Probability of Tree Seedling Establishment Changes Across a Forest–Old Field Edge Gradient[1]

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Forest edges affect many aspects of plant communities, causing changes in microclimate, species composition, and community structure. However, the direct role of edges in regulating forest regeneration is relatively unknown. The pattern of tree establishment across a forest–old field edge was experimentally examined to determine the response of three tree species to the edge gradient. We placed 100 1-m² plots in a 90 × 90 m grid that began 30 m inside the forest, extended across the edge, and ended at 60 m into the old field. Into each plot, we planted seeds of *Acer rubrum*, *Acer saccharum*, and *Quercus palustris*. Emergence increased with distance into the field for both *A. saccharum* and *Q. palustris*. Emergence for *A. rubrum* increased from forest to field, reaching a maximum near 20 m into the field, and then declined with further distance. Nearly all *A. rubrum* seedlings died shortly after emergence. Survival of *A. saccharum* increased with distance into the old field, while survivorship of *Q. palustris* did not respond to the edge gradient. Establishment probabilities increased with distance into the old field for both *A. saccharum* and *Q. palustris*. Growth of *Q. palustris* and allocation patterns of *A. saccharum* also varied across the edge gradient. These results suggest that edges have complex, species-specific effects on tree establishment and growth that can influence the spatial pattern and species composition of regenerating forests.

Key words: *Acer rubrum*; *Acer saccharum*; edge effects; establishment probabilities; *Quercus palustris*; root : shoot ratio.

As landscapes become increasingly fragmented, it is critical that we understand the effects of anthropogenic habitat edges on vegetation dynamics. While environmental and vegetation patterns associated with edges have been described for many ecosystems, the ecological function of these landscape features has not been adequately determined (Pickett and Cadenasso, 1995). Edges have the potential to control the movement and establishment of plants within fragmented ecosystems (Cadenasso and Pickett, 2001), affecting every aspect of a plant community. However, the regulation of forest regeneration by edges is essentially unknown.

At boundaries between deciduous forests and abandoned agricultural land, edge environments have higher light, wind speed, and soil temperature and lower relative humidity relative to the adjacent forested patch (Matlack, 1993; Forman, 1995; Cadenasso, Traynor, and Pickett, 1997). However, the spatial position and abruptness of the transition from field to forest conditions differs greatly depending on the environmental variable examined (Cadenasso, Traynor, and Pickett, 1997) and with edge orientation (Wales, 1972; Fraver, 1994). While the largest changes in microclimate may occur on the field side of the edge (Cadenasso, Traynor, and Pickett, 1997), detectable changes in microclimate may extend 50 m into deciduous forest stands (Matlack, 1993). Edges may locally influence nutrient cycling through enhanced atmospheric deposition rates (Beier and Gundersen, 1989; Lindberg and Owens, 1993) and increased litter inputs (Facelli and Carson, 1991).

The complex environmental changes associated with edges may influence the spatial pattern of tree seedlings in forest remnants (Wales, 1972; Whitney and Runkle, 1981; Chen, Franklin, and Spies, 1992; Young and Mitchell, 1994) and in clear-cuts (Lepage et al., 2000). However, the direct response of tree seedlings to this complex environmental gradient is largely untested (but see Williams-Linera, 1990; Meiners, Handel, and Pickett, 2000). The presence of edges also affects habitat use by animals (Sork, 1983; Linzey, 1989; Cadenasso and Pickett, 2000; McCormick and Meiners, 2000) that may interact with the plant community (e.g., as herbivores, seed dispersers, or seed predators). Consequently, there is the potential for indirect edge effects on the plant community through altered spatial patterns of herbivory or predation (Murcia, 1995; Meiners, Handel, and Pickett, 2000). Furthermore, changes in plant community composition across edges (Fraver, 1994; Matlack, 1994; Meiners and Pickett, 1999) may result in patches of differing invasibility (Hill, Canham, and Wood, 1995), leading to changes in tree establishment. These direct and indirect edge effects may regulate the spatial pattern of tree invasion into successional sites.

Despite the biological and environmental impacts of edges, the role of the forest edge in determining tree regeneration in old fields and clear-cuts has largely been studied as a dispersal phenomenon. In these studies, the forest remnant serves as a source of propagules for the adjacent disturbed site (Johnson, 1988; Hill, Canham, and Wood, 1995; Hughes and Bechtel, 1997). Some investigators have proposed that the spatial pattern of seed dispersal determines the pattern of tree seedlings in successional habitats (Hughes and Fahey, 1988; Johnson, 1988; Hughes and Bechtel, 1997). This idea assumes that establishment does not vary across the edge gradient (Johnson, 1988). However, the spatial pattern of seed dispersal often does not determine the spatial pattern of established seedlings

in plant communities (Houle, 1992; Herrera et al., 1994; Hughes and Bechtel, 1997; LePage et al., 2000). Because dramatic changes in environmental conditions and in plant–animal interactions are associated with edges, we expect the probability of tree establishment to vary across the edge gradient. The final pattern of seedling establishment would therefore be a combination of differential seed input and differential establishment across the edge.

Johnson (1988) acknowledged that modeling spatial patterns of tree seedlings as a function of seed dispersal was based on the untested assumption that postdispersal establishment rates did not vary. To solve this problem, he proposed that "[u]niformity in seedling environment could be checked by sowing known number and quality of tree seeds in plots leading away from seed trees and monitoring predation, recruitment and seedling survival" (p. 185). The goal of our research was to test for changes in the establishment probability of tree seedlings across an edge gradient, evaluating the assumption of constant establishment. We studied a spatial gradient that should encompass the majority of tree seeds dispersed within the site.

Previous work at this site (Meiners, Handel, and Pickett, 2000), has found that tree seedlings respond to edges at small spatial scales (within 10 m of the edge) and that these effects may be quite strong. The present study expands this research, experimentally determining postdispersal tree-seedling edge responses across the potential dispersal range for three tree species common in eastern deciduous forests. We hypothesized that a species' shade tolerance would determine seedling responses to the edge gradient. We predicted that relatively shade-intolerant species (*Acer rubrum* and *Quercus palustris*) would respond to the edge with higher establishment in the field portion of the gradient. Conversely, we predicted that more shade-tolerant species (*Acer saccharum*) would have a higher rate of establishment in the forested portion of the site. Understanding the role of edges in determining tree establishment is critical to predicting forest regeneration at regional scales and to understanding the development of spatial patterning within regenerating stands.

MATERIALS AND METHODS

Study site—The research site was an old field and adjoining early successional forest at the Hutcheson Memorial Forest Center (HMFC) near East Millstone, New Jersey, USA (40°30′ N, 74°34′ W). The edge between the two habitats faced southeast. The young forest was dominated by *Acer rubrum* (23% relative cover), *Fraxinum americana* (38%), and *Quercus palustris* (16%) and was on land that was originally abandoned in the 1950s. *Quercus* spp., *Acer saccharum*, and *Fagus grandifolia* dominated the nearby old-growth forest at HMFC. The field had previously been used to grow corn and had been abandoned for 12 yr at the time of this study. Herbaceous perennial species dominated the old field with scattered trees and shrubs (Meiners and Pickett, 1999).

Experimental design—We established a 90 × 90 m grid beginning 30 m inside the forest and extending 60 m into the old field. Within this grid, we placed 100 1-m² plots at regular 10-m intervals (Fig. 1). The boundary of the young forest with the old growth forest occurred at ~60 m from the study edge, limiting the depth of the grid. Plot position was shifted slightly when necessary to avoid other experimental projects or human-made trails. Wherever possible, we held distance from the forest edge constant within each distance interval, shifting plot position parallel to the edge. For this study, we defined the forest edge as a straight line that approximated the most recent plow line. Several of the plots at 20 m from the edge were adjacent to a
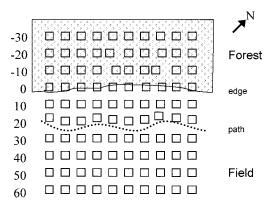

Fig. 1. Diagram of the study site showing actual positions of each experimental plot (plot sizes not drawn to scale). The forested portion of the site is drawn with stippling and the field portion with no pattern. Distance from the forest–old field edge is indicated as negative for forest plots and positive for field plots, with the edge at position 0. A solid line near distance 0 indicates the approximate position of the forest dripline, and a dashed line near 20 m indicates the location of a mown path.

mown path 1.5 m wide. Vegetation at this distance did not reflect the presence of the path, falling within the gradient of vegetation change observed across the edge (Meiners and Pickett, 1999). The spatial range studied should encompass the majority of the seed shadow for seeds produced within the forested portion of the site (Hughes and Fahey, 1988; Greene and Johnson, 1996; Hughes and Bechtel, 1997) and as such, should have illustrated the influences of the forest edge on the vast majority of tree seeds.

Fifty seeds each of *Acer rubrum* and *Acer saccharum* (Marsh.) and 20 seeds of *Quercus palustris* were planted into separate corners of each plot with ~20 cm between species. Seeds of both *Acer* species were planted even with the soil surface and re-covered with any leaf litter. *Quercus palustris* seed were planted so that the top of the acorn was ~1 cm beneath the soil surface. The hole was then refilled with soil and covered with litter. Care was taken to minimize disturbance to the plot vegetation. Planting occurred on 30 April–1 May 1997 for *A. saccharum*, 5–8 May 1997 for *Q. palustris*, and 26 May–3 June 1997 for *A. rubrum* after stratification of *A. saccharum* and *Q. palustris* (Young and Young, 1992). Seeds of *A. saccharum* and *Q. palustris* were purchased from a commercial supplier (Sheffield's Seed Company, Locke, New York, USA). We chose spring planting to avoid high winter losses to seed predators that also respond spatially to the forest edge (McCormick and Meiners, 2000; S. J. Meiners and K. LoGiudice, unpublished data). *Acer rubrum* seeds were collected from a local population in the spring of 1997 and planted immediately. We covered *Quercus palustris* seed with 25 × 45 cm cages of 1.5-cm hardware cloth that were anchored with two 15-cm turf staples. These exclosures prevented mammalian seed predation but did not hamper the emergence of seedlings. Cages were left in place until harvest. While *Quercus palustris* may have somewhat limited dispersal into the field, seeds and seed fragments of this species have been found >40 m from the forest edge (S. J. Meiners, personal observation). This species is also dispersed by blue jays (*Cyanocitta cristata*), which often bury seeds in vegetation openings (Darley-Hill and Johnson, 1981).

We monitored plots every 2 wk for emergence and mortality until 11 August 1997. Upon emergence, each seedling's location was marked with a plastic toothpick to separate from new germinants. We did not observe any seedlings of any of the experimental species germinating outside of the planted area within the plots, so emergence measures should reflect emergence of planted seed only. On 20–26 August, we harvested both above- and belowground biomass for all surviving seedlings. Seedlings were dried at 70°C for 3 d and weighed. We defined establishment as survival to the end of the first growing season (i.e., to harvest). Establishment defined this way is the product of emergence and survival.

Data analysis—The influence of distance from the forest edge on tree seedling emergence, first-year survivorship, and establishment was tested with

TABLE 2. Regression analysis for growth and root : shoot ratio of *Acer saccharum* and *Quercus palustris* on the gradient across the forest–field edge. Dashes indicate nonsignificant variables dropped from analysis.

	Overall model F	Model df	R^2	Intercept	β coefficients	
					Distance	Distance²
Total biomass						
Acer saccharum	0.32NS	1,81	0.00	2.02	−0.0009NS	—
Quercus palustris	26.02****	1,157	0.14	2.54	0.0047***	—
Root : shoot ratio						
Acer saccharum	6.51**	2,80	0.14	−0.22	0.0140**	−0.0002**
Quercus palustris	0.71NS	1,157	0.01	0.04	−0.0057NS	—

Note: NS = Not significant; **$P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$.

logistic regression (Proc LOGISTIC; SAS, 1989). Logistic regression is analogous to traditional regression analysis with the exception that it uses the logit function to analyze binary data such as survival. Logistic regressions included both distance and squared distance from the edge as independent variables and seedling counts as the dependent. Where the squared distance from the edge was nonsignificant, it was dropped from the model and we report only distance effects. Regression coefficients presented refer to changes per meter distance from the edge. Spatial effects perpendicular to the forest edge gradient were found to be nonsignificant and were dropped from all analyses.

The effects of distance from the forest edge on seedling growth and allocation patterns were analyzed with regression (Proc GLM, SAS Institute, 1989). Growth and root : shoot ratio data were log transformed to conform to normality assumptions of regression analyses. Because allocation patterns vary with seedling development (Gedroc, McConnaughay, and Coleman, 1996), a regression between root : shoot ratio and total seedling biomass was first calculated to remove the influence of seedling size on allocation patterns. The residuals from these analyses were then studied to determine changes in root : shoot ratio across the edge gradient independent from seedling developmental stage. Regression analyses of growth and allocation patterns included both distance and squared distance from the edge as independent variables. Regression coefficients presented from the analyses refer to changes per meter distance from the edge.

RESULTS

Likelihood of emergence varied across the edge gradient for all species (Table 1). Emergence for all species was lowest inside the forest and initially increased with distance into the old field. *Acer rubrum* and *Quercus palustris* had significant negative quadratic terms, with the likelihood of emergence decreasing with greater distances into the field (Fig. 2A, C). In *A. rubrum*, this resulted in a peak in likelihood of emergence at ∼20 m into the field. In *A. saccharum*, emergence was lowest inside the forest and gradually increased across the forest edge and into the old field (Fig. 2B).

A 4-wk drought during the early growing season killed nearly all of the *Acer rubrum* seedlings, preventing analysis of the spatial pattern of survival and establishment for this species. The survivorship responses of *A. saccharum* and *Q. palustris* seedlings to the edge gradient differed (Fig. 3; Table 1). *Acer saccharum* survivorship was 0% inside the forest portion of the gradient and increased significantly with distance into the old field (Fig. 3A). However, *Quercus palustris* survivorship showed no response to the edge gradient. Neither species had a significant effect of squared distance from the forest edge.

Establishment probabilities changed dramatically across the edge gradient with both *A. saccharum* and *Q. palustris* having the highest probability of establishment in the old field portion
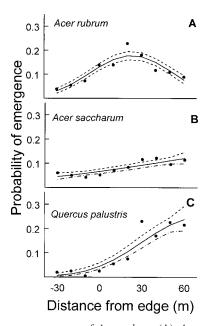

Fig. 2. Emergence responses of *Acer rubrum* (A), *Acer saccharum* (B), and *Quercus palustris* (C) to the forest edge gradient. Negative distances from the edge (distance 0) indicate spatial positions inside the forest. Solid lines represent predicted probabilities of emergence from a logistic regression, with dashed lines representing a 95% confidence interval around that prediction. Points represent proportion of planted seed emerging at that distance.
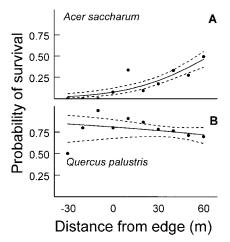

Fig. 3. Survivorship responses of *Acer saccharum* (A) and *Quercus palustris* (B) to the forest edge gradient. Negative distances from the edge (distance 0) indicate spatial positions inside the forest. Solid lines represent predicted probabilities of survival from a logistic regression, with dashed lines representing a 95% confidence interval around that prediction. Points represent proportion of emerged seedlings surviving to harvest at that distance.
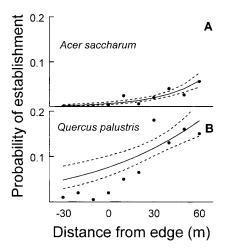
Fig. 4. Effect of the forest edge gradient on the establishment probabilities of *Acer saccharum* (A) and *Quercus palustris* (B). Negative distances from the edge (distance 0) indicate spatial positions inside the forest. Solid lines represent predicted probabilities of emergence from a logistic regression, with dashed lines representing a 95% confidence interval around that prediction. Points represent proportion of planted seed that became surviving seedlings at that distance.
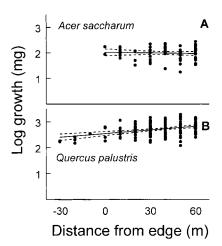

Fig. 5. Growth responses of *Acer saccharum* and *Quercus palustris* to the forest edge gradient. Negative distances from the edge (distance 0) indicate spatial positions inside the forest. Solid lines represent predicted growth from a regression model, with dashed lines representing a 95% confidence interval around that prediction.

of the gradient (Fig. 4; Table 1). Both species showed continuing increases in establishment with increasing distance into the old field. *Acer saccharum* did not become established along the forest portion of the gradient and had overall lower rates of establishment than *Q. palustris*.

Growth of *A. saccharum* had no response to the edge gradient (Fig. 5A) while *Quercus palustris* growth increased significantly from forest to edge to old field (Fig. 5B; Table 2). The relationship between total seedling mass and allocation pattern was weak and only marginally significant in *A. saccharum* ($F_{1,81} = 3.52$; $P = 0.0642$; $R^2 = 0.04$) but fairly strong in *Q. palustris* ($F_{1,157} = 38.00$; $P < 0.0001$; $R^2 = 0.19$). After correcting for biomass effects, root allocation varied significantly with position along the edge gradient in *A. saccharum* but not in *Q. palustris* (Fig. 6). Root : shoot ratio in *A. saccharum* initially increased with distance into the old field but then decreased, resulting in a significant negative quadratic term. The maximum allocation to roots in this species occurred at 40 m into the old field.

DISCUSSION

All species tested showed significant edge effects on seedling recruitment. The variety of edge effects found in this experiment shows that the edge gradient is not a uniform environment for tree recruitment and that tree species respond to this gradient differently. Seedling performance generally was higher in the field than in the forested portion of the site, but the spatial position of optimal performance differed among species and among individual demographic measures. Many of the edge responses in this system show continued changes 30+ m into the old field, showing the potential for long-distance edge influences in fields.

Emergence responses—Emergence in the old field portion of the site ranged from 5 to 25%, which is typical of studies of trees in old fields (Burton and Bazzaz, 1991; DeSteven, 1991; Gill and Marks, 1991; Meiners and Gorchov, 1998; Meiners, Handel, and Pickett, 2000). Shading by woody species

can reduce tree seedling emergence (Callaway, 1992; Meiners and Gorchov, 1998) and may explain decreases in emergence close to the edge and inside the forest. The variation among species in emergence response shows the individualistic nature of species' edge responses and the potential of edges to greatly affect spatial patterns of forest regeneration.

Survivorship responses—While overall survivorship of *A. saccharum* was low, interesting spatial variation was present in the species. Whitney and Runkle (1981) found that this species was more abundant in forest interiors than at edges, attributing this to the shade tolerance of *A. saccharum*. In the current study, *Acer saccharum* seedlings clearly had higher survival in the old field portion of the edge gradient rather than in the forest, as was initially predicted. However, the mortality of *A. saccharum* in the forest may not have been due to physiological limitations, but to slug herbivory. Both *Acer* spe-
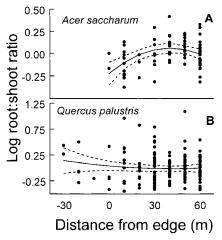

Fig. 6. Allocation responses of *Acer saccharum* and *Quercus palustris* to the forest edge gradient. Negative distances from the edge (distance 0) indicate spatial positions inside the forest. Solid lines represent predicted root : shoot ratio from a regression model, with dashed lines representing a 95% confidence interval around that prediction.

TABLE 1. Summary of logistic regression analyses on the effects of distance from the forest edge on the probability of emergence, survival, and establishment of tree seedlings. Because nearly all *Acer rubrum* seedlings died, analyses for survival and establishment are for *Acer saccharum* and *Quercus palustris* only. Quadratic terms were only included in the model when $P \leq 0.05$. Dashes indicate nonsignificant variables dropped from analysis.

Demographic measure	Overall model χ^2	Model df	Intercept	β coefficients	
				Distance	Distance^2
Emergence					
Acer rubrum	101.73****	2	−1.89	0.0321***	−0.0007***
Acer saccharum	39.83****	1	−2.66	0.0118***	—
Quercus palustris	96.64****	2	−3.07	0.0540***	−0.0004*
Survival					
Acer saccharum	37.63****	1	−2.49	0.0387***	—
Quercus palustris	1.01NS	1	1.45	−0.0084NS	—
Establishment					
Acer saccharum	52.80****	1	−5.05	0.0375***	—
Quercus palustris	17.43****	1	−2.49	0.0161***	—

Note: NS = Not significant; *$P < 0.05$; ***$P < 0.001$; ****$P < 0.0001$.

cies were found to have some damage indicative of slug herbivory in the forest. We frequently observed slugs in the forest plots, but they were never feeding on seedlings. Unfortunately, the direct cause of mortality could not be determined for most seedlings.

Survivorship of *Quercus palustris* was unaffected by the edge. However, growth of *Q. palustris* continued to increase with distance into the field. Because growth rate often determines the survivorship of seedlings (Kobe et al., 1995), we would have expected that survivorship also would have increased with distance into the field.

Growth and allocation responses—The lack of a growth response of *Acer saccharum* to the edge gradient may be explained by its shade tolerance. While able to grow at low light levels, this species may be physiologically unable to take advantage of higher light levels in the field (Bazzaz and Carlson, 1982). For example, growth of this species was unaffected by shading from *Juniperus virginiana* in an Ohio old field (Meiners and Gorchov, 1998). With little change in potential net photosynthetic assimilation across the gradient, *A. saccharum* growth would remain constant. Although not measured in this study, changes in light intensity (e.g., Cadenasso, Traynor, and Pickett, 1997) across the edge gradient probably explain the growth response of *Quercus palustris*. This species is highly shade intolerant as a seedling and can grow quickly with sufficient light (USDA, 1990). The growth response of *Q. palustris* follows the predictions based on its shade tolerance.

After removing the influence of overall plant size, allocation patterns did not change across the edge gradient for *Q. palustris*. This analysis suggests that the seedling-scale environment did not change sufficiently across the site to cause changes in the allocation patterns of first year seedlings or that *Q. palustris* seedlings were not able to change allocation patterns. The hump-shaped response of *A. saccharum* was unexpected. This response may be caused by changes in a combination of factors across the edge gradient such as light availability, soil moisture, and background vegetation. Regardless of the mechanism, this change in seedling allocation patterns represents a very subtle, long-distance effect of forest edges.

Establishment probability and the edge gradient—While the emergence and mortality patterns differed greatly among species, their establishment responses to the edge were similar. Both *A. saccharum* and *Q. palustris* show responses consistent with that predicted for shade-intolerant species. While we predicted this response for *Q. palustris*, our initial prediction was that *A. saccharum* would have higher establishment near the forest because of its shade tolerance. The emergence response drives the pattern of establishment in *Q. palustris*, while establishment for *A. saccharum* is a combination of emergence and mortality.

Most studies of forest fragments have found changes in the numbers of tree seedlings near edges. Several studies have identified species that are less abundant at forest edges than forest interiors (Whitney and Runkle, 1981; Chen, Franklin, and Spies, 1992; Young and Mitchell, 1994). These species tend to be shade-tolerant species characteristic of old-growth forests (Whitney and Runkle, 1981). The majority of species studied to date show increased seedling abundances at the edge of forest fragments (Wales, 1972; Whitney and Runkle, 1981; Williams-Linera, 1990; Chen, Franklin, and Spies, 1992; Young and Mitchell, 1994; this study). These species are often shade-intolerant species that depend on gaps for regeneration (Wales, 1972). These studies show the potential for varied tree responses to edge gradients.

In regional models of forest regeneration, it may be necessary to account for species responses to edges. If increasing rates of establishment with increasing distance from the forest edge are a general edge response in eastern forests, modeling the distribution of these trees by seed dispersal alone would result in the underestimation of seedling abundance at greater distances from the edge. For example, Hughes and Bechtel (1997) studied *Picea rubens* regeneration in a clear-cut, quantifying both seed dispersal and seedling abundance. Seedling abundance did not vary with distance from the edge, while seed dispersal declined exponentially. This response suggests that seeds at greater distances from the edge had a greater probability of establishment, resulting in constant numbers of seedlings regenerating across the site. For this reason, seedling establishment in fragmented systems cannot be modeled purely as a function of seed dispersal (Johnson, 1988; Lepage et al., 2000), but as a combination of dispersal and establishment. While we know little of establishment responses for most species, establishment rates can clearly change dramatically in association with edge gradients.

Conclusions—In order to understand changes in plant community composition and dynamics across edge gradients, both the spatial pattern of dispersal and the edge response of the

species will need to be determined. This study highlights the need to examine the more subtle effects of habitat fragmentation on plant community dynamics. By altering the spatial pattern and species composition of tree invasions, edges may generate long-term patterns in regenerating forests. This spatial legacy may continue long after canopy closure in the disturbed site. We also suggest testing many more tree species to determine the range of edge responses in natural systems.

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