Refining tree recruitment models

C. Calogeropoulos, D.F. Greene, C. Messier, and S. Brais

Abstract: We used a micrometeorological dispersal model to simulate seed and seedling distributions derived from subcanopy balsam fir (*Abies balsamea* (L.) Mill.) source trees in a trembling aspen (*Populus tremuloides* Michx.) dominated forest. Our first objective was to determine the effect of substituting basal area for cone production as a proxy for seed output. The results showed that the r^2 from the regression of predicted versus observed densities increased by ~5% for seeds and ~15% for seedling simulations. Our second objective was to determine the effects of changing the median horizontal wind speed. The median speed in this forest environment varies according to the proportion of leaves abscised. For values of the median expected wind speed between the extremes of leafless and full-canopy forests, the r^2 of predicted versus observed varied between 0.35 and 0.49 for seeds and between 0.33 and 0.62 for seedling simulations. We demonstrated that the simple one-dimensional model can have added precision if the dispersal parameters are chosen so as to allow more fine-scale variation.

Résumé : Nous avons utilisé un modèle de dispersion micrométéorologique pour simuler la distribution des graines et des semis de sapin baumier (*Abies balsamea* (L.) Mill.) provenant de semenciers en sous-étage dans une forêt dominée par le peuplier faux-tremble (*Populus tremuloides* Michx.). Notre premier objectif était de déterminer l'effet d'une substitution de la production de cônes par la surface terrière comme approximation de la production semencière. La valeur de r^2 de la régression entre les densités observées et prédites par simulation a augmenté d'environ 5 % pour les graines et d'environ 15 % pour les semis. Notre deuxième objectif était de déterminer les effets du changement de la vitesse horizontale médiane du vent. La vitesse médiane dans cet environnement forestier varie en fonction de la proportion des feuilles qui se sont détachées. Pour des valeurs attendues de vitesse médiane du vent entre les extrêmes allant d'un couvert forestier sans feuilles à totalement feuillé, la valeur de r^2 entre les valeurs observées et prédites par simulation variait de 0,35 à 0,49 pour les graines et de 0,33 à 0,62 pour les semis. Nous avons démontré qu'un modèle simple et unidimensionnel peut avoir une meilleure précision si les paramètres de dispersion sont choisis de façon à permettre plus de variation à petite échelle.

[Traduit par la Rédaction]

Introduction

Recently the field of ecology has seen a shift from research seeking to describe patterns and generalities to a field seeking to develop simulation models that express these underlying processes. These simulations couple life-history arguments (e.g., recruitment, subsequent growth, competition, and death) as subroutines. A spatially explicit tree recruitment subroutine (e.g., Lepage et al. 2000) is of the following form:

$$[1] \qquad F_{Dx,y} = \lambda B S_{x,y} f(x)$$

where $F_{Dx,y}$ is the density of seedlings in Cartesian space, B is the basal area (m^2) of the source tree with the coefficient λ scaling the relationship between basal area and seed production, $S_{x,y}$ is the expected survivorship during the establishment phase (a function primarily of seedbeds and granivory), and $f(x)$ is the dispersal term. It is assumed that the exponent on B (omitted here for simplicity) is about 1.0 (Greene and Johnson 1994; Clark et al. 1994), but the literature is far too sparse to warrant confidence.

The recruitment subroutine subsequently passes the established seedling density on to subroutines governing growth, light, and thinning-induced mortality (e.g., Pacala et al. 1996). However, a problem that has not been remarked upon involves the coefficient of variation in seedling density. Competition for light will decline with distance between competitors and yet present recruitment subroutines (eq. 1) tend to homogenize density at small scales (i.e., predict a monoculture arrangement). For example, Ribbens et al. (1994; their Fig. 3) predict a relatively uniform distribution of recruits of *Acer saccharum* Marsh. with a coefficient of variation (CV) of 0.33 despite the clumped distribution of the observed recruitment (CV = 0.91). Clearly, with two or more competing species in a system, it will matter greatly in

Received 21 March 2002. Accepted 9 August 2002. Published on the NRC Research Press Web site at http://cjfr.nrc.ca on 10 December 2002.

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doi: 10.1139/X02-154

the subsequent dynamics if all species are essentially found everywhere versus a much more clumped distribution where, most cogently, the inferior competitor can occasionally establish in areas (say a few square metres in extent) that contain no recruits from more competitive species.

Two of the important sources of homogenization arising in present approaches to eq. 1 involve the terms λB (the source-strength term) and $f(x)$ (the dispersal term). There are a number of problems with the source-strength term that we will take up in a separate paper (e.g., the assumption that light receipt is unimportant, and thus, a small tree at the edge of a gap will produce fewer seeds than a large subcanopy stem within an intact stand). Here, we merely point out that while basal area may well be our single best predictor of seed production for a species (cf. Greene and Johnson 1994); nonetheless, the proportion of variation explained is typically only on the order of 0.5 (e.g., Greene and Johnson 1998; Greene et al. 2002). Our first objective is to show that accounting for this unexplained variation in seed production will indeed increase the expected CV of predicted seed or seedling density in a nontrivial manner and, further, will lead to a higher correlation for observed versus predicted recruit density.

Our second objective is to examine the effect of the dispersal term ($f(x)$) on the predicted CV. There are three possible sources enhancing the homogenization of the predicted recruitment. The first factor is the assumption that wind direction can be ignored: that is, an annulus around a tree is expected to have a constant density. Of course, however, wind speed azimuthal distributions are never random or uniform. Further, a number of studies have shown that seed abscission by conifers and hardwoods is much more likely when relative humidity is low; in turn, relative humidity typically shows an azimuthal bias (e.g., Harris 1969; Nathan et al. 2001). Not surprisingly, therefore, a few studies have shown that dispersal curves do indeed show strong azimuthal preferences (e.g., Tanaka et al. 1998; Stoyan and Wagner 2001).

A second dispersal-related factor promoting homogenization is the use of $f(x)$ as a continuous function. In reality, most abscission events occur in a few brief episodes when relative humidity is low and wind speeds are high. For example, with a 15-min averaging time, 2% of the dispersal season (defined arbitrarily as the time from the first to the 99th percentile of the cumulative distribution for abscission) accounted for 57% of all abscised seeds in *Acer saccharinum* L. (Greene and Johnson 1992) and 52% in *Taraxacum officinale* L. (D.F. Greene, unpublished data). Thus, rather than a smooth continuous function, actual one-dimensional dispersal curves should be much more poorly behaved.

The third factor is the choice of $f(x)$ itself. To take an extreme example, Ribbens et al. (1994) and Lepage et al. (2000) used an exponential function with distance taken to the power three. This results in a dispersal curve (density vs. distance) that is virtually flat out to about the mean dispersal distance, and then subsequently declines quite rapidly. Now, if the mean distance between source trees is less than the mean dispersal distance (quite likely given that recruit sample size considerations will encourage one to work with a high density of conspecific trees), then we will predict a very small CV (e.g., Ribbens et al. 1994).

Strangely, given the growing prominence of stand dynamics simulators with spatially explicit recruitment subroutines, the issue of the underprediction of the observed CV has not been examined. In this paper we will look only at the effects of λB and $f(x)$, holding the role of seedbeds (a prime determinant of juvenile survivorship in eq. 1) relatively constant by only examining mineral soil seedbeds.

Materials and methods

Study area

The southern boreal forest study site was located in western Quebec in the Abitibi-Temiscamingue region (79°W, 48°N) on the south shore of Lake Duparquet. Soils are postglacial lacustrine clays. The forest originated from a 1916 fire about 100 ha in size. Bergeron and Charron (1994) provide a detailed description of the long-term dynamics at this site via stand reconstruction. The forest is presently dominated by trembling aspen (*Populus tremuloides* Michx.) with a large amount of post-1916 conifer understory comprised primarily of balsam fir (*Abies balsamea* (L.) Mill.) with small numbers of white spruce (*Picea glauca* (Moench) Voss) and eastern white-cedar (*Thuja occidentalis* L.). The site was chosen because it is bisected by a 530 m long, 3 m wide bladed path created in 1992 by a mining company. This path, initially mineral soil, is now covered by a thick deposit of leaf litter from the adjacent aspen and colonizing herbs. Ring counts on samples (n = 30) of fir seedlings found on the path showed that more than 90% of the recruitment occurred in the period 1993–1996 when there was presumably a great deal of exposed mineral soil remaining. Furthermore, the great majority of these aged seedlings were from the two years 1994 and 1996, corresponding to measured mast years (1993 and 1995, respectively) in the study of Raymond (1998) 500 km to the east of our site.

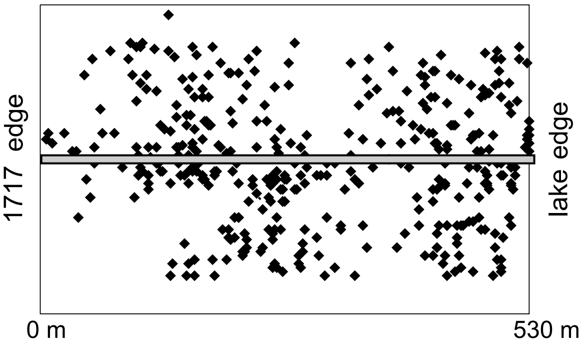
As shown in Fig. 1, the site is bordered on one side by the 1717 forest. In the 1717 forest, the tall canopy fir was removed in the early 1980s by a budworm epidemic. These older stands are now dominated by cedar with some white spruce and aspen. Thus, only the subcanopy fir can presently act as seed sources.

Data collection

For 40 m to either side of the path, within the lakeside and 1717 forest (Fig. 1), we measured the basal area and Cartesian coordinants of every conifer stem taller than 3 m (n = 384). In 1998 we also estimated the ovulate cone production of every fir stem in this same area via binocular counts (n = 9294 cones). Only the portion of the canopy visible to the observer was enumerated for cones. The values were then multiplied by 1.5 to account for the nonvisible portion. Franklin (1968) argued that this method gives a reasonable estimate of the number of cones per tree. An estimate of 25 filled seeds per cone for fir was obtained from a companion study (Greene et al. 2002) using some recently cut stems about 30 km from the study site.

In 1998 along the 530-m length of the path within the 1916 forest, we counted the number of fir seedlings every 10 m in 1 m radius circular plots (n = 305). As mentioned previously, these were mainly from the years 1994 and 1996. In the spring of 1999 we counted the number of filled fir

Fig. 1. Schematic diagram of the location of the 1717 forest edge, lake edge, and source trees (balsam fir) within the 1916 forest. (Shaded band represents the 530-m mineral soil path.)



seeds (derived from the enumerated 1998 cone crop) in these same plots ($n = 792$).

The mean wind speeds (60-s averaging time, one recording each hour) for the study area were obtained from Environment Canada (reporting station at La Sarre, Que., about 50 km from Lake Duparquet) for the months of September and October between 1992 and 1999.

The data collected here were used to generate dispersal curves from each tree within our sampled area. The summed contribution of seeds or seedlings was then used to generate the expected density of recruits every 10 m along the path.

Modelling

To reach our objectives, we adopt for the dispersal term the lognormal distribution (Stewart et al. 1998; Greene et al. 1999; Tanaka et al. 1998). The lognormal has the advantage of being mechanistic and, thus, can be easily parameterized to account for the physical properties of the dispersing units and stochastic meteorological variables. When this $f(x)$ is multiplied by the number of seeds (or seedlings) produced per tree (Q) we have

$$[2] \qquad Q_{Dx} = \left[\frac{Q}{(2\pi)^{1.5}\sigma_{\ln x}x^2}\right]\exp\left[-\left(\frac{0.5}{\sigma^2_{\ln x}}\right)\left(\ln\left(\frac{x}{x_{0.5}}\right)\right)^2\right]$$

where Q_{Dx} is seeds per square metre at the distance x from a point on the path, $x_{0.5}$ is the median dispersal distance, and $\sigma_{\ln x}$ is the standard deviation of the logarithms of the distances traveled.

In eq. 2 the median distance ($x_{0.5}$) traveled by a seed is given by

$$[3] \qquad x_{0.5} = \frac{\bar{u}_{\mathrm{g}}\,\bar{z}_{\mathrm{a}}}{\bar{f}}$$

where $\bar{z}_{\mathrm{a}}$ is the mean height (m) at the time of abscission ($\bar{z}_{\mathrm{a}} = 0.90z_{\mathrm{h}}$, where z_{h} is the mean height of fir trees from this forest (7.47 m)), $\bar{f}$ is the mean terminal velocity (m/s; = 0.85 for balsam fir according to Greene and Johnson 2000), and $\bar{u}_{\mathrm{g}}$ is the median horizontal wind speed (m/s) averaged from z_{a} to the ground. The study site chosen for this modelling exercise was dominated by aspen, a deciduous tree species. Previous modelling exercises employing eq. 2 had been done in conifer-dominated forests. As such, leaf abscission and its effects on the drag experienced at the top of the canopy during the seed dispersal period have not been formally evaluated. Changing the wind speeds ($\bar{u}_{\mathrm{g}}$) will directly influence the median distance at which seeds are deposited. For example, if we take the mean and standard deviation of the natural logarithms of the winds during the 1998 dispersal season and assume dispersal to occur in a full canopy forest, then $\bar{u}_{\mathrm{g}} = 0.116u_{\mathrm{r}}$ m/s (calculated using the protocol from Greene and Johnson 1996), where u_{r} is the measured median wind speed at 10 m at the meteorological reporting station in LaSarre in 1998. Conversely in a leafless canopy this horizontal wind speed is $0.358u_{\mathrm{r}}$ m/s.

The standard deviation of the logarithms of distances traveled ($\sigma_{\ln x}$) can be estimated (Greene et al. 1999) as

$$[4] \qquad \sigma_{\ln x} = \left(\frac{\sigma^2_{\mathrm{w}}}{f^2} + i^2_{\mathrm{u}}\right)^{0.5}$$

where σ_{w} is the standard deviation of the vertical wind speeds (we use the abscission-adjusted default value of Greene and Johnson (2000), $\sigma_{\mathrm{w}} = 0.76$), i_u is the horizontal turbulence (to be measured empirically using the airport data at La Sarre).

In the case of the 1998 seed crop of fir, our basal area measurements allow us to estimate Q in eq. 2 with the empirical value:

$$[5] \qquad Q = \frac{S_D}{B_D}B(i)$$

where S_D is the observed density of seeds (no./m^2) across the 530 m long bladed path, B_D is the mean basal area per area from the 1916 study site, and $B(i)$ is the basal area (m^2) measurements recorded for ith individual tree. For simulations involving seedlings, S_D in eq. 5 was replaced with F_D (the density of seedlings per square metre across the path). Finally, for modelling seed and seedling dispersal using cone counts (as a predictor for productive output of individual trees), B_D and $B(i)$ were replaced with Q_{CD} (density of cones per square metre in the forest transect) and $Q_C(i)$ (number of cones on the ith individual tree), respectively. The estimated source strength here allows us to implicitly include the effect of mortality subsequent to abscission.

Modifications of the micrometeorological model

We used the empirical relative humidity data obtained from Environment Canada (La Sarre, Que.) to examine the effect of this factor on the expected CV of seeds and seedlings. While we know there is a strong bias for abscission during low relative humidity (reviewed in Greene et al. 1999), there is no mechanical model to which we can appeal. Arbitrarily then, we divided days into greater than or less than 50% relative humidity and assumed that all seeds abscised only when the relative humidity was less than 50%. This generated a frequency distribution of eight azimuths, and seeds could only disperse along these azimuths with a frequency dictated by this distribution of low relative humidity. In short, we have, for each tree, applied the weighted one-dimensional model (eq. 2) eight times (eight azimuths). Our initial hypothesis for this exercise is that the bias due to relative humidity will be mild given that the overlapping curves will tend to cancel out any bias in dispersion from individual trees. We attempt it nonetheless so as to determine to what degree the omission of this element decreases fine scale variation.

A final source of fine-scale variation is that of differential survivorship along the path. The present model does not account for seedbed-induced mortality differences but can be explicitly modeled (e.g., Lepage et al. 2000). In our case, however, given that the seedbed from this site was held constant, we can ignore this source of variation as negligible.

Results and discussion

The correlation between the 1998 cone density (cones/m^2) and basal area per area along the 0.5-km path was significant ($r^2 = 0.47$; $p < 0.001$), with the exponent and intercept of the power law regression calculated as 1.38 and 49.7, respectively. This exponent is significantly higher (t test; $p < 0.05$) than the implicit expectation of 1.0 (eq. 1). The sparse literature on seed production in relation to tree size indicates that the exponent varies anywhere from about 0.5 to 1.5 (Greene and Johnson 1994, 1998; Greene et al. 2002). A small amount of the unexplained variation is due to differential light receipt (Greene et al. 2002), as some fir stems find themselves far from or near to gaps. Substituting basal area for cone production in the model led to a decline in the r^2 for the predicted distribution of seeds and seedlings, as well as to a large decline in the predicted CV (Table 1).

The median and the standard deviation of the natural logarithms of the horizontal wind speeds at the LaSarre reporting station were measured as 3.5 and 0.34 m/s, respectively, for the 1998 dispersal season. Thus, the median dispersal distance (from eq. 3) for full- and leafless-canopy forests for our study site was estimated as 3.2 and 9.9 m, respectively. For the combined crop years 1993 and 1995 (responsible for virtually all the seedlings on the path), the median wind speed at the reporting station was very similar (3.3 m/s), and thus, the two extreme median distances traveled are likewise similar (3.5 m (full leaf) and 10.7 m (leafless)). The standard deviation of the natural logarithms of the horizontal wind speeds was 0.44 m/s.

Figure 2 shows the results of the regression analyses (predicted on observed deposited seed densities) using a range of $x_{0.5}$ values based on either cones or its proxy, basal area. The results are shown for median distances ranging from 3 to 20 m where all of the regressions performed were significant ($p < 0.001$). The best r^2 for the 1999 deposited seed densities was for a median distance of 7 m (using cones) and 8 m (using basal area). That is, on average it would appear that the 1998 seeds mainly abscised when about half of the aspen leaves have been removed. This would be roughly early October in our region.

For this range of median dispersal distances the simulations using cone data yielded higher coefficients of determination than our basal area measurements (Fig. 2). This is not surprising given that basal area explains less than half the variation in cone production.

Prediction was better for the seedlings than the 1999 deposited seeds (Table 1). This may be because the seedling data includes two mast years (1993, 1995: Raymond 1998) and, thus, may average out outliers from either year. As with seeds, the model with cones outperforms the model with basal area: the r^2 increases by about 15% (Fig. 3) for the seedlings. The most likely median distance (best r^2) is, however, slightly higher than when we modeled the 1998 seed dispersal, corresponding to the end of the aspen leaf abscission period (say, early November), where the r^2 peaks at 11 m for cones and 10 m for basal area.

Fig. 2. Regression r^2 (for regressions of predicted vs. observed densities) versus the median seed dispersal distance using cones (solid circles) or basal area (open circles) in the model.

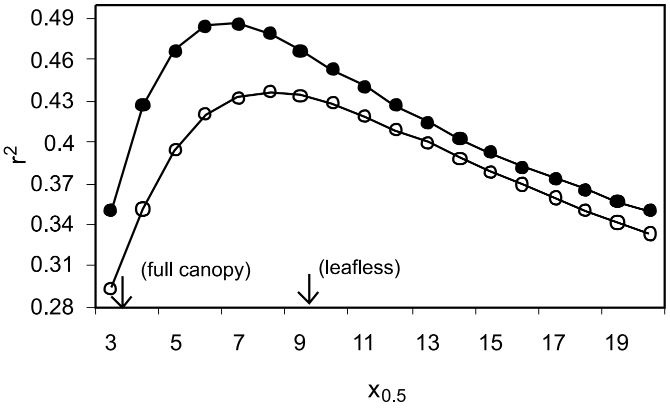
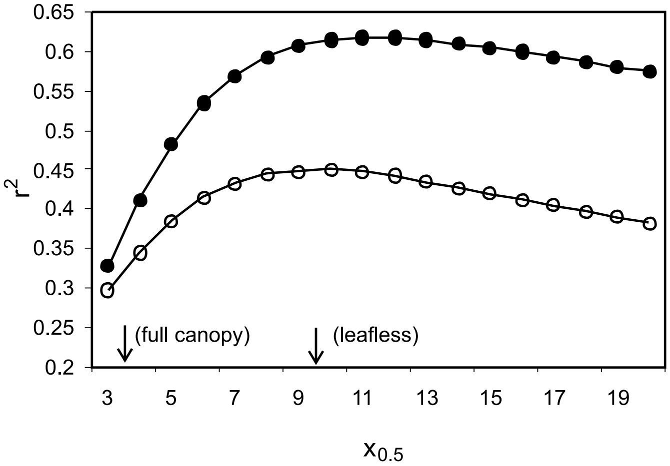


Fig. 3. Regression r^2 (for regressions of predicted vs. observed densities) versus the median seedling dispersal distance using cones (solid circles) or basal area (open circles) in the model.



Most high-latitude tree species abscise their seeds in the autumn over a period of a few months, typically September to early December for 90% of the seeds. Most hardwoods abscise their seeds somewhat earlier (September to early November). We cannot know the precise seed abscission schedules for the three mast years (1998, and the 2 years sponsoring most of the seedlings: 1993 and 1995), but it seems likely, based on our results, that this may occur during the last half of the leaf abscission schedule. Indeed, future modelling in deciduous forest should attempt to include onsite empirical evidence on the timing on leaf and seed abscission.

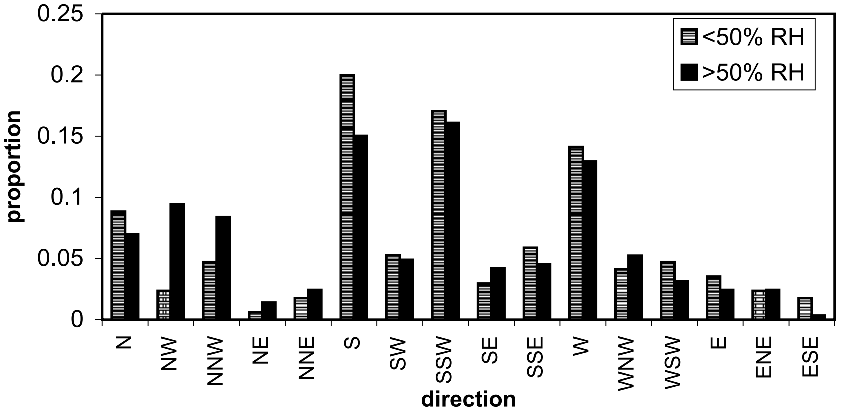
A comparison between the observed and predicted coefficients of variation has not been previously attempted in the literature. The observed CV for our cone-density measurements (total cones per 10-m section of the 0.5-km path)

Table 1. Coefficients of determination (r^2) and coefficients of variation (CV) for simulations involving seed and seedling dispersion using (1) the simple micrometeorological model and (2) the model with azimuthal bias due to relative humidity.

	Cones–seedlings				Cones–seeds		BA–seedlings				BA–seeds	
$x_{0.5}$	r_1^2	r_2^2	CV_1	CV_2	r_1^2	r_2^2	r_1^2	r_2^2	CV_1	CV_2	r_1^2	r_2^2
3	0.33	0.31	1.76	1.58	0.36	0.46	0.30	0.25	1.09	1.05	0.29	0.36
4	0.41	0.38	1.46	1.40	0.43	0.48	0.35	0.30	0.92	0.94	0.35	0.39
5	0.48	0.44	1.28	1.26	0.47	0.48	0.39	0.34	0.87	0.86	0.39	0.41
6	0.53	0.49	1.16	1.17	0.48	0.48	0.41	0.38	0.79	0.80	0.42	0.42
7	0.57	0.52	1.08	1.09	0.49	0.47	0.43	0.40	0.74	0.75	0.43	0.42
8	0.59	0.55	1.02	1.04	0.48	0.46	0.44	0.42	0.70	0.71	0.44	0.42
9	0.61	0.57	0.97	0.99	0.47	0.45	0.45	0.42	0.67	0.68	0.43	0.41
10	0.61	0.58	0.94	0.95	0.45	0.43	0.45	0.43	0.64	0.66	0.43	0.40
11	0.62	0.59	0.91	0.92	0.44	0.42	0.45	0.43	0.62	0.64	0.42	0.39
12	0.62	0.60	0.89	0.89	0.43	0.41	0.44	0.43	0.61	0.62	0.41	0.38
13	0.61	0.60	0.87	0.87	0.41	0.40	0.44	0.42	0.59	0.61	0.40	0.37
14	0.61	0.60	0.85	0.85	0.40	0.39	0.43	0.42	0.58	0.59	0.39	0.36
15	0.60	0.60	0.83	0.83	0.39	0.38	0.42	0.41	0.57	0.58	0.38	0.35
16	0.60	0.59	0.82	0.81	0.38	0.37	0.41	0.40	0.56	0.57	0.37	0.34
17	0.59	0.59	0.80	0.80	0.37	0.36	0.41	0.40	0.55	0.56	0.36	0.33
18	0.59	0.58	0.79	0.79	0.36	0.35	0.40	0.39	0.54	0.56	0.35	0.32
19	0.58	0.58	0.78	0.77	0.36	0.34	0.39	0.38	0.54	0.55	0.34	0.32
20	0.57	0.57	0.77	0.76	0.35	0.33	0.38	0.37	0.53	0.54	0.33	0.31

Note: Results are presented for cone and basal area simulations.

Fig. 4. Prevailing azimuths during periods of low and high relative humidity (RH).



was 1.27 versus 0.56 for basal area/area. The observed CV values for seed and seedling densities across the path were 1.5 and 0.96, respectively. The predicted CV (corresponding to the highest r^2) using cones was 0.91 for seedlings and 1.08 for seeds (Table 1). By contrast, using basal area the CV values were predicted to be 0.64 for seedlings or 0.70 for seeds. Thus, not only is basal area only a modest predictor of cone production, but it is far less variable. Much of this enhanced spatial variation is due to differences in ambient light (Greene et al. 2002). Necessarily then, recruitment models as conventionally formulated (e.g., Clark et al. 1994; LePage et al. 2000) with basal area used as a proxy for female function will greatly underestimate the real CV of seeds or seedlings. A simple way to "restore" the variation for subsequent dynamics simulations would be to draw seed production values from a regression of seeds on basal area that predicts only about half the variance. In summary, using basal area rather than cones leads to a lower correlation and a much lower predicted CV.

Another feature to note in Table 1 is that the predicted CV declines as we entertain larger median dispersal distances. This is not surprising: as the median distance increases, the seed rain (or seedling distribution) becomes more homogenous across the area.

When we modified the simple micrometeorological model to account for azimuthal bias due to low relative humidity, prediction did not improve (Table 1). Only at very short distances did we observe an increase in r^2. Figure 4 depicts the proportions of low and high relative humidity autumnal days. As expected, given the latitude, winds are primarily from the west, southwest, and northwest. Autumnal winds from the west and south are modestly drier than other azimuths. The effect may have been subdued because of overlapping dispersal curves, where any bias due to azimuth or wind speed for a single tree is somewhat cancelled out by the same bias applied to neighboring trees. For coastal or montane environments where azimuthal biases in relative humidity are much more pronounced (e.g., Harris 1969), adequate modelling of seed dispersal will have to include this source of variation. However, in most cases, azimuthal bias will not be an issue.

In conclusion, we have shown that the choice of median wind speed will alter the predictive capacity of the micrometeorological model. For deciduous forests the choice of the appropriate value will depend on the timing of the leaf abscission schedule as well as the seed abscission schedule. Furthermore, we have shown that the choice of parameter for expressing seed production (i.e., cones or the proxy basal area) will also affect the precision in the modelling. Cones invariably have more fine-scale variation than basal area, and thus, using cones as the predictor will allow the coefficient of variation to increase. Future work can include forests stands with a more pronounced azimuthal bias (e.g., montane or coastal environments) so as to determine the effects of wind direction and relative humidity.

Acknowledgements

This project was funded by the Sustainable Forest Management Network. Field assistance was provided by S. Auger, A. Maletto, I. Ritchie, R.B. Clark, and P. Sutherland.

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