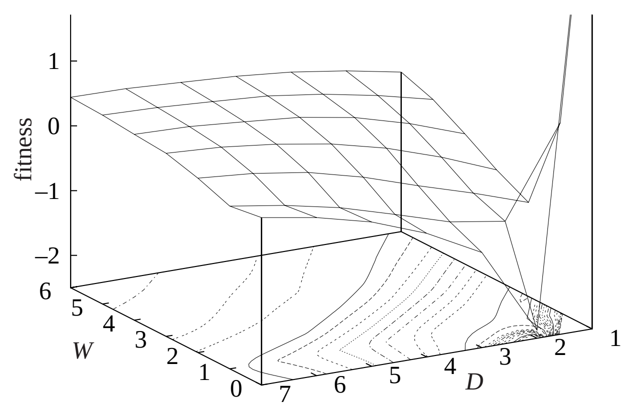


Figure 3: Fitness landscape drawn from the result of ten times of exhaustive matches.

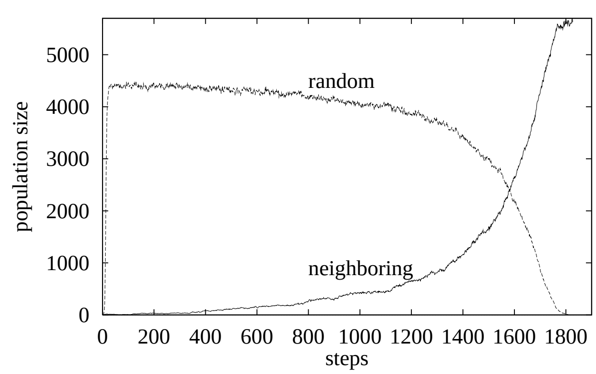


Figure 4: Changes of population sizes in the competition between neighboring and random strategies. One plant for each species is placed in the field at the initial state.

$D \backslash W$	0	1	2	3	4	5	6
1	5.54	0.43	−1.05	−0.80	−0.49	−0.21	−0.04
2	−2.37	−0.95	−0.76	−0.46	−0.19	−0.01	0.13
3	−1.03	−0.81	−0.50	−0.17	0.05	0.16	0.25
4	−0.59	−0.55	−0.22	0.04	0.20	0.28	0.33
5	−0.27	−0.30	−0.01	0.18	0.27	0.34	0.38
6	−0.06	−0.12	0.12	0.28	0.34	0.39	0.43
7	0.08	0.01	0.19	0.33	0.37	0.42	0.44

Table 1: Fitness of species calculated by exhaustive matches.

larger values of both D and W tend to make it tougher except the cases $(D, W) = (1, 0)$ and $(1, 1)$.

To draw the fitness landscape for D and W, we gives h points to the winner defined by the following equation.

$$h = \begin{cases} \dfrac{1000}{M} & \text{if } M < 1000 \\ \dfrac{N_w - N_l}{N_w + N_l} & \text{otherwise,} \end{cases} \tag{3}$$

where M is the number of steps until the match stops, and N_w and N_l are the number of plants at the final step of the winner and the loser respectively. The loser loses the same amount of points after the match. Table 1 shows the average points of each species after ten times of exhaustive combinations by separated random number sequences, and Figure 3 shows its shape for intuitive understanding. It would be reasonable that further and broader region of seed dispersal provides more reproductive success, because it increases a chance to put the seed at an appropriate position.

However, it might seem strange that *neighboring* strategy that puts the seeds at just adjoining side, that is $(D, W) = (1, 0)$, is the best, even though all of the environmental conditions are uniform around the field. There is no evidence of unreliability to sprout and grow anywhere. The fact is that neighboring strategy has beaten all of other species as shown in the upper and left edges of Figure 2. To investigate the process that the neighboring strategy extinguishes others, we examined a match with random strategy that puts seeds at random positions. Figure 4 shows the changes of the number of plants starting from *one-by-one* to the opponent's extinction. The random strategy propagates fastly on the early stage, but the neighboring strategy gradually broadens its territory as shown in Figure 5. The population size of the latter one increases exponentially since the probability of interference by the former one decreases proportionally to that population size itself. One of the reasons why the latter one beats the former one is because placement of a child at neighboring side realizes the minimum distance between plants and leads to higher density of occupation. Higher density brings more reproductive success. The data from our simulation to draw Figure 4 supports this explanation as the maximum size of random and neighboring populations were respectively 4483 and 5713.

The result that the neighboring strategy is the best does not coincide with the phenomena in the nature that we know. Sophisticated mechanisms for seed dispersal could never appear through the evolutionary process if the similar phenomena to our simulation had occurred generally on the earth. The following section gives consideration on some environmental parameters that affects the fitness landscape and provides more reproductive success for long distance dispersal over the neighboring strategy.

Effects of environmental parameters

We designed an evolutionary process to investigate the effects of some environmental parameters, to reduce the CPU time relatively to the above exhaustive method. Each of D and W is represented in a 16 bits unsigned integer that is copied from mother to daughter erroneously under a mutation rate μ, the probability to flip a bit for each. We set $\mu = 0.001$ in our experiments. Each integer is proportionally transformed into a floating point number in $[0, 5]$ from the integer in $[0, 2^{16} - 1]$. We examined 20 trials of separated random number sequences for each parameter settings. Each trial starts with 3,000 plants with random positions and random integers for D and W using uniformly distributed random numbers produced by `drand48` Unix library function.

Scale of disturbance

The advantage of seed dispersal is ability to reach and occupy any new frontier faster, that is, larger D and W would gives more reproductive success than neighboring strategy when large-scale disasters occur frequently. As simulating disastrous disturbance, we introduce a procedure to kill all of the plants within a size of circular area placed randomly with a constant frequency. We examined a variety of diameter A of disturbance area that occurs once per ten steps to investigate the effects of the scale of disturbance. Figure 6 shows the result of the simulation for $A = 10, 15, \ldots, 40$. It indicates the

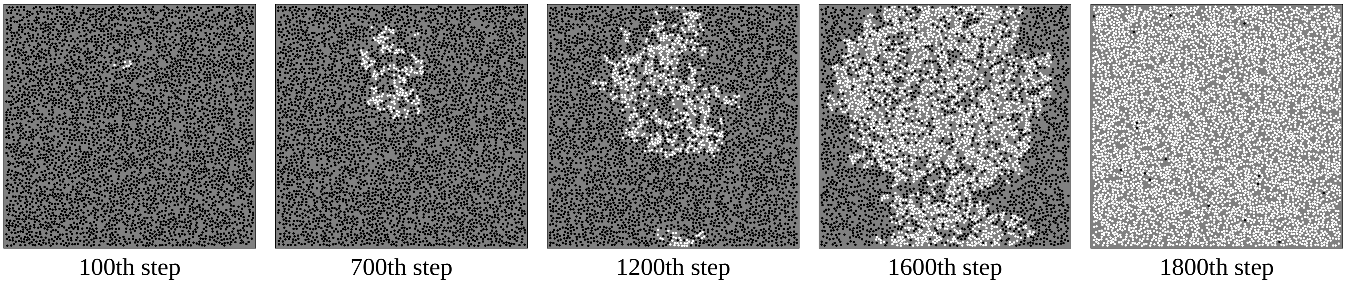


Figure 5: Changes of spatial distribution of plants in the competition between neighboring and random strategies. A black circle indicates a plant of random strategy, and a white circle indicates a plant of neighboring strategy.

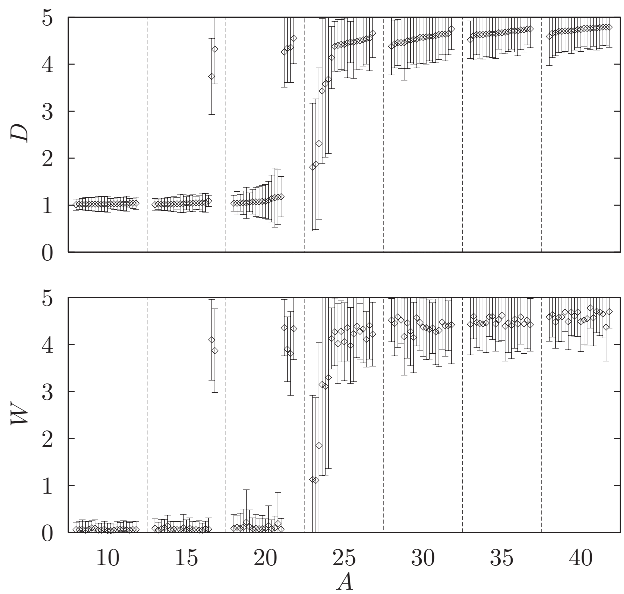


Figure 6: Average values and standard deviation of D and W among plants in the population at 5,000th step with 20 cases for each value of the size of disturbance area A.

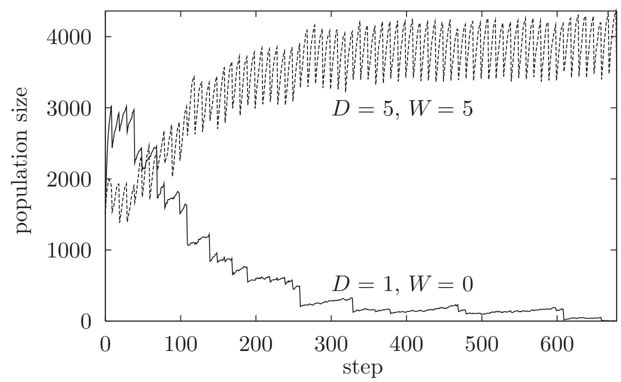


Figure 7: Changes of population sizes in the competition starting from 1,500 plants for each. The diameter of disturbance area $A = 30$ and it occurs once per ten steps.

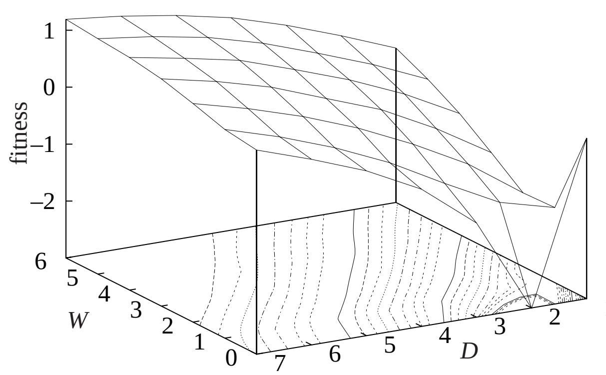


Figure 8: Fitness landscape drawn from the result of ten times of exhaustive matches in $A = 30$.

effect of small scale ($A = 10$) of disturbance is negligible, but large scale ($A \geq 30$) of disturbance exchanges the positions of two strategies. This result supports our prediction.

To see the process of population changes, we examined a competition without mutation between two strategies, $(D, W) = (1, 0)$ and $(5, 5)$. The match starts from 1,500 plants at random positions for each. Figure 7 shows the changes of population sizes when $A = 30$. The result indicates that the sizes of both species shrink at every occurrence of disturbance, and the wider strategy rapidly recovers the diminution, but it is difficult for neighboring strategy. Figure 8 illustrates the shape of fitness landscape drawn by same method described in the previous section, that is, ten times of exhaustive matches. Comparing with Figure 3, it is clear that the fitness of neighboring strategy decreases and further and broader

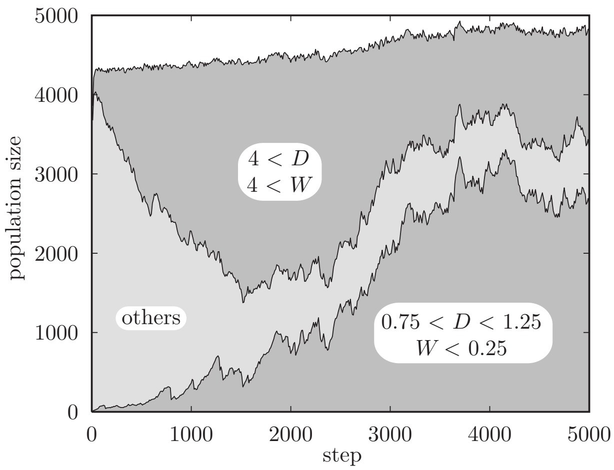


Figure 9: Changes of population sizes in a case of $A = 25$ on three species, neighboring strategy ($0.75 \leq D < 1.25$ and $W < 0.25$), wider dispersal ($4 \leq D$ and $4 \leq W$), and others.

dispersal has more fitness than that.

When $A = 15$ and 20, the population alternatively converges into either strategy. More than half number of cases in $A = 25$ fell into wider dispersal, but the other cases proceeded to mixture of the two optimal species as shown in Figure 9 that illustrates population sizes of three species, $0.75 \leq D < 1.25$ and $W < 0.25$, $4 \leq D$ and $4 \leq W$, and others.

Some readers might be interested in seeing what happen when the frequency is changed. It is obvious that low frequency has small effect but high frequency makes the same effect of large-scale disturbance. The expected damage by disturbance would be proportional to both size and frequency. It would be the similar effect for same value of A/T where T is the number of interval steps. But if both A and T are large, the pattern of population changes would be largely fluctuated. The sudden extinction of neighboring strategy tends to occur, for example.

In the real world, size and frequency of disturbance is various depending on the type such as a flood, storm, landslide, earthquake, volcano's explosion, and so on. It causes fluctuation of the fitness and has affected the evolutionary process of the vegetable kingdom on the earth.

Death-sprout ratio

The reason why the neighboring strategy wins is high probability of a chance that plants touches each other. This probability becomes low if mother plants disappear sooner relatively to the sprout of daughter seeds. We examined evolutionary process for various values of probability of death P_d to see the effect of rapid death of plants. Figure 10 shows the results for $P_d =$

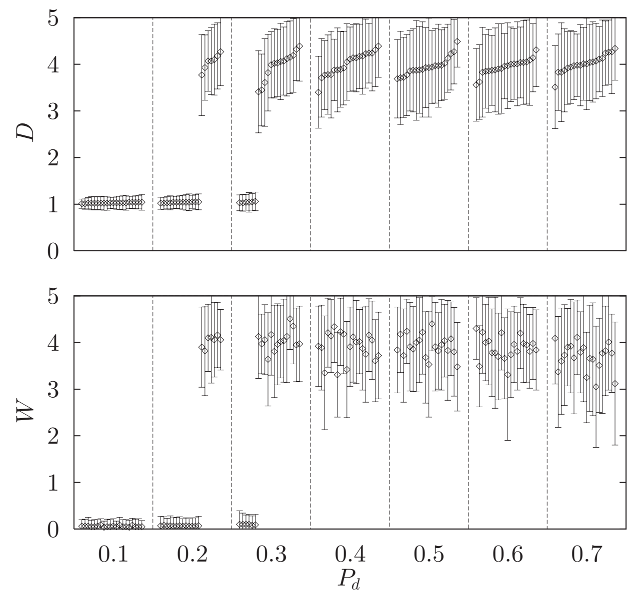


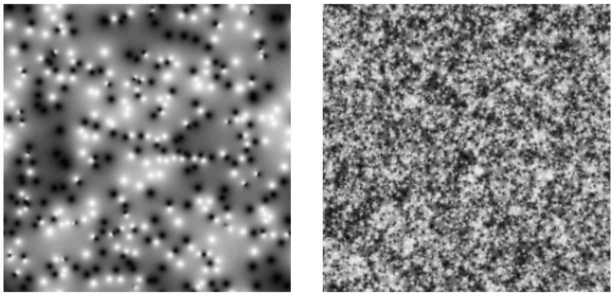
Figure 10: Average values and standard deviation of D and W among plants in the population at 5,000th step for a variety of the probability of death P_d.

$0.1, 0.2, \ldots, 0.7$.

As we expected, high probability of death ($P_d > 0.4$) causes convergence to long distance dispersal. This tendency would accelerate the ability to move to a more fertile field from a barren place. It might have been a factor for acceleration of evolutionary changes. The reason why it is difficult to converge into coexistence of two separated optimal solutions for any value of P_d is that the environmental condition is quite uniform around the field in contrast with the case of disturbance examined in the previous section.

Geographical granularity of fertility

In the real seed, both inner and environmental condition determines the possibility of sprout and growth. The environmental condition includes not only the distance to the other plants but also fertility around the seed. It is difficult to measure the degree of real fertility, but at least it is obvious that the distribution is uneven over the field in any granularity, depending on soil, rocks, water, slopes, and so on. Saying with other words on the reason why the neighboring strategy wins, it is because daughter seeds always grows at the neighbor side of the mother plant where the condition should be good. If the granularity of fertility is too fine relatively to the size of plant, this condition would not be satisfied since it loses a guarantee of fertility around mother plants. To certify this hypothesis, we introduce uneven distribution of probability of seed production P_s on the field, by placing a same number of random points p for $P_s = 1$ and 0, and



$F = 0.4$ ($n = 0.04$) $\quad$ $F = 2$ ($n = 1$)

Figure 11: Example distribution of the seed production rate P_s to test the effect of geographical granularity of fertility.

using the following equations for smooth interpolation.

$$P_s(a) = \begin{cases} P_s(p) & \text{if } a = p \\ \dfrac{\sum_p P_s(p) \cdot w(a,p)}{\sum_p w(a,p)} & \text{otherwise} \end{cases} \tag{4}$$

$$w(a,p) = \frac{\prod_q \mathrm{dist}(a,q)^2}{\mathrm{dist}(a,p)^2} \tag{5}$$

where $P_s(a)$ is the seed production rate at position a, and $\mathrm{dist}(a,p)$ is the Euclidean distance between a and p.

Here we denote the fineness of granularity by $F = 2\sqrt{n}$ where n the number of points p per unit area. Unit area is a square of which edge has same length with the diameter of plant. $1/F$ is theoretically the average value of distances from each point p to the nearest other point[2] . To reduce the computation cost, we use only the points within $\mathrm{dist}(a,p) < 8/F$ for each a. Figure 11 shows examples of the distribution in the field when $F = 0.4$ and 2.

Figure 12 shows the results of evolutionary process for $F = 0.2, 0.4, \ldots, 2.4$. As we predicted, further and broader dispersal surely gains advantage when the granularity is fine ($F \geq 2$). However, the different phenomenon is observed for more even fertility in comparison with the previous two cases. Figure 13 shows the distribution of average values of D and W at 5,000th step, which indicates that combination of small D and large W is also good but combination of large D and small W is not. For more precise analysis, we examined the exhaustive matches again for $F = 0.8$ and 1.6. Figure 14 shows the fitness landscapes drawn from the results. In contrast with the cases described above, large value of D is not good though large value of W is still good when $F = 0.8$ except near values of neighboring strategy. This means that dispersal to wide region provides more reproductive success but it needs to fall seeds also near the mother plant under relatively sparse granularity. The similar effect can be observed even when $F = 1.6$, but large value of D still has enough advantage.

On the real plants, size of plant is different among species. The above result suggests that it is better for a large plant to disperse the seeds in a further and broader region, because granularity of any type of geographical distribution is relatively fine for it. The opposite tendency might be concluded for a small plant, but it would be hard because a small size of community of small plant is easily extinguished by disturbance in the real environment.

[2] The proof is omitted because it is too long. It is trivial that the average value of distances between the nearest points is proportional to $1/\sqrt{n}$ because of the dimension.

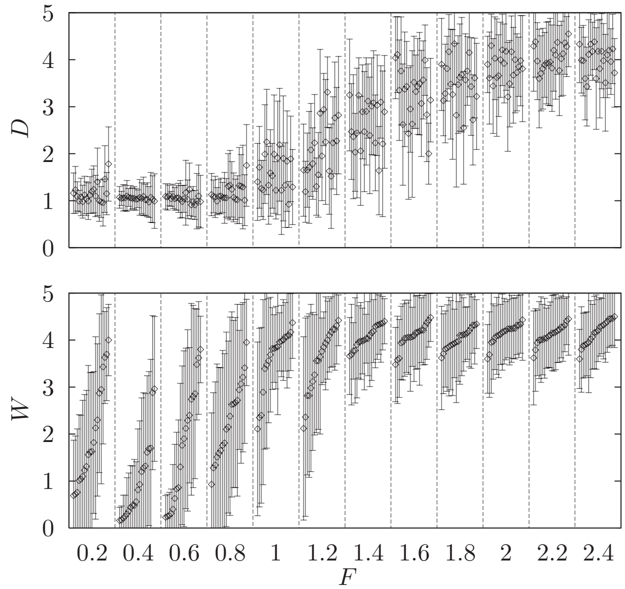


Figure 12: Average values and standard deviation of D and W among plants in the population at 5,000th step for a variety of the geographical granularity of fertility F.

Conclusion

We drew a fitness landscape for distance and width of seed dispersal through a computer simulation. It revealed that both of neighboring and wide range strategies are locally optimal to gain more reproductive success. Contrary to the phenomena in the real world, the neighboring strategy is the best in our first result. We examined a type of evolutionary process to investigate the effects of three kinds of environmental parameters, scale of disturbance, death-sprout ratio, and geographical granularity of fertility. For all of three parameters, the experimental results showed that the probability to converge into dispersal of longer distance becomes greater corresponding to the degree of environmental changes in time and space. Sophisticated mechanisms for seed dispersal are thought to be produced through evolutionary process in changing environment as

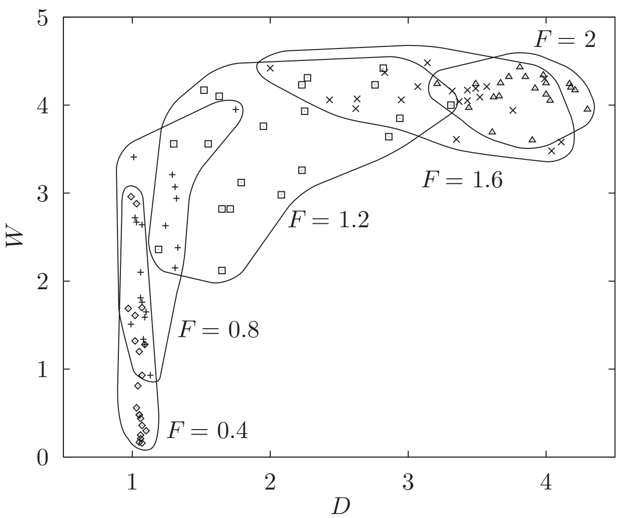


Figure 13: Average values of D and W among each population at 5,000th step for a variety of F.

explained since more than one hundred years ago. The results supports this explanation and shows quantitative characteristics on the balance between these two opposite strategies. Some types of plants have both abilities to realize neighboring and wide range dispersal, such as a lawn, field horsetail, bamboo and so on. This type of function is thought to have evolved under the fitness landscape with two peaks.

Migration of organisms affects evolutionary process as an explanation of large scale evolution, as suggested in (Eldredge 89). Though plants don't move by itself differently from animals, seed dispersal realizes migration of plants for long distance, sometimes over the sea. From this point of view, understanding on the characteristics of seed dispersal could help our understanding on the evolutionary process of organisms.

Considering the real community of plant, there are various size of plants, various number and size of seeds, the cost of long distance dispersal, vertical structures, pollination, geographical boundaries, symbiosis with animals and insects, and other complex relations among all entities in the nature, that we ignored in the simulation. Phenotipic diversity of plants and coexistence of a variety would be caused by these and other factors. It would depend on the objective to decide which factors we should consider in the next work. Specially, local dispersal has disadvantage caused by parent-offspring and inner offsprings conflict. To consider this type of effect, we should introduce the variable size of occupation area determined through competition among plants and seedlings.

We hope this study could be a milestone for Artificial Life approaches to understand some side of evolutionary and ecological characteristics of life.

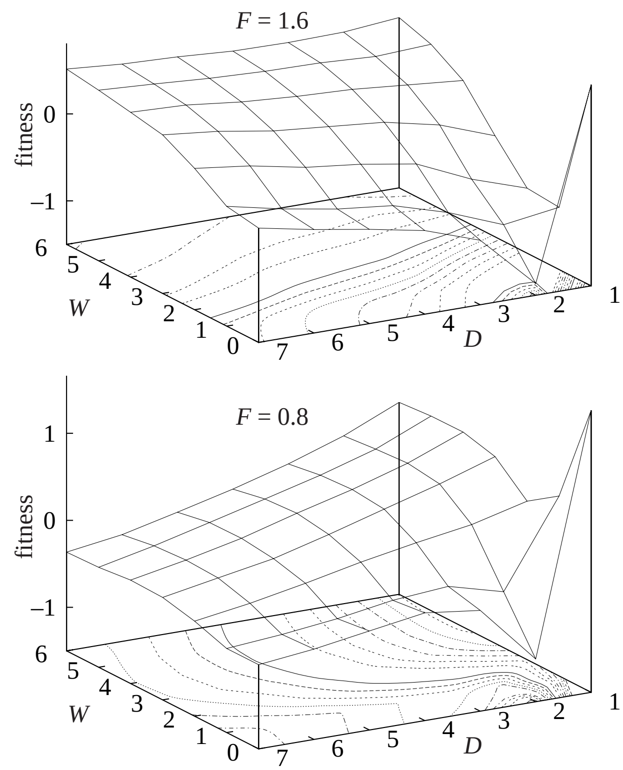


Figure 14: Fitness landscape drawn from the result of ten times of exhaustive matches in $F = 1.6$ and 0.8.

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