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A systematic approach to area-wide tsetse distribution and abundance maps

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Abstract

A raster or grid-based Geographic Information System with data on tsetse, trypanosomosis, animal production, agriculture and land use has recently been developed in Togo. This paper describes the generation of area-wide digital tsetse distribution and abundance maps and how these accord with the local climatic and agro-ecological setting. Results include: (i) a spatial demarcation of ecologically distinct areas, producing a seasonal cluster map based on seasonal weather data and temporal series of satellite derived National Oceanic and Atmospheric Administration (NOAA) AVHRR and METEOSAT variables: (ii) tsetse distribution maps of *Glossina tachinoides* Westwood, *G. palpalis palpalis* (Robineau-Desvoidy), *G. morsitans submorsitans* Newstead, *G. longipalpis* Wiedemann, *G. medicorum* Austen and *G. fusca fusca* (Walker); and (iii) tsetse abundance or 'risk' maps, corrected for within database seasonal fluctuations, for *G. tachinoides* and *G. p. palpalis*. It is concluded that grid-based sampling is the ideal method for rapid assessment of the current vector and disease situation within any country or region, and that remote sensing has an important role to play in planning such a sampling system.

Introduction

Tsetse transmitted trypanosomosis has been identified as a major constraint to increased livestock production in the subhumid ecozone of sub-Saharan Africa. Moreover, tsetse infestations are believed to prevent the successful integration of crop and ruminant production (Jordan, 1986; Jahnke *et al*., 1988; Toure & Mortelmans, 1991; Winrock International, 1992). Apart from the disease situation which develops after an infective tsetse fly bite, it is argued that the mere presence of tsetse creates imbalances in the distribution of susceptible livestock and thus influences the type and number of animals kept, the use of oxen for draught power, manure as crop fertilizer and crop-residues and byproducts as cattle feed (FAO, 1991; Swallow, 1998).

These effects are, however, difficult to substantiate, particularly at the local level. While the general cattle distribution in tsetse affected sub-Saharan Africa shows some 94% of animals distributed at the perimeter of the continental fly belt (FAQ & ILRI, unpublished), it remains to be clarified how this impacts on farming at national and subnational level.

Because of the agricultural and land use dimension of the tsetse problem, there is a need to develop and apply a geographical tool, a Geographic Information System (GIS), for the display, analysis and interpretation of the spatial patterns in tsetse challenge, trypanosomosis risk, clinical disease, livestock biomass, breed distribution, farming system and land utilization. It may be argued that this area-wide knowledge dimension forms the basis for rational trypanosomosis control.

A systematic, area-wide sampling and analysis of geo-referenced data on tsetse, trypanosomosis, animal production, agriculture and land use was performed in Togo. The aim was to develop a grid-based data collection standard and to be able to clarify the local impact of tsetse and trypanosomosis on livestock and agricultural production, and to translate this knowledge at a later stage into practical disease management. This article describes the generation of digital tsetse distribution and abundance maps.

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Published tsetse distribution data, be they at national or regional level, mostly refer to fly presence or absence only and do not consider fly abundance. Comprehensive tsetse distribution maps at continental level have been most recently compiled by Ford & Katondo (1977). Several updates of these tsetse maps have since been published (Katondo, 1984; Moloo, 1985; Gouteux, 1990) but the maps are known to remain rather inaccurate. Tsetse surveys are demanding in terms of staff inputs and have rarely been carried out systematically and over wide areas. In general, data lack detail regarding abundance figures and seasonal fluctuations (e.g. Clair & Lamarque, 1984).

Tsetse distribution data for Togo were reviewed by Mawuena (1988a), discussing fly survey data of the period 1967 to 1972, from the northern half of the country, and survey data from 1977 to 1987, concerning the southern half (Mawuena, 1988b). This work had revealed the presence of three members of the riverine tsetse group, *Glossina (Nemorhina) tachinoides* Westwood, *G. (Nemorhina) palpalis palpalis* (Robineau-Desvoid) and *G. palpalis gambiensis* Vanderplank plus two members of the savannah tsetse group, *G. (Glossina) morsitans submorsitans* Newstead and *G. (Glossina) longipalpis* Wiedemann (Diptera: Glossinidae). No abundance data were available and, except for the southern limit of *G. tachinoides*, no accurate distribution limits were given for the different species.

The present work introduces the principle of area-wide recording of fly presence and abundance, discusses the associated climatic and agro-ecological setting and reflects on how these environmental features explain the picture encountered. It is estimated that this work will assist the production of tsetse maps derived mainly from remotely sensed data, using only a restricted amount of field data.

The present paper is concerned with the ground survey based, spatial tsetse abundance data and follows earlier publication of preliminary results (Hendrickx *et al.*, 1993; Napala *et al.*, 1993; Rogers *et al.*, 1994). Details are now presented on seasonally adjusted abundance of the riverine tsetse species encountered in Togo and fly distribution patterns are related to data on eco-climatic features, both ground measured and remotely sensed, and agricultural activity. The potential for the use of satellite data on environmental features such as vegetation cover, temperature and rainfall measurements, for the prediction of the individual tsetse species presence and abundance is further detailed in a second paper.

Materials and methods

The study area

Togo (fig. 1), 550 km long but never more than 150 km wide, forms a north–south transect of climate (fig. 1a) and vegetation (fig. 1b.A) types representative of subhumid West Africa with climate and vegetation zones or bands running parallel to the coast line, but with local nuances brought about by topography and elevation. In Togo, the Soudanian climate in the north is marked by a single rainy season whilst in the southem Guinean zone the rains become interrupted by a short dry season (fig. 1a). The 450–900 m high Atakora mountain chain divides the northernmost, one third, of the country from the remaining two-thirds and runs south–west to north–east, creating the watershed between the two major river systems (fig. 1b.B).

Existing data sources

A raster or grid-base of 311 identical cells, with each cell side measuring 0.125° latitude / longitude, was adopted as a practical sampling frame for country-wide surveys of tsetse, trypanosomosis and agriculture. Existing data sources on climate and agriculture were also fitted to the same grid, i.e. spatial resolution:

1. An elevation score was obtained for each grid cell using the Digital Elevation Model (DEM) for Africa produced by the Global Land Information System (GLIS) of the United States Geological Survey, Earth Resources Observation Systems (USGS, EROS). The original 0.083°-resolution was resampled to fit the 0.125°-resolution data base.
2. Rainfall features were derived from 30 year rainfall data held by the Togolese Ministry of Agriculture, Livestock and Fisheries; average annual rainfall (mm), the number of months with rainfall exceeding 100 mm (humid months) and the number of months with rainfall lower than 30 mm (dry months). Individual grid figures were obtained from originally drawn monthly isohyets (A4 sheets covering the whole country based on 38 observing stations).
3. Temperatures were interpolated from point records (HMSO, 1983) using a contouring programme in a commercial software package (SURFER, Golden Software Inc.) based on data from a series of observing stations in West Africa (e.g. Togo (8), Ghana (21), Benin (6) and Burkina Faso (7)). Data used were the mean monthly average, maximum and minimum temperatures (°C) and the annual temperature range.
4. Agricultural intensity data (expressed as % of land brought into the cultivation cycle, including fallow, fig. 1b.C) were digitized through scanning existing maps (scale approx. 1 / 500.000), in turn compiled on the basis of aerial photographs (PNUD, 1984).

Remotely sensed data

Remotely sensed data originated from two sources. A first set was derived from the Advanced Very High Resolution Radiometer (AVHRR) on board the polar orbiting National Oceanic and Atmospheric Administration (NOAA) satellites. They included the Normalized Difference Vegetation Index (NDVI), Channel 3 derived data (Ch3) and the Price thermal Index (Ts). Data used have an original (i.e. before adaptation to the databank) spatial resolution of 8 km and a temporal resolution before processing of 10 days to 1 month. The second set was derived from the geostationary METEOSAT satellite, recording data for the whole African continent every 0.5 h with an original spatial resolution of 5 km. Data used were the Cold Cloud Duration (CCD) (Snijders, 1991). Both types of satellite outputs have been reviewed in detail, discussing both their advantages and disadvantages, by Hay *et al.* (1996).

Normalized Difference Vegetation Indices are a measure of the active vegetation biomass (Tucker *et al.*, 1983). They are obtained from measures made in the visible red waveband (Channel 1) and near infrared waveband (Channel 2) using the equation:

$$NDVI = (Ch2 - Chl) / (Ch2 + Ch1)$$

The index is based on the principal that active plant tissue (mainly chlorophyll pigments) absorbs light in the visible red waveband (Ch1) and mesophyll tissue reflects

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light in the near infrared waveband (Ch2) (Sellers, 1985). Healthy plants will thus look darker in the visible and lighter in the near infrared bands than unhealthy or dried out plants, yielding a higher NDVI.

Channel 3, measuring the middle infrared radiation (MIR), both reflected and emitted, has been shown to relate with vegetation canopies (Boyd & Curran, 1996). It was recently recognized to be one of the better predictor variables of landcover type in Nigeria (Rogers *et al.*, 1997).

The Price thermal brightness index, Ts (Price, 1984), simplified by Hay *et al.* (1996), is derived from AVHRR Channels 4 and 5 and has been shown to be a surrogate for the ground temperature variability. The equation used is:

$$Ts = Ch4 + 3.33(Ch4 - Ch5)$$

In this paper we used the maximum value composite images over a period of 10 days of NDVI, Ch3 and Ts derived from the 8 km resolution PATHFINDER data set for the period 1988 to 1990. Mean 10 day average, maximum and minimum values were extracted using the 2×2 pixel array centred as closely as possible on each 0.125° grid square to fit the database. The images were further subjected to temporal Fourier analysis which extracts from the time-series a satellite 'finger-print' of vegetation phenology (Rogers & Williams, 1994). This information was stored as the mean NDVI as well as the amplitudes (i.e. peaks) and phases (i.e. seasonal timing) of the annual, biannual and tri-annual cycles of vegetation activity.

Finally, Cold Cloud Duration from METEOSAT, was derived from measured cloud-top temperatures. In West Africa, cloud-top temperatures between −30 and −60°C have been related to ground measures of rainfall (Snijders, 1991). Cold Cloud Duration was expressed as the number of hours that cloud-top temperatures were below the applicable threshold, depending on the area covered, for a given time period (10 days in this case). Data used were the monthly images from 1989 to 1991 (1988 data were only available for part of the year). Data were processed and stored in the same manner as for NOAA data.

Entomological field surveys

The untreated field data refer to trap catches made at different times of the year for different parts of the country. The first survey period, from 1990 to 1992, covered the major part of the country and in the second, from 1993 to 1995, efforts concentrated on the precise limits at the edges of the fly distributions. All field surveys were conducted by five different mobile teams operating simultaneously. Each team was assigned one out of five administrative regions (fig. la) of the country grossly corresponding to a 1:200,000 map each.

In order to obtain grid cell specific fly density values, 1:200,000 maps were consulted to select survey sites representative in terms of the prevailing dominant vegetation types, and also taking into account the local drainage systems and the accessibility of the terrain. Locally, within each site, the field teams selected what they perceived to be suitable tsetse habitats according to expected fly species, and positioned clusters of a minimum of five and an average of 12-tsetse traps for 24 to 48 h. Throughout all surveys, standard biconical traps (Challier & Laveissière, 1973) were employed. Thus, a total of 653 different survey sites were sampled in 305 of the 311 grid-squares comprising 14,620 trapping days. Traps were unbaited with odour attractants except when determining more precisely *G. longipalpis* distribution limits when ox urine and acetone were employed (producing up to 6-fold increase in trap catches, Hendrickx *et a!.*, unpublished). The species, sex and number of tsetse flies in each trapping site were recorded using classical identification keys (FAO, 1982). More recently published identification software (Glossine Expert, Brunhes *et al.*, 1994) served to identify flies of the *fusca* group (*Austenina*). The subspecies of *G. palpalis* was identified after dissection of the inferior claspers of the genitalia of male specimens, measuring the width of the clasper head with a micrometer (table 1). Specimens of *G. p. gambiensis*, kindly provided by the Centre International de Recherche Développement de l'Elevage en zone Subhumide (CIRDES, Burkina Faso), were used as a reference.

Measured densities were expressed as flies per trap per day and transformed to $\log_{10}(n + 1)$ for further analysis. Since surveys had been carried out during different times of the year in different places, seasonal adjustments were first calculated on the basis of monthly indices, depicted from the seasonal curves (fig. 2) obtained separately for the northern (seasonal clusters A and B) and southern (seasonal clusters C and D) part of the country. Fly density values were thus multiplied with the index of the respective capture month. Fly catches of different survey sites were pooled to obtain the apparent fly density per species per grid. Seasonal curves at the individual fly species level were calculated for the two riverine species (*Nemorhina*), *G. tachinoides* and *G. palpalis palpalis*. Data available for the savannah flies (*Glossina*) *G. m. submorsitans* and *G. longipalpis* were insufficient to obtain these seasonal figures.

Spatial smoothing was carried out through averaging the grid value with that of the eight, or less, adjacent grids. Missing grid-values were also replaced in this way.

Results

Area classification

As a first step, the existing ecoclimatic and satellite derived environmental data were subjected to cell-by-cell classification and clustering, in order to demarcate better the survey area in ecological terms and to establish seasonal clusters of similar setting. For this purpose, the grid cell attribute data which contained information relevant to seasonality, such as the number of humid / dry months, the temperature range and the bi- and tri-annual cycles observed through Fourier processing of NDVI, Ch3 and CCD data, were subjected to a Hierarchical Cluster Analysis, using the commercially available software UNISTAT™. The computed dendrogram, in squared Euclidean space, is shown in fig. 3. The cluster classification is based on the distance between the centroids of all points within each cluster. Table 2 shows the average values and standard error per cluster for the more relevant variables. Differences between clusters were calculated using the standard formula for *t*, equated to *d*, to establish any significant differences between the means of two large samples.

The spatial aggregation of the four main seasonal clusters is depicted in a separate map (fig. 3). Geographically, the results of the cluster analysis suggested a distinct division into two northern and two southern clusters. Table 2 shows some significant differences between those areas. The north,

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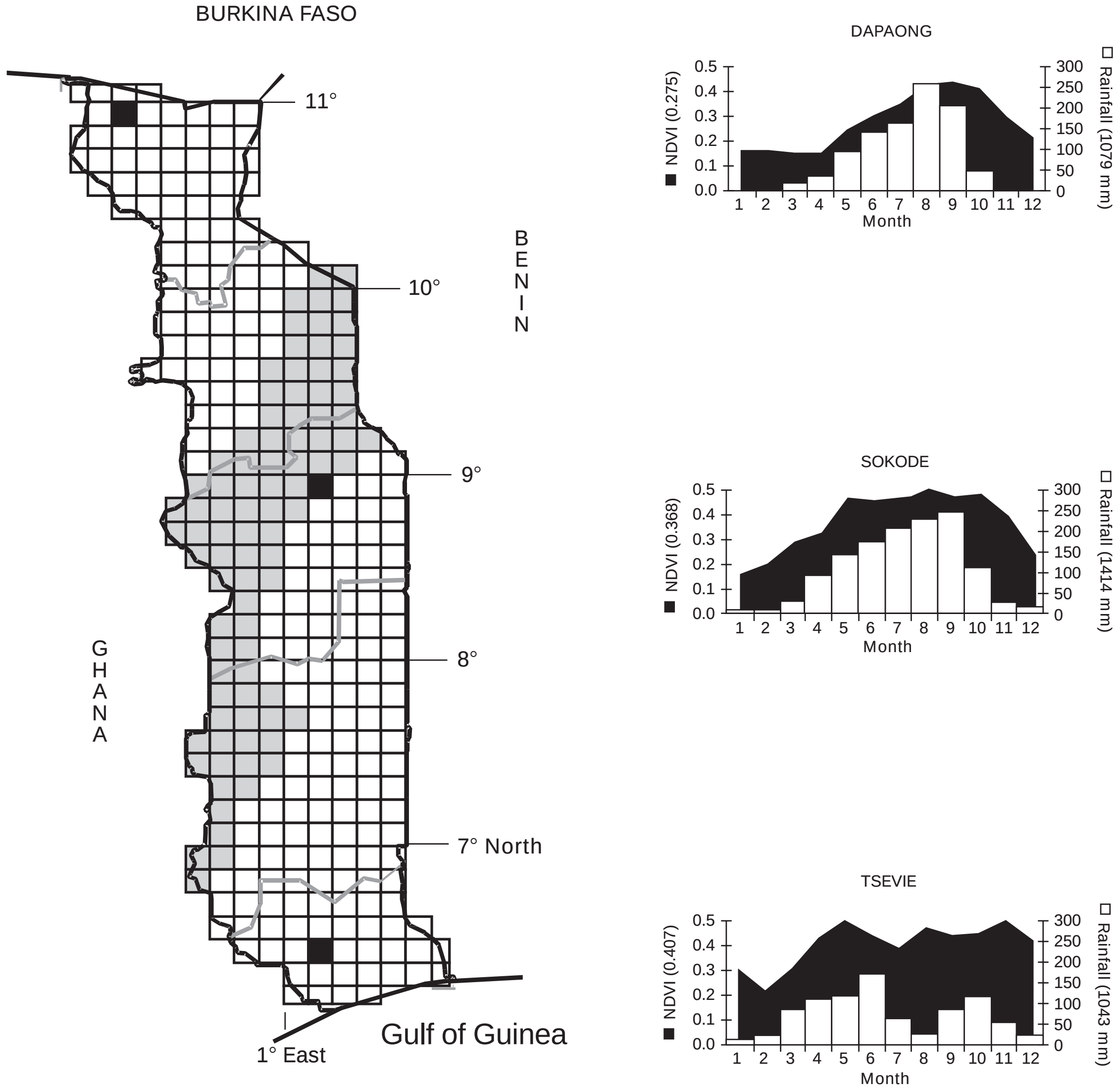

Fig. 1a. Seasonal curves are given for mm rainfall (histogram, white) and Normalized Difference Vegetation Indices or NDVI (surface, black) for respective black grid-squares on map from north to south: Dapaong, Sokode and Tsevie. Average annual values are given between brackets (cfr. Y-axes). See text for more information on NDVI values. On the Togo map the grey shaded grid-squares show the Atakora mountain range. The grey lines represent the administrative regions covered by different field teams, from north to south: Région des Savanes, Région de la Kara, Région Centrale, Région des Plateaux, Région Maritime.

as opposed to the south, is defined by a low ratio of humid over dry months, higher temperature ranges, a dominance of the annual vegetation cycle and a shorter time lag between the timing of the annual cycle of CCD and NDVI. Differences within areas, i.e. between sub clusters A–B and C–D, were also significant. Cluster A is the dry north. Cluster B still has a strong monomodal seasonal component but tends to be more humid further south. This is partly influenced by the Atakora mountain range. Cluster C is the humid south with a bi-modal seasonal cycle and Cluster D is the most humid part of the Atakora, termed the plateau area and which encompasses the lower piedmont area. Within this cluster are the highest grid values for altitude (672 m) and rainfall (1627 mm), and the lowest for temperature (e.g. $Temp_{max}$ 25.2°C).

Tsetse distribution and abundance

General

The distribution and abundance of individual tsetse fly species are presented separately, based on reference material in figs 4–8. Fly abundance maps, before and after smoothing, are shown for both riverine species (fig. 4). Schematic maps depicting the local distribution limits of *G. tachinoides* and *G. p. palpalis* are also given (figs 5–7).

The distributions of savannah (subgenus *Glossina*) and forest tsetse groups flies (subgenus *Austenina*) (fig. 8) were based on untreated fly presence/absence data, with an indication of either low or high density in the case of savannah tsetse. Riverine fly abundance data were regressed against the satellite derived environmental parameters and

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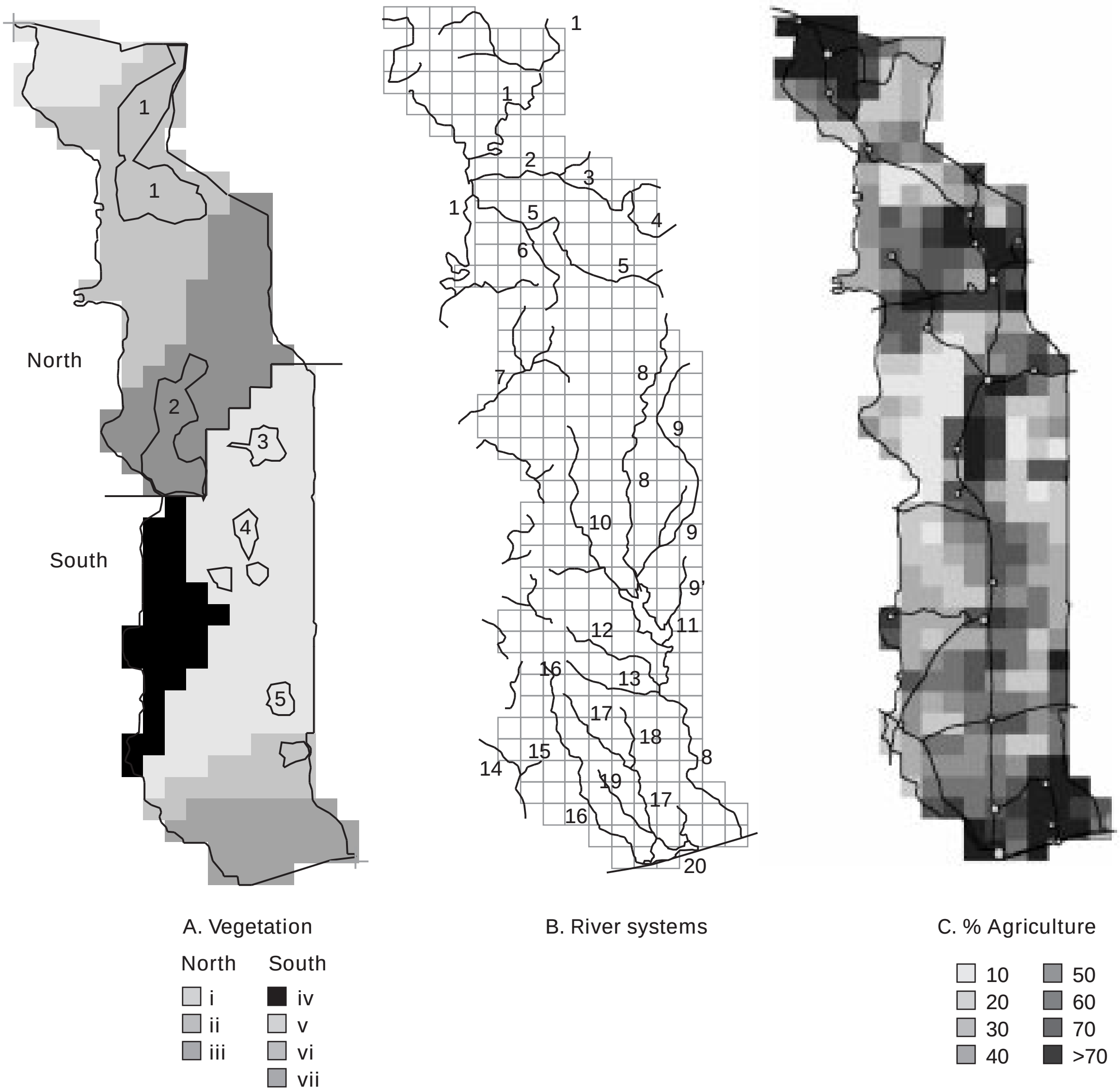

Fig. 1b. A. Vegetation gradient. North Togo: (i) Northern savannah (sandstone); (ii) Sudanian savannah; (iii) Dry forest. South Togo: (iv) Humid forest; (v) Guinean savannah; (vi) Transition zone; (vii) Terre de barre. Protected areas: 1, Oti and Kéran game reserves; 2, Fazao game reserve; 3, Abdoulaye forest; 4, Kpessi and related forests; 5, Tchila Monota and Togodo forests. B. Major rivers: 1, Oti; 2, Koumoungou; 3, Kéran; 4, Binah; 5, Kara; 6, Niantin; 7, Mô; 8, Mono; 9, Ogou; 9′, Nokpé: 10, Anié: 11, Nangbéto dam; 12, Amou; 13, Khra; 14, Todjé; 15, Egbi; 16, Zio; 17, Haho; 18, Yoto; 19, Lili; 20, Lake Togo.
C. Agricultural intensity expressed as the percentage (%) land under cultivation including fallow (adapted from PNUD, 1984) and main roads and towns.

fig. 9 shows the results. Finally, riverine fly abundance is was also plotted against agricultural intensity classes in fig. 10.

Glossina (Nemorhina) tachinoides

As shown in fig. 2, *G. tachinoides* density peaked in February, both in the north and the south, and coincided with the beginning of the dry season when the NDVI value was lowest. A second, less pronounced, peak was observed in the north only, towards the end of the rains, in September.

Comparison of the fly abundance pattern (fig. 4) and the seasonal clustering (fig. 3) confirms the preference of *G. tachinoides* for the northern, drier part of the country. Average densities per grid amounted to 0.34 ± 0.03 and 0.27 ± 0.01 respectively in clusters A and B. In the southem part of the country, in cluster C, densities were much lower (0.09 ± 0.01). Local exceptions were the relatively high fly density pockets at the southern distribution limit. Here, flies may be encountered in the well preserved, dense forest islands, with a tall tree stand, termed ‘forêts sacrées’. These sacred groves were mostly located nearby villages, watering points, and in places with an abundance of domestic pigs. The ‘terre de barre’ (fig. 5), was also exceptional in the sense

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Table 1. Width of the head of the male inferior claspers of *Glossina palpalis*.

Origin (river)	n	Size*	Standard deviation*
Oti	103	105.4	11.0
Koumoungou	261	100.3	9.9
Kara	40	101.4	6.7
Mono	339	97.2	7.8
Ogou	207	95.3	8.4
Anié	199	94.8	8.1
Khra	175	94.4	9.4
Haho	141	108.6	11.7
CIRDES	55	188.4	32.5

*Units: micrometres.

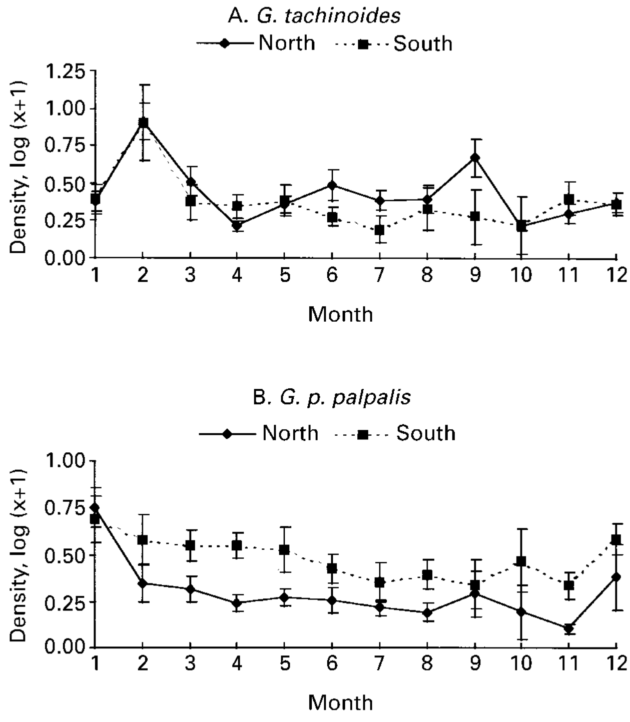

Fig. 2. Seasonal curves per month, with standard errors, for both riverine tsetse species (subgenus *Nemorhina*) separately in the northern and southern part of the country.

that this area was largely devoid of tsetse; this coastal lowland has no more forest relics and agriculture is very intense here. The fly was also absent in the higher altitude areas of cluster D in fig. 3, except in the piedmont area down the escarpment (fig. 6).

The regressions shown in fig. 9 confirm the preference of *G. tachinoides* for a hot, dry mono-modal environment. Densities were highest where the average NDVI was low, the amplitude of the annual cycle of the Price thermal index high and the amplitude of the bi-annual cycle of the CCD low. Channel 3 results were similar to the outcome of the Price index.

As a rule, *G. tachinoides* densities were highest in game reserves and protected forest areas, and lowest in areas with high land pressure and more intensive agriculture. Typical examples from the latter were the extreme northernmost part of the country and the Kara basin, south of the Oti-Keran game reserve. This general trend was confirmed when comparing agriculture intensity and abundance of *G. tachinoides* within the distribution limits of the fly (fig. 10).

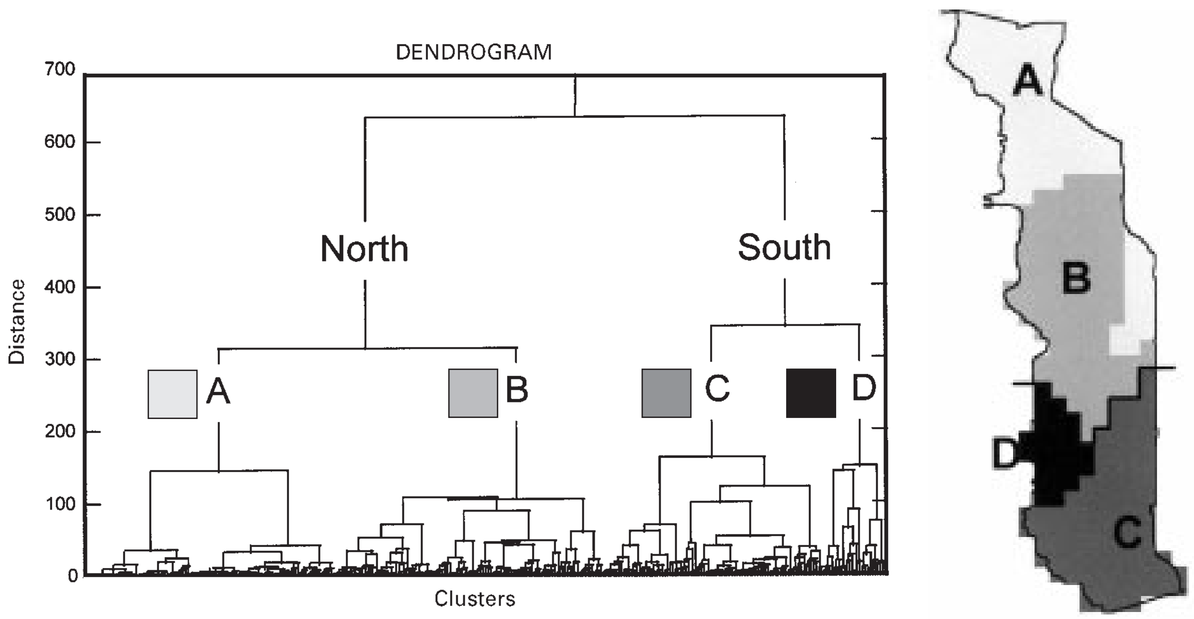

Fig. 3. Seasonal clusters showing a division of Togo in a Northern monomodal zone (A and B) and a southern more humid bimodal zone (C and D). See also average eco-climatic values per cluster in table 1.

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Table 2. Average values and their standard error of selected combined variables per seasonal cluster (cf. fig. 3).

Cluster	$Hum_{months}/Dry_{months}$	$Temp_{range}$	$NDVI_{amp1}/NDVI_{amp2}$	$CCD_{ph1} - NDVI_{ph1}$
A (n=96)	1.23 (0.03)	5.32 (0.04)	6.42 (0.42)	1.65 (0.04)
B (n=105)	1.64 (0.03)	4.56 (0.04)	4.07 (0.23)	1.44 (0.05)
C (n=86)	3.22 (0.22)	3.51 (0.02)	1.80 (0.06)	2.74 (0.04)
D (n=24)	3.99 (0.27)	3.90 (0.08)	1.74 (0.10)	2.65 (0.09)
$North_{AB}$	1.45 (0.02)	4.92 (0.04)	5.20 (0.25)	1.54 (0.03)
$South_{CD}$	3.40 (0.18)	3.60 (0.08)	1.79 (0.05)	2.72 (0.04)
t_{AB}	−11.277	13.637	4.917	3.278
t_{CD}	−2.201	22.241	9.096	−9.228
$t_{North\text{-}South}$	−10.697	27.181	13.486	−24.241

Hum_{months} = number of months with more than 100 mm rain; Dry_{months} = number of months with less than 30 mm rain; $Temp_{range}$ = ground measured difference between the average monthly maximum and minimum temperatures; NDVI = Normalized Difference Vegetation Index; amp_x = peak of the corresponding (x) Fourier cycle; CCD = Cold Cloud Duration; ph_1 = timing of the annual Fourier cycle.

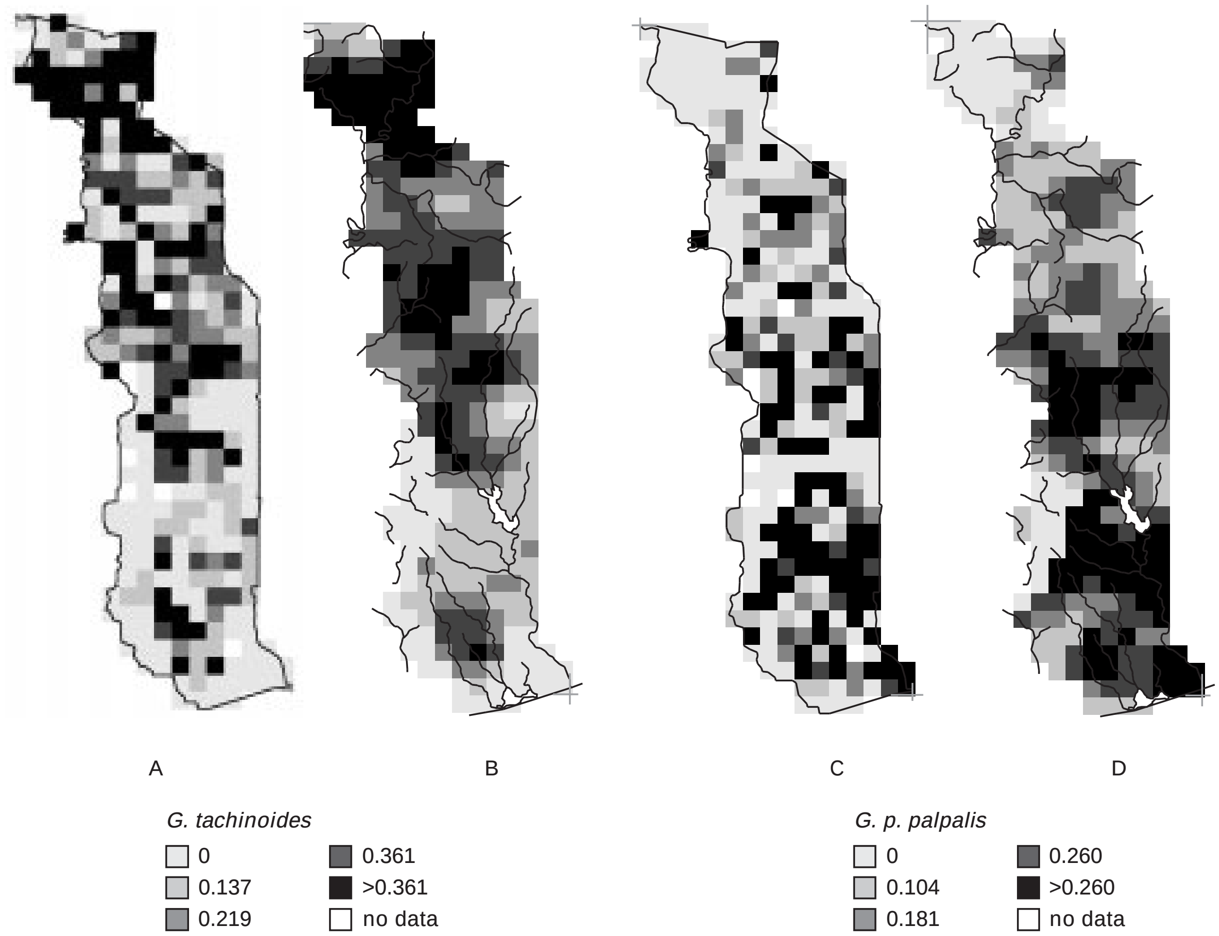

Fig. 4. Abundance maps ($\log_{10}$(fly+1)) of riverine tsetse (sub-genus *Nemorhina*) per grid. Maps A and C show raw data adapted for seasonal influences, maps B and D show 3 × 3 spatial smoothed data (more details in text).

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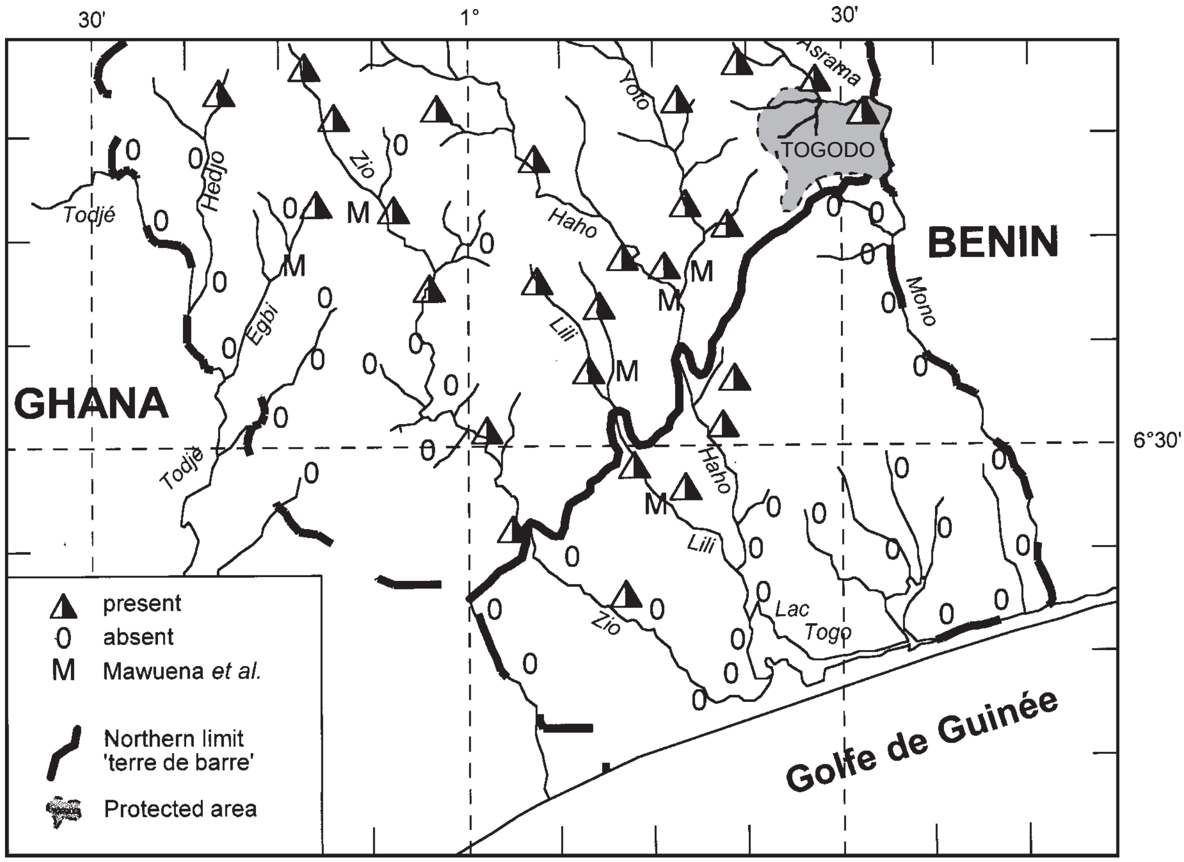

Fig. 5. Schematic map showing the southern limit of *Glossina tachinoides* including actually confirmed sites of presence and absence and past capture sites mentioned by Mawuena (1981, 1988b).

Glossina (Nemorhina) palpalis palpalis

Samples of *G. palpalis* males, collected in different eco-geographically representative sites, were further identified by measuring the width of the head of the inferior claspers; all specimens conformed to the subspecies *G. palpalis palpalis* (table 1). Not a single *G. p. gambiensis* male, or intermediary form, was found.

The distribution of *G. p. palpalis* within Togo shows both a northern and southern limit (fig. 4). In the north (fig. 7) the fly was absent west from the Oti river system and only persisted in well developed islands of riverine vegetation along permanent water sources found in the Oti game reserve. Historical records suggest a much wider distribution in the past (Itard, 1969; Challier *et al.*, 1983).

As with *G. tachinoides*, *G. p. palpalis* was absent from most of the plateau area (cluster D in fig. 3 and fig. 6), but it was present on the tributaries of river Volta in the Akebou and Adele Plateau. In the coastal area, the fly was absent from the lagoonal fringe.

Seasonal densities (fig. 2) showed a peak in the beginning of the dry season in January, both in the south and the north. Ratios between highest and lowest catches were less marked in the south (January, 0.69 ± 0.12 vs. November 0 34 + 0.07) than in the north (January, 0.75 ± 0.10 vs. November, 0.10 ± 0.03). The abundance pattern (fig. 4) suggested the highest densities were also of the Mono river and tributaries. Average densities per grid were highest in cluster C of fig. 3 (0.27 ± 0.02).

The fly was absent from major parts of cluster A and, where its presence was confirmed, densities were generally low except locally on the Oti river and in parts of the northern Atakora. The regressions of fly abundance and satellite derived environmental parameters (fig. 9) revealed curvilinear regression lines with absence of the fly at both extremes of the scale. Also the field results confirmed the preference of the fly for humid areas with a bi-annual rainfall cycle.

Figure 10 suggested that *G. p. palpalis* abundance was hardly altered by the process of agricultural intensification. However the southern shift of its northern limit might at least partially be due to agricultural intensification altering the more fragile biotope on smaller river systems whilst the fly remains present in significant densities on the still preserved denser gallery forests of the Oti river.

Glossina (Glossina) morsitans submorsitans

Glossina m. submorsitans (fig. 8) was found north from 08°30′ latitude, in two distinct areas: (i) the Oti-Keran conservation area, within cluster A of fig. 3; and (ii) the Fazao conservation area in cluster B.

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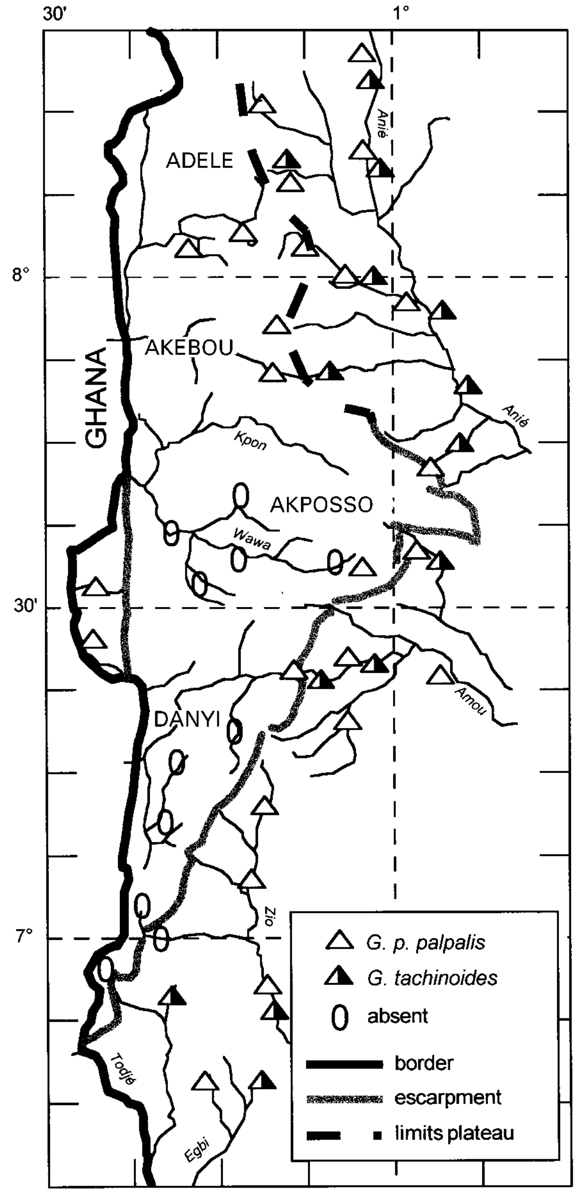

Fig. 6. Schematic map showing the southern sub-humid Atakora plateau area with present day presence and absence sites of riverine tsetse (sub-genus *Nemorhina*).

In both cases, fly abundance appeared to be associated with game and forest reserves. During the first survey round the fly was present in the north on both the Oti and Koumoungou rivers. Around the mid 1990s densities on the Oti river dropped to below measurable levels. The area is known for the occurrence of active poaching and the progressive reclamation of the Oti part of the game reserve by agriculturists. As a consequence, game animals have migrated to Ghana, the Pendjari game reserve in Benin or have remained in the Keran part on the Koumoungou river; it is here where flies also persist.

The Fazao game reserve in the centre of the country is more isolated, less suitable for agriculture and better protected from encroachment by man. As a result, game numbers are more stable and so are tsetse numbers here.

Glossina (Glossina) longipalpis

Glossina longipalpis (fig. 8) was present in clusters within areas B and C of fig. 3. As with *G. m. submorsitans*, this member of the *morsitans* group can readily be associated with intact, well preserved biotopes. In the central parts of the country, in particular the Fazao game reserve, the fly occurred in association with all the other tsetse species found in Togo, except *G. medicorum*. The characteristic habitat resembled open, dry forest types of vegetation. Distribution patterns varied with the season, with a major retraction of flies into the riverine habitat during the dry season. The development of agriculture had a major influence on the extent of fly distribution. The best example was the Abdoulaye forest east of Fazao game reserve in the centre of the country where the fly has been forced to retreat upon the arrival of agriculturists (Dao *et al.*, 1996).

Glossina (Austenina) medicorum

This tsetse was only found in the Tchila-Monota forest in the southern part of the country (fig. 8). It occurred in association with *G. p. palpalis*, *G. tachinoides*, *G. longipalpis* and *G. fusca fusca*, mostly in islands made up of dense vegetation, which may or may not have been linked to riverine galleries.

Glossina (Austenina) fusca fusca

Glossina f. fusca was somewhat more widespread than *G. medicorum*. As a rule, this species was present over the same range as *G. longipalpis* (fig. 8). Within these limits, its presence was mostly restricted to habitats similar to *G. medicorum*. One single specimen was caught on the river Kale in the Mô Plain west of Fazao.

Discussion

The classification of the seasonal clusters (fig. 3 and table 2) is largely based on satellite data. The demarcation thus obtained confirms the notion of a north–south transect of different climate types. Also the entomological survey results can better be explained when reviewed against this classification. However, traditional information sources such as the standard eco-zone maps also contribute to explain the local variability in tsetse abundance (fig. 1b.A). It is believed that satellite imagery, supported by strategic ground truthing and validation exercises, will progressively gain in importance so that apparent discrepancies that now exist between fig. 1b.A and fig. 3 for example will eventually be resolved.

The present tsetse field surveys have shown that it is possible, using a limited number of traps positioned in few selected trap sites, to produce biologically sound fly distribution maps at a resolution of 13.75 km for the different tsetse species present in any part of Togo.

The results of the present, systematic field surveys corroborates with the earlier finding by Mawuena (1988b) that the southern, humid Atakora region is free of tsetse. This area covers a major part of cluster D and has a total surface area of about 2500 km^2. This makes up less than 5%

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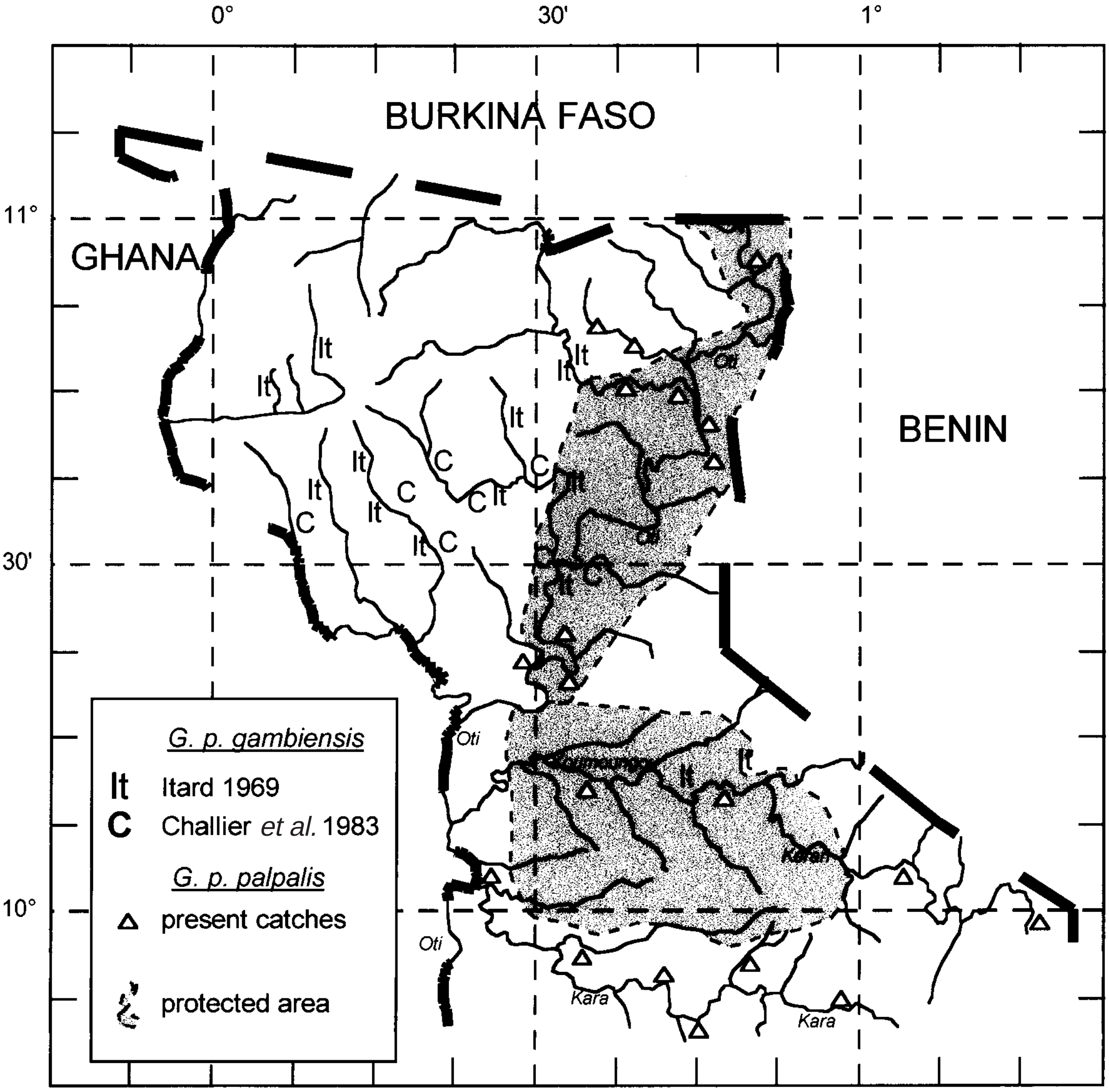

Fig. 7. Schematic map showing the confirmed presence of *Glossina p. palpalis* at its northern limit in Togo and historical capture sites of *G. p. gambiensis* reported by different authors.

of the country area. In the central part of the country all major tsetse species are present in the Fazao game reserve.

Previous work by Mawuena & Itard (1981) suggested a southern movement of *G. tachinoides*. It would appear that this expansion is now halted by adverse climatic conditions and intense agriculture in the 'terre de barre' area. In the north, *G. p. gambiensis* could no longer be detected and the previously identified isolated focus (Challier *et al.*, 1983) may have now disappeared.

The fragmentary knowledge on the exact distribution of savannah species *G. m. submorsitans* and *G. longipalpis* has been clarified. The results suggest that the situation remains fluid and that in areas where demographic and land pressures are high changes may occur, rendering the environment less suitable for these two species. This finding is of relevance to the dynamic land utilization pattern in onchocerciasis freed areas and is consistent with other published results (e.g. Morris, 1934; Popham, 1972). Also important to note here is that the survival of *G. tachinoides* is much affected by ongoing landscape alterations in the drier northern part of the country. While *G. p. palpalis* distributions are still largely unaltered in the more humid south, more fragile habitats appear to be affected at its northern limit. It has to be remembered here, however, that human activity could create new suitable peridomestic habitats at a local level, and thus locally reverse present trends, especially where *G. tachinoides* and *G. m. submorsitans* are concerned (e.g. Madubunyi, 1990; Popham, 1972).

Finally, the distribution of *G. fusca fusca* has been described in some detail for the first time in Togo, and the

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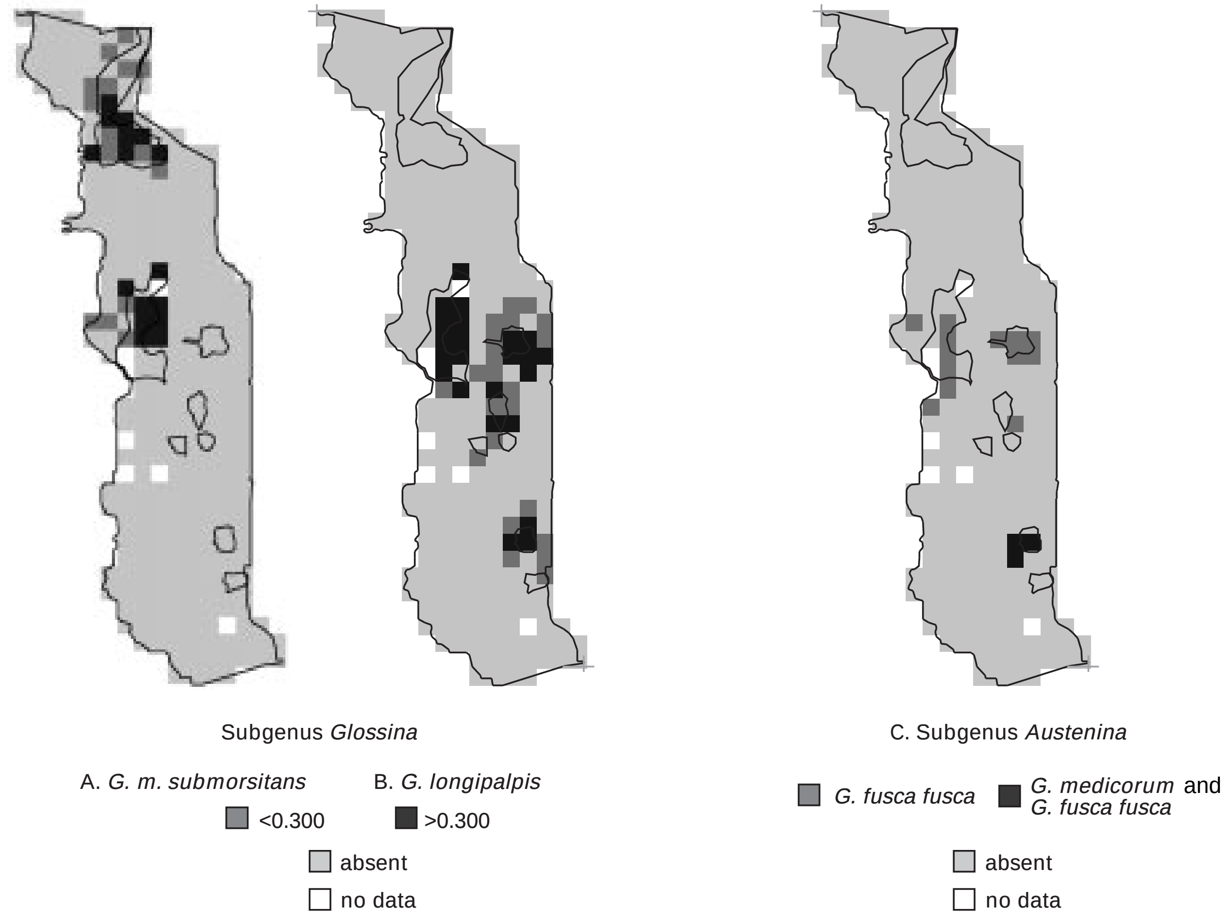

Fig. 8. Distribution and two class raw densities of savannah tsetse (sub-genus *Glossina*) and presence of tsetse from the sub-genus *Austenina*.

disputed presence of *G. medicorum* (Gouteux, 1990) has now been established beyond any doubt.

Besides fly dependent biases such as sex, age and nutritional status (Cuisance, 1989), several biases persist given that the fly density measurement is based on daily trap catches, recorded in a cluster of a limited number of traps per site, positioned according to the expected species of flies. Already mentioned is the spatial aggregation of *G. longipalpis* flies into smaller, wetter areas during the dry season. This finding may help to explain why trap catches during the dry season are highly variable; some traps may capture large numbers of flies and other traps few flies only, or none at all. This suggests a concentration of flies in particularly suitable habitats during that period of the year (Davies, 1977). During the rains, a larger proportion of traps capture close to average numbers of flies suggesting a more even distribution. Similar observations were made in Burkina Faso (Bauer, personal communication) and Benin (Dehoux, 1992). *Glossina tachinoides* in the northern part of the country showed higher average densities during the rains but this may well reflect a true increase in population size.

Some of the variability was removed by adjusting recorded data to seasonal fluctuations and by applying spatial smoothing. The resulting abundance maps, however, reflect relative densities or ‘presence risks’ per species more than actual population estimates.

Fly abundance figures observed for riverine species probably reflect eco-climatic reality. In general, the two riverine species occur together but the fly density of one species is usually inversely proportional to that of the other. This complementarity is also reflected in the distribution range and the results of the regressions between fly abundance and satellite derived environmental parameters (fig. 9). The shape of the curves also suggest that in Togo, *G. p. palpalis* is confined to more specific eco-climatic conditions whilst *G. tachinoides* appears to be adapted to a greater variety of conditions. The relationship between fly abundance and Normalized Difference Vegetation Index values, as shown in fig. 9 for both riverine species, resembles the results obtained by Rogers & Randolph (1991) for the same species in the Ivory Coast.

In conclusion, the field survey approach adopted in Togo allowed us to draw detailed fly distribution and abundance maps of all tsetse species present and to link those results with remotely sensed eco-geographical variables. In future,

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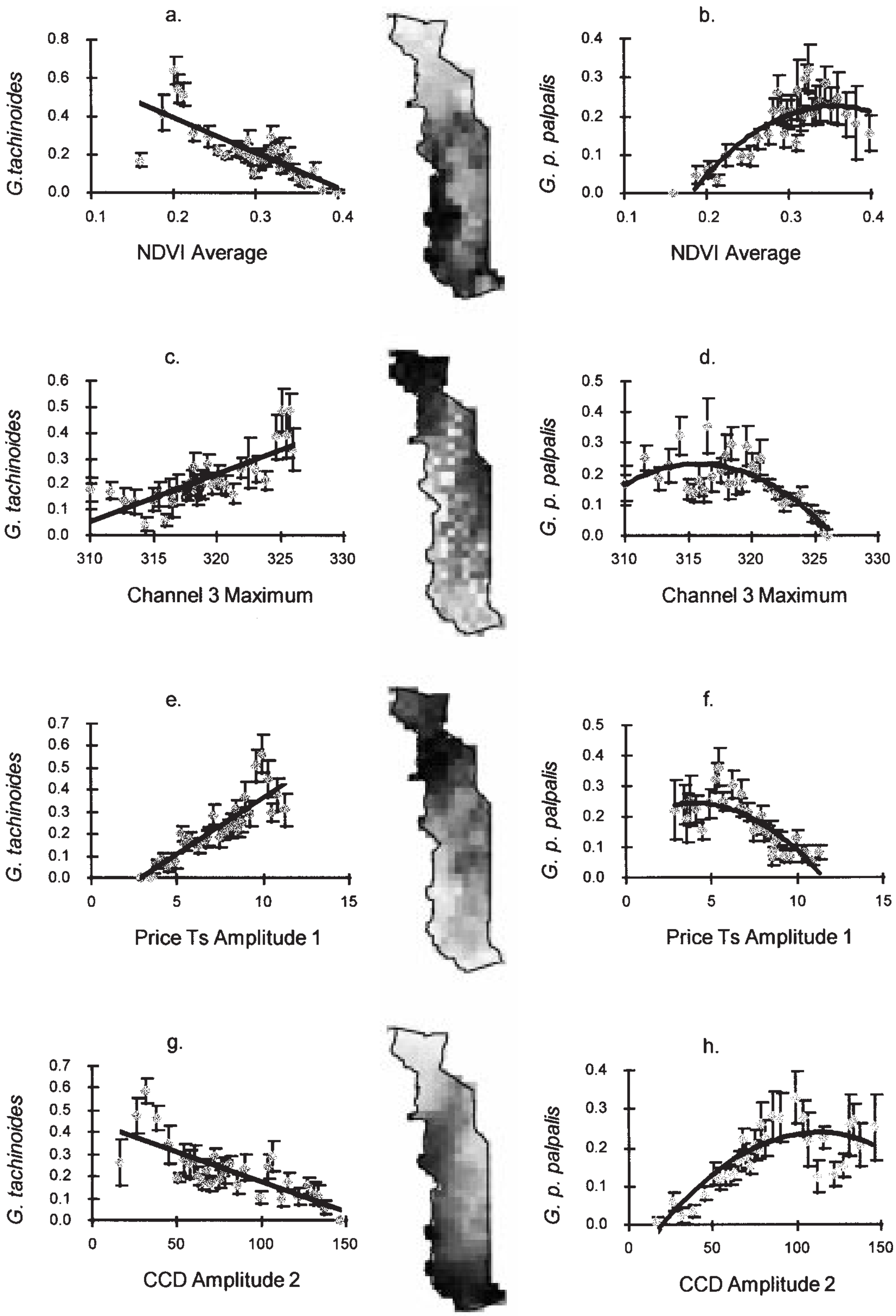

Fig. 9. Correlation between selected remotely sensed variables and abundance figures of riverine tsetse. Classes of 10 subsequent measurements with standard error.

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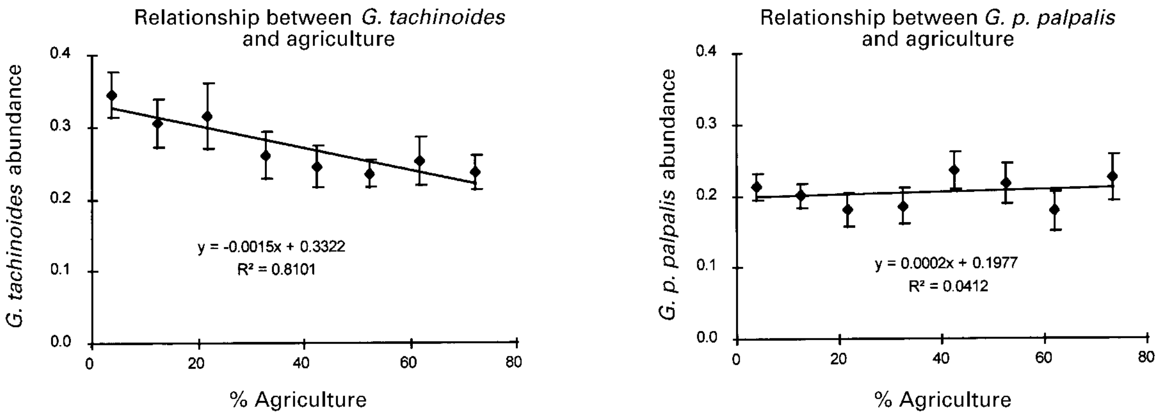

Fig. 10. Correlation between agriculture intensity and riverine tsetse abundance figures within respective fly limits. Classes were defined per 10% agriculture increase with standard error for average abundance. Relationship is significant for *Glossina tachinoides* (n = 8, r = 0.900, $P < 005$) and not significant for *G. p. palpalis*.

this type of map may be generated mainly from satellite-derived variables, using only a restricted amount of field data; this is the topic of a second paper.

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