

Reproduction of a pantropical weed : *Chromlaena odorata* (L.) R. King & H. Robinson

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Reproduction of a pantropical weed: *Chromolaena odorata* (L.) R. King & H. Robinson

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ABSTRACT

GAUTIER, L. (1993). Reproduction of a pantropical weed: *Chromolaena odorata* (L.) R. King & H. Robinson. *Candollea* 48: 179-193. In English, English and French abstracts.

This article considers the reproduction of a pantropical weed: *Chromolaena odorata*. The course of the sexual reproduction is described from observations made in central Ivory Coast. The amount of propagules produced per square meter of *Chromolaena odorata* thicket has been estimated, and their dispersal analysed. The phenology of the reproduction has been studied experimentally in Ivory Coast, and at a world-scale level on the basis of herbaria records. Discussion of the results aims to outline the reproduction strategy of the species, in order to explain its massive invasion of the the paleotropics since the second half of last century.

RÉSUMÉ

GAUTIER, L. (1993). Reproduction d'une adventice pantropicale: *Chromolaena odorata* (L.) R. King & H. Robinson. *Candollea* 48: 179-193. En anglais, résumés français et anglais.

Cet article est consacré à la reproduction d'une adventice pantropicale: *Chromolaena odorata*. On y décrit le déroulement de la reproduction sexuée, telle qu'elle a été observée en Côte-d'Ivoire centrale. La quantité de fruits produits par m² de brousse à *Chromolaena odorata* a été estimée, et le mode de dispersion analysé. La phénologie de la reproduction a été étudiée expérimentalement en Côte-d'Ivoire, ainsi qu'au niveau mondial par la consultation d'échantillons d'herbier. La discussion des résultats cherche à mettre en évidence la stratégie de reproduction de la plante pour tenter d'expliquer la manière foudroyante avec laquelle elle a envahi la région paléotropicale depuis la moitié du siècle passé.

KEY-WORDS: *Chromolaena odorata* — *Eupatorium odoratum* — Reproduction — Phenology — Biogeography.

Introduction

Chromolaena odorata (L.) R. King & H. Robinson (= *Eupatorium odoratum* L.) is a very important neotropical weed of the family *Asteraceae*, which has considerably extended its distribution to the paleotropics in the last 150 years (GAUTIER, 1992 b). It has a bushy habit and forms a very dense thicket 2 m high, in almost pure stands. It is heliophilous and has a quick growing rate, due to a judicious allocation of resources.

Working in Ivory Coast, West Africa, where *Chromolaena odorata* first appeared around 1950, I met it in all types of secondary vegetation in the southern half of the country. It occupies

clearings in the forest zone and often invades plantations. It can also develop in the savannas of the forest-savanna transition zone located in the centre of the country, if they aren't burned regularly.

This paper, partly extracted from a doctoral thesis on the ecology of the species in central Ivory Coast (GAUTIER, 1992 a), is dedicated to the study of the reproduction of the species which could partly explain its success in invading the old world.

The first part describes the reproductive course of *Chromolaena odorata*. The second part deals with the amount of fruits produced and their dispersal. The third part describes its reproduction period, monitored in two sites in the Ivory Coast. The fourth part analyses the reproduction period of the species on a world-wide scale.

Course of reproduction of *Chromolaena odorata*

The first macroscopically visible manifestation of the initiation of flowering is the appearance of very young inflorescence at the apices of the twigs, between the last two pairs of leaves (Fig. 1). This stage will be further referred as the "bud" stage, despite of the relative inadequacy of this term in the family *Asteraceae*.

During a variable period, depending on the meteorological conditions of the site (DELABARRE, 1977), various individuals, or various twigs of the same plant, will initiate flowering events. The development of each inflorescence will go on, the early inflorescence already being at the dispersal stage while "bud" stages might still appear.

In order to follow up the course of the sexual reproduction, an experiment was carried out in the dry season 1988-89, at the Station d'Ecologie Tropicale de Lamto, south of the V-Baoulé, in central Ivory Coast. The climate is transitional between equatorial and tropical, with a mean annual rainfall of 1200 mm and a main dry season of three months. Precipitation occur mainly between march and October, with some years a marked decline in August. The vegetation in the surroundings is a forest-savanna transition mosaic.

In a dense and almost pure *Chromolaena odorata* thicket, derived from the protection of a 62 ha savanna from the annual fires since 1962, 30 twigs of the same site were labelled simultaneously, when they were at the first visible stage of the flowering event. A twig randomly chosen was then harvested twice a week during five months. The sample was immediately pressed and placed in a gas drier to prevent any further development of the inflorescence.

The analysis of these samples led to the constitution of the following chronology (time expressed in days after the first visible manifestation of the inflorescence):

- 11 d.: The axes of the inflorescence are developing. The groups of flowerheads that will form the 3 or 5 cymas of the inflorescence become distinct. At this stage, it can be that new inflorescence appear on the twigs that are located on the same branch, 10 to 20 cm below the labelled inflorescence.
- 25 d.: The lengthening of the peduncles goes on, so that each flowerhead is now clearly distinct from its neighbours. The flowerheads are of an obovoid shape, with an acute apex. They are 5 to 8 mm long (Fig. 2).
- 36 d.: The bristles of the florets begin to appear at the end of the inner bracts, which are the longest. The flowerheads take a cylindrical shape and are now 7 to 11 mm long. At this stage, it becomes obvious that the central cyma is slightly ahead of the lateral ones.
- 39 d.: Anthesis of the central cyma. The bristles of the florets are longer than the inner bracts. The lobes of the corollas appear and the styles are exerted (Fig. 3). Visit of various unspecialized insects (WARD, 1980). True pollination, but also apomixis (MATTHEW & MATTHEW, 1983).



Fig. 1. — The first macroscopically visible manifestation of the initiation of flowering (‘bud’ stage).

Fig. 2. — Young inflorescence.

- 43 d.: The florets of the central cyma fade. Anthesis of the lateral cymas (Fig. 4).
- 46 d.: The whole inflorescence is faded.
- 57 d.: Disappearing of styles and corollas. Development of the fruit.
- 74 d.: Opening of the bracts, exposure of the cypsellas, which place themselves in an hemispherical way (Fig. 5 and 6). I noticed that this opening of the capitula was reversible in case of humid weather. Only a dry capitula allows its cypsellas to be dispersed.
- 81 d.: The fruits are dispersed, the bracts fall, the axes of the inflorescence die.

From this stage on, if climatic condition allows it, the vegetative growth of the plant will resume. The remains of the inflorescence occupying an apical position, the new twigs will appear at the axils of the leaves below. This will occasion a further ramification of the plant. Later in the season, the axes of the inflorescence will fall to the ground, where they will begin to decay.

Dispersal

In order to measure the amount of fruits produced by a *Chromolaena odorata* thicket, five stands of 1 m² were harvested in the aforementioned dense thicket in the surroundings of Lamto. The experiment took place at the end of March 1989, when the fruiting of the thicket was at its climax.

The number of flowerheads in each sample was counted, and the average number of cypsellas in each flowerhead was estimated by counting the cypsellas in 20 flowerheads.

RESULTS	Mean	Standard dev.
Number of fruits per flowerhead (20 samples)	26.8	3.1
Number of flowerheads per square meter (5 samples)	3200	1053

These results multiplied give us ca. 86'000 cypsellas produced per square meter, which is surprisingly close to the 90.000 published by YADAV & TRIPATHI (1981).

In contrast, the estimation of 400.000 cypsellas produced per square meter by a three years old fallow (KUSHWAHA & al., 1981) seems to be a little exaggerated.

Nevertheless, if one considers my own data, the production of one hectare of *Chromolaena odorata* thicket could be estimated to 860.000.000. Taking into account the fact that this estimate is based on a sample harvested at one single moment, and that it is likely that some fruits were already dispersed, it seems reasonable to state that the production of 1 hectare of dense *Chromolaena odorata* thicket exceeds 10⁹.

This data bring to the fore the extraordinary potential of reproduction and invasion of the species. It might explain the massive invasions of new biotopes.

The dispersal of the cypsellas proceeds by two main modes: anemochory and zoo- (and anthropo-)chory.

Concerning wind-dispersal, the lightness of the fruit is of course very important. Weighing a 100 cypsellas of *Chromolaena* gave 0.0215 g, this is scarcely more than 0.2 mg per fruit.

The lift of the fruit is markedly increased by its pappus (Fig. 7). In consequence, the falling velocity of the cypsellas reaches a constant value (final velocity) already after 20 cm. This value has been calculated by measuring the time a fruit takes to cover a two meters fall once the final velocity had been reached. The experiment took place indoors to avoid any disturbance. The fall of 10 cypsellas was measured.

The results showed that the quickest cypsellas had a final velocity of 0.62 m/s, and the slowest of 0.37 m/s. The average on 10 tries was 0.50 m/s with a standard deviation of 0.07 m/s.

This value can be compared with those obtained by SHELDON & BURROWS (1973). They measured the final velocity for 18 species of *Asteraceae*, mainly of temperate origin. The values



Fig. 3. — Anthesis of the central cyma.

Fig. 4. — Central cyma faded, anthesis of the lateral cymas.



Fig. 5. — *Chromolaena odorata* thicket bearing fruits.

Fig. 6. — Mature infructescence.

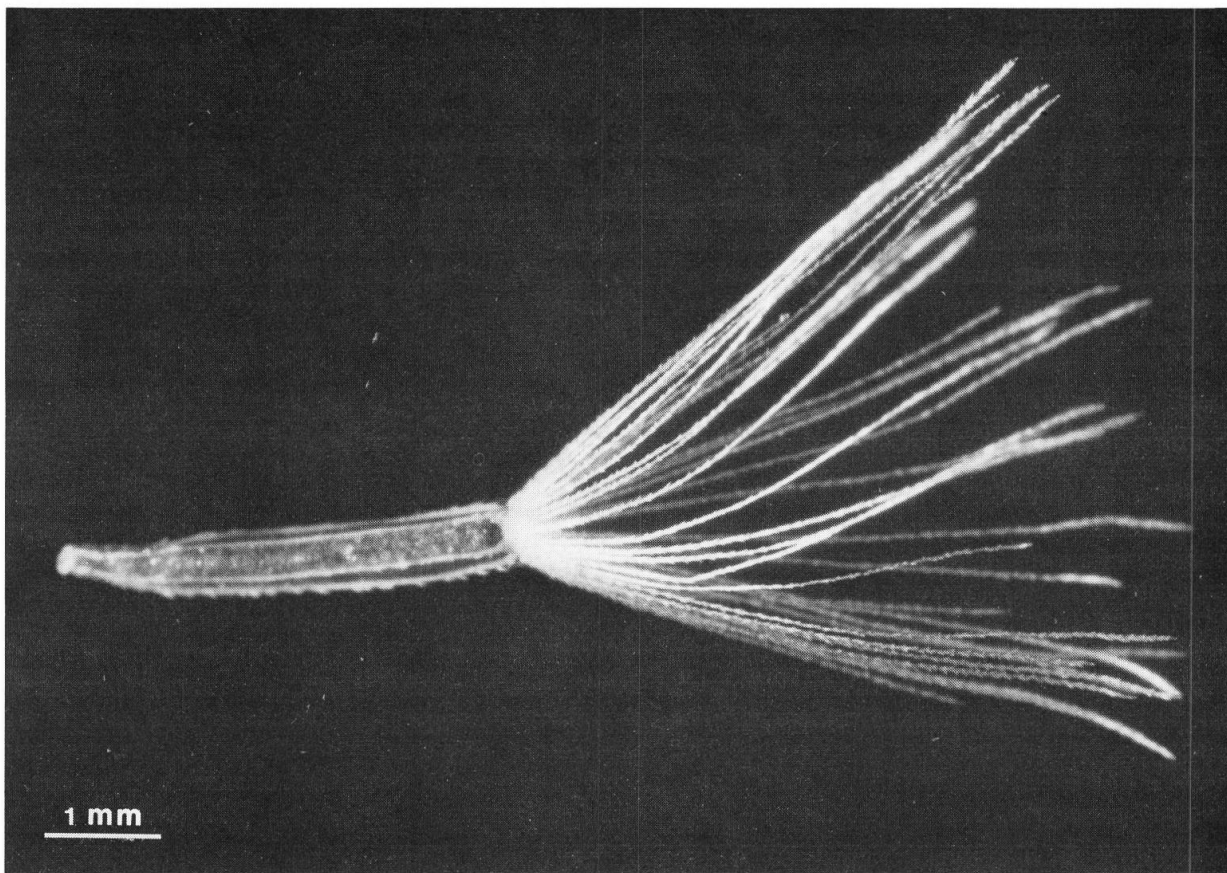


Fig. 7. — Cypsella (photo: M. Kolakowski).

measured by them ranged between 0.19 m/s (*Tussilago farfara* L.) and 2.20 m/s (*Centaurea scabiosa* L.). From my own measurements, *Chromolaena odorata* wouldn't be among the slowest, but has a final velocity close to *Senecio squalidus* L., *Tragopogon porrifolius* L. and *Leontodon autumnalis* L. Taking into account that the cypsellas I tested were stored in a relative compressed way, and although care was taken to choose fruits that looked undamaged, it is possible that this speed could be even lower in natural conditions with a fully open pappus.

Such a slow falling speed is plainly an advantage for dispersal. In climatic conditions such as those that prevail in the intertropical zone, it is not infrequent that convection values are higher than the falling speed of the cypsellas in the middle of the day. Moreover, the stormy winds which often occurs at the beginning of the dry season, allow the seeds to be broadcasted kilometres away. As it is often the case in the *Asteraceae*, fruits are not completely free, even in mature flowerheads. They need a sufficient wind speed to be detached (SHELDON & BURROWS, 1973). On another hand, I have already mentioned above the closing of the flowerhead in humid conditions. It is of course very important that the cypsella should be as dry and light as possible, in order to cover a maximum distance. Dry weather and sufficient wind are thus a prerequisite for the dispersal of *Chromolaena odorata*, and this ensures a maximal efficacy of this crucial stage in colonising species.

I would like to mention here an interesting note by WHITE (1970). Collecting aerial plankton from a plane in Southeast Australia, he met some fruits of *Asteraceae* (mainly *Senecio quadrangularis* Labill., but also *Arctotheca calendula* (L.) Lavyns) at altitudes between 350 and 500 feet, and even a fruit of *Hypochoeris glabra* L. at 2000 feet. I could check the final velocity of the cypsella of these species from the collections in Geneva, and it appeared that they were comparable to the one of *Chromolaena odorata*.

Supposing that a cypsella of our species had been brought by a storm to an altitude of 500 m, and that it would meet there a lateral wind of 5 m/s, the seed would then reach the ground 5 km away from its starting point, even in absence of convection.

Is anemochory sufficient to explain the expansion of *Chromolaena odorata* while invading a new region? DELABARRE (1977) has estimated the spreading speed of the species in Ivory Coast, from his own records on the history of the distribution of the species along the main roads. According to this author, the speed of spread along two chosen directions was of 44 and 45 km/year. We agree with him that this value is too high to be explained by anemochory only.

Another mode of dispersal of the species, which is certainly responsible for such fast spreading speed, is exo-zoo-(and anthropo-)chory. The edges of the seeds have small spines (Fig. 7) that cling to furs, feathers or clothes. Moreover, Delabarre states that long-distance dispersal of anthropochorous nature can take place when seeds of *Chromolaena odorata* are contaminating crop plants that are transported, or by vehicles, especially the ones used for road maintenance.

Thus, the dispersal strategy of *Chromolaena odorata* operates on two different modes. A new region will be reached by long-distance dispersal through exozoochory or anthropochory, whereas the massive invasion of this region will follow, proceeding through anemochory, once a little population has settled.

It should also be noted that the plant can achieve vegetative reproduction. It has the ability to develop adventitious roots if a twig touches the ground. Of 8 twigs that were bent artificially to the ground near Abidjan during the rainy season, 3 had already developed a rooting system sufficient to sustain their autonomous development after 19 days (Fig. 8).

Period of reproduction in Ivory Coast

Two sites were chosen to observe the period of reproduction of *Chromolaena odorata* in Ivory Coast.

The first one is located in the evergreen forest zone, in the "Centre suisse de recherches scientifiques", at Adiopodoumé, 20 km west of Abidjan at an altitude of 25 m, and at a latitude of 5°19'N. The climate is equatorial with an annual amount of rainfall of 2000 mm. Rainy seasons occur twice yearly, separated by a main dry season of 2 months in January and February and a little dry season in August. The mean annual temperature is 26.9°C. The coldest month is January with the occurrence of Harmattan, a dry and cold northerly wind that can some years bring the temperature down to an absolute minimum of 16°C at night.

The second site is the "Station d'écologie tropicale de Lamto", 150 km N.W. of Abidjan, south of the forest-savanna transition zone. The altitude is around 100 m and the latitude is 6°13'N. The amount and dispersion of precipitation has already been presented above (1200 mm, one main dry season from mid November to mid-February). The mean temperature is 27.6°C. The coldest month is again January, also because of the Harmattan, which is here more likely and more pronounced. The absolute minimum temperature is here 13°C.

Ten plants were labelled in the first site and 15 in the second. They were visited twice a month during 25 months. The observer was asked to note, for each plant, the occurrence of the following events:

- "bud" (inflorescence scarcely visible)
- young inflorescence
- flowers (anthesis: corollas and styles visible)
- faded flowerheads
- young fruits (corolla and styles vanished)
- fruits (cypsella arranged hemispherically)
- dispersed fruits (axes of the inflorescences bare)

If none of these stages were visible, the observer writes a "v" for vegetative.



Fig. 8. — Development of adventitious roots on a twig that was bent to the ground during 19 days.

The results of this study are presented graphically on Fig. 9 and 10. Only the stages "bud", flowers and fruit are figured, representing respectively the first macroscopically visible manifestation of the initiation of flowering, the anthesis and the dispersal.

The first remark that can be made is that *Chromolaena odorata*'s reproduction cycle occurs only once a year, and begins in the main dry season on both sites.

It was noticed that during the two years of the survey, flowering started 15 days earlier in Lamto than in Abidjan. It confirms an observation I had made during a journey from the North to the South of the country at mid-November 1986. It had occurred to me that the most northerly plants of *Chromolaena odorata* I could find, around 8°30'N, were ca 1 month earlier in their floral development than those in Abidjan, with a gradient between the two sites.

It is worth mentioning that in Laos, VIDAL (1956) had remarked the same kind of time-lag between Pak Lay and Vientiane, which he attributed to differences in the temperature.

In the case of Ivory Coast, I would prefer to remain prudent on the causes of this time-lag, the initiation of flowering being a complex phenomenon, integrating many climatic parameters.

Another remark that can be made looking at the results is that appearance of new inflorescence occurs in Lamto rather regularly during one and a half months. In Abidjan, on the contrary, new inflorescence appear during almost 5 months, and show a bimodal tendency.

The length of the period where mature cypsellas are present is rather short in Lamto. All the fruits are dispersed before the end of April. On the contrary, in Abidjan, the last fruits ripen in mid-July, as a consequence of the more dispersed period of flowering. It can also happen that the cypsellas remain quite a long time on the plant: in 1988 some fruit were still present in October.

Anyhow, it can be stated that during the dry season, when vegetative growth is hindered by the lack of water, and when additional leaves would only lead to excess transpiration, the species turns its metabolism towards reproduction. This phase will be over with the oncoming of the rainy season, and vegetative growth will resume. At this time, the cypsellas are generally dispersed and ready to germinate in new environments they will soon have colonised.

Period of reproduction on a worldwide basis

Although it is rather clear that the period and duration of reproduction analysed before seem optimal for the intertropical zone where *Chromolaena odorata* has met great successes during the last 150 years, it is not yet clear to what environmental factor(s) the onset of the reproduction event is linked. Analysing data from one single country can only be of little help in this respect.

In a preceding paper (GAUTIER, 1992 b) I had the opportunity to expose the history of the distribution of *Chromolaena odorata*, relying on information extracted from some 900 different herbaria samples. Besides the location of the samples, the date of collection and the phenological status of the specimen were also recorded.

In order to determine the period of reproduction of the species in the various parts of its geographical range, I did the following treatment to these data:

- The vegetative collections and the collections where only the year was known were discarded.
- The collections without the day of the month were attributed to the 15th of the month.

Taking the hypothesis that once initiated, the course of the reproduction should not be very different from one place to another at the level of accuracy I was interested, I relied on my observations at Lamto (cf. first part of this paper) to try to determine at what date the plant from which I had the specimen was at the first visible stage of its reproduction. In this way, for each specimen, a new date was attributed:

- 18 days before for specimen with immature inflorescence
- 42 days before for specimen bearing flowering capitula
- 61 days before for specimen bearing young fruits.

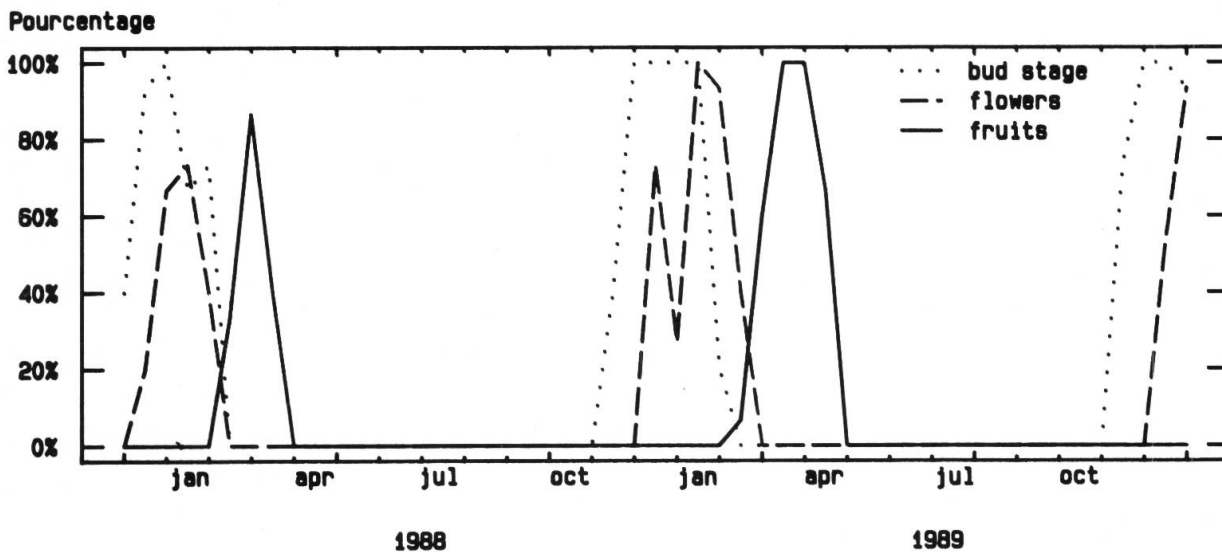


Fig. 9. — Sexual reproduction of *Chromolaena odorata* in Lamto (South of V-Baoulé).

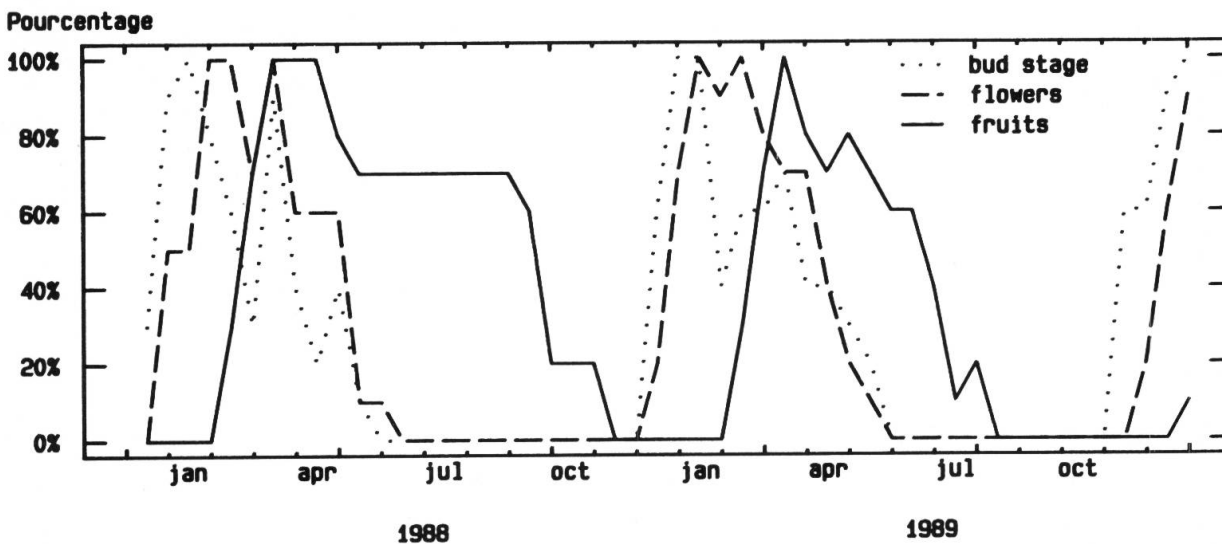


Fig. 10. — Sexual reproduction of *Chromolaena odorata* in Adiopodoumé, in the surroundings of Abidjan.

The specimen bearing only mature fruits weren't taken into consideration because the evolution of the inflorescence stops at this stage, waiting for optimal conditions for the release of the fruits (cf. part 3). Therefore, it was impossible to locate the beginning of the reproduction without the risk of making significant errors.

To the specimen bearing inflorescence at various stages, I attributed more than one date, according to the calculations exposed above. The inflorescence with mature fruits were then again ignored.

In this way, 747 dates, representing an inflorescence at the youngest stage, were listed and plotted, with the latitude of collection in ordinate (Fig. 11). Below the plot, two climatic diagrams are given, illustrating a tropical and an equatorial climate, which prevail in the range of *Chromolaena odorata*.

It is at once obvious that the majority of the points, representing the first stage of a flowering event, are located between September and December for the northern hemisphere, with a maximum in November. Symmetrically, for the southern hemisphere, the majority of the points are located between March and June, with a maximum in May.

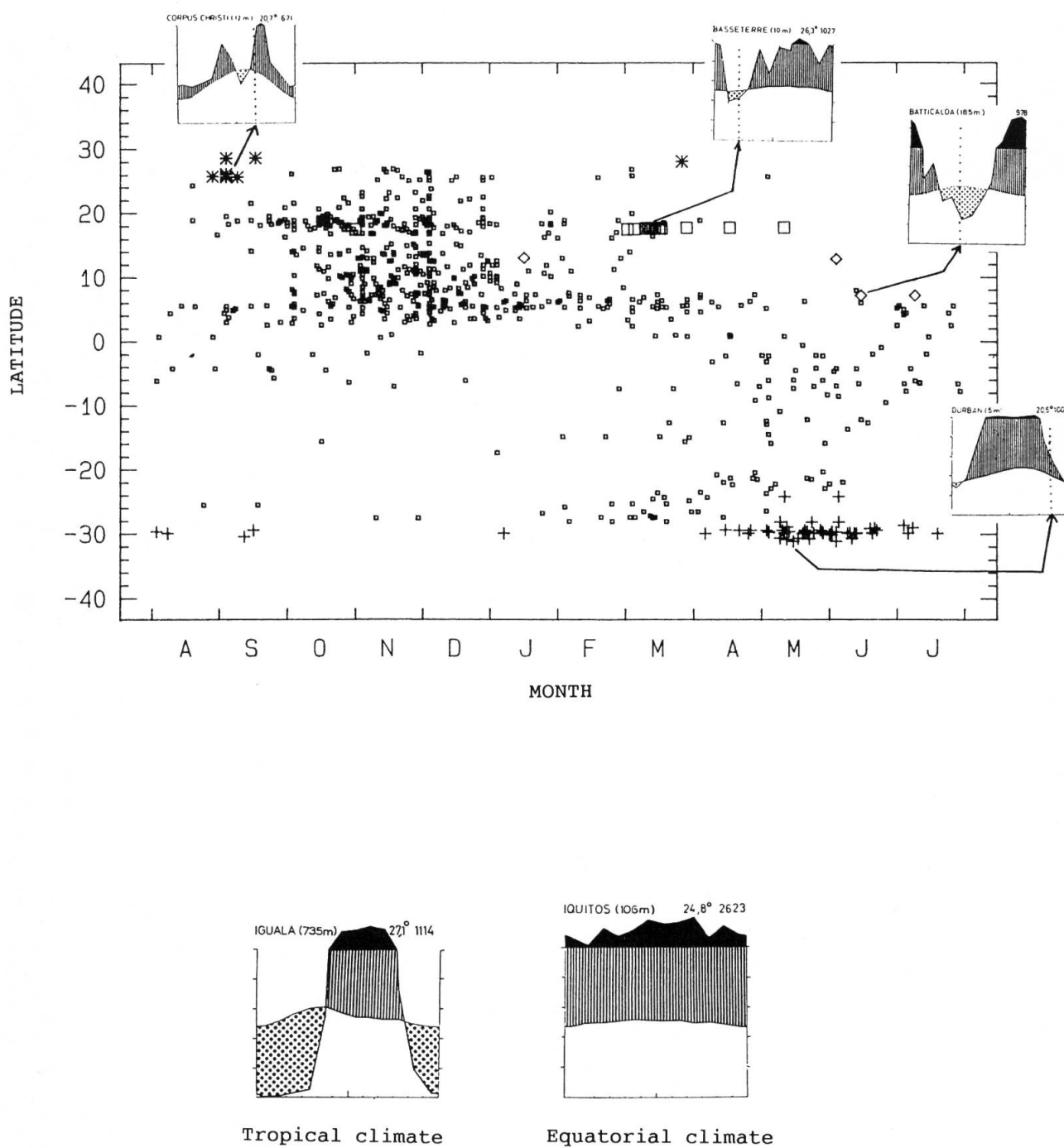


Fig. 11. — Initiation of flowering of *Chromolaena odorata* on a worldwide basis as a function of latitude. (Climatic diagrams from WALTER & LIETH, 1960-1967).

Nevertheless, numerous reproduction events take place out of the peculiar period of each hemisphere. For each of these shifted events, I have tried to find an explanation in the closest climatic diagrams I could find in WALTER & LIETH (1960-1967).

The most important group of these shifted flowerings can be found between 6° North and 6° South. In this belt, it seems that flowering is likely to occur at any time of the year, depending on the site. It can be stated that the climates here are mostly equatorial, being wet the whole year, or with two seasons of decreasing precipitation. The more latitude increases, the deeper we get in tropical climates with only one rainy season. The few abnormalities that can still be found between 6° and 10° N. and S. match local extensions of the equatorial climate.

It is between a latitude of 10° and 25° N. and S. that the exception are the most unlikely. These latitudes correspond to the belts where the tropical climates are predominant, with a well-marked dry season during the winter months.

Nevertheless, a remarkable case has to be mentioned in the northern hemisphere. A group of flowerings seem to be starting between March and May, around 17° N. It happens that the specimens from which these points were extracted were collected in Saba and St Eustatius, in the Dutch West Indies (Fig. 11, big squares). These islands are an exception in the region, having a dry season delayed of 4 months.

Shifted reproduction can still be sporadically observed in both hemispheres for these belts of latitude. In the great majority of the cases, these exceptions can be explained either by an extension of the equatorial climate with heavy rainfall the whole year long (Roatan islands, N. of Honduras, Orizaba in Mexico), or by more contrasting climates with shifted or inverted dry seasons (Madras, India, and East part of Sri Lanka, Fig. 11: diamonds).

Some shifted reproductive events still come from specimens collected in mountainous regions or islands from which we don't have any accurate climatic diagram.

The amount of specimens that seem to show a shifted reproduction under a typical equatorial climate hardly reaches 4.

The two belts of extreme latitude where the plant have been found extend from 25° to 31°08'S. and from 25° to 28°40'N. There, different climate types occur, and as a consequence, flowering seems to start at various times of the year, depending on the region.

In the southern hemisphere, two regions are mainly concerned, the plant being still unknown from eastern Australia. One is located in Natal, on the East coast of South Africa (Fig. 11: crosses). The flowering starts there between May and June, which corresponds to the end of the rainy season. In the other one, continental South America, flowering starts between mid-February and mid-April.

In the northern hemisphere, these maximal latitudes don't occur in Africa, because of the Sahara. In America, they are reached in the Bahamas and in Florida, where flowering follows the tropical model, and from southern Texas to the north of the East coast of Mexico (Fig. 11: stars). There, flowering curiously starts in the second part of the rainy season. It is worth mentioning that this occurrence is located in one of the coldest climates where *Chromolaena odorata* can be found, and that in this way, fruits are dispersed before the winter colds. In an especially dry site in Mexico, reproduction also takes place during the rainy season, but it should be noted that it is likely that the whole aerial part of the plant would die there during the dry season. In Asia, reproduction follows the tropical model in Assam, Northwest India and, with one exception, in Nepal.

The conclusions that can be drawn from this study doesn't support a widespread assumption, which is that in *Chromolaena odorata*, flowering is controlled by the photoperiod (see for example: HOLM & al., 1977). The time of the induction of flowering, which might precede the first macroscopically visible manifestation of flowering by a few weeks, would fall in the majority of cases near the autumnal equinox. But initiation of flowering coincides with this period only as far as the climate is typically tropical. It means that this initiation of flowering also occurs when precipitation decreases, at the beginning of the dry season. It is nevertheless clear that a photoperiodically based induction could explain the anarchy observed at the low latitudes, the variation of day length being too small to be able to induce flowering uniformly. But some facts would lead us to think that flower induction is due to climatic factors.

- The irregularity of flowering in regions with more than 6° latitude, where an equatorial climate occur.
- The shifting of flowering induction in climates where the dry season is also shifted.
- The greater proportion of exceptions at the extreme latitudes.

To my opinion, it would be nonsense to try explaining the induction of flowering of *Chromolaena odorata* by a single factor. If the decrease of precipitation might play in most climates a crucial role, it seems that temperature could also be involved in the cases of extreme latitudes.

It would also be an error to discard the photoperiodic factor. It is not excluded that, in order to be able to reproduce itself at the most favourable time, flowering would respond to a photoperiodic stimuli, in a way peculiar to each population, as an adaptation to a given climate.

I have been trying to initiate flowering of *Chromolaena odorata* by growing plants in a controlled environment. Seeds were collected at the Station d'Ecologie Tropicale de Lamto. After germination, two sets of 24 plants were grown in two phytotrons of different photoperiod (10/14 and 14/10). Every two months, 3 randomly chosen plants in each phytotron were exchanged. After one and a half year, no flowering had been observed, and the experiment was stopped. No final conclusions could be drawn from this experiment, because the plants had to be cut back to stay in the dimensions allowed by the phytotrons.

I have nevertheless been told since (J. Slaats, pers. comm.) that a similar experiment had taken place in the University of Wageningen, with positive results.

If data from a long-time monitoring of *Chromolaena odorata*'s reproduction on one site was available, it would be possible to analyse in which way delays of the usual seasons have an influence on the timing of the phenomenon.

Another interesting experiment would be to cultivate individuals coming from other localities with different climates. Growing a plant from Saba or St. Eustatius in another locality from the northern hemisphere but with a typical tropical climate could show if the shifting of the flowering event is still observed.

Conclusions

Throughout the geographical range of *Chromolaena odorata*, its reproductive cycle starts at various times of the year, depending on the climate. The triggering factor(s) could not be clearly isolated. In the intertropical zone, where the species is most abundant, the onset of the phenomenon coincides generally with the beginning of the main dry season. In this way, the plant turns its production toward sexual reproduction at a time when increase of the vegetative apparatus is not important and could even been deleterious. The duration of the period when *Chromolaena odorata* initiates flowering events also seems to be variable, depending on climatic factors. For instance, in Abidjan, new inflorescence are likely to appear during 5 consecutive months, whereas in Lamto, new flowering events will occur during only 3 months.

From the first visible macroscopically visible manifestation of the reproduction to the ripeness of the fruits, a period of two and a half month seems to be necessary. Because all inflorescence don't start their development at the same time, the total duration of the reproduction event is longer.

The amount of fruit produced is very high. The cypsella are light and, with the help of a pappus, they appear to be adapted to anemochory. The plant only allow the anemochorous broadcasting of its seeds when the weather is dry and when wind speed is sufficient, in order to reach maximum distances.

The dispersion also proceeds by exozoochory and anthropochory, the fruits clinging easily to feathers, furs or clothes. This is probably how the species invades so rapidly a new geographic area.

The strategy of reproduction of *Chromolaena odorata* is very well adapted to its coloniser status. The plant can achieve massive invasions by long-distance dispersal. Owing to the fact that sexual reproduction can intervene as early as the first year of growth, and with the help of its proliferous production of seeds, populations build very quickly in new regions. The anemochory can bring

the species to new sites easily, especially in the secondary landscapes that have become so common in the intertropical belt. The ability of the species to take root from twigs that bend to the ground also increases their competitiveness towards other plants and threatens the surrounding vegetation.

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REFERENCES

- DELABARRE, M. (1977). *Incidence agronomique du développement de Eupatorium odoratum (composée) en Côte-d'Ivoire*. Thèse. Université Nationale de Côte-d'Ivoire. Abidjan.
- GAUTIER, L. (1992a). *Contact forêt-savane en Côte-d'Ivoire centrale: rôle de Chromolaena odorata (L.) R. King & H. Robinson dans la dynamique de la végétation*. Thèse, Université de Genève.
- GAUTIER, L. (1992b). Taxonomy and distribution of a tropical weed: *Chromolaena odorata* (L.) R. King & H. Robinson. *Candollea* 47: 645-662.
- HOLM, L. G., D. L. PLUCKNETT, J. V. PANCHO & J. P. HERBERGER (1977). *The World's Worst Weeds*. University of Hawaii. Honolulu.
- KUSHWAHA, S. P. S., P. S. RAMAKRISHNAN & R. S. TRIPATHI (1981). Population dynamics of *Eupatorium odoratum* in successional environments following slash and burn agriculture. *J. Appl. Ecol.* 18: 529-535.
- MATHEW, P. M. & A. MATHEW. (1983). Studies on the South Indian Compositae V. Cytotaxonomic consideration of the tribes Vernonieae and Eupatorieae. *Cytologia* 48: 679-690.
- SHELDON, J. C. & F. M. BURROWS (1973). The dispersal effectiveness of the achene pappus units of selected Compositae in steady winds with convection. *New Phytol.* 72: 665-675.
- VIDAL, J. (1956). *La végétation du Laos. Première partie: Le milieu*. Travaux du Laboratoire forestier de Toulouse.
- WALTER, H. & H. LIETH (1960-1967). *Klimadiagram-Weltatlas*. Gustav Fischer Verlag. Jena.
- WARD, C. J. (1980). *The plant ecology of the Isipingo Beach, Natal, South Africa*. Memoirs of the botanical survey of South Africa No. 45. Botanical Research Institute, Pretoria.
- WHITE, T. C. R. (1970). Dispersal of exotic weed plants. *Austral. J. Sci.* 32(9): 370.
- YADAV, A. S. & R. S. TRIPATHI (1981). Population dynamics of the ruderal weed *Eupatorium odoratum* and its natural regulation. *Oikos* 36: 355-361.

