Genome Scan of Rice Landrace Populations Collected Across Time Revealed Climate Changes' Selective Footprints in the Genes Network Regulating Flowering Time

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Rice

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Genome Scan of Rice Landrace Populations Collected Across Time Revealed Climate Changes' Selective Footprints in the Genes Network Regulating Flowering Time

Nourollah Ahmadi[1,2*], Mamadou Billo Barry[3], Julien Frouin[1,2], Miguel de Navascués[4] and Mamadou Aminata Toure[3]

Abstract

Analyses of the genetic bases of plant adaptation to climate changes, using genome-scan approaches, are often conducted on natural populations, under hypothesis of out-crossing reproductive regime. We report here on a study based on diachronic sampling (1980 and 2011) of the autogamous crop species, *Oryza sativa* and *Oryza glaberrima*, in the tropical forest and the Sudanian savannah of West Africa. First, using historical meteorological data we confirmed changes in temperatures (+ 1 °C on average) and rainfall regime (less predictable and reduced amount) in the target areas. Second, phenotyping the populations for phenology, we observed significantly earlier heading time in the 2010 samples. Third, implementing two genome-scan methods (one of which specially developed for selfing species) on genotyping by sequencing genotypic data of the two populations, we detected 31 independent selection footprints. Gene ontology analysis detected significant enrichment of these selection footprints in genes involved in reproductive processes. Some of them bore known heading time QTLs and genes, including *OsGI*, *Hd1* and *OsphyB*. This rapid adaptive evolution, originated from subtle changes in the standing variation in genetic network regulating heading time, did not translate into predominance of multilocus genotypes, as it is often the case in selfing plants, and into notable selective sweeps. The high adaptive potential observed results from the multiline genetic structure of the rice landraces, and the rather large and imbricated genetic diversity of the rice meta-population at the farm, the village and the region levels, that hosted the adaptive variants in multiple genetic backgrounds before the advent of the environmental selective pressure. Our results illustrate the evolution of in situ diversity through processes of human and natural selection, and provide a model for rice breeding and cultivars deployment strategies aiming resilience to climate changes. It also calls for further development of population genetic models for adaptation of plant populations to environmental changes. To our best knowledge, this is the first study dealing with climate-changes' selective footprint in crops.

Keywords Climate changes, Selection footprint, Temporal cline, Genome scan, Rice, *O. sativa*, *O. glaberrima*, Flowering time

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Introduction

Climate change is affecting agricultural productivity and its effects may limit global crop production by at least 10% in 2050 (Davis et al. 2016), especially in farming systems dominated by rainfed crops such as in sub-Saharan Africa (Sultan et al. 2019). Adaptation strategies include using better-adapted varieties or switching to more adapted crop species (Pironon et al. 2019). The variety replacement strategy relies on selection of better-adapted varieties among the ones currently cultivated or maintained in gene banks (Rojas et al. 2019), and on creation of new varieties combining adaptive traits scattered among the cultivated species (Haussmann et al. 2012; Watson 2019) and their wild relatives (Cortés and López-Hernández 2021).

Climate change also imposes strong selective pressure on natural populations and on standing genetic diversity of crop species. Predicted consequences include species range shifts, altered phenology, and local extinction (Reush and Wood 2007). Understanding how climate changes affects phenotypic and genetic diversity of crop species can provide clues on which type of material we should produce to withstand the new climatic regimes (Snowdon et al. 2021). It can also provide information on the species vulnerability to these environmental changes (Hoffmann and Willi 2008).

Three mechanisms are commonly distinguished as possible responses to climate change: migration, phenotypic plasticity and genetic adaptation (Hoffmann and Sgrò 2011; Franks et al. 2014). It has been shown that for many plant species the migration pace cannot follow the pace of predicted local climate change (Lorie et al. 2009). Adaptation can occur on a relatively short time if the plant population has sufficient genetic variation upon which selection can act (Hoffmann and Sgrò 2011; Pauls et al. 2013; Messer and Petrov 2013). Organisms can also respond to climate change through phenotypic plasticity, i.e., the ability of a given genotype to modify its phenotype in response to environmental variations (Springate et al. 2011; Kelly 2019).

Understanding mechanisms involved in genetic adaptation linked to spatial or temporal heterogeneity in selection pressures is also an important issue of evolutionary and conservation biology. This implies knowledge about the role of evolutionary processes such as mutation and recombination (Reush and Wood 2007), and about the relative importance of standing genetic variation (i.e. allelic variation that is currently segregating within a population or a species) as opposed to new mutations, as a source of beneficial alleles (Hermisson and Pennings 2017). The role of selection in the adaptation process is also critical to understand, as it shapes the evolution of genes involved in adaptive traits as well as their surrounding genetic diversity (reviewed in Orr 2002; 2005). Answers to these questions may also depend on the biological characteristics of the species under consideration (life cycle, mating system, dispersal rate, etc.). For instance, adaptation to new conditions is expected to be limited in predominantly self-fertilizing populations, due to reduced effective population size and recombination (Anderson et al. 2011; Hartfield et al. 2017). It is thus important to get empirical data on adaptation routes and genetic mechanisms in both self-fertilizing and outcrossing species. Geographic areas where farming systems, not yet affected by the Green Revolution, still rely on a large number of landraces constitute a good setting for such empirical analysis of the genetics of crop species adaptation to climate changes. Indeed, when spread over a broad environmental gradient, those landraces can collectively represent a meta-population harbouring large standing genetic variation (Barry et al. 2007c; Radanielina et al. 2013), that has evolved historically through processes of human and natural selection (Bellon et al. 1997).

Plants phenotypic response to climate changes is as multi-faceted as the changes in environmental parameters. Among the plant phenotypic traits, the reproductive development process and phenology are particularly responsive to climate changes (Gray and Brady 2016; Prevéy, 2020). The initiation of the reproduction phase is a critical life history step and its timing has important fitness consequences. Flowering too early or too late can induce sterility and reduced fecundation rate due to harsh conditions such as high temperatures (Lohani et al. 2020), or incomplete seed development due to adverse meteorological phenomenons such as drought (Fahad et al. 2017; Yu et al. 2019). Regulation of flowering time is a complex process often involving several genetic pathways. In *Arabidopsis thaliana*, it involves a network of more than 60 genes, regulated through four different pathways (Wellmer and Riechmann 2010; Quiroz et al. 2021). In rice (*Oryza sativa*) the list of known regulators of flowering time (termed heading date) includes some 53 genes involved in at least three pathways: photoperiod and circadian clock, chromatin-related pathway, and hormones pathway (Wei et al. 2020).

Several approaches have been developed for the analysis of the genetic bases of adaptation to climate changes (reviewed in Franks and Hoffmann 2012; Aguirre-Liguori et al. 2021) including artificial evolutionary experiments (Hansen et al. 2012), sampling along cline (Bailey and Bataillon 2016; Cruzan and Hendrickson 2020), or sampling across time (Franks and Weis 2008; Hansen et al. 2012) associated with genome scans techniques. However, almost all of the latter studies were focused on natural populations (Bailey and Bataillon 2016). To our best knowledge, the only such study connected to

crop species was the application of the genome scan approach to wild populations of pearl millet, sampled along two geographic clines associated with climate gradient (Berthouly-Salazar et al. 2016). Consequently, little is known about the effects of informal human (farmers) selection in the context of climate change. One probable reason for this situation is the scarcity of relevant study areas, i.e., area not too disrupted by the replacement of the landrace populations with new exogenous cultivars promoted by the formal plant breeding organisations.

Here we present an analysis of the genetic bases of adaptation to climate changes based on sampling across time, in an autogamous crop species, rice, of major significance for the world food security. Our study place was the tropical forest and the Sudanian savannah areas of Guinea in West Africa, not much affected by the Green Revolution. The interval between the two sampling times was approximately 30 years. First, using local historical meteorological data we analysed and confirmed the reality of climate changes in the target area. Second, we analysed and confirmed significant phenological differences between the populations of the Asian rice (*Oryza sativa*) and of the African rice (*Oryza glaberrima*) sampled across time. Third, we implemented two genome-scan methods on those populations and detected several selection footprints. Finally, we were able to connect the loci under selection to known genes and QTLs involved in reproductive development. Our results provide new insight into mechanisms of adaptation of self-fertilizing plant meta-populations, under environmental and human selection. To our best knowledge, this is the first study dealing with climate-changes' selective footprint in crops.

Material and Methods

Study Periods, Geographic Area, and Collection Strategy

Plant material was collected through two collection campaigns in Conakry Guinea. The first campaign (hereafter referred to as Collect-1) took place in 1979 and 1982 (Bezançon et al. 1983). The second collection campaign (Collect-2) was undertaken in 2011 by scientists from Cirad (https://www.cirad.fr/) and IRAG (https://irag-guinee.org/). The collect area stretched from tropical forest to Sudanian savannah agro-ecological regions of Conakry Guinea: latitude 7°34′19.96″ N–12°29′1.50″ N; longitude 8°25′0.0″ O-13°17′59.17″ O (Additional file 1: Fig. S1).

The collect strategy was to drive along major roads and other practicable trails, stop in villages without prior notice, conduct a quick inventory of the rice varieties and collect a sample of each of the identified varieties, in the field or from the granary. The passport data for Collect-1 samples included the village name, the variety name, the species (*O. sativa* or *O. glaberrima*) and, occasionally, the rice growing ecosystem (upland, hydromorphic, lowland) and the type of collect (field/granary, bulk/panicle). Approximately 40% of the accessions were collected in the field.

To prepare the Collect-2 campaign, the geographic coordinates of a large share of the villages visited during Collect-1 was retrieved using Google-Earth software. The collect team borrowed the track of Collect-1 campaign but did not limit its collect to the Collect-1 villages, especially as some villages could not be found. The passport data for samples from Collect-2 included the village name and its geographic coordinates, the variety name and tentative species membership, the rice growing ecosystem and the type of collect. Approximately 80% of the samples were panicles collected in the field.

For Collect-1, 442 accessions were retrieved from the long-term conservation facilities of the Institute de Recherche pour le Development (https://www.ird.fr/). The Collect-2 campaign yielded 776 accessions.

Genotyping

All Collect-1 and Collect-2 accessions were first genotyped with 16 SSR markers using DNA from a plant obtained with a seed visually most representative of the seed stock of each accession. These data served to (i) ascertain the membership of accessions to one of the three genetic groups (*O. sativa indica*, *O. sativa japonica*, and *O. glaberrima*), (ii) detect accessions that could be considered as redundant (i.e. accessions bearing the same allele at each of the 16 SSR loci), (iii) assess the pattern of genetic diversity within each genetic group, for each collect. Based on such information and logistic issues, 600 accessions were selected for genotyping by sequencing (GBS). DNA libraries were prepared at the Regional Genotyping Technology Platform (http://www.gptr-lr-genotypage.com), using the MATAB method for DNA extraction and the *ApekI* enzyme for DNA digestion. The libraries were single-end sequenced using Illumina HiSeq™2000 (Illumina, Inc.) at the Regional Genotyping Platform (http://get.genotoul.fr/). The Fastq sequences were aligned to the rice reference genome, Os-Nipponbare-Reference-IRGSP-1.0 with Bowtie2 (default parameters). Non-aligning sequences and sequences with multiple positions were discarded. Single nucleotide polymorphisms (SNP) were called using Tassel GBS pipeline v5.2.29 (Bradbury et al. 2007). First, the genotypic data for all accessions taken together were filtered for quality score (> 20) and bi-allelic status of SNPs. Second, the genotypic data of accessions from each genetic group were filtered separately for minor allele frequency (MAF > 1%), rate of missing data (< 20%), and heterozygosity (< 5%). The missing data were imputed, separately for

each group, using Beagle v4.0. Table 1 summarizes the results of the process.

Phenotyping

Independent from the above-mentioned selection of accessions for genotyping, 239 accessions from Collect-1 and 412 accessions from Collect-2 were selected (Table 1) to be phenotyped for the duration of the sowing to heading date (DTHD). Accessions from Collect-1 were first seed increased in a greenhouse in Montpellier, France. Phenotyping of accessions collected from the upland and the lowland ecosystems was performed separately. Accessions collected from the upland (see Table 1) were cultivated in an upland field, in the IRAG research station in Guinea (Kindia, 10°00′51.37 N, 12°50′66″ W), in 2012. Accessions collected in the lowland were cultivated in a lowland field, in the same place in 2013. The elementary plot for each accession was three consecutive lines of 1 m long, and the DTHD was recorded on five plants of the middle line. Homogeneity of growing conditions was assessed by the systematic presence of two check varieties every 20 test accessions. There were 364 accessions in common between GBS genotyping and field phenotyping.

Assessment of Genetic Diversity and Population Parameters

Pattern of genetic diversity at the whole accession level and, separately, at the level of each genetic group was investigated using distances between individual accessions estimated by a simple-matching dissimilarity index, computed from genotypes at 1130 SNP common to the *O. sativa indica* (*Osi*), *O. sativa* tropical *japonica* (*Osj*) and *O. glaberrima* (*Og*) accessions. An unweighted neighbour-joining tree was constructed based on this dissimilarity matrix, using DARwin.6 (Perrier and Jacquemond-Collet 2006).

Population parameters were assessed for each genetic group subdivided into two subpopulations representing Collect-1 and Collect-2. This is *Osi*-1 and *Osi*-2 for the *O. sativa indica*, *Osj*-1 and *Osj*-2 for the *O. sativa* tropical *japonica*, and *Og*-1 and *Og*-2 for *O. glaberrima*. The relative importance of genetic diversity among subpopulations, among individuals within a subpopulation and within individuals, was assessed by analysis of molecular variance AMOVA with Arlequin software version 3.5.2. (Excoffier et al. 2010). The same software served to compute nucleotide diversity, expected heterozygosity per locus, the Wright (1965) F-statistics (F_{IS} and F_{ST}) and the population parameter $\theta = 4N_e\mu$, where N_e is the effective population size and μ is the overall mutation rate at the haplotype level.

The speed of decay of linkage disequilibrium (LD) in each subpopulation was estimated by computing r^2 between pairs of markers on a chromosome basis, using the "full matrix" option of Tassel 5.2.6 (Bradbury et al. 2007), and then by averaging the results by classes of distance.

Detection of Loci Under Selection

Presence of loci under selection was investigated through genome scan for loci for which the extent of differentiation between subpopulations Collect-1 and Collect-2 of a given genetic group, summarized by the F_{ST} statistic, is significantly higher than the expected F_{ST} values under neutrality hypothesis, for a given average heterozygosity (h_0) between populations and for a given demographic model (Beaumont and Nichols (1996). Two genome scan methods were implemented: a standard approach assuming outcrossing reproduction (Excoffier et al. 2009) and a method specifically developed for mainly autogamous species (Navascués et al. 2021).

In the Excoffier et al. (2009) approach (hereafter referred to as the "heterozygosity-based" method), first the locus-by-locus differentiation F_{STi} is computed as $\widehat{F}_{STi} = \left(\hat{f}_{0i} - \hat{f}_{1i}\right) \Big/ \left(1 - \hat{f}_{1i}\right)$, where $\widehat{f}_0$ is the average homozygosity within a population and $\widehat{f}_1$ is the probability that two genes from different subpopulations are identical (Weir and Cockerham (1984). Second, Global F_{ST} is computed as a weighted average among loci, where $\widehat{F}_{STi}$ values are weighted by the heterozygosity between populations $h_{1i} = 1 - \widehat{f}_{1i}$ and then the heterozygosity between populations $\widehat{H}_1$ is inferred from the average heterozygosity $\widehat{h}_0$ as $\widehat{H}_1 = \widehat{h}_0/(1 - \widehat{F}_{ST})$. Third, the joint distribution of the neutrality F_{ST} and heterozygosity is obtained by

Table 1 Rice accessions from the two collect campaigns that were genotyped and/or phenotyped for the present study

Genetic group	Number of SNP	Number of accessions genotyped			Number of accessions phenotype		
		Collec-1	Collect-2	Total	Collect-1	Collect-2	Total
O. sativa Indica (*Osi*)	14,775	15	55	70	73	180	253
O. sativa japonica tropical (*Osj*)	9282	96	154	250	107	147	254
O. glaberrima (*Og*)	6250	111	99	210	59	85	144
Total		222	308	530	239	412	651

coalescent simulation under the hypothesis of hierarchical island model of population differentiation. Finally, locus-specific F_{ST} *P* values are obtained from the simulated joint distribution of $\widehat{H}_1$ and $\widehat{F}_{ST}$ by a kernel density approach. Under the hierarchical island model, the population structure is arranged into *k* groups of *d* demes, in which migration rates between demes are different within and between groups. The mutation model implemented is the SNP mutation model, in which a mutation occurs at random along the simulated structured coalescent tree. The approach was implemented using Arlequin 3.5.2 (Excoffier et al., 2010). The value for *k* and *d* was set to 50 and 10, respectively, to mimic a large number of villages each owning less than 10 rice varieties and preferential interactions between varieties of the given village. The number of simulations was set to 50,000.

The Navascués et al. (2021) method (hereafter referred to as "drift-based" method) relies on principles first proposed by Goldringer and Bataillon (2004), that is using the estimated magnitude of drift between two time samples as a null model to test for homogeneity of differentiation across loci. In the case of complete neutrality, all sampled loci should provide estimates of genetic differentiation drawn from the same distribution. Assuming a single isolated population, this distribution depends on the strength of the genetic drift, that is, on the length of the period (*t* in number of generations) and on the effective population size (N_e). Loci under directional selection or linked to such loci are expected to exhibit larger differentiation values than expected under the neutral hypothesis. In order to account for the mainly selfing reproduction system, Navascués et al. (2021) developed an implementation procedure that relies not on the observed allele frequency, but on genotype (*AA*, *Aa* and *aa*) frequency. Indeed, in a mainly selfing species, allele copies within an individual are not independent samples from the population, while genotypes are independent samples. Moreover, in order to account for uncertainty of the initial genotype frequency, assuming the same prior probability for the three genotype frequencies, genotype frequencies in the population are sampled from the posterior probability distribution with $\mathrm{Dir}(\mathrm{K}_0+1)$, where K_0 is the observed genotype counts in the sample of the focal locus at time $t = 0$.

Locus-by-locus differentiation F_{STi} are computed with the Weir and Cockerham (1984) method. Temporal differentiation is measured by estimating the F_{ST} with the analysis of variance approach proposed by Weir and Cockerham (1984). Then, the temporal F_{ST} is used to estimate N_e as: $\widehat{N}_e = \tau(1-\widehat{F}_{ST})/4\widehat{F}_{ST}$, where τ is the number of generations between the two temporal populations. The null distribution of single locus F_{STi} is built through simulations of drift. Each of these simulations consists in (i) drawing the initial genotype frequency K_0 of the locus, conditional on data, (ii) simulating allele frequency change for τ generations, based on $\widehat{N}_e$, (iii) simulating samples by sampling genotypes with genotype frequencies based on $\widehat{F}_{IS}$, and (iv) calculating F^*_{ST} for the simulated sample. The proportion of F^*_{ST} equal or larger than the observed F^l_{ST} provides an estimate of the *p* value for the test. In order to account for multiple tests across the genome, false discovery rates (q-values) are computed from the distribution of the *p* value. Genotype counts observed in the simulated sample of n_0 individuals are modelled as coming from a multinomial distribution $\mathrm{Mult}(\mathrm{n}_0,\gamma_0)$, where γ_0 are the genotype frequencies in the population. In the subsequent generations, allele frequencies π_t are simulated following a binomial distribution as $\pi_t \sim B(2\widehat{N}_e, \pi_{t-1})$ where $\widehat{N}_e$ is the genome wide estimate of the effective population size and π_0 is determined by γ_0. At time $t = \tau$, simulated genotype counts in samples are taken from the multidimensional distribution $K^*_\tau \sim Mult(n_\tau, \gamma_\tau)$, were n_τ is the size of the sampled population at that time, and γ_τ are the genotype (*AA*, *Aa* and *aa*) frequencies in the populations as a function of the allele frequency π_t and the multilocus inbreeding coefficient $\widehat{F}_{IS}$ the estimate from both temporal samples (Weir and Cockerham 1984). Selfing rate is assumed constant across generations. The method was implemented using DriftTest script (Navascués and Vitalis 2020).

The *Osi* group was excluded from search for selection footprint given the small number of accessions available (70) and given the important disequilibrium in the number of accessions in Collect-1 and (15) and Collect-2 (55).

Functional Characterisation of Loci Under Selection

Genes located within an interval of 250 kb on both sides of independent loci detected to be under selection, were determined using the RAP-DB annotation of rice genome (https://rapdb.dna.affrc.go.jp/index.html). The corresponding MSU7.0 gene identity (TIGR) was retrieved using gene-ID converter tool proposed by RAP-DB. The window size of 250 kb was chosen to represent approximately half the distance at which LD decayed to half its initial level, for both *Og* and *Osj* groups, estimated at 450 kb on average across all chromosomes.

Enrichment analysis of genes within the chromosomic segments bearing loci under selection was performed using two gene ontology tools: Agri-GO (Tian et al. 2017; http://bioinfo.cau.edu.cn/agriGO/) and Panther-GO (Mi et al. 2019; http://GeneOntology.org), that use RAP and MSU gene identity, respectively, as input.

The chromosomic segments bearing loci under selection were also investigated for genes known to be involved in reproductive development processes, using available literature (Wei et al. 2020; http://www.model

crop.org/). Likewise, chromosomic segments bearing loci under selection were investigated for enrichment in quantitative trait loci (QTL) involved in DTHD, using the Gramene QTL database (http://www.gramene.org/).

Analysis of the Temporal Evolution of Agro-Climatic Parameters

Climatological data (rainfall and temperature) of the 1961–2010 period were extracted from the archives of Guinea National Weather Service for a weather station in tropical forest area (N'Zérekoré, 7°48′53.2″N, 8°42′14.11″W) and a second station in the Sudanian savannah (Kankan, 10°23′01.65″N, 9°18′18.72″W) of the study region. Evolution of the annual rainfall and of the annual crops' growth season rainfall was characterised using the Lamb index (Lamb 1982): $I = (X_i - X)/\sigma$, where I is the standardised anomaly (Lamb index), X_i is the climatic variable (rainfall) for the year i (or a portion of the year i), X is the average of the same variable in a reference period considered as normal, and σ is the standard deviation of the variable in the reference period. The normal meteorological reference period considered was 1961–1990, as recommended by the World Meteorological Organisation (WMO 1996). The period considered as "crops' growth season" was from June 1st to the end of October. The same methods were used to characterise the evolution trends of the minimum and maximum temperatures.

Results

Temporal Evolution of Major Agro-Climatic Parameters in the Study Area

Patterns of deviation from the normal reference (1960–1990 period), of the annual rainfall total (ART) and of the annual rainfall total during the crops growing season (GSART) along the period 1961–2010, in our two study areas, are given in Fig. 1. These patterns show important temporal evolution of ART and GSART, in both the Sudanian savannah area (Kankan) and the tropical forest area (N'Zérekoré) and a strong correlation between ART and GSART, r = 0.953 in Kankan and r = 0.840 in N'Zérekoré. Three major temporal periods can be distinguished in the two areas, though with not exactly the same year of beginning and end. During the first period (the 1960's), the Lamb index is almost systematically positive, indicating higher rainfalls than during the reference period. During the second period (the 1970's and 1980's), the Lamb indexes are mainly negative indicating abnormally low rainfall. The third period (from the beginning of the 1990's until 2010), is characterized by alternations of years with positive and negative Lamb index, indicating contrasted year-to-year variations of annual rainfall. The second period of abnormally low rainfall is particularly marked in the Sudanian savannah area (Fig. 1). Analysis of monthly rainfall during the crop growth period (Additional file 2: Fig. S2) suggests that during this period, the beginning (June) and the end (September and October) of crop growth season are the most affected months for both the total amount of monthly rainfall and for its inter-annual variability. Thus, rice populations of our two study areas have, actually, experienced a major evolution in rainfalls, between our two collect times.

Regarding the temperatures, patterns of the annual average minimum (T-Min) and maximum (T-Max) in the tropical forest area showed a systematic positive deviation from the normal reference from 1987 on (Fig. 2). The average T-Min and T-Max of the period 1991–2010, were higher than the average T-Min and T-Max of the period 1961–1990, by 1.07 °C and 0.65 °C, respectively. In the Sudanian savannah area also, the annual average T-Max showed a systematic positive deviation from 1987 on, the average difference between the 1991–2010 and 1961–1990 periods being of 1.02 °C. The annual average T-min showed less systematic deviation from the normal reference, and the average difference was −0.14 °C (Fig. 2).

Variation in Day to Heading

A large variability of day to heading (DTHD) was observed among the 651 accessions phenotyped (77 < DTHD < 161 days) and between the three genetic groups (145, 115, and 106 days on average in *Og*, *Osi* and *Osj*, respectively). No significant relationship was found between the accessions' DTHD and the latitudinal coordinate of their place of collect (R < 0.15) in both Collect-1 and Collect-2 subpopulations of each genetic group, suggesting homogenous environmental selective pressure across our study areas stretching between 7°34′19.96″ N and 12°29′1.50″ N.

The distributions of the frequency of accessions of the two collect times in different classes of DTHD, are presented in Fig. 3. These distributions show an important shift of frequencies of Collect-2 accessions toward shorter DTHD, for the genetic groups *Og* and *Osj*, and a more complex pattern for *Osi*. On average, the DTHD of *Og*-2 and *Osj*-2 were significantly shorter than the DTHD of their Collect-1 counterpart: 10.3 days between *Og*-1 and *Og*-2 ($p < 0.00001$) and 3.4 days between *Osj*-1 and *Osj*-2 ($p < 0.002$) (Additional file 3: Table S2). Conversely, the DTHD of *Osi*-2 (118.94 days with confidence interval of ± 1.87) was, on average, 4.3 days longer than the DTHD of *Osi*-1 accessions (114.67 ± 2.97 days). However, in both *Osi*-1 and *Osi*-2 the distribution of DTHD did not satisfy the normality (Shapiro–Wilk test) conditions needed for ANOVA (Additional file 3: Table S2). The most probable reasons for these abnormal distributions of DTHD are the presence of photosensitive accessions of

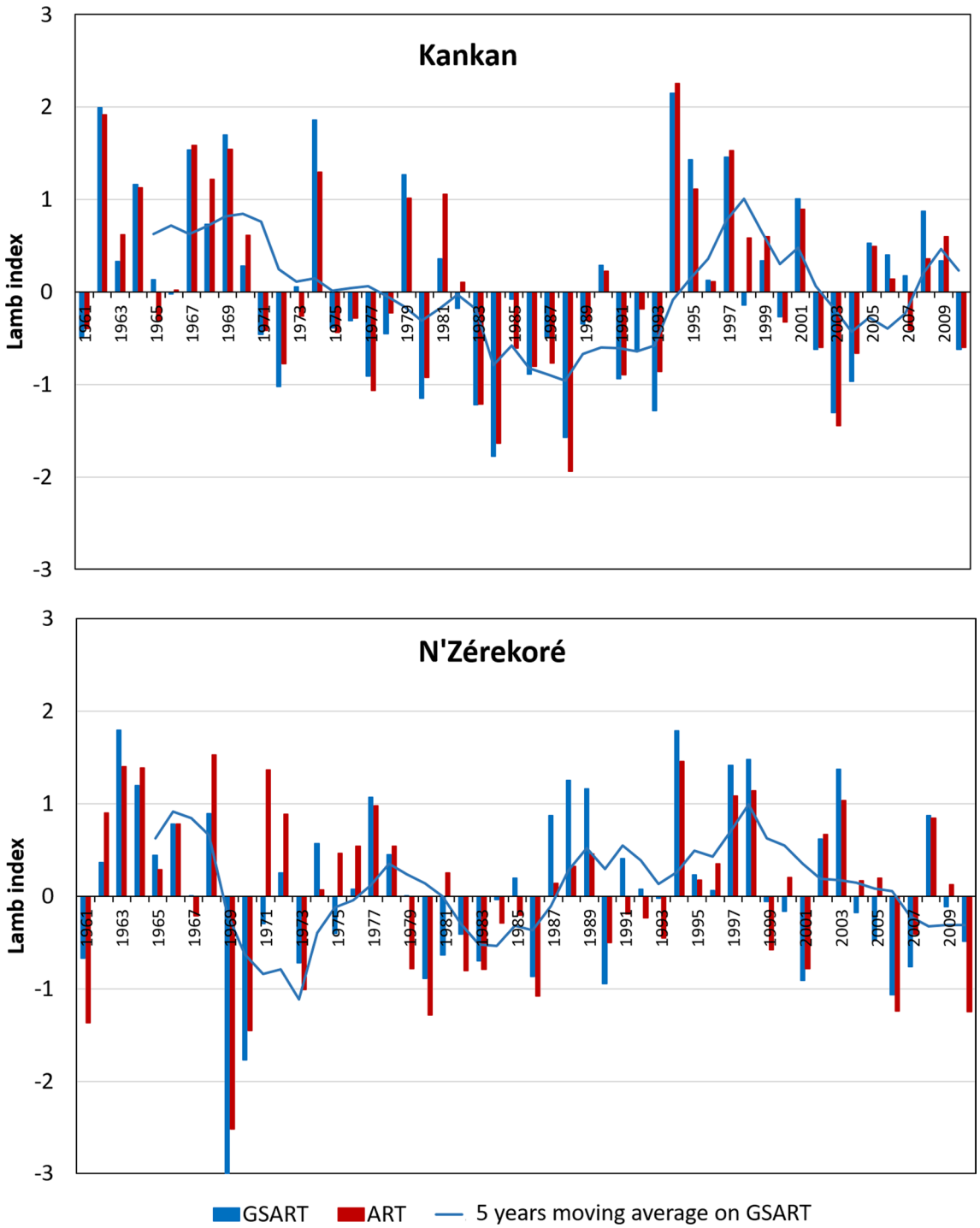

Fig. 1 Pattern of deviation of the annual rainfall total during the crop growth season (GSART) from the normal reference, during the 1961–2010 period, in Kankan (10°23′01.65″ N; 9°18′18.72″ W) and N'Zérekoré (7°′48′53.2″ N; 8°42′14.11″ W) sites of Guinea

long duration and the much larger number of accessions in *Osi*-2 (180 versus 73 in *Osi*-1) that included a larger number of old photosensitive landraces. Indeed, the maximum DTHD reached 161 days in Collect-2, versus 143 in Collect-1 (Additional file 3: Table S2).

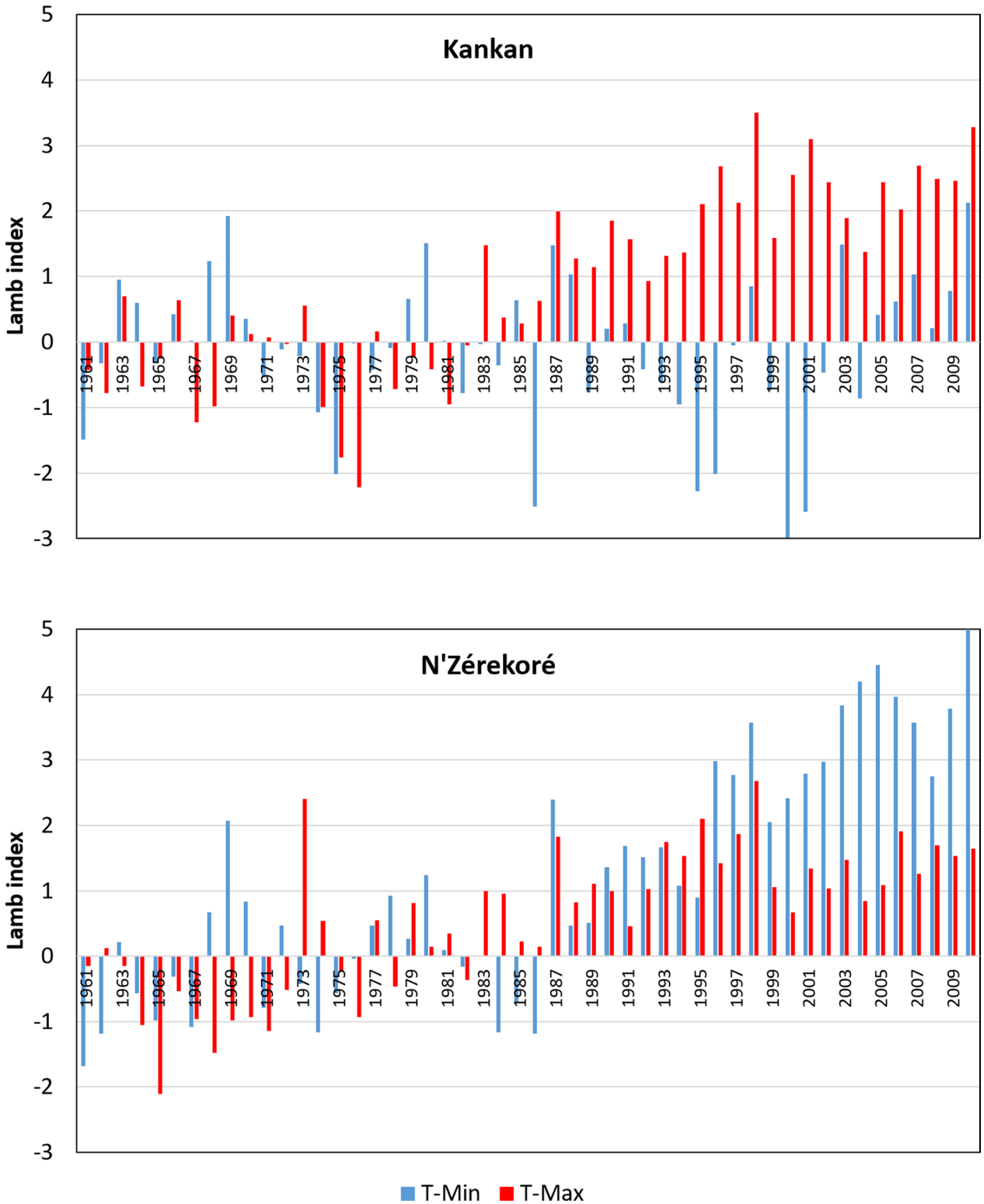

Fig. 2 Pattern of deviation of the annual average minimum (T-Min) and maximum (T-Max) temperature from the normal reference, during the 1961–2010 period, in Kankan (10°23′01.65″ N; 9°18′18.72″ W) and N'Zérekoré (7°°48′53.2″ N; 8°42′14.11″ W) sites of Guinea

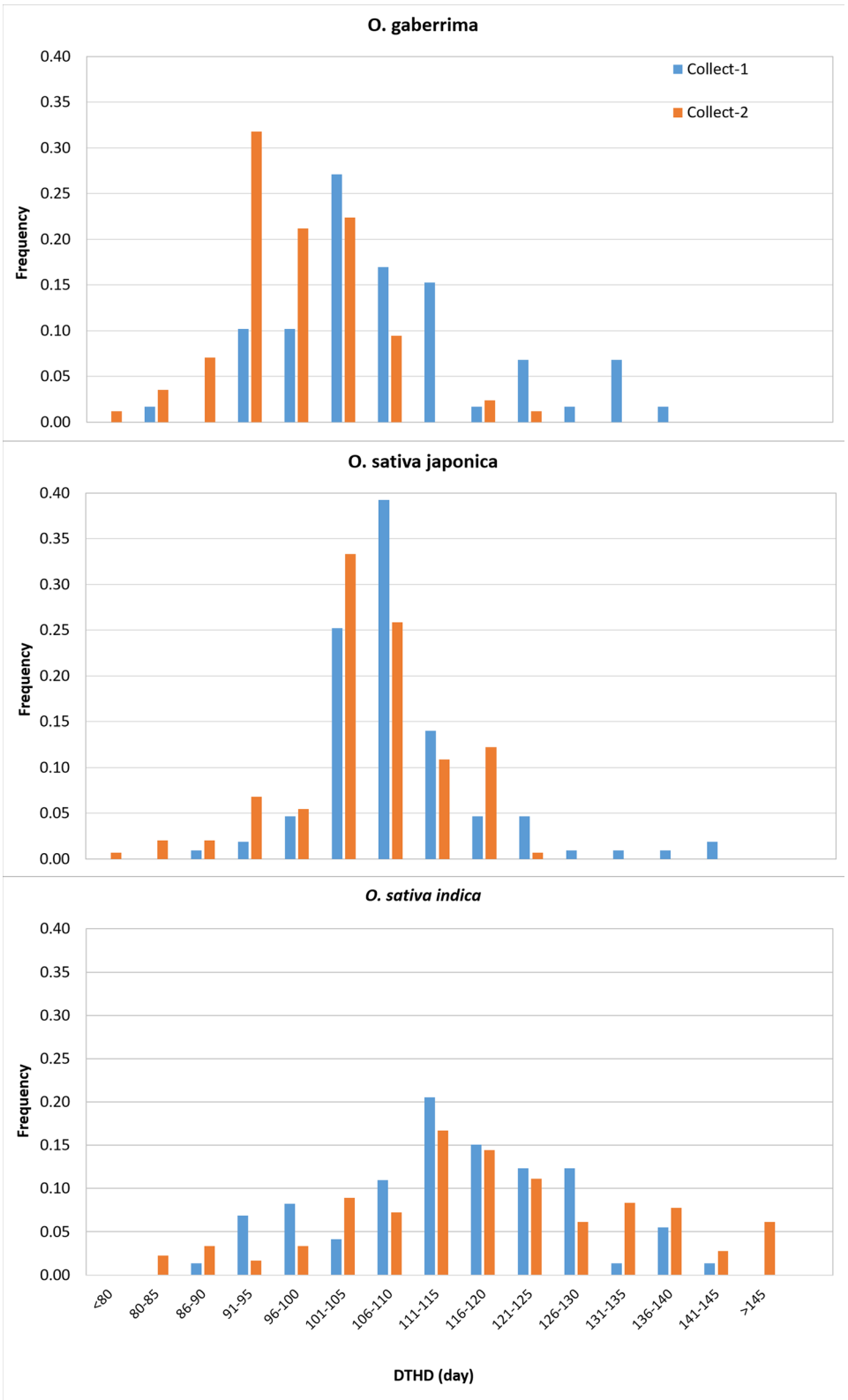

Fig. 3 Distribution of frequency of accessions of the two collect times (Collect-1 and Collect-2) in different classes of duration of the vegetative phase expressed in number of days between the sowing date and the heading date (DTHD)

Genetic Diversity and Population Parameters

Pattern of genetic diversity drawn from genotypes at 1130 SNP loci common to the 530 accessions genotyped with the GBS technology, showed three clear-cut clusters corresponding to the three well-known genetic groups: *Osi*, *Osj* and *Og* (Fig. 4). Within each cluster, accessions from the two collect times did not show plausible preferential grouping (Additional file 4: Fig. S3).

Nucleotide diversity was very low for *Og*-1 and *Og*-2 subpopulations (>0.06), low for *Osj*-1 and *Osj*-2 (>0.09), and of intermediate level (>0.21) for *Osi*-1 and *Osi*-2 (Additional file 5: Table S3). The genetic diversity estimated with the θ parameter showed a similar trend, with the lowest values for *Og*-1 and *Og*-2 (Mean $\theta_{\pi}=319$), the intermediate values for *Osj*-1 and *Osj*-2 (Mean $\theta_{\pi}=798$) and the highest values for *Osi*-1 and *Osi*-2 (Mean $\theta_{\pi}=2867$) (Additional file 5: Table S3). The Tajima's D test detected significant deviations from neutrality in *Og*-1 and *Og*-2 (Mean $D=-2.01$, p value $=0.0010$), almost significant deviation in *Osj*-1 and *Osj*-2 (Mean $D=-1.29$, p value $=0.0575$), and non-significant deviation in *Osi*-1 and *Osi*-2 (Additional file 5: Table S3). The F_{IS} values ranged between 0.0001 (for *Osi*-1 and *Osi*-2) and 0.0303 (for *Og*-2), suggesting a random union of gametes within each population.

Within each group, the "among population" (i.e. among Collect-1 and Collect-2) molecular variance computed by AMOVA was extremely small (<1%) and the "among individuals within populations" variance did not exceed 2.5%. The remaining large share of molecular variance was attributed to "within individuals" variance (Additional file 5: Table S3). Genetic differentiation between the two subpopulations of each group was also very small ($F_{ST}=0.00014$ between *Og*-1 and *Og*-2, $F_{ST}=0.00004$ between *Osj*-1 and *Osj*-2, and $F_{ST}<0.00001$ between *Osi*-1 and *Osi*-2), suggesting random distribution of genotypes across populations (Additional file 5: Table S3).

Important differences were observed between groups for the r^2 estimates of the initial LD, i.e. pairwise distance between markers below 25 kb: 0.7265 for *Osj*, 0.601 for *Og*, and 0.387 for *Osi*-2. The number of accessions in the *Osi*-1 subpopulation (15) was too small to provide a

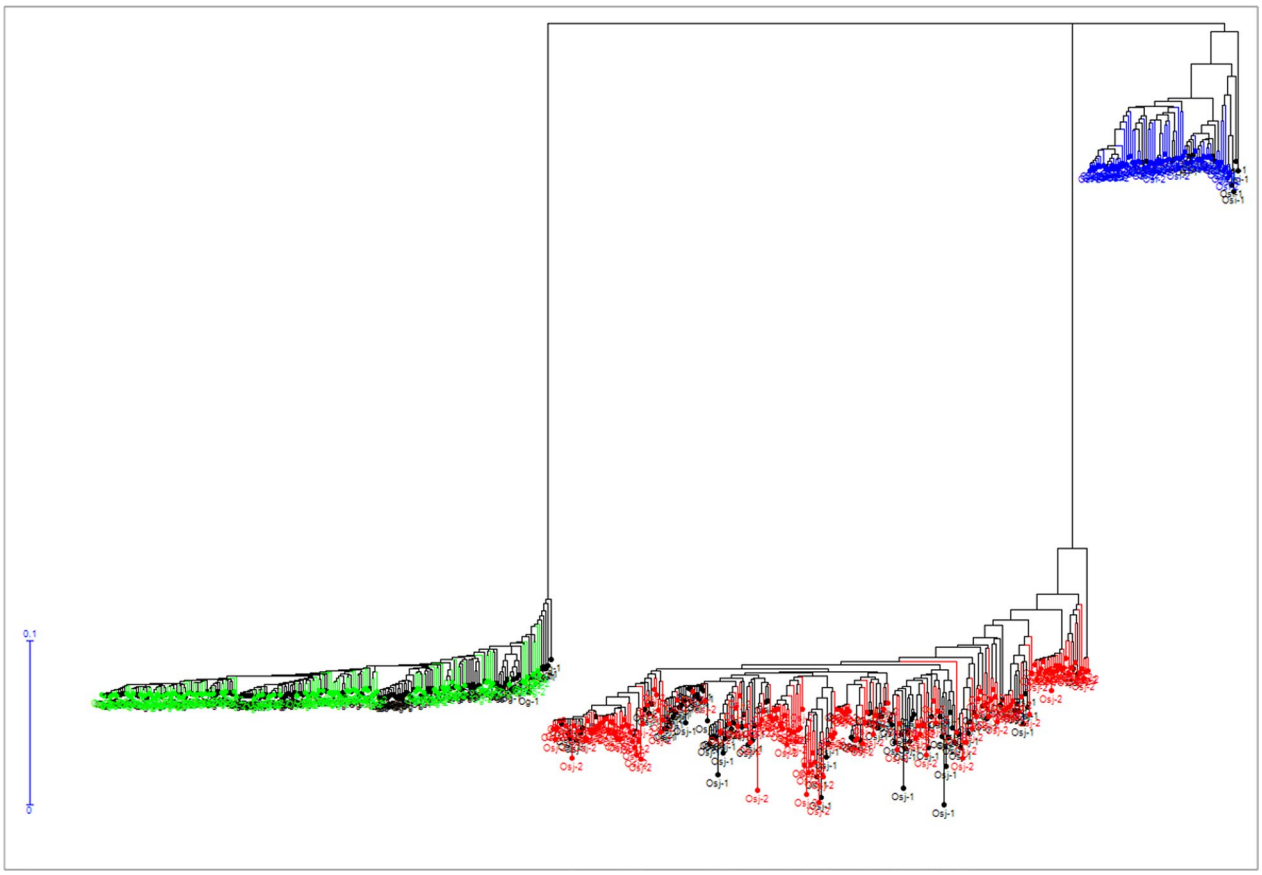

Fig. 4 Unweighted neighbor-joining tree of simple matching distances constructed from genotypes of 530 rice accessions at 1130 SNP loci. Tree branches bearing green, red and blue colors correspond to *O. glaberrima*, *O. sativa indica* and *O. sativa japonica* groups, respectively. Within each branch, accessions from the first collect time (*Og*-1, *Osi*-1 and *Osj*-1) are shown in black

good estimate of LD. The three groups also differed for the subsequent decay of LD (Fig. 5, Additional file 6: Table S4). While the distance at which the LD went below 0.2 was between 200 and 250 kb for *Osi*, it was between 500 and 700 kb for *Og*-1 and *Og*-2, and above 2000 kb for *Osj*-1 and *Osj*-2. The speed of LD decay was slightly higher in *Og*-2 and *Osj*-2, compared to *Og*-1 and *Osj*-1, respectively.

Search for Selection Footprint

Search for selection footprint among the 6250 SNP loci of the *Og* group, using the heterozygosity-based method, identified 20 SNP loci with F_{ST} value beyond the 1% confidence interval limits obtained from simulated data for *Og* group, and 54 additional SNP loci with F_{ST} value within the 1–5% confidence interval limits obtained from simulation (Fig. 6). The former 20 SNP corresponded to 14 independent loci (*IL*), i.e. distance between adjacent SNP loci below 250 kb and strong LD ($r^2 > 0.2$, often close to 1). Among the latter 54 SNP, 21 clustered with five of 14 previously defined *IL*. The remaining 33 SNP formed 16 additional independent loci composed of one to 14 SNP (Additional file 7: Table S5). Distances between each SNP under selection and its two adjacent SNP not under selection were 56.5 kb on average, did not exceed 363 kb, and, thus, were below the distance at which the LD exceeded the value $r^2 > 0.2$. The LD between the SNP under selection belonging to different *IL* and different chromosomes were low ($r^2 < 0.1$); it exceeded 0.2 in 13% cases out of the 242 possible combinations of *IL* but never reached 0.5 (Additional file 8: Fig. S4). The heterozygosity in SNP loci under selection had fallen from 1.56% in the *Og-1* subpopulation to 0.76% in *Og-2* subpopulation.

Search for selection footprint among the 9282 SNP loci of *Osj* group yielded 22 SNP loci with F_{ST} value beyond the 1% confidence interval limits obtained from simulated data for *Osj*, and 88 additional SNP loci with F_{ST} value within the 1–5% confidence interval limits obtained from simulation (Fig. 6). The former 22 SNP corresponded to three *IL*. Among the latter 88 SNP, 16 clustered with the three previously defined *IL*. The remaining 72 SNP formed 11 additional *IL*, including a cluster of 44 SNP (Additional file 7: Table S5). Distance between each SNP under selection and its two adjacent SNP not under selection was 49.6 kb on average, did not exceed 270 kb and, thus, were well below the distance at which the LD exceeded the value $r^2 > 0.2$. The LD between the SNP under selection belonging to different *IL* and different chromosomes was low ($r^2 < 0.1$); the r^2 value exceeded 0.2 in 17% cases out of the 125 possible combinations of independent loci and exceeded 0.5 in two combinations (Additional file 8: Fig. S4). The heterozygosity in SNP loci

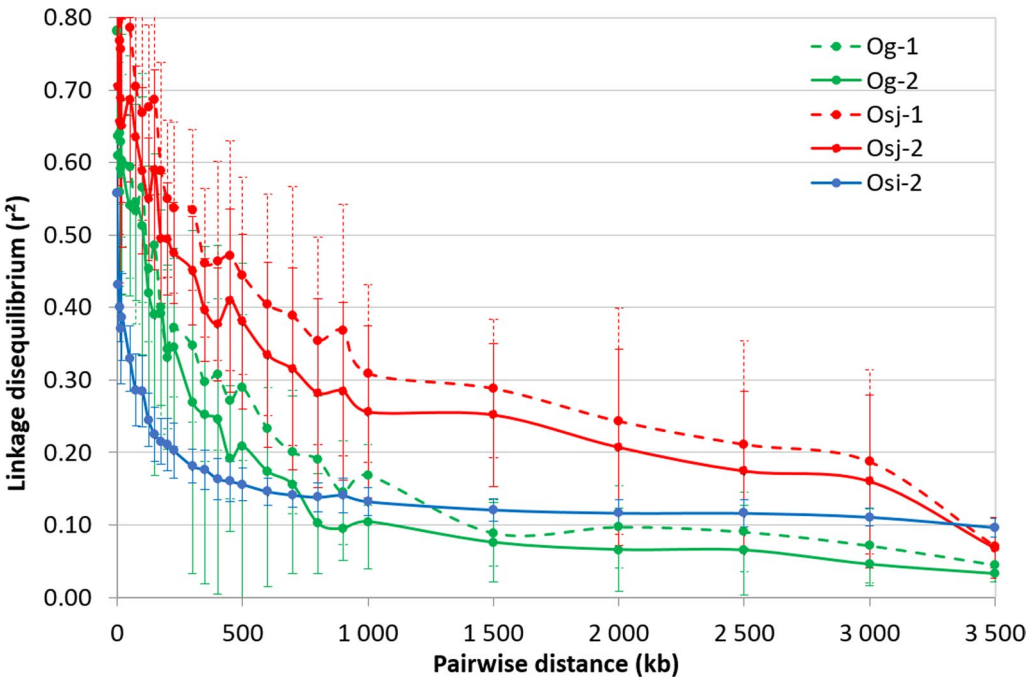

Fig. 5 Patterns of decay in the r^2 estimate of linkage disequilibrium (LD), in the rice populations collected in 1980 (xx-1) and in 2011 (xx-2); *Og*-1 and *Og*-2: *O. glaberrima*; *Osj*-1 and *Osj*-2: *O. sativa japonica*; *Osi*-2, *O. sativa indica*. The LD was estimated from 6250 SNP, 9282 SNP and 14,775 SNP loci for *Og*, *Osj* and *Osi* populations, respectively. The curve represents the average r^2 according to pairwise distance between markers among the 12 chromosomes and the bars represent the associated standard deviation

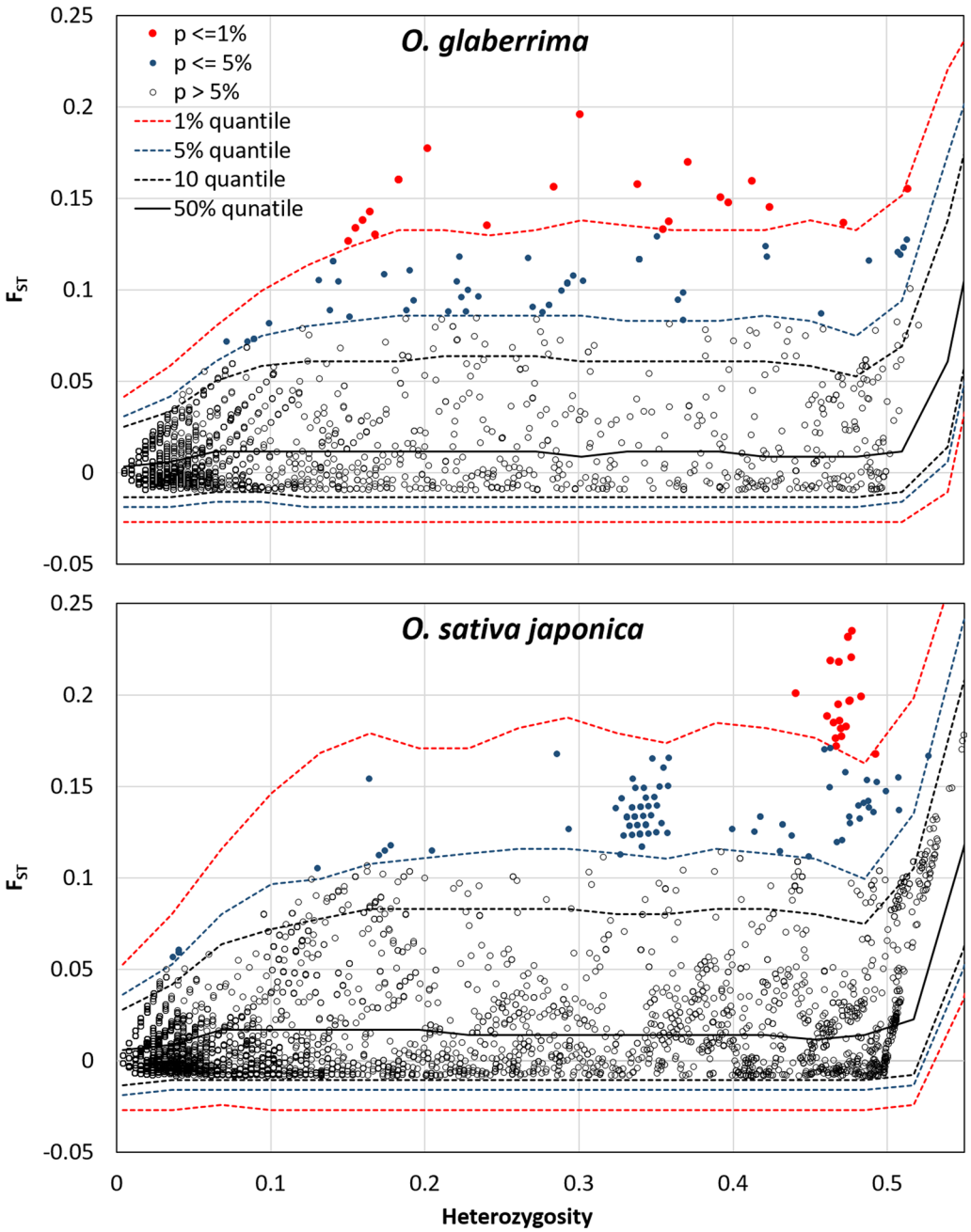

Fig. 6 Plot of the joint distribution of F_{ST} and heterozygosity within populations for the observed loci (circles) and the one-sided confidence interval limits obtained from simulated data (dashed lines). Loci departing from neutrality hypothesis at 1% and 5% significance levels are indicated in red and blue circles, respectively. The number of observed loci was 6250 for *O. glaberrima*, 9282 for *O. sativa japonica*

under selection had fallen from 1.77% in the *Osj-1* subpopulation to 1.02% in *Osj-2* subpopulation.

Search for selection footprint using the drift-based approach, among the 6250 *Og* SNP loci, identified 29 SNP with F_{ST} departing from the neutrality hypothesis with q-value < 0.05 (Table 2; Additional file 7: Table S5). All these loci were also detected to be significantly under selection with $P <= 0.01$ (19 loci) or $P <= 0.05$ (10 loci) with the heterozygosity-based detection method. Likewise, among the *Osj* 9282 SNP loci, 30 showed F_{ST} with q value < 0.05 (Additional file 7 Table S5). All these loci were also detected to be significantly under selection with $P <= 0.01$ (13 loci) or $P <= 0.05$ (17 loci) with the heterozygosity-based detection method. Thus, the results

Table 2 Enrichment in gene ontology terms related to reproductive biological processes, of the chromosomic segments bearing the 24 independent loci most likely under section

Identity of GO term	Description of the biological process	Agri-GO					Panther-GO				
		AN in Ref (24,075)	AN in input (1240)		Fold Enrichment	*q* value	N in Ref (43,658)	N in input (1464)		Fold Enrichment	*q* value
			Obs	Exp				Obs	Exp		
GO:0000003	Reproduction	133	65	6.85	9.49	1.20E−33	587	37	19.68	1.88	3.37E−02
GO:0048608	Reproductive structure development	668	66	26.24	2.51	2.50E−02	–	–	–	–	–
GO:0003006	Reproductive developmental process	668	66	26.24	2.51	2.50E−02	–	–	–	–	–
GO:0009908	Flower development	662	64	26.01	2.46	3.40E−02	–	–	–	–	–
GO:0022414	Reproductive process	114	65	5.87	11.07	1.10E−36	585	37	19.62	1.89	3.38E−02
GO:0009314	Response to radiation	38	31	1.96	15.84	1.80E−20	–	–	–	–	–
GO:0009416	Response to light stimulus	38	31	1.96	15.84	1.80E−20	–	–	–	–	–
GO:0009856	Pollination	114	20	5.87	3.41	3.10E−04	143	18	4.8	3.75	7.96E−04
GO:0009875	Pollen-pistil interaction	–	–	–	–	–	114	14	3.82	3.66	7.94E−03
GO:0048544	Recognition of pollen	–	–	–	–	–	110	14	3.69	3.8	5.86E−03
GO:0050896	Response to stimulus	1026	221	52.84	4.18	3.50E−63	3646	216	122.26	1.77	1.72E−12
GO:0007165	Signal transduction	240	46	12.36	3.72	1.10E−10	1074	60	36.01	1.67	1.86E−02
GO:0009605	Response to external stimulus	25	18	1.29	13.98	5.40E−11	–	–	–	–	–
GO:0023052	Signalling	447	72	23.02	3.13	2.00E−13	1089	60	36.52	1.64	2.51E–02
GO:0009791	Post–embryonic development	2033	167	79.87	2.09	2.50E−02	–	–	–	–	–
GO:0006950	Response to stress	873	164	44.96	3.65	3.80E−39	2109	135	70.72	1.91	3.11E−09
GO:0051716	Cellular response to stimulus	132	55	6.80	8.09	1.10E−25	1874	92	62.84	1.46	3.35E−02
GO:0050789	Regulation of biological process	2027	159	104.40	1.52	1.10E−05	4214	206	141.31	1.46	2.85E−05

AN, and N Number of annotated genes in the *O. sativa* (ref) and in the input genes list, using MSU7.0 or RAP-DB as reference, respectively. *Obs* observed; *Exp* expected

of the drift-based method corroborate the results of heterozygosity-based method, especially for loci most significantly under selection.

Functional Characterisation of Loci Under Selection

Prior to functional characterisation, six independent loci under selection (*ILUS*) in *Og* and in *Osj*, belonging to the same chromosomes and within distance between the component SNP below 250 kb, were merged. The process reduced the total number of *ILUS* to 40, each composed of one to 45 individual SNP. Among these *ILUS*, nine, composed of one SNP and identified to be significantly under selection by one detection method only, were discarded from further analyses. The remaining 31 *ILUS* were divided into two categories: *ILUS* including at least one SNP identified to be significantly under selection by the two detection methods (24 cases, assembling 139 SNP, hereafter referred to as "M2 type") and *ILUS* detected by one method only, namely the heterozygosity-based method (7 cases, assembling 36 SNP), hereafter referred to as "M1 type".

For functional characterisation purpose, the chromosomic interval of each *ILUS* was extended by 250 kb at its two extremities to account for the extent of LD. When concatenated, the 24 M2 type *ILUS* represented a pseudo-chromosomic segment of 23.26 Mb length, bearing 2038 genes endowed with an MSU-TIGR gene identity or 1517 genes endowed with RAP gene identity. The addition of the seven M1 type *ILUS* stretched the length of the pseudo-chromosomic segment to 30.77 Mb, bearing 2706. MSU-TIGER genes or 2612 RAP-DB genes.

The ontology analysis of the 2038 MSU-TIGR genes, on the pseudo-chromosomic segment bearing the 24 M2 type *ILUS*, with the Agri-GO tool, detected highly significant enrichment in genes involved in several biological processes (Additional file 9: Table S6A) including "reproductive processes", "response to light and radiation" and "response to stimulus" (Table 2). Shift to 2706 MSU-TIGER genes (i.e. inclusion of 668 genes underlining the seven M1 type *ILUS*) did not markedly modify the pattern of gene enrichment (Additional file 9: Table S6B). The ontology analysis of the 1517 RAP-DB genes, using Panther-GO tool revealed an enrichment pattern (Additional file 9: Table S6C) that included an important share of the ontology terms related to reproductive processes previously detected with Agri-GO, plus two ontology terms related to biological processes of "recognition of pollen" and "pollen-pistil interaction" (Table 2). Shift to 2612 RAP-DB genes did not markedly modify the pattern of gene enrichment (Additional file 9: Table S6D).

Investigation of the list of genes underlying the 24 M2 type *ILUS* for genes reported to be involved in reproductive processes, identified 12 genes (Table 3, Additional file 10: Table S7) including OsGI ("Gigantea") related to the circadian clock, HD1 ("Constans") involved in induction of flowering under inductive short days, and OsPHYB (Phytochrome B) involved in the regulation of critical day length for flowering. When all the 31 *ILUS* were considered, three additional known genes involved in biological processes related to heading were identified (Table 3, Additional file 10: Table S7).

Investigation of the chromosomic segments bearing the 24 M2 type *ILUS* for the presence of QTLs involved in DTHD, counted 112 such QTL out of the 619 listed in the Gramene QTL database (http://www.gramene.org/) (Table 3; Additional file 10: Table S7). This represented a density of one DTHD QTL every 0.21 Mb, approximately 3.0-fold higher than the expected average density of DTHD QTL, one every 0.62 Mb. The 112 DTHD-QTL counted included a number of major QTL such as Hd1, Hd2, Hd5, Hd6, Hd8 and Hd11. When all the 31 *ILUS* were considered, the count of DTHD QTL reached 162, representing a 3.3-fold enrichment.

Discussion

Understanding changes in the phenotypic and genetic diversity of crop species undergoing environmental selection pressure can provide a wealth of information regarding the genetic processes at work and the adaptation strategies (Snowdon et al. 2021). This study provided insight into the extent of the climate-changes, the related selection pressure on meta-populations of a mainly autogamous crop species, rice, into the extent of its adaptive phenological response, and into the underlying adaptive genetic processes, in the context of a rapid adaptation over 30 generations.

The extent of changes in climate parameters, temperatures and rainfall, between our two collect times (1980 and 2011), were similar to that reported for the entire West Africa (Sultan et al. 2019). It was characterized by approximately a 1 °C rise in mean T-Max and mean T-Min, and by a severely dry period followed by a period of high variability of the annual and cropping season rainfalls. This pejoration of the rainfall regime was particularly severe during the beginning (June) and the end (September and October) of the crops growth season. Analysing N'Zérekoré rainfall data for the 1931–2014, Loua et al. (2017) reported that the higher variability of the annual rainfall during the period 1994–2014 was associated with a shorter duration of the rainy season (later beginning and earlier ending) and a less predictable date for the establishment of the rainy season.

The extent of the heading date advance (10.3 days on average) in our *Og-2* subpopulation, compared to *Og-1*, was among the highest reported for other plant species in

Table 3 Genes and QTLs located on the chromosomic segments bearing the independent loci under selection

Independent loci under selection						Genetic group involved	DTHD QTLs (2)		DTHD genes (3)			
N°	Type	Nb of SNP (1)	Chr	Start	End		Nb	Known name	MSU Identity	Name	GRP	Reference
1	M2	2	chr01	3,930,523	4,504,261	*Og* and *Osj*	1		LOC_Os01g08700	OsGI	1	Izawa et al. (2011)
2	M2	1	chr01	5,540,432	6,040,432	*Og*	14	dth1.1, QHd1a, QHd1a	LOC_Os01g10590	OsFTL8	1	Zhang et al. (2020)
3	M2	9	chr01	18,423,679	19,143,461	*Og*	2					
4	M1	2	chr02	6,762,905	7,267,332	*Osj*	4					
5	M2	1	chr02	24,604,636	25,104,636	*Og*	12	qHD-2, QHd2a	LOC_Os02g41550	OsCRY2	1	Hirose et al. (2006)
6	M2	1	chr03	5,079,703	5,579,703	*Og*	15	dth3.1, QHd3b				
7	M2	3	chr03	10,132,774	12,145,360	*Og*	6	Hd8, dth3.1	LOC_Os03g19480	OsSWN; SDG718	2	Liu et al. (2014)
7	M2	3	chr03	10,132,774	12,145,360	*Og*	6	Hd8, dth3.1	LOC_Os03g19590	OsPHYB	2	Ishikawa et al. (2011)
8	M1	4	chr04	0	827,020	*Og* and *Osj*	1	qDTH-4				
9	M1	9	chr04	1,085,381	3,005,652	*Osj*	12	qDTH-4, QHd4				
10	M2	4	chr04	3,993,589	4,670,203	*Og* and *Osj*	0		LOC_Os04g08034	OsEMF2	3	Luo et al. (2009)
11	M2	1	chr04	32,129,645	32,629,645	*Og*	2	dth4.2				
12	M2	6	chr05	8,974,371	9,788,465	*Og*	2					
13	M2	15	chr05	14,743,007	16,632,418	*Osj*	2	qHD-5				
14	M2	8	chr06	9,422,923	10,942,740	*Osj*	3	Hd1	LOC_Os06g16370	Hd1	1	
14	M2	8	chr06	9,422,923	10,942,740	*Osj*	3		LOC_Os06g16390	OsCLF; SDG711	2	Liu et al. (2014)
15	M2	1	chr06	11,153,613	11,653,613	*Osj*	0					
16	M2	45	chr06	13,095,417	18,074,177	*Og* and *Osj*	5	Hd6b, dth6.1	LOC_Os06g30370	OsMFT1	1	Gao et al. (2014)
17	M2	1	chr07	17,212,559	17,712,559	*Og*	5					
18	M2	1	chr07	29,373,622	29,873,622	*Og*	6	Hd2, QTL7c	LOC_Os07g49460	OsPRR37	1	Hu et al. (2021)
19	M2	2	chr08	4,860,945	5,579,786	*Osj*	3	Hd-5, dth8				
20	M2	14	chr08	17,288,523	18,502,122	*Osj*	21	QHd8, aQHd8, qDTH-8				
21	M1	2	chr08	19,800,834	20,305,131	*Og*	2	qDTH-8				
22	M2	1	chr08	23,308,242	23,808,242	*Og*	2	qDTH-8	LOC_Os08g37490	OsGF14a	3	Liu et al. (2019)
23	M2	1	chr09	14,585,036	15,085,036	*Og*	3	QHd9, FLTQ3				
24	M1	2	chr09	19,597,853	21,078,706	*Og* and *Osj*	18	qHDD9-1, qDTH-9	LOC_Os09g33850	OsFTL4	3	Fang et al. (2019)
24	M1	2	chr09	19,597,853	21,078,706	*Og* and *Osj*	18	qHDD9-1, qDTH-9	LOC_Os09g34070	OsFPA	2	Mouradov et al. (2002)
24	M1	2	chr09	19,597,853	21,078,706	*Og* and *Osj*	18	qHDD9-1, qDTH-9	LOC_Os09g36220	OsPRR95	1	Murakami et al. (2005)
25	M2	2	chr09	22,453,022	22,953,023	*Og*	1	qDTH-9				
26	M1	3	chr11	3,400,294	3,922,487	*Osj*	1	dth11.1				
27	M2	1	chr11	23,361,713	23,861,713	*Osj*	2	QHd11				
28	M2	14	chr11	25,384,918	26,543,152	*Og* and *Osj*	1	hd11				
29	M2	4	chr11	26,942,125	27,922,719	*Og*	0					
30	M1	14	chr12	16,142,460	17,897,080	*Og*	12	dth12.1, QHd12				

Table 3 (continued)

Independent loci under selection						Genetic group involved	DTHD QTLs (2)		DTHD genes (3)			
N°	Type	Nb of SNP (1)	Chr	Start	End		Nb	Known name	MSU Identity	Name	GRP	Reference
31	M2	1	chr12	20,923,730	21,423,730	*Og*	4		LOC_Os12g34850.1	OsVRN5; OsVIL2	2	Wang et al. (2013)

RP heading time regulation pathway. (1) Photoperiod and circadian clock pathway, (2) chromatin-related pathway, and (3) hormones pathway. Type: M1 = Independent loci under selection detected under one detection method; M2 = Independent loci under selection including at least one locus detected to be under selection by the two detection methods implemented. *Og*: *O. glaberrima*; *Osj*: *O. sativa japonica* (1) Number of SNP loci under selection composing the independent loci; *chr* Chromosome; *DTHD* day to heading; (2) source http://www.gramene.org/; (3) see detailed data and references in S Table 7

relation with climate changes. For instance, the flowering time advancement was of seven days on average, for 43 common plant species of North America for a temperature rise of 2.5 °C, over some 150 years (Miller-Rushing 2008). It was of two days in a 22-generations resurrection experiment of the model legume *Medicago truncatula* (Gay et al. 2021), and of 5 to 10 days $°C^{-1}$, according to ecotypes, in *Arabidopsis thaliana*, under experimental conditions (Footitt et al. 2021). In comparison, the advance in DTHD of the *O. sativa* subpopulation *Osj-2* relative to *Osj-1* (3 days on average) was on the lowest side of the reported flowering time advancement.

Shorter growth cycle is a well-known evolutionary process to escape drought, especially during the most sensitive growth phases of meiosis and anthesis (Evans 1993). The advance in DTHD observed in *Og-2* and *Osj-2* subpopulations most probably corresponds to this process, helping the sensitive reproductive phases escape0 the higher drought risk of the end of the rainy season. This hypothesis is also supported by the fact that the shorter DTHD were observed in the two subpopulations *Og-2* and *Osj-2,* almost exclusively cultivated in the drought-prone upland or hydromorphic ecosystems, and not in the *Osi-2* subpopulation, cultivated in the lowland ecosystem, less prone to the effects of changes in rainfall regime. Unfortunately, the adaptive process of shorter growth cycle might have come to the detriment of grain yield potential, due to negative correlation between crop duration and biomass production (Hay 1995), though modern rice breeding programs have managed combining high yield potential and medium-short growth duration (Kush 1995).

Increase in temperatures, within the range of the observed 1 °C, also negatively affects rice grain yield (Chuang et al. 2017) due to an increase in maintenance respiration and to a decrease in grain formation (reviewed in Wassmann et al. 2010). Thus, overall, the changes in rainfall regime and the increase in temperatures observed in our study areas might have resulted in lower average rice yield, by triggering adaptive process that results in reduced biomass production.

Literature describing plant response to climate changes often refers to natural populations and distinguishes three types of responses: migration, temporary (reversible) adaptation through phenotypic plasticity and less reversible genetic adaptation (Franks and Hoffmann 2012; Gray and Brady 2016). When dealing with crop-species populations, one should also consider human (farmers) actions (selection) that can accelerate or slow down plant populations' natural responses. Farmers' actions can take the drastic form of replacement of the existing crop varieties or the more subtle form of selection among the standing diversity or among new diversity emerging from the mutation and/or recombination processes.

In our case, several facts argue against the hypothesis of replacement of the old rice landraces of long DTHD (*Og-1* and *Osj-1* subpopulations) by new exogenous rice varieties of shorter DTHD (*Og-2* and *Osj-2* subpopulations). (i) Penetration of improved *O. sativa* varieties, with shorter duration, in the slash-and-burn based upland rice cropping system of our study area was reported to be extremely limited (Barry et al. 2009) and no breeding program exists for the improvement and release of new *O. glaberrima* varieties. (ii) Distance based neighbour-joining tree did not show any structuring in relation with collect time. (iii) Genetic differentiation between *Og-1* and *Og-2* and between *Osj-1* and *Osj-2* was very low ($F_{ST} < 0.001$). (iv) The genetic diversity (nucleotide diversity and θ parameter) of the Collect-1 and Collect-2 subpopulations had the same order of magnitude. The two latter observations also argue for the fact that the combined human and environmental selection pressure has not given rise to the emergence of a few well-adapted individuals (i.e. shorter DTHD) colonizing the entire area of cultivation of *O. glaberrima* and *O. sativa japonica*. A more subtle selection/genetic adaptation process seems to have been at work, preserving the overall neutral genetic diversity.

According to the theory of genetic adaptation (Orr 2005), when a population is facing a novel environment, its potential for adaptive evolution is provided by the already present "standing genetic variation" or by de novo genetic variation arising during that bout of adaptation. In our case, while the occurrence of adaptive mutations cannot be excluded, their spread to a significant share of the *O. sativa* and *O. glaberrima* subpopulations is unlikely given the length of generation in rice (one year), the rather short interval (31 years) separating our two collect times and the rather low rate of outcrossing in rice. Indeed, the highest natural outcrossing rate reported is 6.8% in *O. sativa* (Sahadevan and Namboodiri 1963) and 5% in *O. glaberrima* (Oka and Morishima 1967). Analysing the distribution of rice genetic diversity at farm, village and ecosystem levels in Guinea, using SSR molecular markers, Barry et al. (2007b; c) reported that (i) rice landraces had a multi-line genetic structure; (ii) the within- and between-farm F_{ST} values were of the same order of magnitude; (iii) within-farm genetic diversity was high, i.e., up to 50% of total genetic diversity observed at the village level; (iv) each village pooled more than half of the regional allelic diversity; (v) regional allelic diversity was comparable to that noted worldwide for the Asian rice (*O. sativa*), but not as high for the African rice (*O. glaberrima*). Thus, one can consider that the *O. sativa* and *O. glaberrima* rice populations of our study area had had

the adaptive evolution potential needed to face the environmental and human selection pressure over the last 30 years. More generally, one can assume that *Og-1* – *Og-2* and *Osj-1* – *Osj-2* subpopulations are independent replicates of the evolutionary process, where migration had a negligible role.

Several methods have been proposed to investigate the role of selection, versus drift, in phenotypic changes between populations (Hansen et al. 2012). The temporal clean approach (Lande 1977; Goldringer and Bataillon 2004) we have implemented offers the advantage of using plant material in which the populations have actually adapted in contemporary times to changes in climate. However, the majority of the statistical methods detecting selection footprint were developed for outcrossing populations, and assumes random mating, making challenging the detection of loci under selection in predominantly selfing populations (Hartfield et al. 2017; Navascués et al. 2021). Indeed, given the extent of LD, selective sweeps in selfing populations can involve large genomic segments and hamper distinction of the genetic features between neutral and adaptive loci. Moreover, selfing can limit adaptation by slowing down pollen-based flow of beneficial variations, can increase drift by reducing the number of independent alleles sampled at reproduction, and can affect the dynamic of polygenic adaptation (reviewed in Hartfield et al. 2017). On the other hand, selfing can facilitate the detection of selective sweeps by reducing (i) the fixation times of beneficial alleles, exposing them faster to selection pressure (Charlesworth 1992) and (ii) the number of new effective recombinations, making it easier to detect sweeps (Smith and Haigh 1974). We implemented two genome scan methods, one assuming random mating (Excoffier et al. 2009) and another that introduces several modifications to the method proposed by Goldringer and Bataillon (2004) to take into account partial selfing (Navascués et al. 2021). The two methods identified several independent loci under selection, in both *O. glaberrima* (25 independent loci distributed on 11 chromosomes) and *O. sativa* (18, distributed on 8 chromosomes) groups, and all the loci, identified by the latter method to be under selection, were also identified as such by the former method, assuming random mating. These results suggest that gene flow and recombination were not the main genetic processes underlying the observed phenotypic adaptation, i.e. earlier flowering time. In other words, the outlier values of change in allele frequency in some loci, detected from the comparison of the observed and expected temporal genetic differentiation (F_{ST}), were mainly the result of selection among the pre-existing allelic combinations. The above-described multiline genetic structure of rice landraces and the rather large and imbricated genetic diversity of rice at the farm, village and region levels (Barry et al. 2007b; c) supports this hypothesis. In a given village, the multiline composition of a given landrace varies between farms, and the landrace can be considered as a meta-population the components of which are subject to farm-to-farm customary exchanges (Barry et al. 2007c). The same imbricated picture can be applied to groups of adjacent villages and farther. This setting of genetic diversity allows the environmental selection pressure to operate either directly (individuals plant/line with long DTHD fails to complete their life cycle when the rainy season ends earlier) or indirectly through farmers' selection of panicles bearing well-filled grains that will serve as seed for the next generation. Indeed, hand-picking of individual panicles is the most widely shared harvesting practice, in the slash-and-burn itinerant rice cropping system of our study area.

The 31 independent loci detected to be under selection were scattered among 11 chromosomes out of the 12 that compose the rice genome. Their length did not exceed 1500 kb (560 kb on average), save one case on chromosome 6 of *Osj*, composed of 45 significant SNP and extending over 4478 kb. Distance between these loci and their two adjacent SNP not under selection was around 50 kb on average and seldom went beyond the values at which the LD exceeded $r^2 = 0.2$. This almost absence of selective sweeps confirms the presence of the adaptive variants on multiple genetic backgrounds, well before the time *Og* and *Osj* populations undergone environmental selective pressure. The selective pressure has halved the heterozygosity rate of the loci under selection, already highly homozygous (> 98%), like all other loci not under selection. This adaptive process resembles the "evolutionary rescue" process in selfing plants described by Uecker (2017). However, in the case of *Og* and *Osj* populations, the variants were already, largely, in homozygous state, and the number of independent loci involved was quite high, 25 in *Og* and 18 in *Osj*.

Among the *ILUS*, a relatively small share (13% in *Og* and 17% in *Osj*) were in LD above $r^2 > 0.2$. This limited long-distance LD between the independent loci, on each chromosome and across chromosomes, testifies that, though polygenic, the adaptive process involved in *Og* and *Osj* did not translate into predominance of multilocus genotypes, as is often the case in selfing plants (Hartfield et al. 2017; Gay et al. 2021). Though rare in selfing populations, such a pattern of genetic basis of adaptation is in accordance with the complex polygenic genetic basis of the phenotypic adaptation involved, the DTHD. Indeed, the 31 *ILUS* showed significant enrichment in genes involved in the reproduction processes, and 29 of the loci could be connected to QTLs or genes (or both) involved in DHTD.

Rice is a short-day plant in which the heading date is regulated by a network of genetic components that can be organized into at least three pathways: photoperiod and circadian clock, chromatin-related pathway, and hormonal pathway (reviewed in Wei et al. 2020). Representatives of each of these pathways are present among the 15 DHTD genes we identified to be located on chromosome segments under selection (Table 3). For instance, *OsGI*, the orthologue of *GIGANTEA* in *A. thaliana*, is strongly involved in the circadian clock system and *Hd1*, the orthologue of *CONSTANCE* in *A. thaliana*, is a major photosensitivity gene in rice. Over-expression of *GI* triggers higher expression of *Hd1* and rapid flowering under any day length (Wei et al. 2020). *SDG711* and *SDG718* genes, involved in the chromatin pathway, also regulate the expression of *Hd1* and, thus, flowering in short days (Liu et al. 2014). *OsphyB* regulates the *Hd1*-mediated expression of the rice Florigen *Hd3a* and critical day length; its function in floral induction is not affected by the photoperiod (Takano et al. 2005; Ishikawa et al. 2011). *OsEMF2* (embryonic flower) gene belongs to the polycomb group proteins that play important roles in the epigenetic regulation of gene expression. Alteration of *OsEMF2* has pleiotropic phenotypic consequences including early flowering time (and even skipping the vegetative phase) even under long-day conditions, and abnormal flower organs (Luo et al. 2009). *OsGF14* is strongly induced by soil-drought stress and triggers the abscisic acid-dependent response pathway (Liu et al. 2019). It also acts as a negative regulator of flowering by interacting with *Hd3a* (Purwestri et al. 2009). Thus, the most probable underlying genetic bases of the observed DTHD responses to climate changes are subtle changes in the genetic network regulating rice DTHD and not the drastic turning off/on of one major gene. Given the number of genes involved, it would be difficult to extract the effects of individual genes, especially as the changes in the genetic network most probably vary from one rice landrace to another according to farms and villages.

The genetic bases of plant adaptations to environmental changes are often described in terms of soft and hard sweeps. In a mutation-limited world, recent adaptation leads to hard sweeps and leaves clear and well-understood footprints in genomic diversity (Hermisson and Pennings 2017). The complex footprints of selection due to climate changes (higher temperature, reduced rainfall and less predictive start and end of the rainy season) that emerges from our empirical study in rice does not seem to be covered by those models and calls for further model development. Implication of our finding for the development of crop varieties resilient to climate changes is the application of principles enunciated as early as the sixteenth century by Olivier de Serres (1600) "some level of intra-varietal diversity is guarantee for stability." Such stability requires moving from the conventional paradigm of creation of uniform and genetically stable cultivars toward evolutionary plant breeding (reviewed in Döring et al., 2011), i.e. crop populations with some level of genetic diversity capable of adapting to the conditions under which they are grown.

Abbreviations

ART	Annual rainfall total
Collect-1	Rice accessions collected in 1980
Collect-2	Rice accessions collected in 2010
DTHD	Days to heading date
F_{ST}	Fixation index, a measure of population differentiation due to genetic structure
GBS	Genotyping by sequencing
GSART	Annual rainfall total during the crops growing season
IL	Independent loci
ILUS	Independent loci under selection
LD	Linkage disequilibrium
M1 type	SNP detected to be under selection by one of the detection method implemented
M2 type	SNP detected to be under selection by the two detection method implemented
MAF	Minor allele frequency
N_e	Effective population size
Og-1	*O. glaberrima* Accessions collected in 1980
Og-2	*O. glaberrima* Accessions collected in 2010
Osi-1	*O. sativa indica* Accessions collected in 1980
Osi-2	*O. sativa indica* Accessions collected in 2010
Osj-1	*O. sativa japonica* Accessions collected in 1980
Osj-2	*O. sativa japonica* Accessions collected in 2010
T-Max	Average maximum temperature
T-Min	Average minimum temperature

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12284-023-00633-4.

Additional file 1: Fig. S1. Area and road map of the two collect campaigns of rice samples in Guinea. Adapted from Bezançon et al. (1983).

Additional file 2: Fig. 2. Pattern of deviation of the monthly rainfall during crop growing season (June–October), from the normal reference, during the 1961–2010 period, in Kankan (10°23′01.65″N, 9°18′18.72″W) and N'Zérekoré (7°48′53.2″N, 8°42′14.11″W) sites of Guinea.

Additional file 3: Table S2. Summary statistics and ANOVA of days to heading (DTHD) of rice accessions collected in 1980 (Collect-1) and in 2011 (Collect-2) and phenotyped in 2012 (Year-1) or 2013 (Year-2).

Additional file 4: Fig. S3. Unweighted neighbor-joining tree of simple matching distances constructed from genotypes at 1.130 SNP loci, for *O. glaberrima* (Og) *O. sativa indica* (Osi) and *O. sativa japonica* (Osj) groups. Accessions from the first collect time (Og-1, Osi-1 and Osj-1) are shown in black.

Additional file 5: Table S3. Molecular diversity and population parameters and relative importance of different diversity compartments revealed by AMOVA.

Additional file 6: Table S4. Variability of decay of pairwise linkage disequilibrium with distance between markers among the 12 chromosomes in five rice populations.

Additional file7: Table S5. Loci under selection detected by heterozygosity-base method (Excoffier et al. 2009) and by drift-based method (Navascués et al. 2020), in *O. glaberrima* (Og) and O. *sativa japonica* groups.

Additional file 8: Figure S4. Linkage disequilibrium between SNP loci under selection in *O. glaberrima* and *O. sativa japonica* (74 and 110 SNP loci respectively). Triangle above and below the bisectrix represent the r^2 and the r^2 *p* value respectively.

Additional file 9: Table S6. Detailed results of gene enrichment analyses using Agri-Go (Tian et al. 2017; http://bioinfo.cau.edu.cn/agriGO/) and Panther-GO (Mi et al. 2019; http://GeneOntology.org) enrichment analysis tools.

Additional file 10: Table S7. Presence of QTL and genes involved in days to heading (DTHD), on 31 chromosomic segments bearing the 31 independent loci under selection.

Additional file 11: Table S1. Passport data of the 530 rice accessions from the collected campaigns of 1979-82 and 2011, genotyped for the present study.

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Benefit-Sharing Statement
This work was undertaken in the framework of collaboration between scientists from IRAG- Guinea and Cirad-France. All collaborators are included as co-authors. The results of research have been shared with the provider communities through a number of meeting with farmers community and extension services. The aim of the present paper is to share the results with the broader scientific community. The rice accessions collected were sent to the Africa-Rice's gene-back for long-term conservation. In relation with this research, an IRAG young scientist (Mamadou Aminata TOURE, co-author of the present manuscript) spent one year in France for his Master degree in genetics & plant breeding.

Author contributions
NA and MBB conceived the study and assembled the rice accessions; JF produced the genotypic data. MAT produced the phenotypic data; MN Contributed to genome scan analysis; NA analysed the data and wrote the manuscript. All authors have reviewed the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials
Passport and phenotypic data of the rice accessions studied are provided Additional file 11: Table S1. Genotypic data can be downloaded in HapMap format from http://tropgenedb.cirad.fr/tropgene/JSP/interface.jsp?module=RICE study Genotypes, study type G-panel_GBS_data.

Declarations

Ethics approval and consent to participate
Doesn't apply.

Consent for publication
Doesn't apply.

Competing interests
The authors declare that they have no conflict of interest.

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