Climatic Change (2012) 112:673–685
DOI 10.1007/s10584-011-0230-6

Modeling the role of rainfall patterns in seasonal malaria transmission

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Received: 7 July 2010 / Accepted: 21 August 2011 / Published online: 6 December 2011

Abstract Seasonal total precipitation is well known to affect malaria transmission because *Anopheles* mosquitoes depend on standing water for breeding habitat. However, the within-season temporal pattern of the rainfall influences persistence of standing water and thus rainfall patterns can also affect mosquito population dynamics in water-limited environments. Here, using a numerical simulation, I show that intraseasonal rainfall pattern accounts for 39% of the variance in simulated mosquito abundance in a Niger Sahel village where malaria is endemic but highly seasonal. I apply a field validated coupled hydrology and entomology model. Using synthetic rainfall time series generated using a stationary first-order Markov Chain model, I hold all variables except hourly rainfall constant, thus isolating the contribution of rainfall pattern to variance in mosquito abundance. I further show the utility of hydrology modeling using topography to assess precipitation effects by analyzing collected water. Time-integrated surface area of pools explains 70% of the variance in simulated mosquito abundance from a mechanistic model, and time-integrated surface area of pools persisting longer than 7 days explains 82% of the variance. Correlations using the hydrology model output explain more variance in mosquito abundance than the 60% from rainfall totals. I extend this analysis to investigate the impacts of this effect on malaria vector mosquito populations under climate shift scenarios, holding all climate variables except precipitation constant. In these scenarios, rainfall mean and variance change with climatic change, and the modeling approach evaluates the impact of non-stationarity in rainfall and the associated rainfall patterns on expected mosquito activity.

1 Introduction

Malaria continues to cause severe suffering and death in much of the world, and is particularly severe in sub-Saharan Africa. Globally, an estimated 781,000 people lost their

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lives to malaria in 2009, and 709,000 (91%) of these deaths were in sub-Saharan Africa (WHO 2010). Serious health and associated economic costs of this disease dictate the need to understand the spatial and temporal determinants of transmission. The ability to provide early warnings of impending epidemics and to allocate resources for the fight against malaria depends on such an understanding. Social, economic and other factors can influence malaria transmission, however environmental drivers often play a dominant role (Craig et al. 1999; Martens 1998; Molineaux and Gramiccia 1980; Patz et al. 1998; Zhou et al. 2004). Average temperature, daily maximum and minimum temperatures, humidity, precipitation and hydrology all affect mosquito populations and influence malaria transmission in various ways. Precipitation and hydrology are particularly important environmental determinants of malaria, because the *Anopheles* mosquitoes responsible for spreading the parasite depend on standing water for breeding and aquatic-stage development (Gillies and DeMeillon 1968; Bomblies et al. 2008). In environments where water availability limits mosquito populations, interannual variability in the seasonal rainfall affects interannual variability in *Anopheles* mosquito density. While many studies have documented positive correlations between mosquito density and annual rainfall (e.g. Molineaux and Gramiccia 1980; Zhou et al. 2004; Kelly-Hope et al. 2009; Koenraadt et al. 2004; Patz et al. 1998), the correlations are not strong, and none have considered the potentially significant contribution of intraseasonal variations in rainfall patterns to variance observed in seasonal mosquito abundance. In this paper I analyze the effects of intraseasonal rainfall variability and use a numerical model to show a pronounced contribution of rainfall pattern to interannual variability in seasonal mosquito activity in water-limited environments. Furthermore, I investigate changes in rainfall patterns resulting from climate change in the Sahel zone to isolate the sensitivity of *Anopheles* mosquito abundance to changes in seasonal precipitation mean and variance. Because of the intractability of isolating the effects of rainfall patterns alone in the field, this analysis relies solely on numerical model predictions.

In arid, water-limited but highly malarious environments of Africa such as the Sahel, individual rainfed breeding pools of the type heavily utilized by the dominant vector mosquito *Anopheles gambiae sensu lato* form in topographic low points in response to rainfall. Topography dictates the bathymetric dimensions of typical breeding pools and their hydrologic catchments. These can vary significantly, leading to a wide distribution of pools' persistence times and surface areas at a certain location for a given rainfall amount. In arid, rapid-drying environments such as the Sahel, the persistence of an individual pool must exceed the temperature-dependent maturation time of aquatic stage mosquitoes (~7 days) for a new cohort of mosquitoes to emerge. Thus, microtopography and storm frequency can impact adult mosquito abundance. Both the seasonal rainfall amount and the temporal distribution of those rainfall events can influence mosquito population dynamics. As an illustration, a gravid female mosquito seeking breeding habitat near a typical Sahel village can choose from a number of open water bodies with a wide distribution of sizes (and persistence) following a 50-millimeter rainstorm. A number of the pools will disappear before the next rainfall occurs, and if the mosquito oviposits (lays eggs) in a pool destined to desiccate, that cohort of mosquitoes will be lost in the rapidly-drying soil. However, if the mosquito chooses a pool destined to persist through the interstorm period (the time elapsed between discrete rainfall events) and that pool is replenished with runoff from subsequent rainfall, adult mosquitoes can ultimately emerge. A storm total of 40 mm instead of 50 mm with the same duration until the next storm would yield a higher fraction of pools that will desiccate because of overall lower persistence. A 50 mm storm with a longer duration until the next storm would also cause more pools to disappear. Thus, the impact of lost cohorts on overall mosquito population dynamics depends on host pool persistence for a given rainfall amount as well as the interstorm return period, and therefore the potential for intraseasonal rainfall patterns to add to variance in seasonal mosquito abundance must be considered. The distribution of pool sizes is governed by microtopography, and their persistence depends on bathymetry, soil type, antecedent wetness, duration until the next water inflow, and evaporation, suggesting the use of high resolution distributed hydrology models to investigate this effect.

The Sahel across West Africa sees only one wet season each year, and the rain falls mainly from large organized convective systems (Mathon and Laurent 2001). The convective storms very rarely exceed 1 h in length, although trailing stratiform precipitation (the nonconvective rainfall that typically follows a leading convective line) typically yields low-intensity rainfall for several hours directly following the passage of the storm (Lebel et al. 1998). LeBarbe and Lebel (1997) have shown that the number of precipitation events, instead of the mean event rainfall, constitutes the primary mode of interannual rainfall variability in the Sahel. They noted that the mean rainfall total from individual storms does not significantly differ between rainy seasons, and differences in annual precipitation depend only on the number of events, and not on strength of those events or differences in the length of the rainy season (LeBarbe and Lebel 1997). It follows that for lower precipitation years, the intervals between rainy days tend to be longer, and for higher precipitation years, intervals between precipitation events are generally shorter over the course of a rainy season (May–October). As described above, this mode of rainfall variability has significant implications for pool persistence and the longevity of the vulnerable subadult mosquitoes within that pool, leading to a nonlinear rainfall/mosquito connection. Very few models have attempted to simulate the effects of pool persistence on mosquito abundance, and those that do rely primarily on compartmental model structure with “perfect mixing” assumptions, eliminating the benefits of representing individual pools (e.g. Hoshen and Morse 2004). With a highly detailed, distributed hydrology model that represents the formation and persistence of individual pools, the problem of representing nonlinear rainfall frequency effects becomes tractable.

The dependence of seasonal rainfall on the number of events, rather than the magnitude of those events, can be extended to climate shift scenarios in the Sahel. Several significant climate shifts have occurred in the Sahel during the last 10,000 years, translating isohyets northward for wetter conditions and southward for drier conditions (Bomblies and Eltahir 2009). Current global climate change could influence Sahel rainfall climatology, and in such a scenario the current mode of interannual rainfall variability is expected to continue to dictate seasonal rainfall totals. A shift toward wetter conditions will increase the number of events, thus decreasing the interstorm period. Conversely, a shift toward drier conditions will result in increasing the time between rainfall events, allowing more desiccation. In this study I evaluate the impacts of future potential climate shifts on vector mosquito abundance, which naturally extends to village-scale malaria transmission intensity.

2 Materials and methods

In order to isolate the effect of varying precipitation regimes while keeping all other inputs constant, I employ the coupled hydrology and agent-based entomology model HYDREMATS that predicts the topographically-determined location and persistence of individual pools, in a spatially explicit manner (Bomblies et al. 2008). An example of HYDREMATS output, superimposed on a satellite image of Banizoumbou, Niger is shown in Fig. 1. Individual

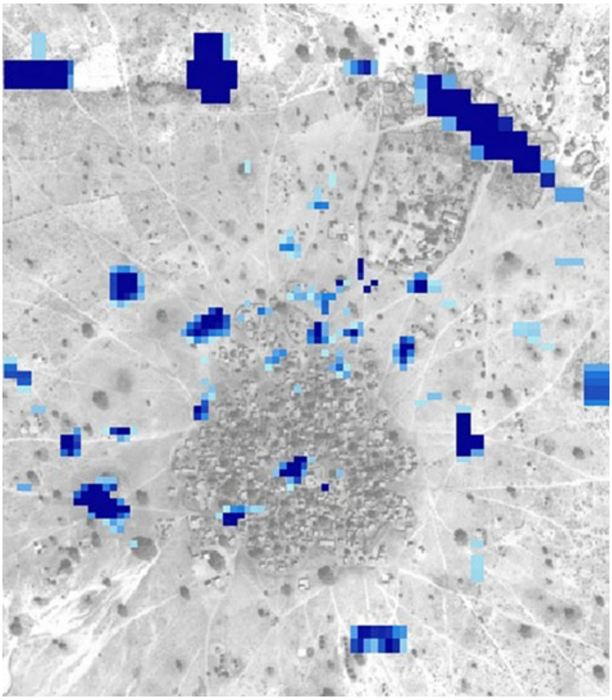


Fig. 1 An example of hourly model output surrounding Banizoumbou, Niger, showing a number of simulated pools following a 60 mm precipitation event. A subset of the depicted pools will persist long enough to allow subadult mosquitoes to mature and emerge as adults. The rest will desiccate. The figure shows simulated water depths overlain on an aerial photograph of the village. Simulated water depth for this particular snapshot range from 0 to 100 cm. Low water levels are light blue and get progressively darker with depth, with the darkest blue corresponding to 100 cm

pools of varying sizes surrounding the village are evident in this figure, which represents one hourly time step in the simulation. An agent-based mosquito population model is coupled to the hydrology model component to simulate the hydrology/mosquito population dependency at high spatial and temporal resolution. In this model, individual mosquitoes emerge from pools (represented by the hydrology model) that are sufficiently persistent to allow full development of adult mosquitoes. Individual simulated adults fly through the model domain, interacting with their immediate environment. They cycle through stages of seeking a blood-meal, egg-development, and seeking pooled water for oviposition (egg-laying), which then repeat until the mosquito dies. Behavioral decisions (such as whether to utilize a pool for oviposition, or in which direction to fly) are determined probabilistically. The model simulates the entire life history of individual mosquitoes constituting a population around a village, including the necessary temperature-dependent aquatic stage development within individual pools, and assumes that pool desiccation results in complete loss of the cohort hosted by that pool (a reasonable assumption in the arid Sahel where soil rapidly dries, but not necessarily in wetter environments where mud persists and can allow mosquito larvae to survive (Koenraadt et al. 2003)).

HYDREMATS has been successfully applied to the southwestern Niger village Banizoumbou to reproduce observed interannual differences in mosquito abundance (Bomblies et al. 2008). From that field study, correlation between 2005 and 2008 field-measured abundances and seasonal rainfall totals yields a positive but weak correlation with a correlation coefficient of 0.35. In 2007, an environmental management intervention effort in Banizoumbou depressed mosquito abundance (Gianotti et al. 2008), and with this year removed, seasonal rainfall still only explains 44% of the variance of mosquito abundance. However, the HYDREMATS model was successful at predicting the interannual differences in observed mosquito abundance for the 2 years of the study (2005 and 2006).

For this simulation, hydrology model resolution is 10 m and the model domain spans a 2.5 km×2.5 km area surrounding Banizoumbou. These model parameters are the same as for the previously published calibrated hydrology model for the site (Bomblies et al. 2008). At Banizoumbou (considered representative of the Sahel) tiny pools with scales less than 10 m (such as tire ruts and hoofprints) disappear rapidly after a rainfall event when distant from larger topographic low points and the primary breeding habitat in the area is generally tens of meters (Bomblies et al. 2008). Topography data was derived from a combination of Shuttle Radar Topography Mission (SRTM) data and a topographic survey done in the field using a Topcon total station to fill in details.

Daily rainfall in the Sahel can be described statistically using a first-order stationary Markov Chain model for rainfall probability on any given day, combined with the sampling of a Weibull distribution for event magnitude (Ali et al. 2006; Gerbaux et al. 2009). This combined method is used to generate a sequence of 50 realistic hourly time series of rainfall that is then used as a rainfall forcing for the deterministic HYDREMATS model. The first-order Markov Chain model involves two parameters: transition probabilities P_{01} and P_{11} which represent respectively the probability that it rains the day after a specific day given that it has not rained that day, and the probability that it rains on the day after a certain day, given that it *has* rained on that day. These parameters change throughout the season to reflect the greatest chance of precipitation during the August peak of the rainy season and much lower chances during the early rainy season in late May/early June and the late rainy season in mid-September. The parameterization derives from rainfall data from the Banizoumbou meteorological station (IRD, France), from 2002 to 2008. The derived parameters match very well those of Gerbaux et al. (2009) from Senegal, at another Sahel site with similar climate. Figure 2 shows the seasonal average transition probabilities assigned to the model for Banizoumbou.

The Weibull distribution has been noted to fit rainfall data well in the Sahel (Gerbaux et al. 2009). At the Banizoumbou meteorological station, the fit is good (R^2=0.993), and so the Weibull distribution is used to synthesize daily rainfall amount. To generate a realization of daily rainfall for a season, for each day during the rainy season transition probabilities are compared to a uniformly distributed random number. If the random number is less than the appropriate transition probability for the tested day (P_{01} or P_{11} depending on whether or not it is raining on the tested day), then it rains on the following day. Once the rain/no rain

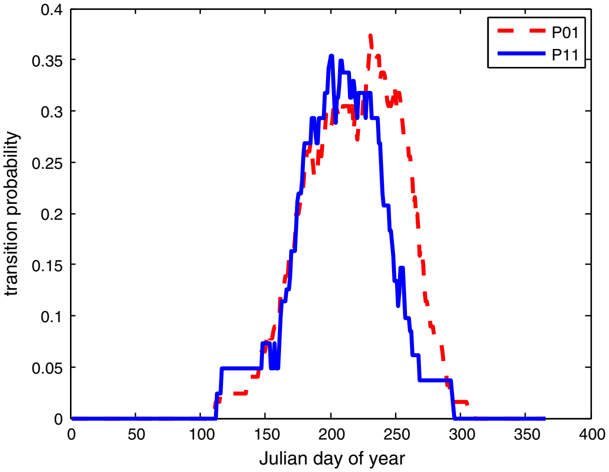


Fig. 2 Average Markov Chain model parameters (transition probabilities) for the Banizoumbou meteorological station

assignment has been made for each day based on the seasonally-changing transition probabilities, the Weibull distribution (with fitted parameters k=0.7 and λ=9.3) is sampled to determine the daily rainfall amount. I assume that only one storm can occur during each day, and that the hyetograph follows the generalized hyetograph of Guillot and Lebel (1999) for the Sahel. The parameters for the synthetic hyetograph model were the same as those used by Balme et al. (2006) for southwestern Niger. The time of day of the storm is random, and rainfall intensity from the trailing stratiform clouds is assumed to be a constant 1.5 mm/h after the convective cell has passed. The method is repeated to generate 50 realizations of seasonal rainfall as an hourly time series of rainfall for input into the HYDREMATS model.

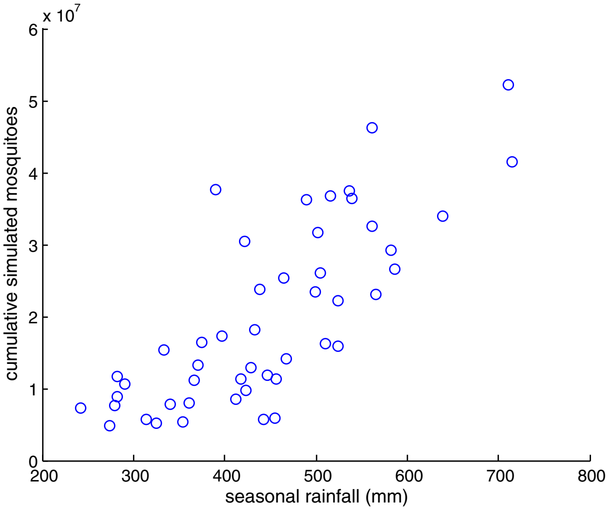
The Sahel has been subjected to several climate shifts in the past 5000 years that have shifted isohyets north when conditions have become wetter, and south for a shift toward drier conditions. Impacts of such climate shifts on malaria transmission have been simulated for Banizoumbou (Bomblies and Eltahir 2009). At this same village, assuming that under a climate shift scenario the number of rainy days changes rather than individual storm magnitude as observed by LeBarbé and Lebel, climate shift conditions can be simulated in the Markov Chain model by varying transition probabilities by the same factor as the climate change-induced change in precipitation (Gerbaux et al. 2009). For example, an increase in annual rainfall from 450 to 540 mm (20% increase, factor of 1.2) can be simulated by raising observed transition probabilities by a factor of 1.2. In this study, the effect of climate change-induced rainfall variability on mosquito abundance is explored using factors 0.4, 0.6, 0.8, and 1.2. The ratios of average rainfall to the baseline case do not always match the factors, due to the stochastic nature of the rainfall model.

The observation of LeBarbe and Lebel (1997) that Sahel interannual rainfall variability is characterized by year-to-year changes in the number of precipitation events instead of mean storm totals is assumed to hold under climate change scenarios as well. A hypothetical climate shift in the Sahel might translate isohyets 90 km to the north (Bomblies and Eltahir 2009), resulting in a 90 mm gain in annual precipitation from the 1 mm km^{-1} rainfall gradient (Lebel et al. 1992). For Banizoumbou, with average annual precipitation of approximately 450 mm, this scenario corresponds to a precipitation increase of 20%. Because seasonal rainfall increases are not brought about by increases in storm average rainfall, the number of storms during a season must increase by 20%. Daily probability of rain must increase by 20% to yield the necessary 20% seasonal precipitation increase. Therefore, increasing the transition probabilities P_{01} or P_{11} by 20% is consistent with a hypothetical 90 mm increase in Banizoumbou seasonal rainfall from climate change. In this analysis, I use the same procedure to test the effect of various scenarios (−60%, −40%, −20%, and +20%) on mosquito abundance in Banizoumbou, and compare the results to the unperturbed scenario. The expected translation in isotherms accompanying southward or northward migration of Sahel isohyets during a climate change event is ignored in order to isolate the effect of intraseasonal rainfall variability on mosquito activity.

3 Results

Figure 3 shows the simulated mosquito abundance as a function of total seasonal rainfall in Banizoumbou, Niger. The seasonal rainfall is generated for current conditions as described in *Methods* and represents 50 time-series realizations assuming stationarity in seasonal rainfall. All environmental variables except precipitation are held constant for all model runs. The cumulative simulated mosquitoes in Fig. 3 are time-integrated over each

Fig. 3 Cumulative simulated mosquitoes vs. rainfall for the baseline scenario. For this correlation, r^2=0.60 and the mean rainfall is 449 mm. The only difference between individual runs is intraseasonal distribution of rainfall, yielding varying seasonal rainfall amounts. Temperature, humidity, and other environmental variables known to affect mosquito populations are held constant for each run



time step of the model. Using this simple correlative approach, annual total precipitation explains 60% of the variance in mosquito abundance. Because all of the other environmental variables are held constant, the remaining variance in the mosquito abundance can be attributed to the direct and indirect effects of intraseasonal rainfall patterns, as well as the internal stochasticity within the model. Model results are summarized in Table 1.

Variance due to the internal stochasticity within the model must be accounted for, because mosquito behavior is simulated probabilistically. Individual simulated mosquitoes' decisions are based on uniformly-distributed random numbers compared to model-assigned behavioral parameters (for example, the chance that a female mosquito will lay eggs in a

Table 1 Statistics summarizing rainfall and mosquito abundance for all 50 model runs done for each change factor. Correlation coefficients for several climate change factors are included. The r^2 values show the proportion of the variance in total mosquito abundance described by each of the variables (seasonal rainfall, time-integrated surface area, or time-integrated surface area of pools that have persisted longer than 7 days). The only variable that is different between the individual runs is rainfall pattern

	Climate change factor				
	0.4	0.6	0.8	1	1.2
Average rainfall (mm)	207	300	354	449	503
Rainfall variance (mm^2)	475	782	1010	1313	1396
Abundance mean (individuals)	4.12×10^6	5.43×10^6	1.17×10^7	1.98×10^7	2.56×10^7
Abundance variance	8.10×10^{12}	9.93×10^{12}	7.51×10^{13}	1.56×10^{14}	2.36×10^{14}
Fraction of abundance variance due to model stochasticity	8.4%	3.1%	0.4%	2.7%	2.0%
	r^2 values (correlation of mosquito abundance with variable):				
Seasonal rainfall	0.37	0.19	0.54	0.60	0.69
Surface area	0.41	0.38	0.56	0.70	0.75
Surface area (t>7 days)	0.65	0.58	0.71	0.82	0.85

particular pool that she encounters). The model is deterministic, and therefore the behaviors of simulated individuals will depend on the random number seed in the model. The model was run 20 times using a fixed precipitation, varying only the random number seed. This was done for all of the climate change scenarios, and the resulting fractions of total variance that can be attributed to internal stochasticity for each scenario are summarized in Table 1. Once this variance is accounted for, the remaining variance results from rainfall patterns exclusively. For example, in the baseline scenario (change factor=1.0) rainfall pattern explains 38.9% of the variance in mosquito abundance because 2.7% of the variance not due to seasonal rainfall (40%) can be attributed to internal model stochasticity.

The coefficient of determination for the regression of seasonal rainfall with simulated mosquito abundance (r^2=0.6) is greater than published field observations that investigate the correlation between rainfall and vector abundance. Although rainfall is clearly influential and often limits mosquito abundance, generally in Africa precipitation alone does not correlate strongly with mosquito abundance or activity. For example, Koenraadt et al. (2004) noted a statistically significant correlation between lagged weekly rainfall and adult *An. gambiae s.l.* mosquito density in a Kenyan village for only the first 6 weeks of observation (r^2=0.59), and much worse, insignificant correlation thereafter. Kelly-Hope et al. (2009) found insignificant correlations for precipitation with *An. gambiae s.s.* density (r^2=0.246) and for *An. arabiensis* density (r^2=0.315) in southeastern Kenya. Patz et al. (1998) noted poor correlation of human biting rates with rainfall (r^2=0.05) in Kisian, Kenya. They significantly improved predictive ability by correlating with lagged modeled soil moisture from a computer model, which resulted in a better correlation with human biting rate (r^2=0.45). This result clearly demonstrated the importance of land surface hydrology in linking rainfall to mosquito breeding and population dynamics. The extensive Garki Project of northern Nigeria noted a poor correlation of seasonal rainfall with mosquito abundance (Molineaux and Gramiccia 1980), without stating the correlation coefficient. Garki, Nigeria is in the Sudano-Sahelian zone, and environmental conditions are thus similar to those of southern Niger. All of these prior results from field studies show that many determinants affect vector mosquito abundance and activity, and not just rainfall. These may include temperature and humidity effects, variations in vegetation (for availability of shaded resting sites or larval nutriment), differences in human behavior (e.g. irrigation, bednet usage, housing construction, etc.) or the variable presence of animals as alternate blood meal sources, for example. Many diverse factors are expected to contribute to interannual variability in mosquito abundance. In the model, all of these other potential factors are held constant to isolate the effects of rainfall, resulting in the coefficient of determination of r^2=0.6 for seasonal rainfall.

The processes of runoff generation and subsequent overland flow into topographic depressions are simulated. Because the formation of pools resulting from precipitation depends strongly on local topography and because mosquitoes seek out such open water, the simulated total surface area of standing water is more strongly correlated with mosquito abundance than precipitation alone. Integrated total surface area through each model run explains 70% of the variance in adult mosquito populations, an improvement over a correlation with precipitation alone. Because many of these pools do not persist long enough to allow adult mosquitoes to develop from their aquatic subadult stages, a correlation of surface area of pools persisting longer than 7 days (a typical development time for mosquito larvae) with adult mosquitoes improves the correlation. Cumulative time-integrated surface area of pools that have persisted longer than 7 days explains 82% of the variance in total adult mosquito abundance.

Climate change simulations yield similar trends. Correlation of mosquito abundance with precipitation is relatively weak for all scenarios presented in Table 1. More variance in the mosquito abundance is explained by pool surface area and the most variance is explained by integrated surface area of pools persisting longer than 1 week.

Figure 4 shows the average of time-integrated mosquito abundance of all 50 hourly precipitation time series for each change factor. Figure 4 also includes baseline mosquito abundance (factor 1.0) times the ratio of the each factor's precipitation total to the baseline (449 mm). Model results diverge from this line to show a more complicated relationship between climate change factors and resulting mosquito abundance than a simple linear proportional dependence on rainfall. Two related effects can explain this difference. First, the increased interstorm duration with decreased change factor reduces the number of pools persisting long enough to yield adult mosquitoes. This depresses the mosquito abundance. Second, a reduced number of mosquitoes seeking oviposition habitat near the village will have a decreased chance of laying eggs in the few pools that can host the subadult mosquitoes to adulthood. Simulations for change factor 0.4 show a slight leveling of the curve, because two large persistent pools with large catchments nearby the village begin to dominate and become the exclusive sources of adult mosquitoes. Small pools tend to disappear before gravid mosquitoes can find them, and thus become less important.

The variance of mosquito abundance increases as

$$V_m = 1.102 M_m^{1.95} \left(R^2 = 0.98\right)$$

Where V_m is the variance of total annual time-integrated mosquito abundance for all realizations for a given change factor and M_m is the mean in mosquito abundance of all model realizations. The increase in variance in mosquito numbers is due primarily to differences in annual rainfall variance associated with the precipitation change scenarios. Change in rainfall variance naturally accompanies change in the mean (Mearns et al. 1997; Waggoner 1989), and the resulting change in the model precipitation forcing variance clearly affects population variance. From the application of the first-order Markov Chain model, climate-change induced changes in the annual precipitation variance depend on mean in the following manner:

$$V_p = 5.848 M_p^{1.26} \left(R^2 = 0.99\right)$$

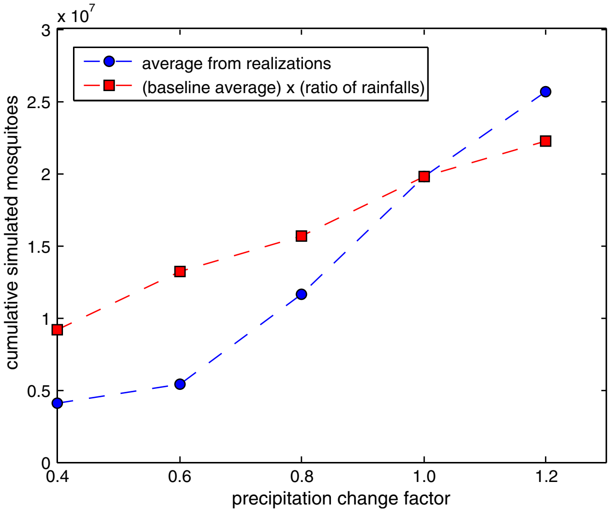


Fig. 4 Mean cumulative mosquitoes over 50 realizations for each change factor (*circular marker*) and the mean cumulative abundance of the baseline scenario (factor 1.0) multiplied by the ratio of precipitations (*square marker*). The divergence is attributed to the pool persistence effect

Where V_P is the variance of total annual precipitation for a given change factor and M_p is the mean annual precipitation. This relation is close to that found by Waggoner (1989). He inferred the impact of climate change- induced changes in mean precipitation on precipitation variance from observed differences in present rainfall climatologies, and determined that "the variance increases as the mean raised to the ~1.3 power" (Waggoner 1989).

4 Discussion

Modeling results suggest that intraseasonal rainfall patterns can affect *Anopheles* mosquito population dynamics. Adequate breeding pool persistence is a requirement for adult mosquitoes to emerge in arid, water-limited environments. Thus, the interplay of microtopography, land surface hydrology, rainfall intensity and rainfall patterns that dictates the formation and persistence of mosquito breeding pools can exert a control on mosquito abundance. In this study, I have examined the contribution of this effect to variance in time-integrated seasonal mosquito populations in Banizoumbou, Niger. Many model runs were made varying only precipitation pattern, and the incomplete rainfall-mosquito correlation ($r^2=0.6$; Fig. 3) demonstrates the influence of temporal distribution of rainfall as an additional mosquito population control in this model system. This is distinct from the well-established role of seasonal rainfall totals in regulating mosquito abundance. Simulation of mosquito population variance dependent only on within-season differences in rainfall pattern is a highly artificial scenario and can only be performed in mathematical models. In reality, precipitation events would coincide with changes in temperature and humidity, which are both known to influence mosquito populations.

In this modeling study, mosquito population variance was explained better by time-integrated pool surface area than by precipitation alone. This points to the important role of local topography. Rainfall would have little effect on mosquito abundance if micro-topography were too smooth, because indentations with sufficient catchment area are necessary to impound water. A further improvement in the explanation of mosquito variability was noted by correlation of mosquito abundance with surface area of pools that have persisted longer than 1 week. One week is approximately the length of time necessary for subadult mosquito development. This improved correlation reaffirms the important role of pool persistence—influenced by topography, rainfall patterns, air temperature and humidity and soil and vegetation conditions—in regulating mosquito populations. Some leftover variance derives from individual mosquito agent behavior. For example, lower total mosquito abundance reduces the chance that an individual pool near the village will be found and utilized for oviposition. With more mosquitoes arriving at that pool and choosing to deposit eggs there, the pool controls mosquito populations to a greater extent, and its control on populations is diminished if it is only rarely found by gravid females. An evaluation of the internal model stochasticity has shown that behavioral decisions account for approximately 2.7% of the total variance. In drier climate shift scenarios, the contribution of internal stochasticity to total variance in abundance is higher because there are fewer mosquitoes, and the impacts of individuals' decisions are greater.

Precipitation pattern changes resulting from climate change are simulated to have pronounced impacts on *Anopheles* mosquito abundance. In modeled climate change scenarios with 50 realizations for each precipitation change factor (0.4, 0.6, 0.8, and 1.2 times the base case), variance of predicted mosquito abundance rises with mean predicted mosquito abundance at a greater rate than precipitation variance rises with precipitation mean ($M^{1.95}$ vs. $M^{1.26}$). The only difference between realizations for a given change factor is intraseasonal rainfall pattern. This suggests that differences in rainfall patterns between individual realizations add variance to the naturally-occurring variance increase that accompanies a mean increase. The mechanism causing this added variance is the same mechanism at play in the base case: highly persistent pools allow the uninterrupted development and emergence of more cohorts of mosquitoes. Conversely, lower annual rainfall amounts with unfavorable precipitation patterns for pool persistence yield low mosquito abundances. In the case of lower rainfall amounts, the impact of ephemeral pools is reduced because fewer mosquitoes tend to find intermittent pools before they disappear, thus depressing the variance in population more than natural precipitation variance would suggest.

In water-limited transmission environments, an increase in the variance of mosquito populations can have significant consequences (Pascual et al. 2008). In desert fringe regions with very high interannual climate variability such as the Sahel, alternating high and low transmission years can amplify malaria burden due to variations in natural immunity (Kiszewski and Teklehaimanot 2004). In a wet year preceded by dry years, a huge population of *Anopheles* mosquitoes transmit malaria in an immunologically naïve population, thus contributing to devastating epidemics (Kiszewski and Teklehaimanot 2004). Moreover, years of reduced transmission resulting from low mosquito abundance may allow natural immunity to wane, thus priming the population for another serious epidemic. In this fashion, altered mosquito population variance can have deleterious effects on human health.

Mean mosquito abundance increases with increased precipitation, as expected. However, this increase is not exactly linear. In low precipitation scenarios (factors 0.4 and 0.6), a few large pools dominate mosquito emergence as they are the only ones to contain water long enough to allow mosquitoes to develop to adulthood. Small pools susceptible to desiccation between rainstorms are extremely unlikely to persist long enough for adult mosquitoes to emerge. As precipitation factor increases in wetter scenarios, more of the small ephemeral pools with small catchments and flat bathymetry begin to persist long enough for adults to emerge (approximately 1 week). These pools are susceptible to long interstorm periods, and may rapidly dry out if not regularly replenished with water. With the highest mean annual precipitation scenario, these pools regularly persist long enough to allow adult emergence, and only occasionally disappear. An additional effect results from the increased chance that a particular pool will be utilized—and thus factor into mosquito population dynamics—if the population is already quite large from previous wet conditions.

High resolution modeling of hydrology is computationally expensive and not feasible for large areas. However, for larger areas, estimates of the extent of breeding habitat for certain rainfall regimes can be made using remotely sensed topography. Previously available remotely sensed topography products such as SRTM were too coarse for the level of modeling detail necessary to simulate mosquito breeding. Fortunately, new satellite technology designed to measure topography at a high resolution consistent with the characteristic scale of Sahel *An. gambiae* breeding sites is becoming a reality. The TerraSAR-X and TanDEM-X synthetic aperture radar satellites will generate digital elevation models at such as spatial resolution, on the order of meters. While it will not be possible to run detailed hydrology models for large regions at this spatial scale, it may be possible to generate a descriptive index at a coarser scale that represents the level of microtopographic relief and hydrological characteristics that will yield breeding pools, when coupled with a certain rainfall regime that must be described stochastically for a region. Such a regional indicator of mosquito breeding pool persistence would not be computationally expensive and may aid in the identification of areas susceptible to high mosquito activity during rainfall anomalies.

5 Conclusion

This study has evaluated the contribution of intraseasonal rainfall pattern variability to variance in malaria vector mosquito populations for a water-limited environment in the Sahel using a field-validated numerical model. The interplay of land surface hydrology (vegetation and soil types), topography and precipitation regimes can yield a significant effect in water-limited transmission environments that should not be ignored in the development of models linking malaria transmission to environmental drivers. In this modeling study, seasonal precipitation accounts for only 60% of the variance in mosquito abundance. The remaining 40% is attributed to the effects of rainfall patterns and internal model stochasticity. An analysis showed that 2.7% of the 40% was due to this randomness governing individual mosquito behavior. As a result, rainfall pattern accounts for 39% of the variance in modeled mosquito abundance in Banizoumbou. This result could not be obtained without explicit simulation of individual pools and their persistence, underscoring the value of high-resolution (both spatial and temporal) mechanistic simulation to resolve these necessary details. In this study, surface area of pooled water from the model explained more variance in mosquito abundance than seasonal precipitation alone, and surface area of pools persisting longer than 1 week explained even more variance in mosquito populations. Such approaches can be used to estimate the effects of nonlinearities in the rainfall/mosquito connection.

Acknowledgements This study was funded by National Science Foundation EPSCoR grant “Complex Systems Modeling for Environmental Problem Solving”. I acknowledge the helpful comments of two anonymous reviewers.

References

Ali A, Amani A, Lebel T, Ibrahima S (2006) In: Demuth S, Gustard A, Planos E, Scatena F, Servat E (eds) Climate variability and change-hydrological impacts. IAHS, Wallingford

Balme M, Vischel T, Lebel T, Peugeot C, Galle S (2006) Assessing the water balance in the Sahel: impact of small scale rainfall variability on runoff Part 1: rainfall variability analysis. J Hydrol 331:336–348

Bomblies A, Eltahir EAB (2009) Assessment of the impact of climate shifts on malaria transmission in the Sahel. Ecohealth 6(3):426–437

Bomblies A, Duchemin J-B, Eltahir EAB (2008) Hydrology of malaria: model development and application to a Sahelian village. Water Resour Res 44:W 12445. doi:10.1029/WR006917

Craig MH, Snow RH, LeSueur D (1999) A climate-based distribution model of malaria transmission in Sub-Saharan Africa. Parasitol Today 15:105–111

Gerbaux M, Hall N, Dessay N, Zin I (2009) The sensitivity of Sahelian runoff to climate change. Hydrol Sci 54(1):5–16

Gianotti RL, Bomblies A, Dafalla M, Issa-Arzika I, Duchemin JB, Eltahir EAB (2008) Efficacy of local neem extracts for sustainable malaria control in an African village. Malar J 7:138

Gillies MT, DeMeillon B (1968) The Anophelinae of Africa South of the Sahara. S. Afr. Inst. of Med Res, Johannesburg

Guillot G, Lebel T (1999) Disaggregation of Sahelian mesoscale convective system rain fields: further developments and validation. J Geophys Res – Atmos 104(D24):31,533–31,551

Hoshen MB, Morse AP (2004) A weather-driven model of malaria transmission. Malar J 3(32). doi:10.1186/1475-2875-3-32

Kelly-Hope LA, Hemingway J, McKenzie FE (2009) Environmental factors associated with the malaria vectors *Anopheles gambiae* and *Anopheles funestus* in Kenya. Malar J 8(268). doi:10.1186/1475-2875-8-268

Kiszewski A, Teklehaimanot A (2004) A review of the clinical and epidemiological burdens of epidemic malaria. Am J Trop Med Hyg 71(suppl 2):128–135

Koenraadt CJM, Paaijmans KP, Githeko AK, Knols BGJ, Takken W (2003) Egg hatching, larval movement, and larval survival of the malaria vector *Anopheles gambiae* in desiccating habitats. Malar J 2:20

Koenraadt CJM, Githeko AK, Takken W (2004) The effects of rainfall and evapotranspiration on the temporal dynamics of *Anopheles gambiae ss* and *Anopheles arabiensis* in a Kenyan village. Acta Trop 90:141–153

LeBarbe L, Lebel T (1997) Rainfall climatology of the HAPEX-Sahel region during the years 1950–1990. J Hydrol 189(1–4):43–73

Lebel T, Sauvageot H, Hoepffner M, Desbois M, Guillot B, Hubert P (1992) Rainfall estimation in the Sahel: the EPSAT-Niger experiment. Hydrol Sci J 37:201–215

Lebel T, Braud I, Creutin JD (1998) A space-time rainfall disaggregation model adapted to Sahelian mesoscale convective complexes. Water Resour Res 34(7):1711–1726

Martens WJ (1998) Health and climate change: modelling the impacts of global warming and ozone depletion. Earthscan, London

Mathon V, Laurent H (2001) Life cycle of Sahelian mesoscale convective cloud systems. Quart J Roy Met Soc 127(572):377–406

Mearns LO, Rosenzweig C, Goldberg R (1997) Mean and variance change in climate change scenarios: methods, agricultural applications, and measures of uncertainty. Clim Chang 35(4):367–396

Molineaux L, Gramiccia G (1980) The Garki Project. World Health Organ, Geneva, p 311

Pascual M, Cazelles B, Bouma MJ, Chaves LF, Koelle K (2008) Shifting patterns: malaria dynamics and rainfall variability in an African highland. Proc Roy Soc B 275:123–132

Patz JA, Strzepek K, Lele S, Hedden M, Greene S, Noden B, Hay S, Kalkstein L, Beier JC (1998) Predicting key malaria transmission factors, biting and entomological inoculation rates, using modeled soil moisture in Kenya. Trop Med Int Health 3(10):818–827

Waggoner PE (1989) Anticipating the frequency distribution of precipitation if climate change alters its mean. Agric For Meteorol 47:321–337

World Health Organization (2010). *World Malaria Report 2010*. Geneva: WHO, 2010. http://www.who.int/malaria/world_malaria_report_2010/worldmalariareport2010.pdf

Zhou G, Minakawa N, Githeko AK, Yan G (2004) Association between climate variability and malaria epidemics in the East African highlands. Proc Nat Acad Sci 101(8):2375–2380