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Secondary seed dispersal and its role in landscape organization

Sally Thompson[1] and Gabriel Katul[1]

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[1] Mathematical models of banded vegetation patterns predict rapid upslope migration of vegetated patches not realized in field observations, a key point of disagreement between theory and observation. It is shown that the disagreement between model results and field observations can arise from seed dispersal dynamics. Two representations of biomass movement are used to test the hypothesis that secondary seed dispersal in overland flow inhibits band migration. The first is based on coupling down-slope water transport and seed advection. The second uses a kernel-based representation of seed transport where an anisotropic dispersal kernel combines the effects of isotropic primary and downslope secondary seed dispersal, and ensures that conclusions about secondary dispersal are independent of diffusive representations of biomass movement. The analysis demonstrates that secondary seed dispersal can retard upward movement of banded vegetation irrespective of the precise representation of biomass movement as long as the anisotropic effects are accounted for. **Citation:** Thompson, S., and G. Katul (2009), Secondary seed dispersal and its role in landscape organization, *Geophys. Res. Lett.*, *36*, L02402, doi:10.1029/2008GL036044.

1. Introduction

[2] Banded vegetation, consisting of interspersed bands of vegetation and bare soil, occurs in arid ecosystems worldwide in association with biological soil crusts, intense, infrequent rainfall, and slopes of 0.2–2 % [*Valentin et al.*, 1999]. Vegetation patterns are thought to arise from a positive feedback between soil moisture availability and biomass density, emergent properties of coupled hydrological and ecological processes [*D'Herbes et al.*, 2001]. The dynamics of these systems have attracted interest due to their occurrence in areas prone to desertification [*Goutorbe et al.*, 1997], their importance as a source of forage [*Safriel and Adeel*, 2003], and numerical predictions suggesting the patterns are indicator of desertification [*Rietkerk et al.*, 2002, 2004]. Numerical models repeatedly predict upslope migration of vegetated patches due to increased facilitation at the upslope edges of the bands, encouraging expansion at rates of 10–100 m/year in many models [*Klausmeier*, 1999; *Rietkerk et al.*, 2002; *Thiery et al.*, 1995; *von Hardenberg et al.*, 2001]. This prediction remains one of the most debated questions regarding band dynamics [*Seghieri and Dunkerley*, 2001; *Worrall*, 1959]. Measures of upslope vegetation movement at rates of 0.10 to 0.15m/year have been reported [*Leprun*, 1999], but other studies found no evidence of migration over 5–8 years [*Cornet et al.*, 1992; *Montana*, 1992]. Over short observation windows, systematic upslope migration is difficult to distinguish from temporary expansion/contraction of bands [*Tongway and Ludwig*, 2001]. Increasingly, field studies are concluding that spatial variation of band vegetation reflects niche partitioning and not upslope migration [*Couteron et al.*, 2000].

[3] Mathematical models of banded systems predict an unequivocal and rapid (10–100 m/year) migration of the vegetation bands, 2–3 orders of magnitude faster than observations [*Klausmeier*, 1999; *Rietkerk et al.*, 2002; *Thiery et al.*, 1995; *von Hardenberg et al.*, 2001]. This is a key point of disagreement between theory and observation. It is argued here that this disagreement can be resolved by consideration of seed transport, or more precisely, its representation in the modelling framework used in previous studies. Although seed dispersal is critical for migration of vegetation communities, these processes are only now being incorporated into models of patterned vegetation [*Pueyo et al.*, 2008; *Thompson et al.*, 2008].

[4] We hypothesise that the rapid band migration generated by contemporary models arises from the failure of diffusion-based representations of biomass migration to capture important features of seed dispersal in these systems. Seed banks in banded systems are concentrated within vegetated bands, where the seed density can be 180 times greater than in the bare interband [*Mauchamp et al.*, 1993; *Seghieri et al.*, 1997]. Seeds are transported down slope from bare sites by runoff [*Aerts et al.*, 2006]. This advection can be the dominant dispersal mechanism for some species, even in dry environments [*Friedman and Stein*, 1980]. Recruitment of seedlings on the biological crusts in the interband is minimal [*Montana et al.*, 2001; *Prasse and Bornkamm*, 2000], and this exaggerates tendency for recruitment to occur within the bands rather than at their edges.

[5] Two different approaches are taken to incorporate secondary dispersal of seed. The first approach adds advection of seeds to a process-based model that couples water and biomass dynamics to predict upslope migration of vegetation bands [*Rietkerk et al.*, 2002]. Promisingly, previous qualitative examination of secondary seed dispersal by similar mechanisms suggests that it may alter band migration dynamics [*Saco et al.*, 2007]. The second uses the kernel-based approach of *Thompson et al.* [2008] to improve the realism of dispersal modelling. In this kernel-based model framework, an anisotropic seed dispersal kernel parameterises the combined effect of isotropic primary dispersal and directional (downslope) secondary seed dispersal. The use of the two different models of seed transport allows conclusions about secondary dispersal to be decoupled from the exact treatment of seed movement. It should be understood that the underlying ecological and hydrological representation of banded vegetation dynamics

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[1] Nicholas School of the Environment and Earth Sciences, Duke University, Durham, North Carolina, USA.

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Table 1. Model Parameters (Dimensional and Nondimensional) Used in Analysis

Dimensional Parameters	Value	Nondimensional Parameter	Value
c (g mm^{-1} m^{-2}) Water uptake: plant growth ratio	10	$b = \dfrac{d}{cg_{\max}}$	0.8
$g_{\max}$ (mm m^{2}g^{-1} day^{-1}) Maximum specific water uptake	0.05	$r = \dfrac{r_w}{cg_{\max}}$	0.2
R (mm day^{-1}) Precipitation	0.75	$R' = \dfrac{R}{k_1 cg_{\max}}$	0.5
k_1 (mm) Half saturation constant of water uptake	3	$k = \dfrac{k_2}{k_1 c}$	0.1667
k_2 (g m^{-2}) Half saturation constant of infiltration	5	$D'_p = \dfrac{D_p \alpha^2}{V_o^2 cg_{\max}}$	0.00002–0.008
D_{p} (m^2 day^{-1}) Biomass diffusion coefficient	0.004–1.6	$D'_w = \dfrac{D_w \alpha^2}{V_o^2 cg_{\max}}$	0.00008
α (day^{-1}) Maximum infiltration rate	0.1	$V'_p = \dfrac{V_p}{V_o}\dfrac{\alpha}{cg_{\max}}$	0.08–0.2
V_o (m day^{-1}) Surface water velocity	2	$\gamma = \dfrac{cg_{\max}}{\alpha}$	5
D_w (m^2 day^{-1}) Soil water diffusion coefficient	0.01	$x' = \dfrac{x\alpha}{V_o},\ y' = \dfrac{y\alpha}{V_o}$	0.2
V_p (m day^{-1}) Seed advection velocity	0.4–2	$t' = tcg_{\max}$	0.5
dx, dy (m) Cartesian increments	1		
dt (day) Time increment	1		
d (day^{-1}) Mortality rate	0.1		
r_w (day^{-1}) Water loss to deep drainage/evaporation	0.1		

is equivalent between the two models, which differ only in their precise depiction of seed transport.

2. Model

[6] The starting point is *Rietkerk et al.*'s [2002] reaction-diffusion model on a slope:

$$\frac{\partial P}{\partial t} = c\, g_{\max} \frac{W}{W + k_1} P - d\,P + D_p \nabla^2 P$$
$$\left(\mathrm{P:\ \ plant\ biomass,\ \ g\ m^{-2}}\right)$$

$$\frac{\partial W}{\partial t} = \alpha\, O \frac{P + k_2 W_o}{P + k_2} - g_{\max} \frac{W}{W + k_1} P - r_w W + D_w \nabla^2 W$$
$$\mathrm{(W:\ \ soil\ water\ depth,\ \ mm)}$$

$$\frac{\partial O}{\partial t} = R - \alpha\, O \frac{P + k_2 W_o}{P + k_2} + V_o \frac{\partial O}{\partial x}$$
$$\mathrm{(O:\ \ surface\ water\ depth, mm)}$$

The terms in this model are given in Table 1. The modification consists of the addition of a term representing down slope advection of seeds to the biomass equation. This term is the spatial derivative of the advective biomass flux, a product of the mobile biomass (κP) and its advection velocity V_p. To first order, it is assumed that the proportionality constant κ and the biomass velocity are spatially uniform, so that $\frac{\partial \left(V_p \kappa P\right)}{\partial x} = V_p \kappa \frac{\partial P}{\partial x}$. Advection in surface runoff is assumed to be primarily responsible for seed transport down-slope, so $V_p \le V_o$. In this refined model seed dispersal is a two-stage process. The first stage of isotropic primary dispersal of seed from the plant to the ground is parameterized by $D_p{}'$, and subsequent, directional secondary dispersal in overland flow occurs with rate $V_p{}'$. Selection of an appropriate value of κ is problematic given that the continuous model allows biomass movement to occur continuously rather than seasonally. Plants commit a wide range of biomass to reproduction, up to 50% for some annuals [*Aronson et al.*, 1993]. An intermediate value of κ = 0.2 was used for all simulations. The revisions can be incorporated in other models of banded vegetation and the Rietkerk model is used here primarily as a case study.

[7] The model was nondimensionalized to facilitate numerical investigations. The nondimensional equations are (see Table 1 for definition of parameters):

$$\frac{\partial P'}{\partial t'} = \frac{W'}{W' + 1} P' - bP' + D_p{}' \nabla^2 P' + V_p{}' \kappa \frac{\partial P'}{dx'}$$

$$\frac{\partial W'}{\partial t'} = O' \frac{P' + W_o}{P' + 1} - k' \frac{W'}{W' + 1} P' - rW' + D_w{}' \nabla^2 W$$

$$\gamma \frac{\partial O'}{\partial t'} = R' - O' \frac{P' + W_o}{P' + 1} + \frac{\partial O'}{dx'}$$

The properties of the original model are examined in several other papers [*HillerisLambers et al.*, 2001; *Rietkerk et al.*, 2002] and are not repeated here. Instead the focus is on band migration and the related control parameters $V_p{}'$ and $D_p{}'$. The impact of varying $V_p{}'$ and $D_p{}'$ on band migration, while holding all other parameters constant (Table 1), was investigated in a 1D model, following the observation that patterns tended towards a 1D steady state. $V_p{}'$ was varied with $D_p{}' = 8 \times 10^{-4}$, while $D_p{}'$ was varied while holding at $V_p{}' = 0.1$, corresponding to realistic dimensional parameters [*Rietkerk et al.*, 2002]. Initial conditions consisted of equally spaced bands of varying wavelength k.

[8] The premise that biomass movement is diffusive remains questionable given the non-Gaussian nature of many dispersal kernels. The kernel-based model of *Thompson et al.* [2008] was used as a reference to test if the retardation of upslope band movement is linked with biomass diffusion. This model represents biomass movement processes in a

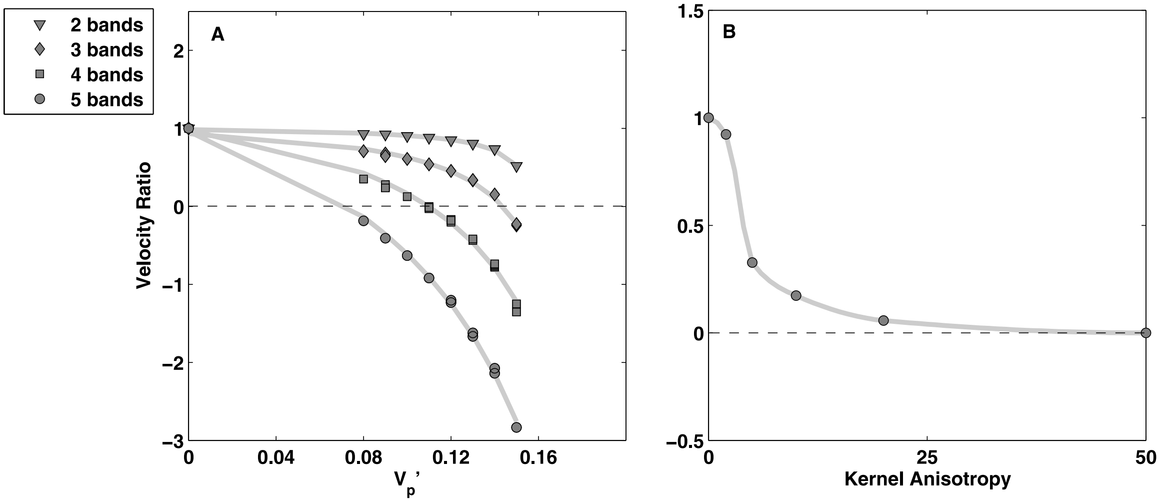

Figure 1. Band velocities shown as ratios between the anisotropic test cases and the equivalent isotropic model. The same initial conditions are used for each set of data points on a given line. (a) Decline and eventual reversal of the velocity ratio with increasing downslope advection. (b) Decline of the velocity ratio as the degree of anisotropy in the kernel is increased from a factor to 2 to a factor of 50.

seed dispersal kernel that captures the statistics of seed transport from an individual plant. This model modifies the biomass equation as follows:

$$\frac{\partial P}{\partial t} = \left(c\, g_{\max}\frac{W}{W+k_1}P - d\,P\right)(1-\phi) + \phi\left(\int\int \vartheta(x-x', y-y')P(x',y')dx'dy'\right).$$

Here ϑ is the dispersal kernel (that can account for secondary dispersal mechanisms if known), ϕ represents the proportion of standing biomass dispersed per unit time (on the order of 4×10^{-4} g/m^{2}day [*Thompson et al.*, 2008]) and x' and y' define the distance seeds move from the parent, integrated over the domain.

[9] No measured dispersal kernels ϑ accounting for both primary and secondary transport in banded systems were available. A qualitative approach was adopted by taking an isotropic Wald or Inverse Gaussian kernel, often used to represent wind dispersal of seed [*Thompson and Katul*, 2008]. The anisotropy associated with secondary dispersal was incorporated by weighting the upslope half of the kernel to one fiftieth of the value of the downslope half (a conservative value compared to the 180-fold discrepancy observed in seed bank density) and normalized.

[10] The precise treatment of all eco-hydrological processes in both modelling approaches can be criticized ad infinitum. However, to address the study objective here, it suffices to demonstrate that banded vegetation migration rates can be significantly retarded when a primitive treatment of secondary dispersal is included. The model results here should not be viewed as providing 'finality' to the migration of banded vegetation problem but are logical first steps highlighting processes that require further consideration.

3. Results

[11] Band migration velocities produced by the unmodified Rietkerk model [*Rietkerk et al.*, 2002] were on the order of 20–200 m/year, depending on the band wavenumber, with the parameter values in Table 1. The isotropic kernel-based model [*Thompson et al.*, 2008] generated velocities of approximately 10 m/year. Both models in their unmodified form therefore generated band migration at rates at least an order of magnitude greater than field observations could support, although we emphasise that the models have not been calibrated to a specific ecosystem, and that these results are included solely to provide a frame of reference for typical model output.

[12] The hypothesis that band migration is inhibited by the inclusion of anisotropy in seed dispersal was explored through the advection-diffusion and a kernel-based model. The band velocities for varying degrees of secondary dispersal are presented as a ratio of the band velocity when dispersal was purely isotropic in Figure 1. Snapshots of the band evolution for the two models in isotropic and anisotropic modes are provided in Figure 2.

[13] In the case of the advection diffusion model, systematic variation of the parameters $V_p{}'$ and $D_p{}'$ slowed and eventually reversed the band migration velocity (Figure 1a). The band velocity was also found to depend upon the wavenumber of the pattern, with upslope movement favoured at low wavenumbers. Downslope movement of the bands occurred at large values of the dimensionless seed advection velocity $V_p{}'$, and small values of the dimensionless seed diffusion coefficient $D_p{}'$. Phase diagrams detailing the effects of $V_p{}'$, $D_p{}'$ and the wavenumber in terms of the direction of band migration are provided as auxiliary material.[1] As will be elaborated on in the discussion, the prediction of bands downslope band migration should be treated with caution. These results should be interpreted as indicating the regime in which upslope migration is precluded.

[14] For the kernel-based model, an increasing degree of anisotropy in the kernel slowed and eventually halted band evolution in the direction of the slope gradient, so that band migration dynamics occurred primary across the slope. In

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[1] Auxiliary materials are available in the HTML. doi:10.1029/2008GL036044.

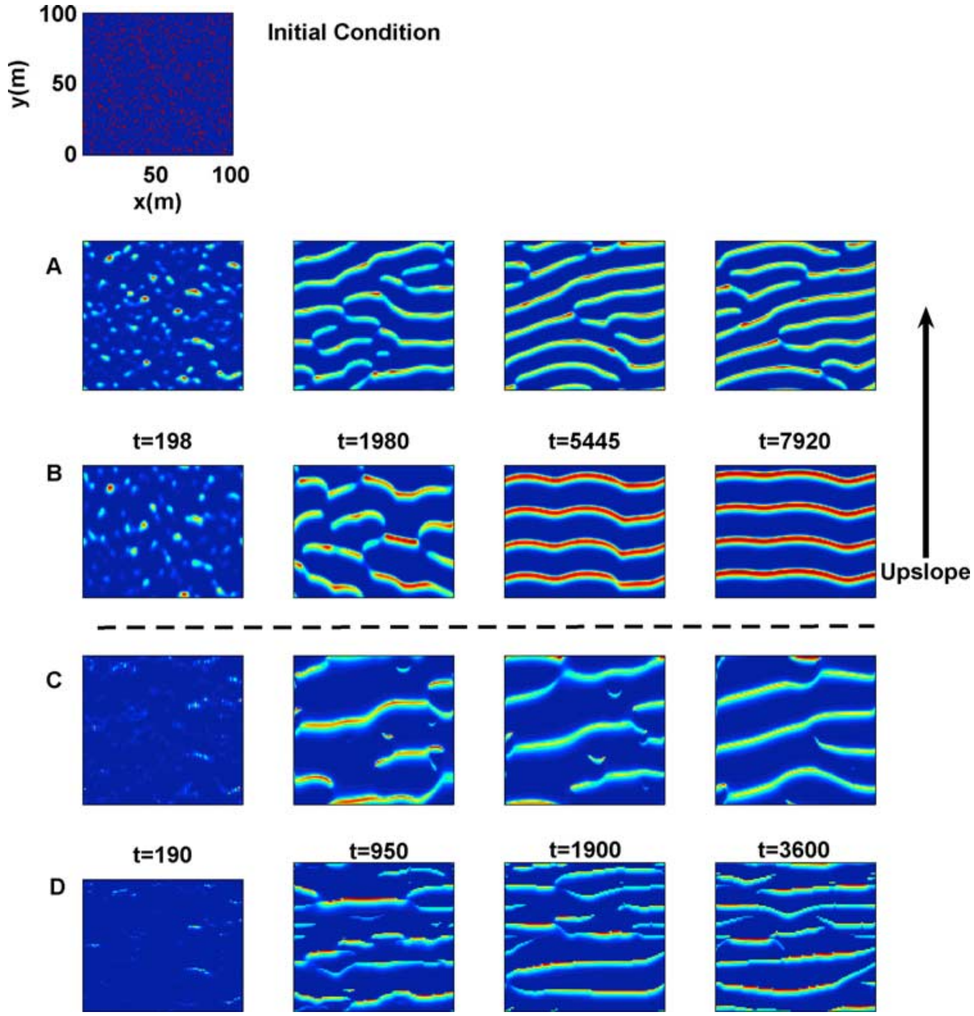

Figure 2. Snapshots in time of the modelled spatial biomass density. The same initial condition was used in each case. (a) Results from the reaction-diffusion model with diffusive biomass transport. The bands move rapidly upslope. (b) Model output when a downslope biomass velocity of 0.46 m/s was added. Band migration rates approach zero, and the bands evolve towards a 1D pattern. (c) Kernel model output with an isotropic kernel. Bands rapidly migrate upslope. (d) $same model in which the kernel is weighted by a factor of 50:1 downslope. Band migration is essentially confined to the cross-slope direction.

the absence of information to constrain the possible forms of the anisotropic kernel, only the effects of upslope-downslope anisotropy were tested, generating the velocity ratio data shown in Figure 1b.

4. Discussion and Conclusions

[15] The model results indicate that a down-slope flux of biomass associated with secondary dispersal of seeds in overland flow is sufficient to freeze or even reverse the upslope migration of vegetation bands. This result can be physically understood by relating the model parameters $V_p{}'$ and $D_p{}'$ to more commonly used measures of seed and dispersal properties. Seed transport in overland flow can be described as saltation [*Bagnold*, 1973], in which V_p equals V_o minus a thrust term accounting for particle re-suspension. This thrust approximately equals the seed terminal velocity V_g, that may be estimated from gravity (g), the seed drag coefficient C_d, diameter d, and specific gravity γ_g of a seed.

$$\text{So, } V_p' = \frac{1}{\gamma}\frac{V_p}{V_O} = \frac{1}{\gamma}\frac{V_O - V_g}{V_O} = \frac{1}{\gamma}\left(1 - \frac{1}{V_O}\sqrt{\frac{4gd}{3C_d}\gamma_g}\right)$$

Dimensional analysis offers an interpretation of $D_p{}'$. Firstly a definition of $D_P = \frac{C_p^2}{4r}$, where r is the average growth rate of the population is used. C_p the migration velocity of the vegetation population can be derived from the properties of most seed dispersal kernels using the procedure described by *Thompson and Katul* [2008]. Substituting for D_P and γ, $D_p{}' = \frac{C_p^2\alpha}{4rV_o^2}\frac{\alpha}{cg_{\max}}$. When water is plentiful $r \Rightarrow cg_{\max}$, and so $D_p{}' = \left(\frac{C_p}{2\gamma V_o}\right)^2$. The control parameters thus give the ratio of biomass transport induced by primary seed dispersal to the rate of water transport ($D_P{}'$), and of seed to flow velocity ($V_P{}'$). Upslope band migration ceases when $C_p < V_o$, or as $V_p \rightarrow V_o$.

[16] The effect of wavenumber on band migration can be understood in terms of resource delivery to the upslope edge of the band, which is maximised for low wavenumbers and declines as wavenumbers increase. At low wavenumbers the increased availability of resources upslope of the band results in high survival and rapid growth of the relatively few seeds dispersed there. As resource availability and upslope survival declines (higher wavenumbers), the higher density of the downslope seed bank becomes the dominant driver of band migration.

[17] Although the model results predict downslope migration of the bands, this is probably a consequence of the simple representation of dispersal. Vegetation bands are effective in trapping particles and slowing the velocity of water. The difference in the seed bank density within and outside bands [*Seghieri et al.*, 1997] suggests that bands are effective at trapping seeds. Advection of seeds in runoff is likely to transport seed to, but not through, the bands. Down-slope migration should be interpreted as indicative of a regime where upslope migration is prevented.

[18] Models of banded vegetation have consisted of primarily hydrological models focused upon surface water dynamics with minimal representation of vegetation [*Ludwig et al.*, 1994, 1999; *Mauchamp et al.*, 1994], or reaction-diffusion models coupling simplified vegetation and hydrological dynamics (as used in this study) [*Barbier et al.*, 2008; *Klausmeier*, 1999; *Rietkerk et al.*, 2002; *Thiery et al.*, 1995; *von Hardenberg et al.*, 2001]. This distinction is not surprising given the timescale separation between the fast hydrologic and slow biomass movement dynamics. The results here suggest that a reconciliation of these approaches is needed to formally scale up over the fast timescales determining water and seed redistribution, to the slower timescales determining vegetation growth. This averaging approach will require stochastic treatment of input parameters, particularly rainfall distributions, to evaluate infiltration and biomass responses. It may be facilitated by tracer studies in the vadose zone [*Allison et al.*, 1994; *Allison and Hughes*, 1978; *Scanlon*, 2000], offering insight into soil moisture residence time, transport paths, and the water sources used by plants.

[19] New approaches should also extend the use of kernel-based descriptions of seed dispersal dynamics. This work suggests that the heretofore little studied process of secondary seed dispersal in overland flow may alter the macroscopic spatial dynamics of vegetation communities. This process is physically mediated and readily amenable to physical analysis. Detailed studies of such processes, in combination with relevant field measurements of primary and secondary dispersal (e.g., through release of buoyant tracers [*Boedeltje et al.*, 2004; *Merritt and Wohl*, 2002]) would allow the elucidation of the full anisotropic seed dispersal kernel, and the quantitative use of kernel based models.

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G. Katul and S. Thompson, Nicholas School of the Environment and Earth Sciences, Duke University, Durham, NC 27707, USA. (gaby@duke.edu; set8@duke.edu)