Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Virology

# The biogeography of viral emergence: *rice yellow mottle virus* as a case study

Agnès Pinel-Galzi[1], Oumar Traoré[2], Yacouba Séré[3], Eugénie Hébrard[1] and Denis Fargette[1]

*Rice yellow mottle virus* (RYMV) exemplifies the key role in plant virus emergence of the early steps of crop extension and intensification in traditional agriculture. In East Africa, RYMV emerged in the 19th century after rice intensification along the Indian Ocean coast, and later spread inland concomitantly with rice introduction. In West Africa, the contrasted history of rice cultivation among regions differently shaped RYMV populations. A biogeographical approach — which jointly considers the spatial distribution of the virus and its hosts over time — was applied to reach these conclusions. We linked the evolution of RYMV over the past two centuries to a geographical map of the history of rice cultivation in Africa.

**Addresses**
[1] Institut de Recherche pour le Développement (IRD), UMR RPB (IRD, CIRAD, Université Montpellier 2), Montpellier, France
[2] INERA, 01 BP 476, Ouagadougou 01, Burkina Faso
[3] AfricaRice, P. O. Box 33581, Dar es Salaam, Tanzania

Corresponding author: Fargette, Denis (denis.fargette@ird.fr)

**Current Opinion in Virology** 2015, **10**:7–13

This review comes from a themed issue on **Emerging viruses: interspecies transmission**

Edited by **Antoine Gessain** and **Fernando Garcia-Arenal**

For a complete overview see the Issue and the Editorial

Available online 26th December 2014

http://dx.doi.org/10.1016/j.coviro.2014.12.002



## Introduction

In animal virology, a major distinction is made between epidemics caused by interspecies transmission through spillover from wild hosts (animals) to humans (man being an ecological dead end for the virus), and those mainly driven by intra-specific human-to-human infection [1,2]. By analogy, what is the respective role of wild and cultivated hosts in virus emergence and spread in plant virus ecology, that is, inter-specific and intra-specific transmission, respectively? On the one hand, the role of wild hosts in plant virus ecology, already documented [3–5], is still reevaluated in the light of metagenomics studies [6–8]. On the other hand, the links between virus emergence and agriculture in modern times [9] may also be relevant during the early stages of agriculture ([10–12], but see [13•]). These key questions underlined the crucial need of studies of plant–virus interactions at the agro-ecological interface [14•], considering the role of wild plants [15] and the level of human management [16•,17]. Accordingly, the case of subsistence agriculture — in which the relative impacts of wild and cultivated hosts are less imbalanced — is of particular interest.

*Rice yellow mottle virus* (RYMV) is considered here as a case study of plant virus ecology at the wild/cultivated interface in subsistence agriculture, as rice has been cultivated traditionally until the recent decades in most regions of Africa. Did the emergence of RYMV and the current epidemics in cultivated rice result from recurrent spillovers from the wild reservoirs? Alternatively or complementarily, did the inoculum come from infected rice, even when and where this crop was cultivated by subsistence methods? If the diversification of RYMV mainly occurred in cultivated rice, close relationships between the history of rice and virus evolution are to be expected. In this review article, we looked for the impact of intra-species and interspecies transmission on the emergence and spread of RYMV from the early diversification of the virus to the current epidemic phase in rice.

## RYMV ecology and epidemiology

*Rice yellow mottle virus* is a single-stranded RNA species of the genus *Sobemovirus* [18]. RYMV is transmitted by various biotic and abiotic means, but no evidence of seed-borne transmission has been found [19]. The natural host range of RYMV is limited to the two species of cultivated rice *Oryza sativa* L. and *Oryza glaberrima* Steud., the wild rice species *Oryza barthii* A. Chev. and *Oryza longistaminata* A. Chev. et Roehr, and the wild grasses *Echinocloa colona* (L.) Link, *Eragrostis atrovirens* (Desf.) Trin. ex. Steud and *Panicum repens* L. [20]. RYMV has a narrow experimental host range restricted to the *Oryza* genus and a few wild *Poaceae* species most of which belong to the tribe *Eragrostidae* [21]. Only the crow-foot grass *Dactyloctenium aegyptium* (L.) P.Beauv. is a differential host of RYMV strains [22]. RYMV was first detected in 1966 near Kisumu in Kenya along the north-east shore of Lake Victoria [21]. This report coincided with the development of one of the first major intensive rice production schemes in Africa. Since then, most epidemics have been associated with rice intensification. This reflects the impact of changes in methods of rice cultivation on RYMV ecology. Under subsistence rice cropping, transmission and spread are greatly restricted

**Box 1 History of rice cultivation in Africa according to Roland Portères.**

Portères [39] proposed that the African rice *O. glaberrima* was domesticated ca. 3000 years ago in the inland delta of the upper Niger River and had diffused to two secondary centers of domestication, one along the Senegambian coast and the other in the interior Guinea highlands. Recent analyses of the genome of *O. glaberrima* [38,40••] are consistent with the theory of the domestication of the African rice developed by Portères. Portères further proposed that *O. glaberrima* cultivation extended to Lake Chad at the north, and to the Atlantic Ocean at the south in the 16th century between the Senegal River and Axim, a coastal town in Ghana close to the Côte d'Ivoire border [32]. To the east, rice cultivation was not practised then. The Asiatic rice introduced by the Portuguese along the West African coast since the 16th century was more readily accepted where the African rice had been grown previously, because suitable cultivation methods were known. As a consequence, Portères identified a region of dense rice cultivation at the west (named the rice belt) and a region of sparse rice cultivation at the east (referred to as the yam belt because of the traditional yam cultivation). These two areas of rice cultivation in West Africa (also named by Portères the continuous and the discontinuous rice domains, respectively) are referred to collectively as the old rice domain. In Central Africa, the Asiatic rice was grown more recently, in the early 20th century. Accordingly, it was referred to by Portères [41] as the new rice domain.

In East Africa, rice was introduced recurrently by Indian and Arabic traders since at least the 10th century, and since the 16th century by the Portuguese. Rice was grown until the 19th century along the coast within a narrow and extended band alongside the Indian Ocean. Rice cultivation intensified in the 19th century, and was introduced from the coast into its hinterland by Swahili traders in the second half of the 19th century. Rice was grown first around the African Great Lakes: Lakes Victoria, Tanganyika, and Malawi. Interestingly, a recent map of rice in Africa [42] identified an area of dense rice cultivation in West Africa which matched the old rice domain of Portères [39,41], an area of low rice cultivation in Central Africa similar to the new rice domain of Portères [32,41], and an area of dense rice cultivation in East Africa which encompassed the coastal band and its hinterland [39,41].

by spatial and temporal discontinuities. FAO statistics (http://faostat.fao.org/) indicated a four-fold increase in area of rice grown between 1960 and 2013 in Africa to reach a total of 11 millions ha. The current rice intensification favors RYMV emergence and spread in rice [19]. Introduction of irrigation allows large areas of cultivation and double-cropping, reducing spatial and temporal discontinuities. The associated practice of using rice nurseries also facilitates virus build-up and spread to neighboring fields. Consequently, cultivated rice must be a major source of inoculum during the current epidemic phase.

## RYMV emergence in rice: a biogeographical approach

What was the role of cultivated rice in RYMV emergence *before* the epidemic phase of the second half of the 20th century, and how to address the question? A biogeographical approach — which jointly considers the spatial distribution of the virus and its hosts over time — is applied here to assess the role of cultivated rice in RYMV emergence at different times and in different regions. The phylogeography of RYMV over the past two centuries (Figure 1) is linked to a geographical map of the history of rice cultivation in Africa (Figure 2). Four situations — two in East and two in West Africa — which are contrasted and sufficiently documented to test the links between rice cultivation and RYMV evolution are discussed below.

The genetic diversity of RYMV has been assessed in most of the countries of Africa where the virus occurs. It has revealed a high diversity, up to 11% along the 4450 nt long genome, a clear-cut phylogeny with well-defined strains not obscured by frequent recombination events, and a marked geographical distribution of the strains not blurred by repeated long-range movements. The distribution of the strains throughout Africa had a marked geographical basis with different strains in East, Central and West Africa (Figure 1). RYMV phylogeny is split into three lineages (S5, S6 and S4-S1) with discrete geographical distributions. The S5 lineage is confined to Kilombero, a region along the Indian Ocean at the latitude of the Zanzibar Archipelago. The S6 lineage is present in East Africa only, mainly on the coastal zone alongside the Indian Ocean. Strains of the S4-S1 lineage are spread all over Africa. RYMV is a measurably evolving population [23], and the age of the major strains/lineages can be estimated. The pattern of genetic diversity of RYMV has been interpreted as resulting from a concomitant diversification and spread of the virus from East to West Africa since the 19th century [19]. It is shown here that, at a finer scale of spatial resolution, the geographic distribution of the strains has been shaped by the history of rice cultivation in Africa.

## RYMV emergence in East Africa

(i) In East Africa, rice has been cultivated for centuries in a narrow and extended band along the coast of the Indian Ocean (Figure 2). Rice cultivation intensified in this region during the 19th century. The Kilombero region is the only area in Africa which harbors isolates of the three lineages S6, S5 and S4-S1 [24•]. The time of their most common ancestor (TMCRA) is estimated to ca. 180 years, that is, ca. year 1830 (Figure 1). Then, RYMV first emerged in East Africa in the 19th century in a region and at a time when rice cultivation became sufficiently intense to sustain successful virus transmission and spread.

(ii) In East Africa, rice was introduced from the coastal zone into its hinterland in the second half of the 19th century. Rice was first cultivated around the African Great Lakes: Lakes Victoria, Tanganyika, and Malawi (Figure 2). The virus strains found in this region diversified ca. 100 years ago (Figure 1). This spatio-temporal link suggested that RYMV spread followed rice introduction inland East Africa. Yet, only a subset of the diversity was introduced from the coast, reflecting the presence of spatial bottlenecks