The Impact of Obstruction on a Model of Competitive Exclusion in Plants

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Abstract—This study extends an earlier work on an agent based model of competitive exclusion in plants by adding obstructions to a toroidal agent world. The agents are called *grid plants*, whose genome specifies their pattern of growth and when they make seeds. Seed production is the figure of merit used to assess the success of grid plants. Barriers are found to substantially inhibit seed production, out of proportion to the amount of space they occupy. Two types of barriers are used, ones that occupy productive space in the simulation and ones that block growth between grids of the simulation but occupy no space. Both sorts of barriers are found to inhibit seed production well in excess of the physical space obstructed, nor is fraction of obstruction a strong determinant of the level of inhibition. There is a cooperative effect from both seed mortality and barriers: past some threshold dependent on both, the plants take much longer to achieve exponential growth, if at all. A very strong effect of nonlocal adaptation is apparent in the results, where plants evolved under increasing hardship are initially better adapted, even to other boards, but the effect reverses when evolutionary pressure becomes too high.

I. INTRODUCTION

Garret Hardin defined the term *competitive exclusion* in 1959 as the simple rule that "Complete competitors cannot coexist. [5]". The *competitive exclusion principle* is even older and is attributed to G. F. Gause [4]. Within ecology it is stated as Gause's law: *two species competing for the same resources cannot coexist if other ecological factors are constant*. Competitive exclusion permits species to compete indirectly through scarce resources such as nutrients or space. This competition can even potentially drive species to extinction. Selection pressure can cause species to avoid competitive exclusion by evolving to a state of greater specialization. Darwin's Finches [6] are a classical example of this phenomena. When one finch species lives on an island, its beak evolves to utilize a broad variety of food sources. When a pair of finch species live on an island their beaks and the food sources they can effectively utilize evolve in divergent directions. Competitive exclusion differs from other exclusion principles in grid based models in that it arises over long time scales and multiple generations.

Plants can engage in multiple forms of competitive exclusion. These range from competing to attract pollinators, competition for scarce nutrients in the soil, and competition for space. This study builds on an earlier study [1] and

continues modeling of competitive exclusion for available space in a two-dimensional world. An earlier study [3] using a related model examined the question the degree to which competitive ability increases with time of evolution.

In this study we extend the model by placing obstructions to plant growth into the model environment. The types of obstructions used include filled-in cells of the grid that completely block plant growth as well as walls between grids that block plant growth across them. The obstructions used in this study are shown in Figure 2. There are two different encodings used for obstructions. Boards 2, and 9–12 place barriers as the walls of grids meaning that while the barriers obstruct plant growth, they to not use up space that could be occupied by grid plants. Boards 3–8 fill grid cells with obstructions.

The modeling technique used is agent based and the agents are called *grid plants*. An exclusion principle, permitting only one plant to occupy a square of the grid the plants grow on, established space as a scarce resource for which the agents compete in a multi-generational game in which both an energy balance and seed placement by the plants are modeled.

A given grid plant genome has several goals relative to survival. Recall that the genome may have many instances present in the world at a given time.

1) A plant must make at least one seed and it is good if it can make several seeds.
2) The plant must obstruct non-relatives with its pattern of growth and, to the greatest degree possible, permit relatives space to grow.
3) The genome must work well in unobstructed worlds and those filled with other plants and/or obstructions (see Figure 1). This strongly constrains the plant to produce a seed relatively early because it may not grow large enough to gather the energy for a late seed.

This list of constraints makes it clear that, if we view competitive exclusion as a mathematical game scored in seeds, the game is a very complex one. The map from genome to strategy is non-obvious and context dependent. The game is multi-player with hundreds of players, which come in groups in the form of dozens of players that are close relatives.

The algorithm used to evolve grid plants has differences from a standard evolutionary algorithm. The principal one is that it does not have an explicit fitness function. The number of seeds a given plant has that survive long enough to sprout serves as an implicit fitness function, and one that is far closer to the selection function that drives biological

evolution. Another important difference is that the population size of the algorithm is variable and self-regulating.

The remainder of the study is structured as follows. Section II discusses some other models of competition in plants. Section III gives a careful definition of the extended model. Section IV specifies the design of experiments used. Section V gives and discusses results while section VI draws conclusions and outlines potential next steps.

II. BACKGROUND

This study focuses on the impact of introducing barriers into a relatively abstract model of plant competition; Much more complex models exist, which can deal with more complex issues. In [9] the authors add functional diversity of plant types to a grid based, mass balance of plants over a large area. This study is intended to permit modeling of the impact of climate change and is tested against satellite data. In model of this sort, isolation by distance[10] might be an important feature, but not in this study were there is no distance to speak of.

Another phenomenon that can be treated with this type of model is the impact of invasive species. In [2] the authors show that invasive species with initial large impacts decline in impact over time, presumably because the local ecosystem adapts to the invader. This work suggests that invasive species are not as problematic as their initial behavior suggests.

It is possible to crowd-source the tuning of the parameters of ecological models of plant spread and growth. In [8] the authors tune the parameters of an agent based model of clonal plants in this fashion. The model is used to research questions about the persistence of species. The role of local disturbances in the maintenance of diversity of plants within an ecology is explored in [7]. Local disturbances cause a greater variety of local environments with a resulting increase in diversity of species.

III. THE MODEL OF COMPETITIVE EXCLUSION

Grid plants implement a model of competitive exclusion in plants in a toroidal 2-D world. *Toroidal* means that the world wraps at its edges. This is done to avoid edge effects, except when they are intentionally restored as a type of barrier. Grid plants start as a single occupied cell in a grid, the initial growth tip, and grow thereafter in some direction (up, down, right, left) from the growth tip. The growth tip is the most recent cell generated. The chromosomes for grid plants are strings over a five character alphabet: **L**eft, **U**p, **R**ight, **D**own, and **S**eed, the last of which means the plant attempts to place a seed beneath its growth tip. Grid plants grow on a rectangular grid, set to 100×100 cells in this study, that implements two exclusion rules, in addition to barriers:

1) A plant cannot grow into occupied grids or filled-in cell obstructions.
2) A plant cannot grow across a wall obstruction.
3) No more than one seed may be placed at a given location.

Cell and seed layers of the simulation are maintained independently. This grid plant model differs from that published in [3] in a number of ways. The parameters, given in Section IV are set to different values and this version of the model implements a model of pollination, and with it sexual reproduction.

When a seed sprouts, the simulator performs a random walk in steps of ± 1 in the x and y directions for up to 30 steps. The steps of the random walk are also constrained by the barriers in the same way as plant growth; an obstructed step is wasted. The first other seed it encounters is presumed to be from the plant that pollinated the seed under consideration. If no other seed is found the plant undergoes self-fertilization. Waiting until the seed sprouts, and using seeds to identify the male parent, is done to reduce the possibility of self-pollination if the random walk was performed until a plant cell was encountered. The seeds generated by a plant serve as a surrogate for its position in the world.

A growing grid plant is constrained by a number of factors. The emplaced barriers added in this study and the other plants occupying grids of the simulator are direct constraints on growth. In addition to these physical constraints the plant is constrained by its available energy. A seed starts with four units of energy and a single grid cell occupied. The basic execution loop for gene expression is given in Figure 1. Figure 1 shows a grid plant world in years 1, 2, 4, and 8. These years were chosen because they show both sparsely and densely populated worlds. The world shown in Figure 1 has a very low rate of death among new seeds and so rapidly arrives at a very dense state in which plants fill one or two cells. The seed mortality rate is a critical parameter of the grid plant model, as is the number of time steps in a growing season. Note that at lower seed mortality rates, plants rapidly become very small making the space of plant shapes and the associated search problem for an effective shape far simpler.

Algorithm 1: Genome Expression Algorithm
Occupy initial cell
Energy=4
Set state=-1
Repeat
  if(state=-1)read next loci into state
  if (action is seed)
    If(energy$\geq$5)
    and(no seed here)
      Make seed
      Energy-=5
      State=-1
  else if desired cell empty
    if (Energy$\geq$3)
     Grow into cell
     Energy-=3
     State=-1
  Energy+=number of cells in plant
Until(No loci remaining or out of time);

The grid plant simulation is a model of annual plants. Seeds sprout and the plants grow for some number of time steps, occupying cells and placing seeds. At the end of the growing season all live plant cells are removed from the simulated world and a new year starts. Seeds placed in the previous year are subject to mortality and then the survivors sprout,
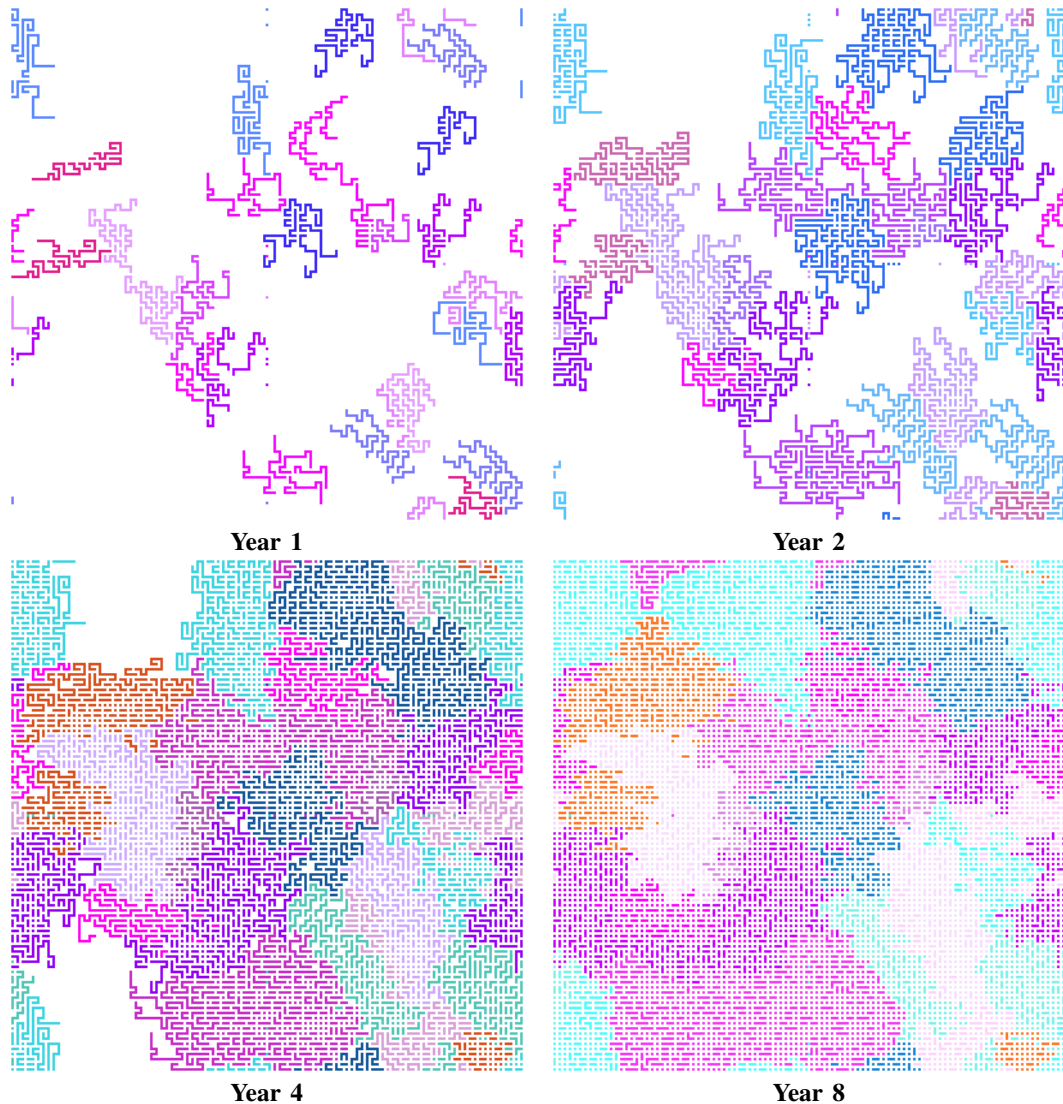
Year 1

Year 2

Year 4

Year 8

Fig. 1. Shown is the state of a simulation for Board 1 at years 1, 2, 4, and 8 after the initial placement of seeds. Different colors represent plants with different genomes. The simulation shown here has a low level of seed mortality and rapidly fills so that plants have an mature size of one or two grid cells.

with pollination. The *rate of seed mortality* is the probability a given seed will be removed. This represents death due to environmental factors such as rot or animal foraging. The genome of seeds that sprout is the result of uniform crossover between the plant that generated the seed and the plant that supplied pollen or it is a clone of the parent if no pollen donor was encountered. This latter situation is quite rare once the world fills in. New seeds also may have one loci modified to a new value based on a per-seed mutation rate specified in the design of experiments.

IV. DESIGN OF EXPERIMENTS

A collection of 84 experiments were performed using 100×100 versions of the boards shown in Figure 2 with the following rates of random seed mortality: 80%, 82.5%, 85%, 87.5%, 90%, 92.5%, and 95%. The grid plant genomes are length 60. A given experiment is initialized by generating

ten random grid plant genes and placing a seed with each at ten random, empty locations. The genes are over the alphabet $\{U, D, L, R, S\}$.

A growing season lasts 40 time steps. In each time step a plant adds its current size in cells to its energy. It reads one loci of its genome, at a cost of one energy, and then executes it if it has sufficient energy remaining. Energy and actions to be executed are saved into subsequent turns and actions are executed in the next turn with sufficient energy. In each time step the plants are executed in a random order with a new random order generated for each time step. There is an energy cost of 3 points for a grid plant to grow into a new cell and five to generate a seed under the growth tip. If a growth action is obstructed the plant does not pay the energy cost for the growth, and the instruction is used up. Note that regardless of the amount of stored energy in a plant, it may
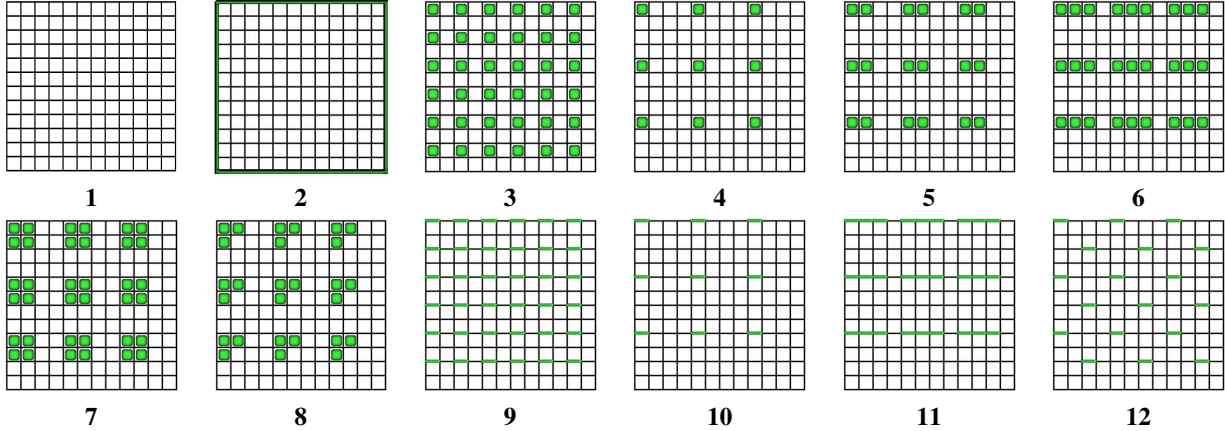
Fig. 2. Shown are the boards used in the experiments, in a 12x12 version for clarity. Green squares represent obstructed squares, green edges represent obstructions between squares. Except for Board 2, the tiling patterns shown are continued periodically in the 100x100 boards used in the experiments.

only execute one action in a time step.

At the end of the growing season all plant cells are removed from the cell layer and the seed layer is subject to seed mortality. The probability of death is modified by not killing the last ten seeds in a layer no matter what, a provision that is needed only early in the evolution of the plants or at very high seed mortality rates. Seeds then perform their random walk to find pollen. If a seed finds itself or fails to find any partner then it self-pollinates. Then, at a rate of 10%, one single point mutation uniformly at random is used to modify the plants and the new seed layer is used to start another growing season.

Each of the 84 experiments is comprised of 100 runs of the algorithm. Each instance of the algorithm is run for 5000 growing seasons. In each growing season, over all 100 runs, statistics were saved for the number of plants, number of seeds, area covered by plants, and total energy.

A. Cross-board adaptation

At the end of each experiment, the entire population of seeds is saved. To test for whether seeds evolved on a particular board are non-locally adapted to similar boards, we transplant the evolved seeds into the other boards and allow them to grow. For each of these runs, 10 seeds selected at random from the same evolved population (to allow for kinship effects) are placed on a new, empty world, with some possibly different type of obstruction. 100 growing seasons are run and we save the same statistics of plant count, seed count, area covered, and total energy.

These experiments are repeated for each board type evolved on, transplanted to each board type, including their own. For each of these 12×12 possibilities, we seed independent worlds with 3 samples of 10 from each of the 100 evolved populations, for 300 total replicates. This is further repeated for each seed mortality rate; the rate remains the same between evolution and evaluation after transplantation for consistency.

V. RESULTS AND DISCUSSION

Figure 3 shows how the number of (pre-mortality) seeds evolved over the course of time, shown for the four lowest mortality rates used. The left side of the figures shows the results restricted to the first 100 growing seasons for clarity and comparison with prior experiments. It is important to notice that the vertical scales of the four panels are dramatically different.

For 80% and 82.5% seed mortality, the simulated ecosystem is capable of generating large numbers of seeds, on relatively unobstructed boards. Increasing to 85% seed mortality, a lower but still significant number of seeds is produced, while at 87.5% the number of seeds drops under 2% of the total number of available cells in the world, as low as 0.5%. For higher seed mortality rates, we see that the mortality factor completely dominated the simulation, forcing the use of the rule that preserved the last 10 seeds. This drastically changes the behavior of the system, and so we will generally present results only on the four lowest rates of seed mortality.

There is a very strong effect from obstructions — compare boards 1 and 3 which have the lowest and highest levels of obstruction. At all four seed mortality levels, the seed production is substantially higher on board 1, and the difference is far greater than simple change in available space would suggest: board 3 obstructs 25% of the space, but at the lower seed mortality levels, has more than ten times fewer seeds. The type of barriers in board 6, which occupy 18.75% of the available space, are also associated with nearly ten-fold lower seed production.

For the most part, the ranking order of how effective the obstructions are at lowering seed production is stable. Board 3 and 6 are the two worst obstructions, followed by boards 7, 8, and 2 for high obstruction, boards 5, 9, and 12 close together for medium obstruction, and boards 4, 11, 10, and 1 for low to no obstruction. One interesting result is that effectiveness is not strongly related to the coverage of the obstructions: board 7 covers 25% of the space, more than board 6, yet board 6 is significantly harsher for the plants.
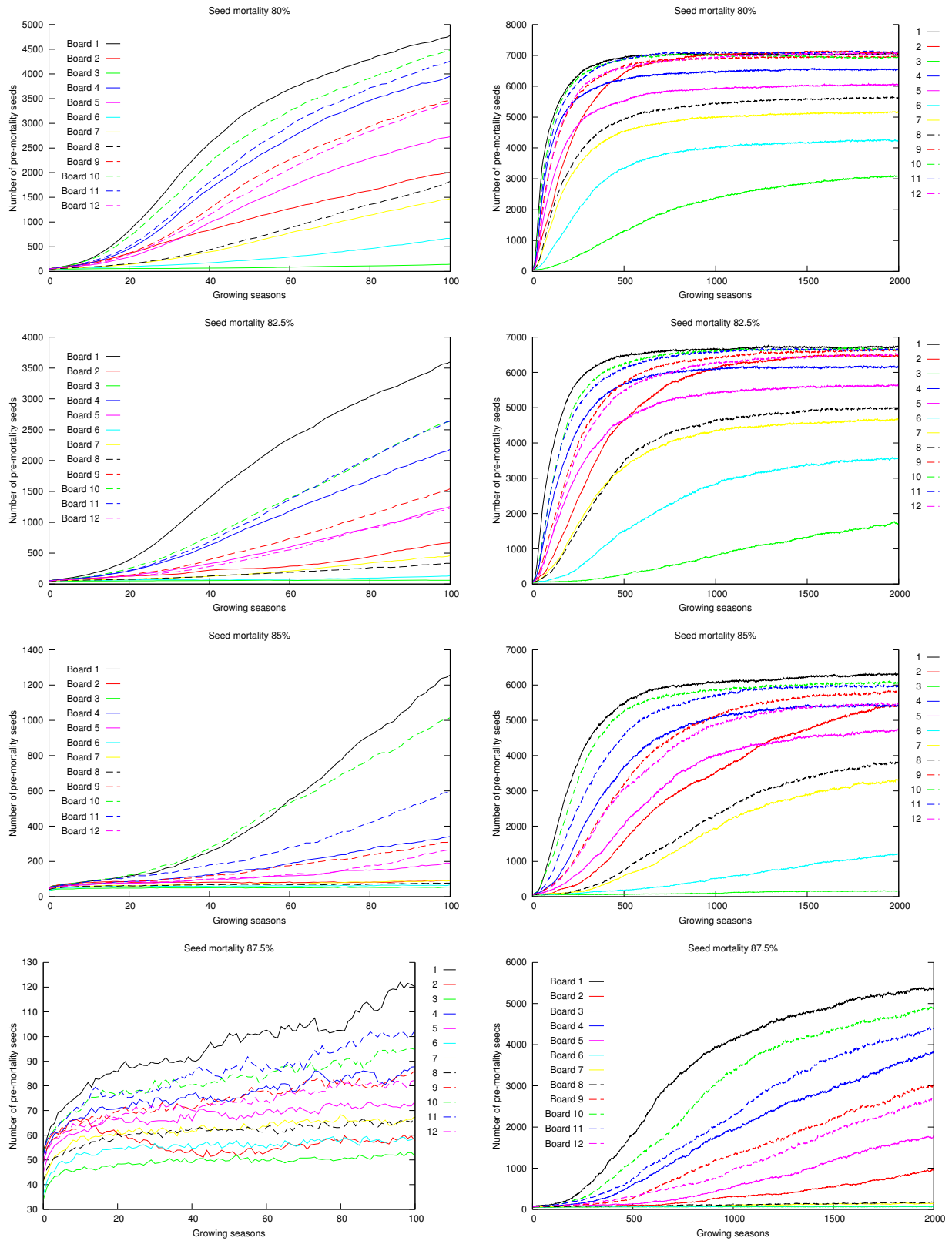
Fig. 3. Seed production from all plants in a year over the first 100 (left) and 2000 (right) growing seasons of the four lowest seed mortality rates (from top to bottom: 80%, 82.5%, 85%, 87.5%) for all twelve boards; average of 100 replicates. Note the vertical scales are not equal; line types correspond to the same boards across all plots.
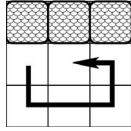
Fig. 4. Shown is one of the several ways that a barrier can curtail the growth of a grid plant. Barriers are represented by blocks while the arrow shows the pattern of growth of the grid plant. In this model, the shown plant is completely incapable of any further growth.

Boards 9–12 use a more complex model of barriers in which the obstructions are on the sides of the cells, leaving 100% of the actual cells available as space to the grid plants. Board 2, which 4 long walls not only take up no growth space, but hardly cover 1% of the placement possibilities for walls, ranks 5th in terms of inhibition of seed production, ahead of board 5, which physically renders 12.5% of the cells inaccessible. Thus the space covered is not the major driving effect of obstruction.

One way of interpreting these results is via their effects on the plants. Figure 4 shows one of the ways a barrier can disrupt the growth of a grid plant and completely prevent any further growth. From this direction, it is clear the presence of long stretches of walls, or from inspection of boards 3 and 6, presence of bottlenecks maximizes the ways in which the plants can entrap themselves. Additionally, the presence of barriers also gives opponents (other grid plants) more tools to obstruct growth; in combination, this makes the problem of evolving effective growth strategies much more difficult.

A. Seed production curvature

Note the curvature of the plots in Figure 3. Since the presence of barriers makes the problem of producing seeds more difficult, and higher seed mortality rates also make it harder, thus evolution is naturally divided into an epoch where the curve is concave up and one where it is concave down. The concave up portion represents exploration and discovery for solving the problem of producing seeds, culminating in a period of exponential-like growth. The concave down portion represent reaching carrying capacity, when the entire world becomes as filled as the plants can make it, and thus settling down into a consensus strategy for coexisting.

Looking at the same board across different seed mortality rates suggests that mortality represents a substantial source of problem difficulty. Increasing seed mortality is roughly equivalent to requiring longer evolutionary timescales to learn to compensate. The right-hand side of Figure 3 shows the same experiments, but plotting the first 2000 growing seasons instead. From direct comparison, the profile of seed production for the first 100 seasons under 80% mortality is similar to the first 2000 seasons under 87.5% mortality, an effective 20-fold timescale delay.

Widening the scope of the plots, especially for lower seed mortality which may be construed to be deeper in relative time, shows another anomalous effect of board 2, the standard square. In short timescales, board 2 was the 5th worst board in terms of obstructiveness, but this is belied by the difference is asymptotic behavior: it is clear that the plants can, and have, eventually learned to cover the entire board. The effect of board 2 is to significantly lengthen the time required for that exploration to happen. Instead of simply requiring a growth pattern which can tile the plane (as for board 1), the long walls require the plants to create a pattern that can handle edges.

In combination, the obstructed grid plant seed production problem has cases that are particularly hard, with the difficulty in terms of evolutionary time required to solve them independently changeable, to some degree, from the amount of space obstructed either from blockages or walls.

B. Cross-board adaptation

Plants that are evolved to handle particular barriers may also be able to handle similar types of barriers. To test this, we took the seed populations after 5000 growing seasons, selected 10 seeds from the same population (to not neglect possible kinship effects), and transplanted them into a new, empty world with a different obstruction board pattern. The number of seeds produced after the 100th season post-transplantation is recorded for each combination of original board evolved on vs. board evaluated on. Seed mortality is kept constant between evolution and evaluation.

Results are tabulated in Table I, for 80%, 85%, and 87.5% seed mortality. To aid in interpretation, the cells are colour-coded, ranging from red for the lowest number through light purple, blue-green, and to green for the highest number. The standard expectation is that the diagonal of the table, representing seeds evolved for that specific board, will dominate relative to seeds evolved for different boards. The results are generally in agreement, especially for the worst obstructions. At 80% mortality, seeds specifically evolved on board 3 are twice as good as seeds from other boards; seeds from boards 6–8, the next worst obstructions, are the next best. The pattern is repeated for testing on boards 6–8, although less strikingly.

A more interesting finding is that planting seeds from boards 6–8 on board 1, completely unobstructed, actually beat seeds evolved on the empty board. This has precedent in the literature, in that solving the harder problem, with higher evolutionary pressure, leaves the agents better equipped to handle easier problems. The effect diminishes with planting from board 3 to 1, indicating that like other results, too much pressure eventually generates a retrograde effect.

The results from 85% mortality generally conform to the same pattern, that the highest obstructions are unsolvable by seeds not specifically adapted to it, but solutions partially transfer and confer a nonlocal advantage. Interestingly, board 3 seeds, while more than thrice as good on their home board, notably fails to thrive anywhere else, relative to other seeds, clearly showing the effect of retrograde adaptation.

Moving up to 87.5% mortality, which was previously established to allow further evolutionary time to have an effect, displays the extreme effects of adaptation. Board 3 seeds cannot grow well, even on their own board, where their home board advantage is wiped out. This indicates they are

80% Seed mortality
Board evaluated on

	1	2	3	4	5	6	7	8	9	10	11	12
1	7013	6607	1850	6252	5667	3478	4526	4800	6474	6874	6736	6462
2	7057	7043	1610	6300	5679	3316	4474	4767	6505	6962	6799	6513
3	7224	5747	3340	6501	5894	3642	4710	4978	6542	7106	6964	6552
4	7203	6713	1886	6482	5879	3722	4751	5052	6740	7100	7001	6637
5	7347	6916	1950	6605	6025	3820	4877	5151	6901	7218	7098	6782
6	7490	6745	2168	6809	6254	4316	5141	5496	7047	7380	7271	6852
7	7557	6930	2049	6869	6267	4041	5180	5472	7242	7480	7388	7087
8	7665	6927	2082	6980	6348	4157	5250	5632	7334	7594	7515	7170
9	7259	6727	1890	6483	5873	3651	4825	5085	7038	7163	7101	6838
10	7036	6672	1787	6288	5695	3506	4586	4845	6571	6939	6795	6554
11	7189	6663	1877	6436	5838	3619	4743	5041	6847	7077	6994	6698
12	7270	6922	1989	6484	5809	3485	4735	5004	6910	7191	7103	6958

85% Seed mortality
Board evaluated on

	1	2	3	4	5	6	7	8	9	10	11	12
1	6347	4995	134	5181	4390	1053	2972	3095	5089	6020	5687	5114
2	5972	5744	123	4745	3896	540	2312	2386	4508	5615	5263	4647
3	3573	523	400	2283	1475	263	733	709	1803	3076	2729	1577
4	6482	4873	171	5485	4678	1528	3301	3525	5419	6241	5973	5327
5	6542	4407	195	5552	4866	1823	3464	3638	5408	6259	6038	5285
6	6136	1716	247	5113	4542	2592	3314	3580	4692	5740	5432	4201
7	6652	3212	195	5684	4953	2165	3776	3910	5760	6411	6160	5413
8	6730	3103	188	5809	5030	2335	3799	4229	5905	6536	6317	5552
9	6493	3991	180	5479	4601	1322	3397	3545	5936	6292	6135	5570
10	6406	4873	149	5312	4482	1179	3055	3248	5296	6110	5854	5306
11	6425	4478	178	5368	4509	1264	3188	3405	5494	6195	5986	5362
12	6425	5342	170	5298	4350	860	3003	3239	5462	6189	5949	5622

87.5% Seed mortality
Board evaluated on

	1	2	3	4	5	6	7	8	9	10	11	12
1	5567	2904	130	4027	2903	162	926	1124	3345	5039	4475	3430
2	3076	2564	129	1764	994	139	219	262	1234	2587	2126	1336
3	782	124	126	264	162	130	143	147	479	321	182	
4	5683	1959	132	4350	3280	237	1386	1642	3832	5201	4823	3601
5	5149	1152	130	3941	3101	321	1380	1502	3335	4671	4290	2809
6	735	131	122	303	188	130	150	147	226	524	364	189
7	1786	179	125	985	648	197	388	403	705	1392	1080	547
8	2056	198	127	1265	945	211	513	658	959	1682	1388	781
9	5389	1370	125	4039	2726	187	1377	1418	4520	5109	4907	4025
10	5557	2427	129	4109	2824	160	1031	1193	3922	5169	4818	3830
11	5684	2068	133	4327	3024	205	1293	1654	4280	5343	5060	4041
12	5319	1755	131	3811	2280	159	861	963	3823	4977	4588	4130

(*Board evolved on* is the left-side row label for all three tables.)

TABLE I

NUMBER OF SEEDS PRODUCED AFTER THE 100TH SEASON, WHEN TRANSPLANTING 10 SEEDS FROM THE SAME WORLD EVOLVED FOR 5000 SEASONS ONTO A NEW, EMPTY WORLD, WITH A DIFFERENT OBSTRUCTION PATTERN BOARD; AVERAGE OVER 300 REPLICATES EACH. SEED MORTALITY IS THE SAME FOR INITIAL EVOLUTION AND EVALUATION AFTER TRANSPLANTATION; EACH OF THE THREE TABLES HAS A DIFFERENT PARAMETER SETTING.

maladapted due to overly high pressure and cannot even solve the seed production problem properly. Seeds from boards 6–8 show the progressively worsening effect of retrograde adaptation, where they start becoming unable to grow at all.

Due to the striking display of nonlocal adaptation present in the results, from the phase of positive adaptation up through and beyond retrograde adaptation, we retabulate some of the results in Table II. Here, we vary the seed mortality rate (still kept the same between evolution and evaluation) and the original board for evolution, while fixing the board where the saved seeds are transplanted into.

Board 1, no obstruction, is shown first. The trend of adaptation granted by evolving under harsh obstruction/mortality can now be clearly seen, as it starts reversing around 85% mortality. Under extreme 90% seed mortality, seeds from the home board are the least maladapted and can grow somewhat; board 10, the least nontrivial obstruction, comes in second. The 92.5% mortality results are only shown to illustrate complete failure of evolution under insurmountable pressure; these are unreliable flatline numbers, nonzero only due to the mercy rule keeping the last 10 seeds.

Board 3, with the worst obstruction, is recorded next. The nonlocal adaptation is very strong, but again starts failing around 85% mortality; any higher and no seeds can successfully thrive at all. The paradoxical increase in seeds as mortality increases beyond 90% is a pure artifact of the mercy rule and can be disregarded. Finally, board 12, which is in the middle of the rankings for obstruction, is displayed. The results corroborate the conclusion that a combination of board obstruction and seed mortality creates the evolutionary pressure, which manifests as a period where plants are initially well-adapted to other boards, even unobstructed, but

Evaluated on Board 1

Seed mortality, both for evolution and evaluation

		80%	82.5%	85%	87.5%	90%	92.5%
	1	7013	6743	6347	5567	1876	272
	2	7057	6522	5972	3076	193	245
	3	7224	6580	3573	782	203	267
	4	7203	6930	6482	5683	229	262
	5	7347	7161	6542	5149	194	251
Board	6	7490	7079	6136	735	200	259
evolved	7	7557	7306	6652	1786	205	267
on	8	7665	7262	6730	2056	194	278
	9	7259	6973	6493	5389	251	251
	10	7036	6786	6406	5557	608	270
	11	7189	6871	6425	5684	354	267
	12	7270	6989	6425	5319	232	266

Evaluated on Board 3

Seed mortality, both for evolution and evaluation

		80%	82.5%	85%	87.5%	90%	92.5%
	1	1850	772	134	130	157	191
	2	1610	459	123	129	140	184
	3	3340	2542	400	126	154	188
	4	1886	882	171	132	155	192
	5	1950	882	195	130	146	181
Board	6	2168	1142	247	122	153	182
evolved	7	2049	867	195	125	143	182
on	8	2082	920	188	127	158	183
	9	1890	768	180	125	150	190
	10	1787	735	149	129	147	180
	11	1877	790	178	133	153	193
	12	1989	734	170	131	151	191

Evaluated on Board 12

Seed mortality, both for evolution and evaluation

		80%	82.5%	85%	87.5%	90%	92.5%
	1	6462	5952	5114	3430	253	232
	2	6513	5692	4647	1336	172	229
	3	6552	5581	1577	182	183	233
	4	6637	6206	5327	3601	189	241
	5	6782	6256	5285	2809	181	225
Board	6	6852	6126	4201	189	180	235
evolved	7	7087	6561	5413	547	189	223
on	8	7170	6437	5552	781	178	241
	9	6838	6379	5570	4025	197	231
	10	6554	6078	5306	3830	204	234
	11	6698	6167	5362	4041	195	229
	12	6958	6498	5622	4130	190	230

TABLE II

NUMBER OF SEEDS PRODUCED AFTER THE 100TH SEASON, WHEN TRANSPLANTING 10 SEEDS FROM THE SAME WORLD EVOLVED FOR 5000 SEASONS ONTO A NEW, EMPTY WORLD, OBSTRUCTED AS ONE OF THREE PARTICULAR BOARD PATTERNS; AVERAGE OVER 300 REPLICATES EACH.

then retrograde adaptation sets in.

VI. CONCLUSIONS AND NEXT STEPS

While the difficulty of the gridplant problem is mostly due to the seed mortality rate, as measured by seed production, this is not the major object of this study. The experiments performed demonstrate that adding barriers into the simulation environment drastically increases the difficulty. That seed production dropped on Boards 2, 9–12 when the barriers took up no productive space, shows the mere constraint on which direction a plant may grow has an impact on their growth.

The experiments also demonstrated that there is a non-linear, compounding effect between the seed mortality rate and the type of barriers on the grid. Barriers are roughly

equivalent to an increase in the effective mortality rate, and the worst ones can make the seed production problem unsolvable starting at lower mortality rates.

There is a strong nonlocal adaptation effect where seeds evolved on obstructed boards are better at other types of obstruction when transplanted, beating out seeds from relatively open boards. This can be partially explained by the higher evolutionary pressure from the effective mortality rate speeding up the rate of evolution. Unexpectedly, the effect *reverses* itself when the evolutionary pressure becomes extreme, and the seeds evolved become completely unsuccessful at any board. This phenomenon of retrograde adaptation merits further study: whether it inevitably occurs in deep evolutionary time or only from excessive pressure.

A artificial feature of the simulations presented here is the exceedingly regular seed mortality. Replacing fixed rates of seed mortality with variable levels would be more natural and would also drive the evolution of plants in a different manner. Seed mortality also occurs uniformly at random. Another common type of disturbance is zonal [7], e.g. all plants in a roughly circular area are destroyed by gophers making a burrow, or an area is flooded. When seed mortality happens in such contiguous zones, the ability of plants to spread into a new area becomes advantageous, requiring an elongated growth pattern. This, however, would increase the plant's probability of interaction with barriers, and the interplay between the two effects is unknown. This suggests that changing the pattern of seed mortality should be a priority for future research.

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