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Rainfall and air humidity: non-linear relationships with termite swarming in Amazonia*

by

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Abstract

The daily flight activity patterns of reproductive forms of termites (alates) in Central Amazonia were investigated in a case study with one light trap that was run continuously for over 3 years. The trap was situated in a secondary forest on terra firme in Manaus, Brazil. Light trap catches of termites were not significantly correlated to rainfall, relative air humidity, evaporation and barometric pressure. However, non-linear relationships were revealed by a regression tree analysis in which high Kalotermitidae flight activity was related to low air humidity (<75.5 %) at 8:00 of the morning of the catch night. Also, a MARS (multiple adaptive regression splines) analysis which fits regressions to non-linear data revealed that total Isoptera flight was non-linearly dependent on intermediate daily rainfall levels.
Keywords: **Rainforest, secondary forest, termites, dispersal flight, climate factors.**

Resumo

O padrão diário de atividade de vôo das formas reprodutivas de térmitas (alados) na Amazônia central foi estudado num estudo de caso, usando-se uma armadilha luminosa durante um período contínuo de 3 anos. A armadilha encontrava-se numa capoeira (floresta secundária) em terra firme em Manaus, Brasil. As coletas de cupins na armadilha luminosa não estavam significativamente correlacionadas a precipitação, umidade relativa do ar, evaporação e pressão barométrica. Porém, relações não-lineares foram reveladas numa análise de árvore de regressão na qual a atividade de vôo na família de Kalotermitidae estava relacionada com baixa umidade do ar (<75.5 %) ás 8:00 horas da manhã seguinte ás capturas noturnas. Também, uma análise com MARS (splines regressivos múltiplos e adaptivos) a qual aplica uma regressão a dados não-lineares revelou que o vôo de Isoptera no total foi dependente, de uma forma não-linear, de níveis intermédios de precipitação diária.

Introduction

The swarming of termite alates is a still little understood biological phenomenon. In these social organisms that spend most of their life as modular, sessile colonies or "superorganisms" (BEGON et al. 1996; MORITZ & SOUTHWICK 1992), the swarming guarantees the two basic biological functions of gene recombination and dispersal. Alate

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swarming in central Amazonia occurs throughout the year (REBELLO & MARTIUS 1994; MARTIUS et al. 1996), but the swarming patterns of termites of the three families that occur in the region (Kalotermitidae, Rhinotermitidae, and Termitidae) are distinct, clearly seasonal and seem to be adaptive to environmental conditions: whereas overall alate swarming frequency in non-flooded terra firme forest (SIOLI 1983) is reduced during the dry season, the lowest frequency in the floodplain forests (JUNK 1997) is observed during the flood phase which occurs in the season when alate swarms in rain forests show a high frequency (REBELLO & MARTIUS 1994). However, little is known about the factors that trigger the simultaneous release of alates of one species. Often, termite swarms are synchronized over a distance of several hundred kilometers (NUTTING 1969). Rainfall (MEDEIROS et al. 1999), light intensity, temperature, moisture, and wind and atmospheric pressure (NUTTING 1969 and literature herein) have been shown to control termite alate flight.

Here we report on a 3-year study during which termite alates were captured continuously in a light trap exposed in a secondary forest in central Amazonia. The trap was emptied every day over that period. These catches allow to assess the day-to-day patterns of swarming in Amazonia, and to evaluate air moisture, rainfall, evapotranspiration and air pressure as possible trigger factors of termite alate flight.

Material and methods

Central Amazonia is mainly covered by dense primary lowland "terra firme" rainforest; stands are 30-40 meters high and of high tree species diversity (KLINGE et al. 1975; GENTRY 1990). However, the present study was carried out in a secondary forests. These are of widely varying aspects and occur where land stripped of the original forest has been left for regrowth (SMITH et al. 1997).

The study area was a 30-40 year old secondary forest site of approximately 10 ha, on the campus of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil. It was surrounded by larger and smaller remnants of former primary rain forest (terra firme forest in Brazil) and in part by urbanized areas, intersected by streets with lamps and buildings.

The average annual rainfall between 1971 and 2000 was 2554±273 mm (MARTIUS et al. 2003a). A short dry season (monthly precipitation below 100 mm) lasts from July to September and average monthly temperatures are between 25 and 27 °C (RIBEIRO & ADIS 1984). The soil in the region is a Xanthic Ferralsol (FAO/UNESCO 1990).

Termite assemblages in rain forests consist of up to one hundred species per hectare (MARTIUS 1994). In secondary forests, both their density and diversity are generally reduced (BANDEIRA 1978, 1989; MARTIUS et al. 2003b). Nevertheless, termite swarming still is considerable; at least half of the termite species registered with direct sampling in similar stands was also recorded in light trap catches (REBELLO 1997).

To collect flying termite adults (alates) we used a light trap type "WALZ" (MÜHLENBERG 1989) equipped with a fluorescent lamp (manufacturer: Ecotech, Bonn, Germany). The trap was plugged via an extension cable into an electrical socket at a building in 15 m distance. An interruptor coupled to a photosensitive element switched the light off and on at dawn and sunset. This means that predominantly those termites swarming at night were collected by the trap. The trap was suspended in dense secondary growth behind that building at a height of 1.60 m above the ground. The collector vial was filled with 150 ml of water with some drops of detergent. The system was run continuously, the vial being emptied daily. The collected material was immediately transferred into 70 % alcohol, then termites were sorted out and identified to the family level. No attempt was made to sort termites into species because alates are rarely described; also we found that catches of single species generally are not sufficient for pattern analysis (REBELLO 1997). The trap was run from August 28, 1990 to November 30, 1993 (39 months). Data for the period September 1990 to August 1993 (3 full years) were used in Figures 1, 2 and Table 1.

The data were analyzed based on total catches (individual numbers per day). A transformed data set with binary presence-absence (1-0) data was also tested but without significant results. Besides standard statistical analysis (linear regression, Pearson correlation) we looked for non-linear data relationships with two computer-intensive data mining tools, MARS and CART.

Building regression trees with CART

In view of the failure of linear regressions on our data set, CART (classification and regression trees) was used as a parameter-free procedure (BREIMAN et al. 1984; STEINBERG & COLLA 1998; references for CART applications are given in MARTIUS et al. 2003b). The software program CART (also from Salford Systems) classifies data into binary "trees" in a computer-intensive iterative trial-and-error process (cf. Fig. 3). For each of the individual lines of a given data set, a decision has to be made based on a single question (e.g., "is air humidity ≤75.5 %?"). The answer to this question decides whether the given line of the data set is to be sent to the right- or to the left-hand node of the actual bifurcation. Both the choice of the questions and the decision upon where the threshold for the split is set are made on the basis of "misclassification costs" that occur when a case is sent to the wrong side of the split (cf. BREIMAN et al. 1984; STEINBERG & COLLA 1998 for details). The program tries to minimize these costs in a computer-intensive iterative process. CART can handle data sets with missing values (BREIMAN et al. 1984). This was an advantage with our data set which had 10 % missing values due to trap failure. CART regression trees were grown with the defaults given by the program except that a 50-fold cross validation was used.

MARS

Multivariate Adaptive Regression Splines (MARS) is a novel exploratory analysis technique that quickly and automatically detects non-linear relationships between data by piecewise fitting a linear regression over parts of the whole non-linear function (FRIEDMAN 1991) in a computer-intensive, data-driven procedure. Data transformation is automatically performed by the program to account for non-linear structure in complex data sets. The program detects interactions between the predictor variables and can handle missing data. The procedure has performed equally well as or often better than neural networks (DE VEAUX et al. 1993). The MARS tool of Salford Systems (San Diego, California) was used following the analysis with CART. CART allowed to narrow down the number of predictor variables, and MARS was then used to search for eventual regressions, i.e. smoother relationships than those detected with CART. This two-fold procedure is recommended by STEINBERG et al. (1999).

Results

The total catch period comprised 1191 nights. Termites were collected in 42 % of the nights in which the traps were active (given the mentioned 10 % failure rate). Of the total 11683 alates collected in the course of this study, 85.2 % belonged to the family Termitidae, 13.5 % to the Kalotermitidae, and only 0.4 % to the Rhinotermitidae (Table 1). However, Kalotermitidae were present in 30 % of the catches, but Termitidae (18 %) and Rhinotermitidae (3 %) were much less frequent.

The daily abundances of Termitidae were higher in September to Mid-January (days 1-150 in Fig. 1), and again in May to July (days 250-300) in all years. Kalotermitidae catches peaked throughout the period of July to November (days 300-365 and then 1-100; Fig. 2). Both groups consistently had low catches from mid-February to mid-April (days 170-230) in all years; i.e. during the end of the rainy season. The total abundances of all families were higher in 90/91 and 92/93 (Table 1). Rhinotermitidae data are too scarce for further analyses.

Linear regressions between daily catch numbers per family and daily rainfall were not significant (Annex 1). Also, Pearson product moment correlations between daily catches and climate data were not significant (Annex 2). Although satisfactory P values were obtained for some climate data and Kalotermitidae catches, all correlation coefficients were too low for a consistent relationship. Equally, when the termite catch data were lagged by one day to account for an eventual delay in the termites' reaction to climatic events, no significant correlations were found.

Regression tree analysis

The analysis of termite catches in the light trap with a regression tree (CART) approach only yielded significant trees with Kalotermitidae catches modeled on air humidity. Air humidity at 20:00 hrs the night before the catch (UR20) separated the data set into a simple tree with two final nodes of approximately equal size. With UR20 below 80.5 %, average daily catch number of Kalotermitidae was 2.8 ind. day^{-1} (n = 523 cases); whereas UR20>80.5 % yielded much lower catches (0.5 ind. day^{-1}, n = 549). However, when UR20 and UR08 (the air humidity at 8:00 hrs on the morning after the catch) were used together as predictor variables, UR20 was overrun by UR08 which split the data set at UR08>75.5 % (Fig. 3).

That means that a dry evening (UR20<80.5 %; almost half of the cases) yielded on average about five times more Kalotermitidae per catch than a moist evening (UR20>80.5 %). However, if the air humidity early on the morning that follows the night of the catch was lower than 75.5 % (indicating a very dry night; this was the case in 59 catches only), the average Kalotermitidae catch a high 8.2 ind. day^{-1}, about six times higher than in moister nights (1.3 ind. day^{-1}). This shows that Kalotermitidae swarming is not linearly correlated to air humidity but rather is triggered when a certain threshold is reached. It also confirms earlier findings (REBELLO & MARTIUS 1994) that Kalotermitidae (dry-wood termites) swarming is related to dry climate.

MARS analysis

The analysis using multivariate adaptive regression splines (Table 2) points at a non-linear relationship between total Isoptera flight and rainfall. The other data sets (single termite families and other climate variables) did not yield any results. Total Isoptera have a sharp peak at a daily rainfall of 10-15 mm (Fig. 4). That suggests that daily rainfall of this size may be sufficient to trigger alate flight. Only again with very high daily rainfall of several 100 mm the Isoptera flight activity increases weakly, probably either because then swarming is higher or, more probably because only a few species show activities with those very high rainfall events. This pattern of reaction to rainfall explains why no linear correlations were detected.

Rainfall of more than 40-50 mm per day is generally associated with either strong storms or with long-lasting whole-day precipitation. This points at a need to differentiate, in further studies, between events of different rainfall types rather than a rainfall gradient alone.

Discussion

At first sight, the results of the MARS and CART may appear to be contradictory. CART showed that Kalotermitidae swarming is related to dry nights, whereas MARS showed that total Isoptera flights were related to rainfall, although not linearly correlated. The fact that Kalotermitidae only account for 15 % of the total Isoptera might explain this inconsistency. Although Kalotermitidae swarm preferentially in dry nights, the effect is overrun by the majority of Termitidae in the total termite catch.

It was not possible to obtain similarly consistent results for the single families with MARS, or to grow regression trees for the other families than Kalotermitidae using CART. This shows that still considerable effort is needed to make consistent statements on the factors that trigger termite swarming. More traps would allow for better statistics and a species-specific analysis of data. However, the approach chosen here was successful in showing that relationships between termite catches and climate data are non-linear and can not be detected with simple regressions or correlations.

Conclusions

In view of the observed seasonality of termite alate swarming (cf. also REBELLO & MARTIUS 1994; MARTIUS et al. 1996; MEDEIROS et al. 1999), it is interesting that a correlation between termite catches and climate data is difficult to obtain even when a high-resolution data set, based on extremely work-intensive daily catches, is used. This might in part be due to the fact that when families are pooled, different species with different reaction are mixed which blurs the correlations. Analyses of termite swarming based on individual species are under way (REBELLO 1997). However, the analysis based on non-linear data mining techniques undertaken in the present study shows that the reason for a lack of correlation might be the non-linearity of the reaction of termites to climate factors. Non-linear relationships to rainfall (with MARS; for all termites) and air moisture (with CART; for Kalotermitidae) were achieved. It was confirmed that rainfall is one of the trigger factors for termite flight, and that swarming of Kalotermitidae, dry-wood termites, is related to lower moisture content in the atmosphere. This holds a promise for future collections of similar data sets which should be carried out with a larger number of replicate sampling (replication of traps) and on a species rather than family basis.

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Table 1: Total number of termite alate catches in a light trap in a secondary forest site, Manaus, Amazonia, Brazil. Annual periods last from September to August.

Period	Kalotermitidae	Rhinotermitidae	Termitidae	Total Isoptera
90/91	798	16	5626	6538
91/92	251	11	1326	1601
92/93	532	15	2997	3544
Total period (1990-93)	1581	42	9949	11683

Table 2: Basis functions (BF) generated by the MARS model of total Isoptera catches (ISOPTT) vs. rainfall (RAIN).

BF1 = max(0, RAIN - 13.000);
BF3 = max(0, RAIN - 11.600);
BF5 = max(0, RAIN - 15.000);

Y = 5.472 - 421.418 * BF1 + 247.949 * BF3 + 173.633 * BF5;

model ISOPTT = BF1 BF3 BF5

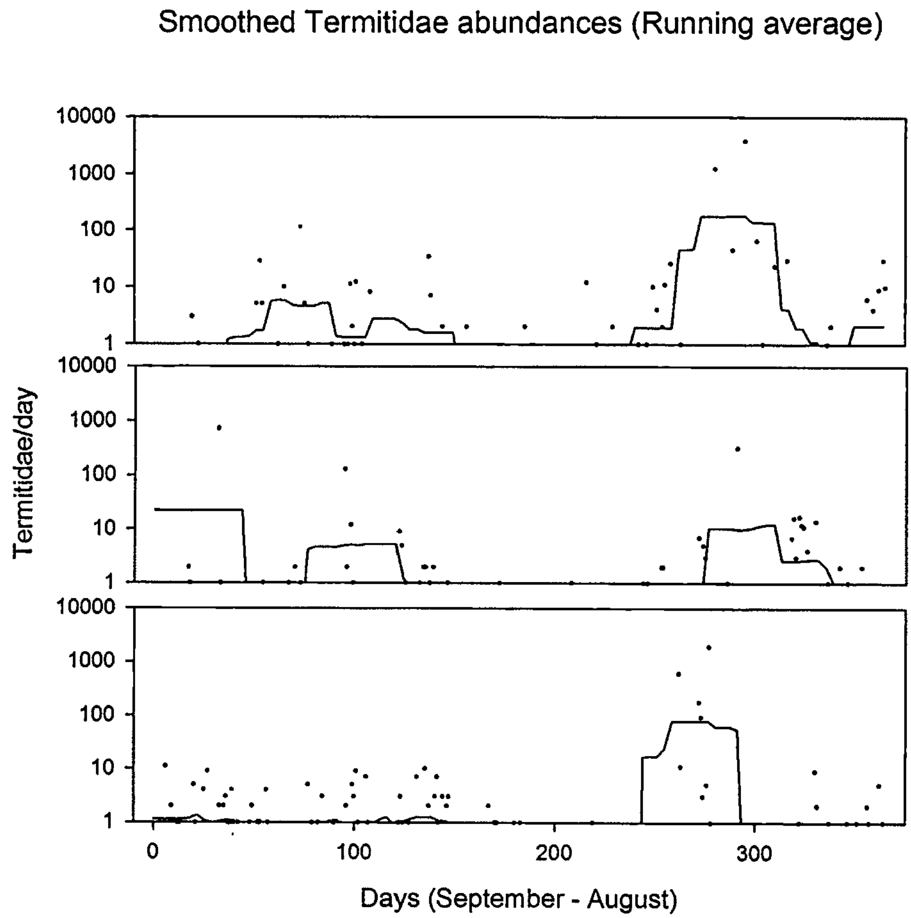

Fig. 1:
Smoothed daily Termitidae abundances show peaks during September to January and May to July. Proportion of total sample for calculating the running average is 10 % of the data set. Dots = daily catches; line = smoothed values.

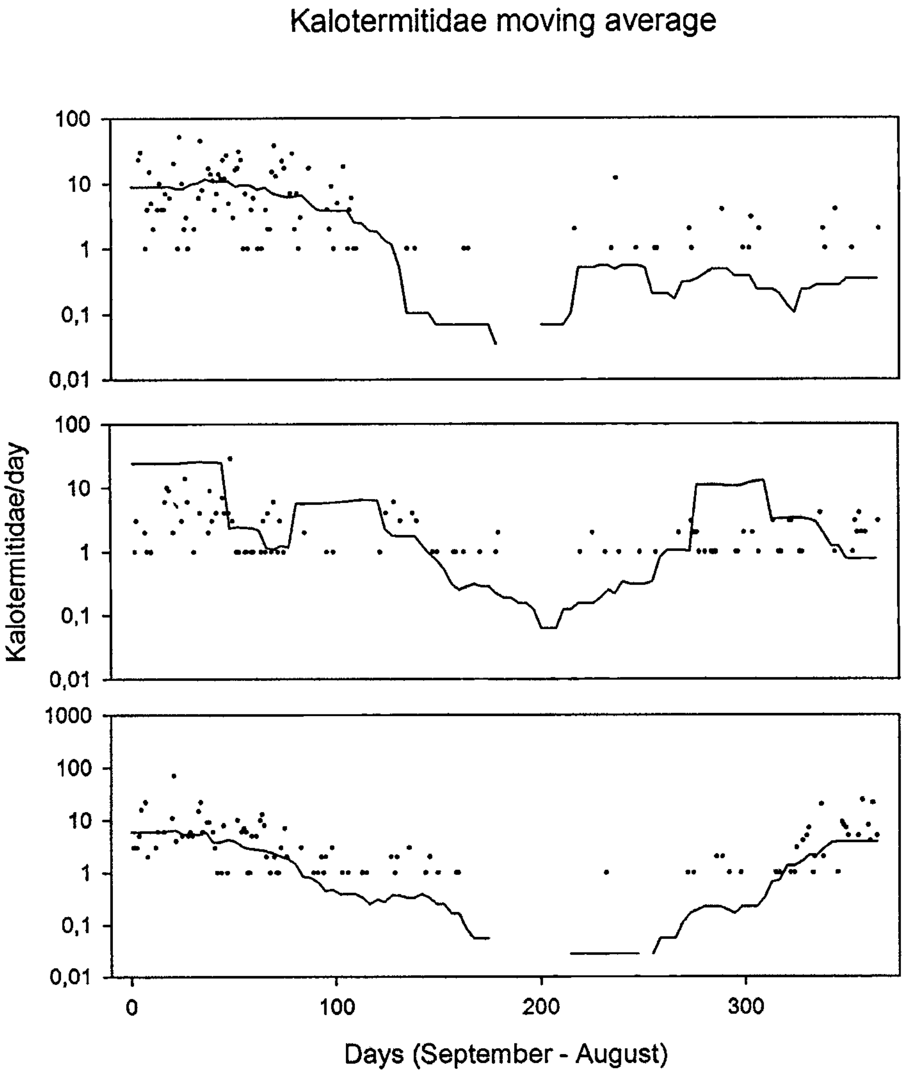

Fig. 2:
Smoothed daily Kalotermitidae abundances peak from July to November. Proportion of total sample for calculating the running average is 10 % of the data set. Dots = daily catches; line = smoothed values.

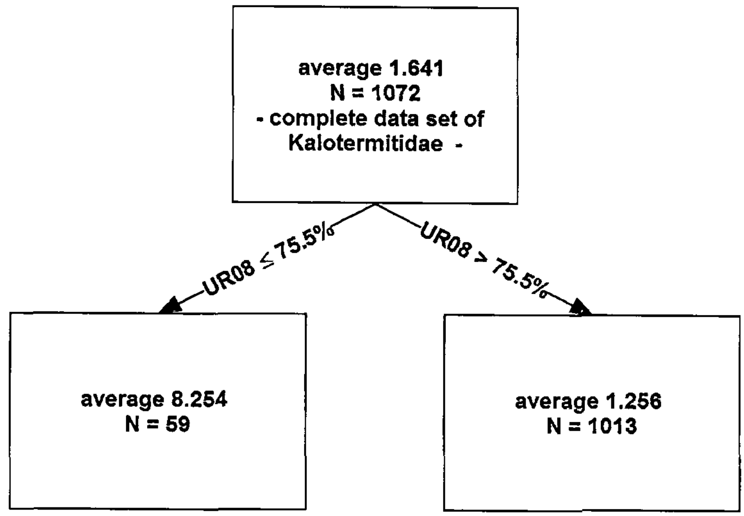

Fig. 3:
Two-node CART regression tree for Kalotermitidae catches. Cases with relative air humidity at 08:00 on the morning of the catch night (UR08) of less than 75.5 % go to the left side and average 8.2 ind. day^{-1}.

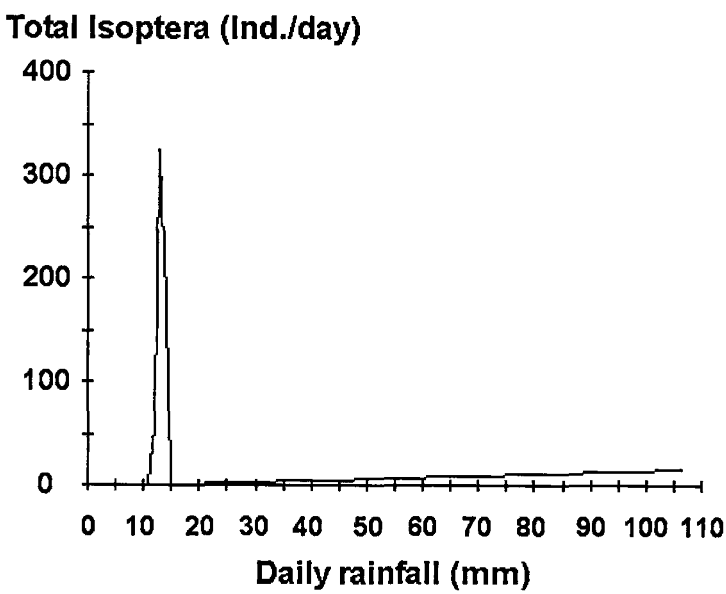

Fig. 4:
Multivariate adaptive regressions splines (MARS) analysis of the relation between daily total Isoptera catches and rainfall shows a sharp peak of swarming at a moderate daily rainfall level.

Annex 1: No linear regression between daily catches per termite family (K, R, T) and daily rainfall (Prec) on the preceding day was observed (data from August 1990 to December 1993).

Family	**Regression**	**N**	**r^2**
Kalotermitidae	K = 1.88 - 0.0042*Prec	1071	0,011
Rhinotermitidae	R = 0.04 + 0.0003*Prec	1062	0,001
Termitidae	T = 7.65 + 0.315*Prec	1062	0,001

Annex 2: Pearson product moment correlations between daily climate factors and daily catches per termite family in a light trap (August 1990 to December 1993). R = correlation coefficient; P = P value; N = number of samples. UR08, UR14, UR20 = relative air humidity at 8, 14 or 20 hours on the day before the catch. Pres = atmospheric pressure. Lagged Variables = catch data were postponed by one day (24 h) with relation to climate data to allow for delayed reaction of termites to trigger factors.

Climate	**Kalotermitidae**			**Rhinotermitidae**			**Termitidae**		
factor	**R**	**P**	**N**	**R**	**P**	**N**	**R**	**P**	**N**
Rainfall	-0,105	**$6.1*10^{-4}$**	1071	0,01	0,749	1062	0,028	0,355	1062
Evaporation	0,23	**$4.6*10^{-14}$**	1047	-0,03	0,325	1038	0	0,969	1038
UR08	-0,02	0,572	1060	0	0,921	1051	0	0,963	1051
UR14	-0,243	**$7.2*10^{-16}$**	1068	-0,02	0,539	1059	0,017	0,591	1059
UR20	-0,228	**$5.1*10^{-14}$**	1068	0,036	0,24	1059	0,025	0,42	1059
Pres08	0	0,767	1062	0	0,924	1053	0	0,961	1053
Pres14	-0,09	**3**	1068	0	0,761	1059	0	0,868	1059
Pres20	-0,01	0,646	1069	0	0,865	1060	0	0,929	1060
				Lagged Variables					
Rainfall	-0,1	**2**	1070	-0,02	0,483	1061	0	0,935	1061
Evaporation	0,22	**$6.4*10^{-13}$**	1048	0	0,381	1039	-0,03	0,298	1039
UR08	0	0,612	1059	0	0,9	1050	0	0,925	1050
UR14	-0,205	**$1.45*10^{-11}$**	1068	-0,01	0,65	1059	-0,02	0,485	1059
UR20	-0,198	**$7.1*10^{-11}$**	1068	0,037	0,235	1059	-0,01	0,695	1059
Pres08	-0,913	0,766	1061	0	0,928	1052	0	0,962	1052
Pres14	-0,08	**6**	1068	-0,05	0,105	1059	-0,02	0,489	1059
Pres20	-0,01	0,646	1068	0	0,865	1059	0	0,929	1059