Inheritance of anther culture response in rice

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F_1 hybrids of a set of crosses involving the highly-responding *Japonica* cultivar, Taipei 309 and the three low-responding *Indica* cultivars, IR72, IR64, and IR54, as well as the parents were studied for their response to anther culture in terms of callus induction and plant regeneration frequency. Diallel analysis revealed the high-response in Taipei 309 to be governed predominantly by recessive alleles as against the low-responding *Indica* cultivars which were largely due to dominant alleles. Although it is difficult to suggest precisely the number of genes that control anther culture response, the study amply demonstrated that these traits followed quantitative mode of inheritance. Furthermore, our studies on the estimates of genetic components of variation for callus induction revealed that additive variance largely govern the response indices, suggesting thereby that transfer of the high callusing ability of Taipei 309 to low-responding genotypes by simple selection techniques should be feasible.

RESEARCH on anther culture in rice has generated large volume of information and material of basic and applied value over the past three decades. Nevertheless, exploitation of this technique in crop breeding and genetics research is hampered due to very low regeneration frequency of anthers of rice in general, and *Indica* cultivars in particular. Factors that restrict the use of anther culture to certain species/cultivars have been extensively reviewed recently[1]. Among them, influence of genotype is considered to be the most important in rice, as evidenced from inter-varietal and intra-varietal differences in anther culture response[1–3]. Research efforts on the enhancement of response to anther culture have, however, been confined mostly to manipulation/refinement of callus-induction and plant-regeneration protocols.

Earlier efforts to understand the genetics of anther culture response in some of the cereals including barley, wheat, maize, and rice revealed no consistency as the reported mode of inheritance varied from simple Mendelian to complex quantitative mode of inheritance[4–8]. Furthermore, the reports on number of genes or gene blocks that control anther culture response in rice is quite conflicting. Whereas Miah *et al.*[7] reported callus induction from anthers to be controlled by a single block of genes, Takeuchi *et al.*[9] opined involvement of two dominant genes governing callus induction, and plant regeneration. A recent report[10] on the molecular basis of anther culture response reveals the possible involvement of five quantitative trait loci (QTL) in the control of callus induction in the *Japonica* variety JX17, suggesting that the trait could be genetically as complex as the well-established quantitative traits, like yield. Since adequate information is lacking on the genetic control of callus induction and green plant regeneration from anthers, and also since inconsistency still persists on the nature and mode of gene action governing them, the present study was therefore, undertaken to elucidate further the genetic basis of anther culture response.

For the experimental studies four parents consisting of three low-responding *Indica* cultivars, viz. IR72, IR64, and IR54; and a high-responding *Japonica* cultivar, Taipei 309 were crossed in all possible combinations, including reciprocals. The material was evaluated in a randomized complete-block design with three replications. Anthers from these plants were plated for callus induction following the procedure described by Balachandran *et al.*[11]. The N6 basic medium[12] supplemented with 5% maltose, 2.0 mg/l 2,4–D, and 0.5 mg/l kinetin for callus induction; and MS medium[13] comprising 3% sucrose, 2.5 mg/l BAP, 0.5 mg/l kinetin, and 1.0 mg/l NAA for regeneration were used. Diallel analysis was carried out following Hayman's model[14,15] and heritability was estimated using the method of Mather and Jinks[16].

Analysis of variance showed highly significant differences among the parents and hybrids for callus induction (Table 1). The mean response to callus induction was higher in Taipei 309 (25.8%) than in the *Indica* cultivars, viz. IR72, IR54, and IR64 (Table 2). Likewise, F_1 hybrids with Taipei 309 as one of the parents also showed moderately high response compared to *Indica* x *Indica* hybrids. Similarly, in respect of plant regeneration, the F_1 hybrids having Taipei 309 as one of the parents invariably regenerated green plants at higher frequency than the *Indica* x *Indica* hybrids. The parents that yielded more calli exhibited a tendency to regenerate plants proportionately at higher frequency. Further, no significant reciprocal differences were observed among the hybrids for both the traits (Table 2).

The estimates of genetic components of variation for callus induction revealed the magnitude of D (additive genetic variance) and H_1 (dominance variance) to be

Table 1. Combined ANOVA for callus induction in 4 x 4 diallel cross

Source	DF	SS	MSS	F-value
Parents	3	1037.50	345.83	94.29**
F_1 hybrids	5	330.37	66.07	18.02**
Parent x F_1 hybrids	1	9.89	9.89	2.70
Replication	2	27.52	13.76	3.75*
Error	18	66.02	3.67	1.00

*, **Significant at 5% and 1% level of probability respectively.

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positively significant. As the D value was much higher than H_1, we can conclude that the additive component is predominant in the expression of the trait. This is in agreement with all the earlier reports that have associated callus response to both the additive component as well as the dominance component[7,8,17,18]. The observation that recessive and dominant alleles are possibly associated with both positive and negative effects, respectively, on callus induction (Figure 1), is in conformity with the findings of Imuta *et al.*[19]. Regression coefficient ($b = 1.24 \pm 0.27$), significantly different from zero but not from unity, is suggestive of the absence of epistasis as well as correlated gene distribution in the parents. Estimate of the mean degree of dominance over the loci ($H_1/D^{1/2}$) was less than unity (0.76), suggesting partial dominance. Relatively low (0.20) estimates of the ratio of negative to positive alleles, $H_2/4H_1$, indicates unequal distribution of alleles at the loci, exhibiting dominance in the parental genotypes. Although the positive sign of F suggests involvement of largely dominant alleles rather than recessive ones in controlling callus induction in the parents, it is implicit from high proportion of K_d/K_r (2.08) that the alleles responsible for high-callus induction were recessive. The estimated value of narrow sense heritability was high (70%), confirming further the major contribution of additive component to callus induction (Table 3).

Table 2. Relative anther culture response and reciprocal effects in intersubspecific hybrids*

Parents (P)/cross	Mean (%) Callus induction	Mean (%) Green plant regeneration
Taipei 309 (P)	25.80a	20.17a
IR72 (P)	5.97de	10.47b
IR64 (P)	2.77ef	2.50c
IR54 (P)	4.73ef	6.30bc
Taipei 309 × IR72	13.53b	4.33bc
IR72 × Taipei 309	12.50bc	5.27bc
Taipei 309 × IR64	9.27cd	6.73bc
IR64 × Taipei 309	10.90bc	4.67bc
Taipei 309 × IR54	10.57bc	4.70bc
IR54 × Taipei 309	10.63bc	3.77bc
IR72 × IR64	1.70f	0.0c
IR64 × IR72	2.70ef	2.10c
IR72 × IR54	4.33ef	0.0c
IR54 × IR72	2.67ef	0.0c
IR64 × IR54	1.93f	0.0c
IR54 × IR64	1.63f	0.0c
C.D. (5%)	4.55	7.78

*Mean of three replications; Means followed by the same alphabet are not significantly different at 5% level by DMRT.

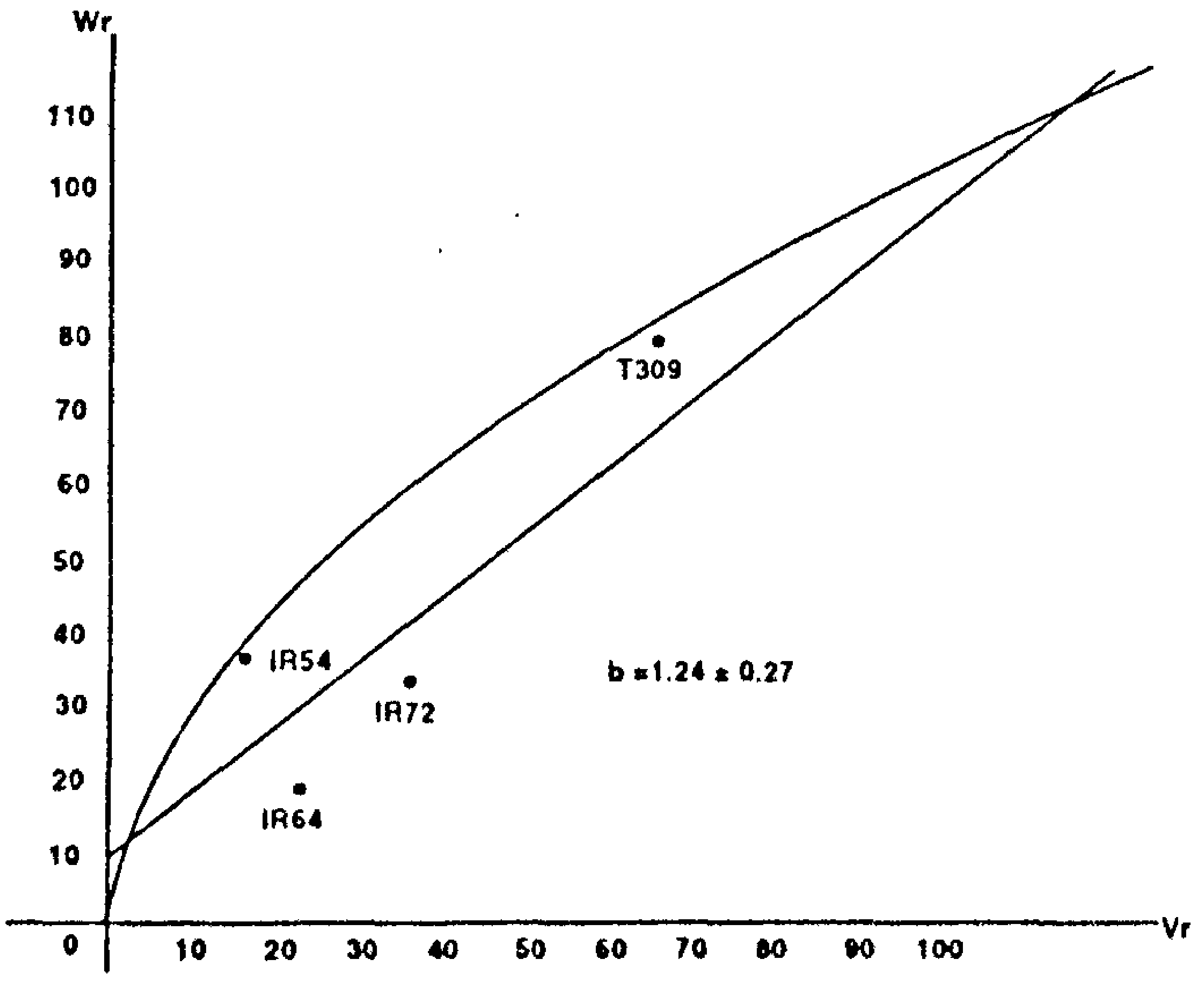

Figure 1. Graph of (Wr, Vr) for callus induction in 4 × 4 diallel cross.

The nature of gene action revealed that high-callusing ability is governed by recessive alleles, and that it would respond to selection as it is being governed predominantly by easily fixable additive component. By virtue of its being controlled by additive component, transfer of the high-callusing ability of Taipei 309 to low-responding *Indica* genotypes by adopting simple selection techniques should be feasible, as has been demonstrated in barley[20].

In one of the crosses, viz. Taipei 309 × IR64, anther culture response of 50 randomly selected F_2 plants was compared with the F_1 plants, and a continuous variation was observed, showing skewness either on the low or high-response direction in the F_1 itself. The frequency distribution of plants varying in callus-induction response was near normal in the F_2, encompassing the range of both high-response parents as well as the low-response ones, and the skewness showed a tendency towards low-response parents (data not shown). Because of the failure to fit the data on the different response groups into possible oligogenic Mendelian ratios, and also because the distribution pattern showed higher number of plants in the F_1 and F_2 generations falling in the low-response

Table 3. Estimation of genetic and environmental components of variation for callus induction in 4 × 4 diallel cross

Component	Estimated value ± SE
D (Additive)	113.91 ± 10.31**
H_1 (Dominance)	66.42 ± 29.96*
H_2 (Dominance)	52.52 ± 27.65
h^2 (Dominance)	2.06 ± 18.76
F (Additive, dominance, gene asymmetry)	61.09 ± 26.48*
E (Environmental)	4.61 ± 1.37
Proportional values	
[$H_1/D^{1/2}$]	0.76
[$H_2/4H_1$]	0.20
[K_d/K_r]	2.08
Heritability (ns)	0.70

*,**Significant at 5% and 1% probability levels respectively.

range, the data is not only indicative of the typically quantitative nature of the trait but also confirms the recessive nature of genes that control anther culture traits. Thus, the findings of present study as well as reports from both conventional and molecular studies stress further, the involvement of complex quantitative mode of inheritance governing anther culture traits. But, in-depth study using molecular tools is warranted to understand still more precisely the number of genes involved and their nature of control of anther culture response.

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Palaeomagnetism of Deccan Traps from the Killari borehole flows

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Borehole drilling in Deccan Traps at the Killari village, Latur District, Maharashtra, revealed nine Deccan Trap flows with a thickness of 338 m resting over a Precambrian basement. A palaeomagnetic study of drill core samples from these flows using laboratory AF and thermal demagnetization methods revealed downward pointing magnetic inclinations with a mean value of + 56.3°. This suggests that these flows were erupted during a reverse polarity period of the geomagnetic field. The mean magnetic inclination of these flows is equal to the reported inclination of the eastern and south-eastern part of the Deccan Traps. From this correlation it appears that most of the Deccan Traps in the region were poured out at the same time supporting the suggestion that the Deccan flood basalts were erupted in a very short period of time.

THE Deccan Traps occupying an area of half a million square kilometers in the western part of peninsular India constitute a single geologic unit, the palaeomagnetism of which was well studied. Several geochronologic results were also reported on these rocks giving the most probable age for the eruption of these flood basalts. Vandamme *et al.*[1] summarized the palaeomagnetic and geochronologic data of several flows of the trap country and made the following important inferences. Only two field reversals of the geomagnetic field occurred with a chron sequence of N–R–N. About 80% of the flows were poured out during the reverse chron which was correlated with Chron 29 R. Most of the Deccan Traps were poured out in a very short period of time (less than one million years). The Ar/Ar dating of the Deccan Traps assigns an absolute age of 65.5 ± 2.5 Ma for the volcanic eruption.

The large magnitude earthquakes ($M > 6.0$) at Koyna (1967) and Latur (1993) point towards a relatively enhanced level of seismotectonic activity of the Deccan Volcanic Province (DVP) in the Indian shield which is otherwise considered to be a stable region. With a view to understanding the configuration and structure of the basement, several boreholes were drilled jointly by NGRI and AMD in the Deccan Traps near Killari village (18°03′07″N, 76°33′20″E), the site of the 30 September 1993 earthquake. We have carried out palaeomagnetic investigation of the Deccan Trap flows encountered in the borehole about 2 km north-west of the Killari village to find out only the magnetic polarity. This is a unique opportunity to study a vertical sequence in the region.

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Results of this investigation are presented in this communication.

Deccan Traps around Latur, Maharashtra, reveal atleast 12 different flows with gentle gradient[2]. Borehole drilling at Killari village revealed a Deccan Trap thickness of 338 m underlain by a basement consisting of peninsular gneiss and an intervening 8 m thick infra-trappean sequence[3]. A detailed chemical stratigraphic study by Jaffri *et al.*[4] of samples from four boreholes near Killari identified nine flows – a top set (thickness 174 m) consisting of four subsurface flows and a partly eroded one at the surface and a bottom set of four flows (thickness 160 m) separated by a 4 m thick red-bole horizon. Thickness of these flows ranges between 15 and 75 m. These are correleated with Ambenali and Poladpur formations, respectively on the basis of minor, trace and isotope geochemical criteria. These basaltic flows are porphyrytic medium to fine grained rocks with minor alteration effects. Phenocrysts are either plagioclase or clinopyroxene at times seen as clusters. Magnetite is the main opaque mineral occurring as euhedral specks, needles, well developed tabular and skeletal grains. Two generations of magnetite are inferred from the petrographic studies on these flows. The magnetite content varies from 3–4% to 10%.

Five to eight drill cores covering the entire thickness of each flow encountered in the borehole were obtained and the top and bottom were marked. Vertical cores of 2.5 cm diameter and 5 to 8 cm length were drilled from each drill core. From each core 2–3 specimens of 22 mm length were cut. A total of 117 cylindrical specimens were prepared from the 55 samples.

Natural Remanent Magnetism (NRM) of the specimens was determined with reference to an arbitrary line drawn on the core as there is no bearing of the N–S line and there is every possibility for the core to rotate during drilling. The measured inclinations of all the specimens are downward and steep. Remanent intensity (J_n) and susceptibility (K) were also measured and the Koenigsberger ratio (Q_n, ratio of remanent to induced intensity in a field of 0.05 mT) was computed. These are listed in Table 1. The stability of the magnetic inclination in these specimens was studied using both AF and thermal demagnetization methods on a pilot basis. Two specimens from each flow were subjected to progressively increasing peak fields of 2.5, 5, 10,15, 20, 30, 40, 50, 60, 80 and 100 mT and remanent magnetism measured after each step of demagnetization. Similarly, one specimen from each flow was also subjected to thermal demagnetization in steps of 100, 200, 300, 400, 450, 500, 540, 580 and 600°C and the remanent magnetic vector measured after cooling to room temperature. The specimens exhibited extreme stability of the remanent vector during both these tests revealing the stable magnetic inclination in these rocks. After removal of weak viscous components at lower alternating magnetic fields (5 mT) and temperatures (200–300°C), the vectors exhibit the characteristic component. Typical examples of behaviour of these rocks to these pilot tests are shown as Zijderveld diagrams in Figure 1. On the basis of results of these tests, atleast one specimen from each core of all the samples was demagnetized at either 15 mT AF field or a temperature of 400°C to recover the stable magnetic inclination. Magnetic inclinations of all the specimens studied were averaged to get the flow-wise mean inclinations for all the flows encountered in the Killari borehole and listed in Table 1 along with other properties investigated.

The flow mean magnetic inclinations obtained by detailed laboratory demagnetization studies vary between + 64.5 and + 49.3. Only one flow registered a low value of + 37.8 which is not considered in evaluating the mean magnetic inclination of these flows. The Koenigsberger ratio of these rocks varying between 0.92 and 10.53 indicates the stable nature of the remanent magnetic vector in them[5,6]. Thus, the Deccan Trap flows encountered in the borehole drilled at Killari reveal a mean magnetic inclination of + 56.3. This mean inclination is very similar to the mean inclination reported for the

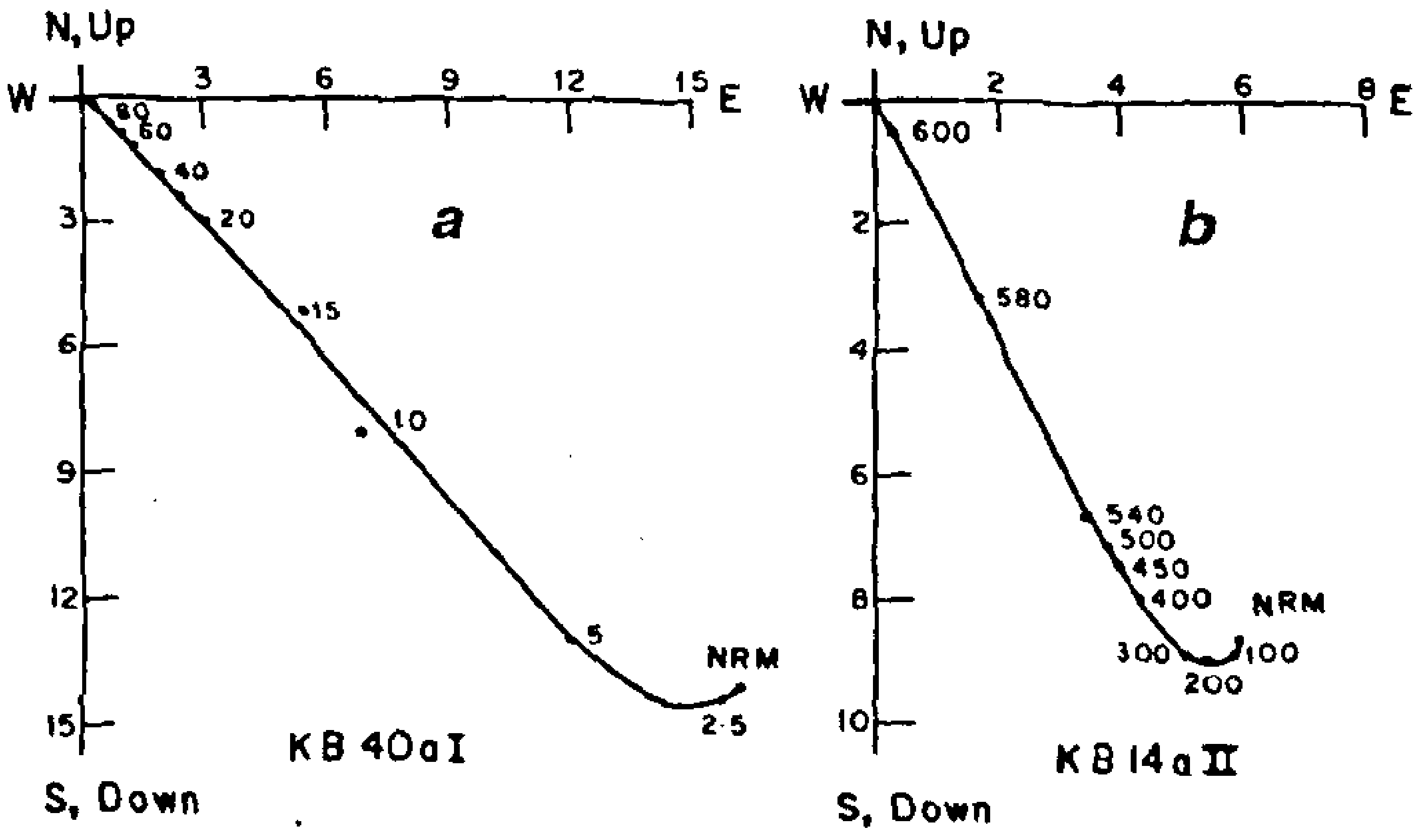

Figure 1. Response of Killari borehole basalt flows to AF and Thermal demagnetizations. Typical Zijderveld plots depicting the vector behaviour to (*a*) AF and (*b*) thermal treatment during a pilot study. These are plots of the vector on N–S vertical plane. Numbers are peak AF fields in (*a*) and temperatures in (*b*). Intensity is in A/m.

Table 1. Palaeomagnetic and magnetic properties of Deccan Traps from Killari borehole basalt flows

Flow	*N*	*n*	I_m	J_n A/m	*K* $10^{-3} \times$ SI	Q_n-ratio
1	5	12	+ 64.5	6.57	1.20	10.53
2	5	12	+ 62.5	8.37	2.94	5.22
3	5	10	+ 63.9	2.90	2.34	7.26
4	5	11	+ 61.6	2.81	2.54	2.90
5	5	10	+ 59.5	5.01	1.59	7.00
6	8	17	+ 51.2	2.46	2.32	2.19
7	6	17	+ 56.7	1.31	3.17	0.92
8	6	12	+ 49.3	1.93	1.68	2.72
9	7	16	+ 37.8	2.02	1.91	2.21
Mean	–	–	+ 56.3	3.61	2.19	4.56

N = Number of samples; *n* = Number of specimens; I_m = Mean inclination; J_n = NRM intensity; *K* = Susceptibility; Q_n = Koenigsberger ratio.

Deccan Trap flows from other places (see Table 2) and corresponds to a reverse magnetization in the southern hemisphere acquired at the time of their eruption.

Palaeomagnetic data of the Deccan Traps from some sites[7–17] are examined to see whether there is any similarity with the mean remanent magnetic inclination observed in the subsurface flows encountered in the borehole at Killari. These sites include Buldana, Aurangabad, Ellora, Amaravati, Harsul, Jalna, Lonar, Nagpur, Durgada, Umrer, Dongargaon, Kurdwadi, Latur, Gulbarga, Chincholi and Vikarabad (Figure 2). Palaeomagnetic data reported from these sites are given in Table 2. It is evident from the data that the Deccan Traps exposed at all these sites are reversely magnetized. This corresponds to a reverse magnetic direction during early Tertiary period when the Indian subcontinent was in the southern hemisphere. The mean magnetic inclination of these flows is between + 31 and + 62. The remanent magnetic inclination (+ 56.3) corresponding to a reverse magnetization observed in the vertical sequence of nine flows in the Killari borehole is also similar to these mean inclinations. From this comparison it is evident that the Deccan Traps at all these places in the central, eastern and south-eastern regions were erupted more or less during the same period when the geomagnetic field was reversed.

Table 2. Remanent magnetic data of Deccan Traps from some sites

Locality	Latitide N	Longitude E	D_m°	I_m°	Reference
Buldana	20°31′	76°18′	149	+ 53	7
Aurangabad	19°54′	75°24′	150	+ 48	8
Ellora	20°06′	75°18′	158	+ 53	9
Akola	20°40′	77°05′	164	+ 48	10
Amaravati	20°58′	77°50′	179	+ 31	10
Harsul	19°54′	75°24′	186	+ 61	11
Jalna	19°54′	75°54′	160	+ 46	12
Lonar	19°59′	76°34′	136	+ 42	13
Nagpur	21°10′	79°12′	149	+ 54	10
Durgada-Umrer	20°36′	78°45′	148	+ 53	14
Dongargaon	20°31′	79°12′	155	+ 54	10
Kurdwadi	18°15′	76°00′	165	+ 42	15
Latur	18°24′	76°31′	154	+ 50	16
Gulbarga	17°18′	76°56′	145	+ 58	17
Chincholi	17°29′	77°28′	153	+ 62	17
Vikarabad	17°20′	77°00′	140	+ 60	17

D_m = Mean declination; I_m = Mean inclination.

The magnetic polarity in the Deccan Traps was used as a tool in stratigraphic classification of flows at several places. Several suggestions were made in the past with regard to the division of the Deccan Traps on the basis of record of the geomagnetic field reversals in them. The Deccan Traps are considered to decrease in age from east towards the west and those along the fringes are the earliest phases of eruption, making them older than the western flows[18]. A number of proposals were made with regard to their stratigraphic classification on the basis of their magnetization. As many as 5 to 7 reversals of the geomagnetic field changes were reported in Deccan Traps and correlated the flows from several regions[14,15,19–22]. In view of the available reliable Ar/Ar dating results on Deccan Traps it is probable that these traps recorded 2–3

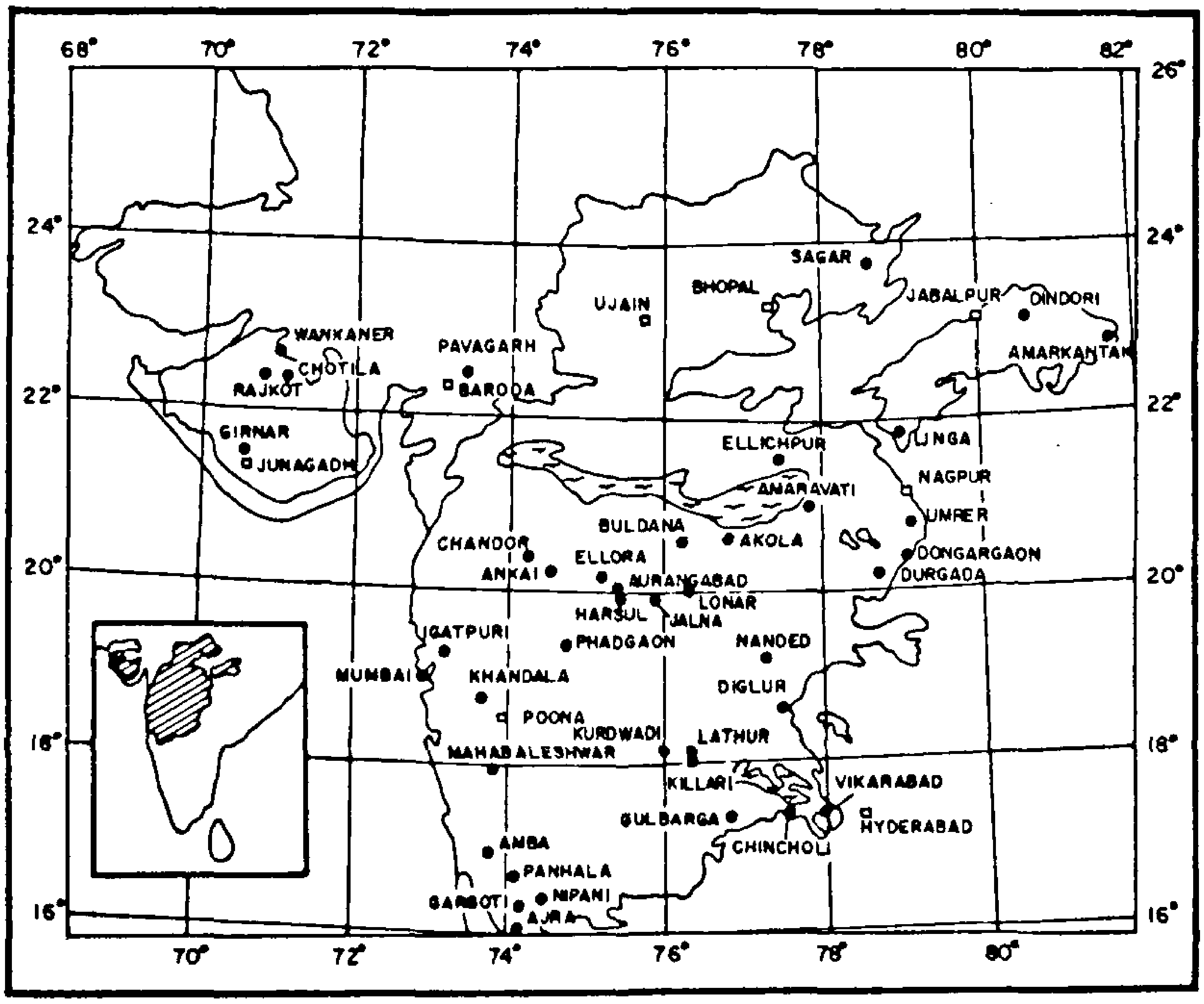

Figure 2. Geological map of Deccan Traps showing the sites from where palaeomagnetic studies were reported along with the location of the borehole drilling site at Killari village, Latur District, Maharashtra.

reversals of the geomagnetic field during their eruption. Courtillot *et al.*[10] and Vandamme *et al.*[1] notice that about 80% of the Deccan Traps were reversely magnetized with a chron sequence of N–R–N at the K–T boundary. They further argue that this reverse chron is Chron 29 R and the most active phase of Deccan volcanism lasted for a period of approximately one million years. In such a situation the subsurface flows encountered in the borehole at Killari with their reverse magnetization resting above the Precambrian basement located in the S–E fringes might represent the earliest eruptions of the Deccan flood basalts along with other flows in the central, eastern and south-eastern regions of the Deccan Traps. This might also mean that the older flows belonging to the Narmada Normal epoch[22] are missing or did not erupt in the Killari region.

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Probabilities of occurrence of great earthquakes in Himalaya

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The long-term conditional probabilities of occurrence of great earthquakes along the Himalaya plate boundary seismic zone have been estimated. The chance of occurrence of at least one great earthquake along this seismic zone in a period of 100 years (beginning with the year 1999) is estimated to be about 0.89. The 100-year probability of such an earthquake occurring in the Kashmir seismic gap is about 0.27, in the central seismic gap is about 0.52 and in the Assam gap is about 0.21. The 25-year probabilities of their occurrence are 0.07, 0.17, and 0.05 for the Kashmir, the central and the Assam seismic gaps, respectively. These probabilities will serve in the assessment of the seismic hazard in the Himalaya and the adjoining Ganga plains.

THE Himalaya have risen out of a process involving fracturing and stacking of rocks over a period of long geologic time. The occurrence of great earthquakes is inherent in such a process. Although the historical evidence is quite incomplete, a number of such earthquakes in this region have been recorded since 1250 BC[1]. In the most recent sequence four great earthquakes have ravaged the Himalaya: 1897 in Assam, 1905 in Kangra, 1934 in Bihar–Nepal, and 1950 in Assam taking a toll of over 30,000 human lives and causing heavy economic losses (Figure 1). As the relative convergence of India and Eurasia, which provides the energy released in the earthquakes, is continuing unceasingly, similar great earthquakes are expected to occur in the future also. In order to assess the seismic hazard from such earthquakes we estimate the probabilities with which they are likely to occur in various sections of the Himalaya in a given interval of time in the future. We also estimate the combined probability of the occurrence of one or more such earthquakes in any section of the Himalaya.

We employ the time-predictable model of earthquakes to obtain the probabilities. The model envisages that strain builds up in a steady manner in a fault zone under a geodynamical process. After the same is released by an earthquake, the recovery of strain begins preparing the region for the next one to occur. The probability of occurrence of the next strain-relieving earthquake on a particular fault segment is proportional to the time elapsed since the last one[2,3]. That such a process is operative in the Himalaya has been shown by the analysis of the repeat levelling data on the Saharanpur–Mussorie profile[4].

The active tectonics in Himalaya is imaged by the earthquakes occurring there. An arcuate belt of moderate-