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Within the past decade interactions among plants and animals have received increasing attention, mostly pertaining to selection of plants that produce toxic secondary compounds as a direct result of herbivory (Gilbert and Raven, 1975; Feeny, 1975; and Rhoades and Cates, 1976) and in turn selection of animals that detoxify these plant compounds (Freeland and Janzen,1974). Indeed, the plant-herbivore association has been regarded in the context of predator-prey relationships, especially for seed eaters (Scott, 1970, 1976; Janzen, 1971; Smith, 1975; and Pulliam and Brand, 1975). However, there are other important plant-animal associations. Regulation of plant nutrients (Mattson and Addy, 1975; Chew, 1974; Owen and Wiegert, 1976) and productivity by both vertebrate and invertebrate and host plant associations (Harris, 1974; Dyer, 1973, 1975; Dyer and Bokhari, 1976) also have been described. Thus it appears there are many associations which affect populations of plants and animals in evolutionary time (Janzen, 1976) and others which have short-term effects in "physiological time," i.e., periods ranging from minutes to a single growing season. It is this latter phenomenon that I am examining in this paper.

A question has been raised about the overall effects of Redwinged Blackbirds (Agelaius phoeniceus) feeding on ripening ears of field corn in the east and middle west of North America (Dyer, 1973, 1975). In several instances, fields in which Redwings fed produced more corn than fields in which feeding levels were lower; this is true for plots within fields as well (ms. in preparation). On a regional basis the question is complex. Can birds recognize more productive corn fields, or even more productive patches within fields, or is there an interaction between the animal and the corn plant that triggers higher levels of production? Of the two alternatives, I have suggested that the more likely event is that avian herbivory stimulates grain production (Dyer, 1973, 1975). Thus it is of heuristic value to examine growing field corn ears in fields of the midwest in order to determine whether there is the possibility that one or more "herbivorous events" may trigger processes which lead to compensatory growth. The approach to identifying the possibility of compensatory growth has been through simulating bird damage on maturing corn ears by mechanical manipulation. The study was conducted during 1971 in hybrid field corn raised for seed.

METHODS AND MATERIALS

In August 1971 a field of field corn, a 3-way cross of A632 x B37 - 43 x 619, destined for seed production in Erie County, Ohio was selected for the study. It was planted May 10, 1971; fertilized at the rate of 169 kg N, 135 kg K, and 56 kg P ha $^{-1}$; and had weeds controlled by 2.8 kg atrizine and 0.34 1 of 2,4-D ha^{-1} post emergence, plus one mechanical cultivation. The experiment was started August 5. Four plots in two adjacent rows, selected at random, were used for the experiment. In each of the plots two classes, consisting of damaged and undamaged were utilized. A small metal cone, constructed with interior "teeth," was designed to macerate the corn ear tips to a constant distance down each ear (2.1 cm average distance). On alternate plants 125 ears were damaged, and 125 ears were left as controls. Five-day periods separated the treatments, i.e., on 5-day intervals the four plots were damaged. The entire damage simulation process thus extended over a 20-day period, giving a range of differing phenological conditions, or phenophases, during the maturation of the corn grain (Total samples = 1000 = 2 treatments x 125 samples x 4 phenophases).

The corn ears were allowed to mature in the field and were harvested on October 4-6, 1971. All ears were bagged individually and taken to the laboratory for analysis. Many measurements were taken, but those pertinent to this report were (1) total ear length, (2) total length of kernels of each ear, (3) shelled weight of kernels, (4) moisture content, (5) diameter at base, middle, and standard distance from ear tip, and (6) total amino acid content at base, middle, and tip from each ear class (damaged or control treatment from each of the four phenophases). Amino acids reported were alanine, valine, glycine, isoleucine, leucine, proline, threonine, serine, methionine, hydroxyproline, phenylalanine, aspartic acid, glutamic acid, tyrosine, lysine, histicine, arginine, and half-cystine.
Statistical analyses were conducted at the Natural Resource Ecology Laboratory, CSU using standard package analysis of variance (ANOVA) and covariance analysis of variance (COVANOVA) programs.

RESULTS

Contrary to my earlier reports (Dyer, 1973, 1975) that biomass of corn grain apparently increases during avian herbivory, these simulated-damage results outwardly do not indicate compensatory recovery (Table 1): the mean weight of the control class was signigicantly heavier than the damaged class for all four phenophases ($p < 0.01$). The picutre is complex. In order to address the problem an important criterion to measure is biomass distribution per unit length along the ear, since it is difficult to compare damaged and control ears directly. [Note that the damaged ears are shorter (Table 1), owing to shrinkage following the damage procedure.] Using this measure, the biomass distribution is signgicantly higher for the damaged classes when compared to the control (Table 1 ($p < 0.01$) for 2-way ANOVA; effect of phenophase is not significant ($p > 0.1$)). The reason for the apparent increase in biomass per unit length is at least partially explained by differences in ear diameter. The diameter of the damaged ears for the three ear locations for all phenophases was significantly larger than the control ($p < 0.025$, paired t-test). Even though the mean difference is small (0.03 mm), it does provide evidence that biomass is increased by mechanically damaging the corn ear tip.

Further evidence of biomass compensation is available from comparisons of production values expected from various length classes for the control and mechanically damaged classes. The regression for the control class ear production was $Y = 33.724 + 8.573X$ ($r^2 = 0.837$), where Y = weight in g and X = length in cm. By using this regression to predict corn production for the mechanically-damaged class, it is obvious that in all phenophases the damaged group produced more than expected (Table 2).

Stronger evidence of compensatory growth in damaged conditions exists with measures of amino acid levels. The totals of all amino acids, giving total percent protein, show a significant increase ($p < 0.05$) for the mechanically damaged classes over control classes; there was no difference in amino acid levels in any location on the ear ($F < 1.0$). The range of amino acid production (Δ%, damaged compared to control) was from 13.1% for mid-ear locations in phenophases 1 and 2 and -2.9% for the base in phenophase three. The earliest phenophase showed the greatest increase (11.8%), and samples from the middle part of the ear over all phenophases and ear sample locations was 6.3% (Fig. 1). The amino acid level differences were higher for the two earliest phenophases and varied less from the control class values for phenophases 3 and 4, a result expected because of growth and maturation of the corn ear. A higher growth response in treated ears would be expected at an early phenophase in contrast to later stages when the flow of carbohydrates and nutrient materials to the ear is shutting down. A covariance analysis, used to determine the influence of normal variability on the mechanically damaged levels, indicates that the damage treatment per se was influential ($p = 0.057$,3,7 d.f.).

DISCUSSION

Overall, the control class produced slightly more total N (3.21 g N per ear for damaged class contrasted to 3.36 g N for controls), but the results are mixed and as yet inconclusive. Nonetheless, using the average values of 10.49% total protein for the control class and 11.15% for the damaged class and grain production values for damaged and undamaged field reported from Southwestern Ontario (Dyer, 1975), estimates of total N production in bird-damaged fields range from 24.1 to 30.1% higher than non-damaged corn. Thus overall, the greatest impact on the corn crop in areas subject to avian depredation may be an increase in total N, as long as nitrogen is not limiting in either the field or the plant tissue.

Phenology of the association also is important, witness the total amino acid reaction obtained for the various phenophases in this experiment (Fig. 1). Avian depredation at one stage of development predictably would affect the corn differently when compared to depredation at another stage.

All of these results suggest that one of two alternative hypotheses can explain these experimental results:

(1) photosynthate that was channeled into the developing damaged ear was neither increased nor decreased, and available carbohydrate and amino acids were partitioned into kernels remaining on the damaged ears, thus concentrating biomass and protein, or

(2) there was a physiological response that increased photosynthate flow into the damaged ear and compensatory growth resulted. The effect was then caused by changes due to mechanical damage in the apical portion of the corn ear.

Even though the methods are indirect, an approach necessitated by the fact that I must attempt to determine potential compensation in the face of biomass removal, this study suggests that mechnaical damage alone to growing corn ears results in increased biomass. As noted previously (Dyer, 1973, 1975), if biomass compensation does indeed result from herbivory, there would then be a real drop in total biomass. Such a relationship would constitute a "herbivory optimization curve" and has been observed for other herbivore-plant associations (S. McNaughton, pers. comm.).

At this time not all of the responses reported here are consistent. For instance, it is suggested in Table 2 that there were increasing levels of biomass added to the damaged ear in older phenophases. On the other hand evidence presented for amino acid changes shows the largest response in earliest phenophases. No matter what the response ultimately proves to be, there remains strong evidence that mechanical damage results in certain growth responses that are counterintuitive.

This evidence puts herbivory in a new potential light. Janzen (1976) presented convincing evidence that certain tropical legume seeds showed decreased fitness when subjected to simulated herbivory after maturation. From evidence presented here and that of Scott (1970), I pose the hypothesis that certain types of herbivory performed before maturation of seeds may give entirely different results. Indeed, Maun and Cavers (1971) were able to manipulate seed size and ultimately change conditions of dormancy and enhance germination of curled dock (Rumex crispus) simply by removing certain proportions of flowers at anthesis. The implication is that such physiological changes also may affect fitness of seed-producing plants in the next generation. That many animals might participate in these processes under normal circumstances refocuses their potential role as ecosystem controllers, because herbivory could result in selective advantages for many plant groups.

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DISCUSSION

Question: You presented four different components of simulated bird damage. Could you offer a program that incorporates these factors?

Dyer: Yes, sir, I can. As far as the simulation model, there is an ecosystem input function, and it's already been developed; it's already functioning. It uses biologically real data; it has well-established theoretical basis. It's widely published. It's called MODEL BIRD, developed by John Haynes and George Eddis, Colorado State University. And it has a great deal of power; it does have some problems, however, and I think that it needs new input Information. It doesn't need any theoretical update; it simply needs more field experience. And it needs a lot of people willing to address it, willing to work with it, and willing to use that model in collaboration with their field data. The model is essentially worthless unless somebody is willing to pick it up and say I have a testable situation in an environment. Given these series of questions and these series of hypotheses, can. I get new information from this model, or from a model like Richard Dolbeer has, to answer these environmentally important questions, most of which will never be able to be answered in collecting field data? So that's my response to that question.

I think there are several groups, including ours, in the country that have obtained this level. We have several working that have experience in this area and like myself are all doing lots of other things. In fact, I don't have time to spend any more because I have other duties. We need to recognize these potentials, recognize the validity of these models, and recognize the cost savings. I feel confident that I can sit down and using this BIRD model and in one generation simulate a lot of these models that we've been hearing about today. I can come up with numbers, but until we understand what those numbers mean and handle those problems with numbers, or guess back to field data, we won't go anywhere. But I can run a simulation of the model roost and compare the data with that A1 Stickley and Richard Dolbeer and Steve White are getting; and I can do it for $25.

Question: Are we to assume that all the so-called successes of Avitrol, where it has apparently protected crops compared to those of other studies where the crop was not protected, are artifacts?

Dyer: That's a reasonable question. I wish I could give you an answer on that. The only answer I can give you is that I've not had a chance to compare my philosophy and your reasoning. I can think of some reasons for its being an artifact. I have my name on one publication confusing similar things, and I have really questioned why is there this difference. I sort of know why there's this difference in data, because we run into this all the time in our lands program.

The problem that we encounter that's really discouraging me is that we cannot pour biological data in an ecosystem with the same degree of confidence that we can run our models. Now that's a far-out blatant statement, and people really can object to it. We have the largest single data bank on ecological material that exists anywhere in the world. We know the standard deviation is larger than the mean. If you have a situation like that that means that you can make a wild guess and any answer is going to be pretty close. That's what these models are doing. These models are built on really basic information that has very little variability. This is information, you realize, that has less variability than measuring corn. We build up these series of associations, and we apparently carry the small variations all the way through- By the time we know what we're doing then we have fairly good predictive capability. If we don't know what we're doing, then it's been a waste of time. But so far a lot of ecological models, BIRD being among them, has been validated in a lot of interesting ways.

Let me show you a slide; I think that will expalin what I'm trying to get to. I think we're looking at perceptions of the real world in this box, and then to explain those perceptions we have word models. We have data, we have conceptual models, empirical models, numerical models, static models, all of which have the same capability of explaining what our perceptions are in the real world. I think what most biologists feel they're doing in this particular season is moving data into this box, but the models are no better than the data. Pay attention to constraints in Information theory that dictate the level of organization. And then put together the data, argue about it, which is what we've been doing here, and finally come up with some sort of day-to-day perception of the real world that's acceptable, and I have no doubt that I could sit down and do that.

TABLE 1. Length of corn and biomass for control and mechanically-damaged ears, Erie County, Ohio 1971. Phenophase groups start with corn in "early milk" stage and are separated by 5-day intervals.

	Phenophase				
	1	2	3	4	Averages
Length of ear (cm)					
Control	19.07	19.14	19.21	18.73	19.04
Damaged class	18.56	18.74	18.92	18.46	18.67
Difference, C > D*	0.51	0.40	0.29	0.27	0.37
Length of corn distributed on cob (cm)					
Control	18.66	18.73	18.62	18.24	18.56
Damaged class	16.66	16.59	16.58	16.57	16.60
Difference, C > D*	2.00	2.14	2.04	1.67	1.96
Weight of shelled corn (g)					
Control	193.99	194.99	192.15	190.33	192.87
Damaged class	177.93	178.54	179.85	182.94	179.82
Difference, C > D*	16.06	16.45	12.30	7.39	13.05
Weight per unit length ($g\ cm^{-1}$)					
Control	10.40	10.41	10.32	10.44	10.39
Damaged class	10.68	10.76	10.85	11.04	10.83
Difference					
Damaged > Control	0.28	0.35	0.53	0.60	0.44
Δ%	2.69	3.36	5.14	5.75	4.24

*Comparison of length and weight differences (control over damaged) is significant ($p < 0.05$, 1-way ANOVA).

TABLE 2. Estimates of biomass compensation in mechanically damaged corn ears.

	Phenophase			
	1	2	3	4
Increase in biomass (g) of damaged ears, predicted over measured	1.38	2.59	3.96	7.16
Δ%	+0.70	+1.47	+2.26	+4.07

Estimates are derived from regression analysis of undamaged control ears, where total biomass of kernels per ear are compared to ear length ($Y = 33.724 + 8.573X$, $r^2 = 0.837$ for control ears, where Y = weight in g and X = ear length in cm). Values given in table are then differences of measured mean weights over predicted weights in the damaged ears using the control ears as a basis. Even though the overall effect of the mechanical damage simulating herbivory was a loss in total biomass, these estimates suggest a compensatory effect at each of the phenophases. (See text for experimental procedures.)

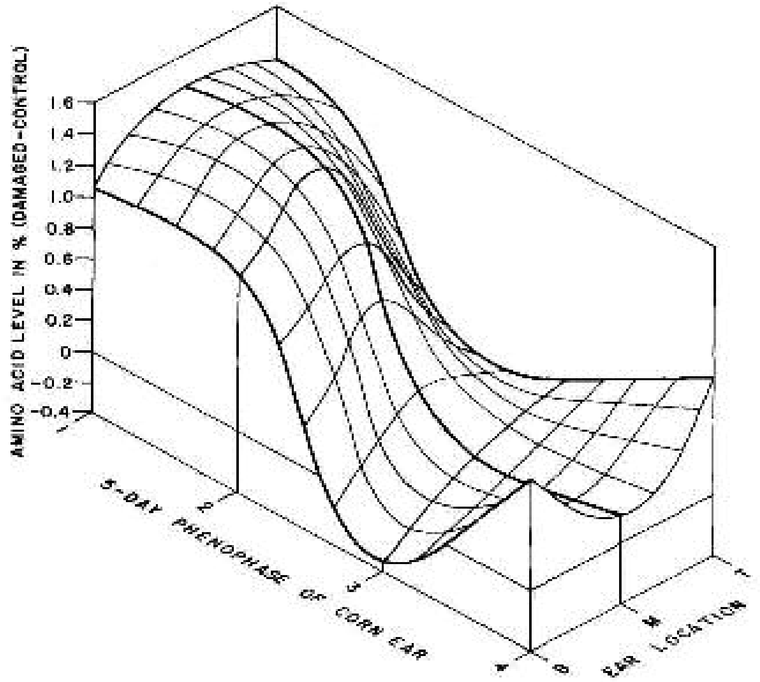

Fig. 1. Graphical interpretation of amino acid levels in relation to ear location and development.