

From eq. (6) it is clear that the magnetic field may be obtained by carrying out the same numerical calculations as those needed for the gravity field, except that $(-G\sigma)$ needs to be replaced by $(C_m\sigma)$. Therefore, the same computer code can be used for computing the gravity and magnetic fields separately or simultaneously.

Keeping the geometry and physical properties same as above, the Poisson's relation¹⁴ which is commonly used for the transformation of gravity to magnetic anomalies may be given as,

$$H_x = \frac{M}{G\rho} \sum_i \frac{\partial F_{xi}}{\partial I}, \quad (7)$$

where M is the intensity of magnetization and I is the direction of magnetization.

It is interesting to note that the new relation derived between gravity and magnetic field components (eq. (6)) differs from the well-known Poisson's relation (eq. (7)). The new approach provides a direct relation between the corresponding field components, whereas Poisson's approach gives a relation between the components of magnetic field to the gradient of the gravitational attraction in the direction of magnetization. It is apparent therefore that the new algorithm is computationally more efficient in the transformation of gravity field components to the magnetic fields and vice versa.

A new relation is derived between the components of the gravity and magnetic fields resulting from an arbitrary three-dimensional object bounded by plane polygonal facets having uniform volume density and magnetization. Gravity and magnetic field components have been expressed as the field due to an equivalent distribution of surface mass-density and surface pole-density over the bounding surface of the source body. This facilitates construction of a unified algorithm for the computation of gravity or magnetic anomalies separately or simultaneously. This algorithm will substantially simplify and speed-up the numerical modelling of gravity and magnetic anomalies and may find wide applications in the joint inversion of potential field data. The gravity field can be computed at all points, including points on the surface of the body or at any of its corners. However, the magnetic field has a singularity at the corner. Our formulation does not require coordinate transformation, as with all previously published schemes. It appears to be computationally efficient compared to the well-known Poisson's relation normally used for the transformation of one field to another.

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ACKNOWLEDGEMENTS. We thank the Director, National Geophysical Research Institute, Hyderabad for his kind permission to publish this work.

Received 16 February 2001; revised accepted 7 November 2001

Differential influence of pollen and stylar genotypes on lifespan of pistillate flowers in a monoecious herb, *Momordica tuberosa* (Cogn.) Roxb. (Cucurbitaceae)

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The floral lifespan of pistillate flowers of *Momordica tuberosa* is terminated by abscission of petals, intentionally, when they are still fully turgid within sixty-five minutes following their pollination; the staminate flowers do not abscise their petals, but progressively wilt. Petal abscission was found to depend on the type of pollination: hand pollination using out-cross pollen induced an early petal abscission than the self-pollen (geitanogamy). At least six pollen grains were critical to initiate successful petal abscission in freshly-bloomed flowers, below which the petals did not abscise even at the end of the day. There exists a quantitative relationship between the number of pollen grains deposited onto the stigma and the time taken for petal abscission; greater the pollen grain deposition, quicker the rate of abscission. The time required to induce petal abscission seems to be controlled by pollen genotype, genotype of pollen recipient and the interaction between the two. By invoking the theory of sexual selection it is explained that strategies of pollen genotype and those of stylar genotype may not always coincide,

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while shaping the rate of petal abscission. The adaptive significance of this phenomenon has been discussed.

ABSCISSION of petals following pollination has been documented in a few angiosperms¹⁻⁸. Based on the nature of petal abscission, angiosperms have been grouped into: (a) those showing gradual physiological changes in their petals such as loss of turgor, degradation of corolla cells and finally wilting; and (b) those in which the lifespan of the flower is terminated by abrupt abscission of the petals when they are still fully turgid^{7,9}. A few workers have documented the differences in the rate of corolla abscission in response to self- and cross-pollination^{6,10,11}; petal abscission has also been investigated as a function of number of pollen grains deposited on the stigmatic surface⁶. However, the mechanism of pollination-induced petal abscission is not clear; a few workers have ascribed this to hormonal synthesis^{1-4,6,8,12}.

Petal abscission in plants has been viewed as being adaptive^{7,11}. It might help in (a) minimizing superfluous visits of pollinators to already pollinated flowers; (b) diverting pollinators to receptive and rewarding flowers thereby leading to a greater floral residence time and effective pollination¹³; (c) reducing the visibility of pollinated flowers to floral predators which might take the same cues as that of pollinators¹⁴.

However, there could be potential costs associated with floral abscission¹¹. For instance, premature petal abscission might shorten the length of the active phase of a flower, and consequently opportunities to increase progeny variability as well as mate choice might reduce. Therefore, flowers must remain functional until they receive sufficient pollen grains to ensure maximum seed set and generate ample progeny variability, such that they contribute ultimately towards plant fitness. In fact, it has been demonstrated that pollen grains strongly influence the rate of petal abscission¹¹. It is likely that different pollen sources may have different effects on the floral lifespan following their deposition onto the stigma¹¹. A pollen genotype which initiates an petal senescence might eliminate the potential competition to sire ovules from conspecific pollen sources. We are not aware of any studies focusing on this possibility, specially among self-compatible species. *M. tuberosa*, a wild monoecious cucurbit, offers a good opportunity to test some of these issues.

We report here the results of the experiments designed to know whether (i) there is a threshold pollen load required to initiate successful petal abscission; (ii) pollen donors differ in their ability to induce petal abscission, and (iii) pollen donors and recipients interact in shaping the effective lifespan of pistillate flowers.

The study was conducted at Raichur (16°15'N; 77°20'E; 389 m above msl), Karnataka, India.

M. tuberosa Cogn. (Cucurbitaceae) (syn. to *Luffa tuberosa* or *Momordica cymbalaria*) is a monoecious, self-compatible, insect-pollinated (generally bees), tuber-forming perennial herb. It colonizes the fallow and cultivated alluvial soils of arid regions of southern India. Many scandent branches radiate from the underground tuber. Both primary and secondary branches bear at each node, either male (in 2- to 5-flowered racemes) or female (solitary) flowers¹⁵. The yellowish staminate flowers are large ($N=74$; $X=2.05 \pm 0.03$ cm) and are distinguishable from the pistillate flowers ($N=64$; $X=1.41 \pm 0.02$ cm; t test significant at $P<0.01$) by having a dark yellow spot at the base of the petals. The ovary contains five to six ovules arranged linearly. *Momordica* plants exhibits male-biased sex ratio (defined as number of male flowers per female flower)^{16,17}.

Pistillate flowers of *M. tuberosa* possess five petals arranged in imbricate aestivation and are found to abscise them following pollination, when they are still fully turgid. Petals of pollinated flowers abscise abruptly within sixty to seventy minutes, while those of bagged or unpollinated flowers remain fresh throughout the day. Pistillate flowers which do not abscise their petals will not develop into fruits; instead they gradually fade and drop-off. Staminate flowers do not abscise their petals, but gradually wilt and drop-off (personal observations).

Bagged pistillate flowers on naturally-occurring plants ($N=28$) were hand-pollinated using the pollen obtained from the male flowers borne on the same plant or on different plants, collected at random, to effect self- or cross-pollination respectively, in the early hours of the day (6.00 to 9.00 h). Lifespan of pistillate flowers was recorded as the duration, in minutes, taken by individual flowers to abscise at least one petal from the time of pollination.

The number of pollen grains that had deposited and germinated on the stigmatic surface was counted from flowers that had abscised their petals and from those in which petals were intact at the end of the day, under natural conditions. The stigma were observed under an epifluorescence microscope after staining with aniline blue¹⁸.

To study the effect of the number of pollen grains on the stigmatic surface and the rate of petal abscission, fresh pistillate flowers were pollinated with a known number of pollen grains (for instance, one, two, three, four, ... etc.) derived from known donors by careful observation under a dissection microscope. The time taken for abscission of petals was recorded after pollen deposition.

Pistillate flowers of six plants maintained in greenhouse condition (collected from locations separated by over 5 km) were pollinated with abundant pollen in a diallele fashion, such that all plants were used as pollen

Table 1. Time taken for petal abscission, in minutes, following self- and cross-pollination in *M. tuberosa*

Type of pollination	No. of flowers pollinated	Time to abscise petal mean \pm SE	<i>t</i> test
<i>Natural habitat</i>			
Self	60	68.77 \pm 1.01	$t = 3.07; df = 168; P < 0.005$
Cross	110	64.97 \pm 0.73	
<i>Greenhouse condition</i>			
Self	134	56.59 \pm 0.70	$t = 4.28; df = 559; P < 0.001$
Cross	427	53.56 \pm 0.33	

KS test. Natural habitat – $d_{max} = 0.22; \chi^2 = 7.512, 0.05 > P > 0.02; df = 2$; Greenhouse condition – $d_{max} = 0.23; \chi^2 = 7.008, 0.05 > P > 0.02; df = 2$.

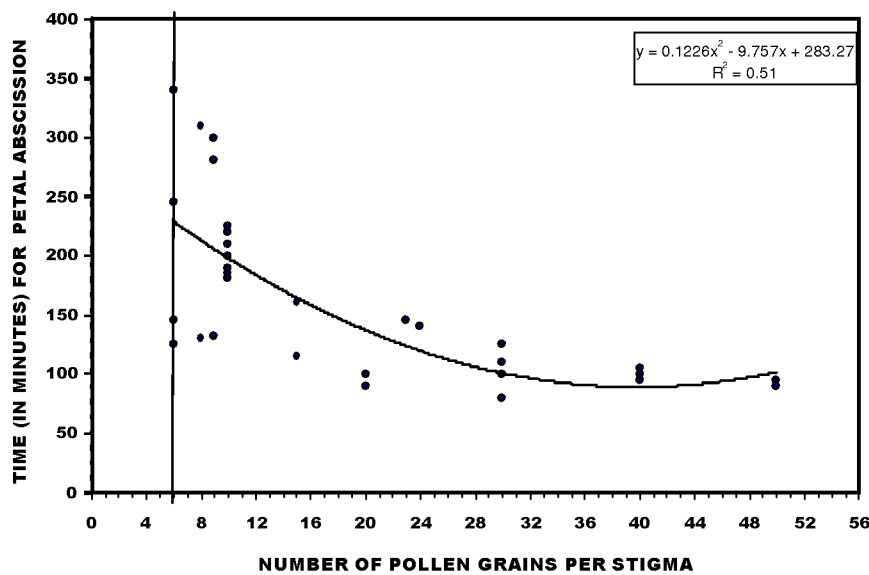


Figure 1. Pollen load on stigmatic surface vs time for petal abscission. Flowers receiving less than six pollen grains did not abscise their petals even at the end of the day. Therefore, the points are not plotted (the line indicates this critical pollen grain number).

donors as well as pollen recipients. Mean time taken for petal abscission was subjected to Two-way ANOVA with donor, recipient and donor \times recipient interaction as sources of variation.

The means were compared using Student's *t* test and difference in frequency distribution was compared by Kolmogorov–Smirnov test (KS test)¹⁹.

The rate of petal abscission in pistillate flowers of *M. tuberosa* was found to depend on the type of pollination and pollen load on the stigmatic surface (Table 1; Figure 1). Flowers receiving cross-pollen grains abscised their petals significantly earlier, by five minutes under natural conditions and by a little over three minutes under greenhouse conditions, to those receiving self-pollen (Table 1).

Controlled pollination with known number of pollen grains indicated that pistillate flowers receiving less than six pollen grains did not abscise their petals even

at the end of the day (Figure 1). This suggests that a threshold number of six pollen grains is necessary to initiate successful petal abscission. Further, the time required for petal abscission reduced with the number of pollen grains deposited on the stigmatic surface (Figure 1). The variation in the time required for petal abscission was higher when a fewer pollen grains were deposited, than when the number of pollen grains deposited was more. Under natural conditions too, pistillate flowers, which had their petals intact even at the end of the day, possessed, on an average, around six pollen grains on their stigma (of which only 24 per cent were germinated; Table 2). Over 70 per cent of the flowers had captured less than 10 pollen grains on their stigma under natural conditions (Figure 2), whereas flowers that had their petals abscised at the end of the day possessed around 35 pollen grains, of which 78 per cent were germinated (Table 2).

Table 2. Number of pollen grains deposited, germinated on stigma and petal abscission in natural habitats

Whether or not petals abscised at the end of the day	Petals abscised	Petals not abscised	t test
Number of stigma examined	41	44	
Number of pollen grains deposited per stigma	35.36 ± 5.01	6.67 ± 1.12	t = 9.30; df = 83; P < 0.001
Number of pollen grains germinated per stigma	22.85 ± 2.27	2.84 ± 0.69	t = 8.75; df = 83; P < 0.001
Per cent pollen grains germinated per stigma	78.50 ± 3.28	24.03 ± 0.69	t = 15.55*; df = 83; P < 0.001

*Computed for angular transformed values.

KS test for pollen deposition: $d_{max} = 0.66$; $X^2 = 37.38$; $df = 2$; $P < 0.001$.

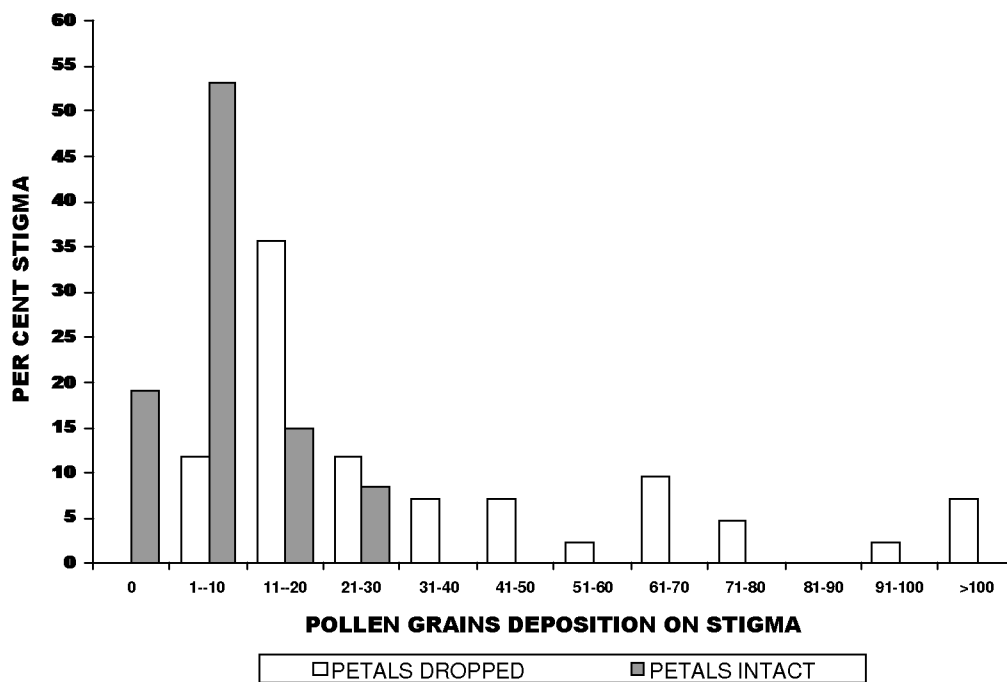


Figure 2. Number of pollen grains deposited on stigma in flowers with their petals intact and petals abscised in their natural habitat (KS test: $d_{max} = 0.66$; $P < 0.01$).

Table 3. Two-way analysis of variance of mean time required for petal abscission

Source	df	MSS	F-ratio	Significance
Recipient	5	979.95	34.85	P < 0.001
Donor	5	133.43	4.75	P < 0.01
Recipient × donor	25	46.42	1.65	P < 0.05
Error	209	28.12	-	

CD for recipients @ P = 0.05 is 2.30; CD for donors @ P = 0.05 is 2.30; CD for interaction @ P = 0.05 is 5.64.

Six genotypes involved in the crossing programme differed significantly with respect to the mean time taken for petal abscission when self-pollinated (Figure 3; F value = 34.85, df = 5; 209; P < 0.001). Their effect on petal abscission time was also significant, both as pollen donors and as recipients (Table 3). The significant interaction term in the ANOVA suggests that the

effect of pollen donor genotype on mean time taken for petal abscission is not independent of the pollen recipient genotype (Table 3).

Cross-pollination induced early petal abscission than did self-pollination (viz. geitonogamy, since pollen grains from different flowers of same plants were used in pollination) in *M. tuberosa*. This result is in line with those established by Gilissen⁶ and Linskens¹⁰. Working with a self-incompatible species, *Campanula rapunculoides*, Richardson and Stephenson²⁰ also have shown that cross-pollination induced early flower senescence while self-pollination did not affect floral lifespan. In a particularly autogamous *Portulaca umbraticola*, self-pollination, contrary to the present study, shortened flower lifespan in comparison with either cross-pollination or absence of hand-pollination¹¹.

Consequent to abscission of petals only in pistillate flowers, the Operational Sex Ratio (defined as number

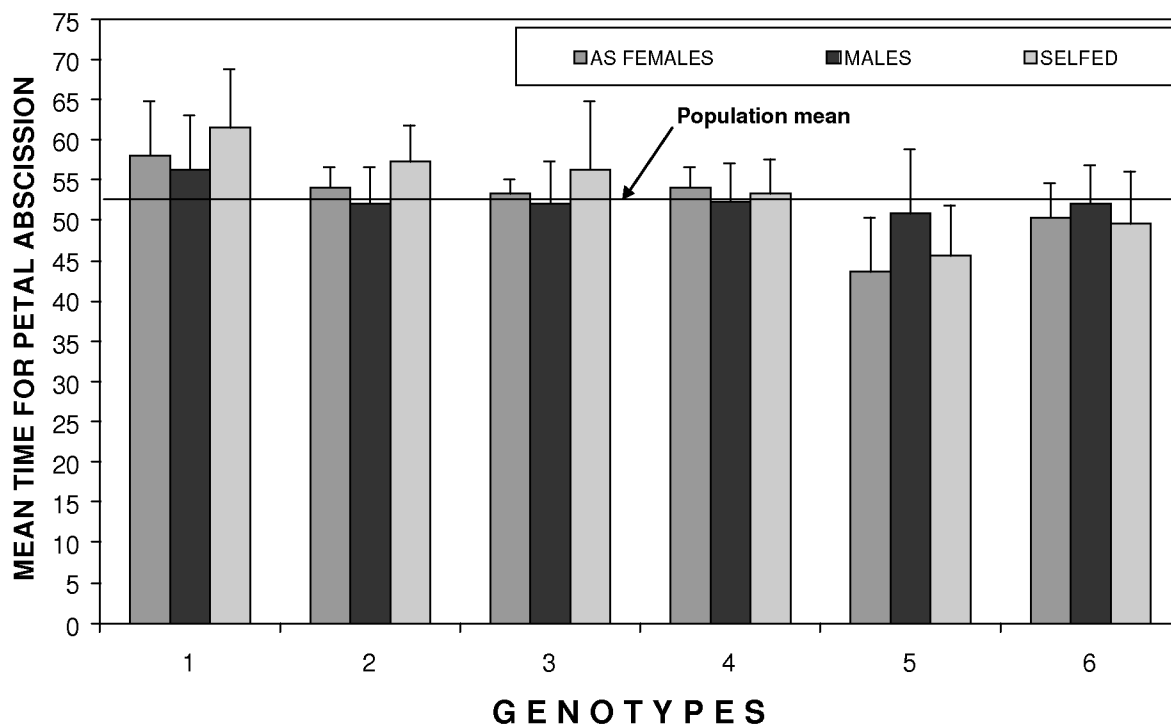


Figure 3. Mean time taken for petal abscission by genotypes when they were used as (i) pollen recipients, (ii) pollen donors, and (iii) when they were selfed.

of bloomed male flowers to female flowers in a day in a defined area) in *Momordica* will be altered¹⁷. The number of male flowers available to an unpollinated pistillate flower would increase with time in a day and the probability of being pollinated would also increase even under limited bee activity. Delayed petal abscission by self-pollination certainly encourages possibility for later out-crossing and hence progeny variability.

There was a quantitative relationship between the number of pollen grains on the stigma and the time taken for petal abscission in *Momordica*. An interesting feature is that a threshold load of six pollen grains on the stigmatic surface is critical to initiate successful petal abscission. This threshold is akin to the number of ovules present in the ovary. Perhaps, *Momordica* represents the only system where pollination-induced petal abscission responds in a dose-dependent manner after a threshold, which ensures pollen grains just adequate to fertilize all the ovules.

The time taken for petal abscission seems to be controlled by genotypes of pollen recipient, pollen donor and the interaction between the two. Significant variation in the ability to induce petal abscission among pollen genotypes suggests that the competition among potential pollen donors to sire ovules might well extend up to their influence on floral longevity. By 'manipulating' floral longevity, pollen donors might attempt to out-compete other donors. However, this donor effect was not independent of the pollen recipient genotype.

The interaction among pollen donors genotype and that of pollen recipient also suggests that pollen and stilar genotypes might strongly interact over floral lifespan. This interaction might be manifested as a conflict around the critical pollen load, because the pollen donors would be selected to initiate petal abscission soon after they reach the stigma, while stilar genotypes would be selected to initiate petal abscission after receiving adequate pollen grains, such that progeny variability is ensured.

The wide variation observed in Figure 1 in the time required to initiate petal abscission in the early part might in fact represent such an interaction. The reduction in this variation with increase in number of pollen grains on the stigma suggests that pollen and stilar strategies might coincide. Because majority of the plants are bisexual, the gene for early induction of petal abscission selected through male function might also be expressed through female function. In such a case, this would lead to a negative effect on functional lifespan of flowers. However, mechanisms such as 'parent sex-specific activation of gene' have recently been put forward to explain such intricacies²¹⁻²³. Evidence is now accumulating to show that the gene derived from pollen might show contrasting effect to the same gene that is derived from the ovules^{24,25}. The physiological mechanism required to trigger-off petal abscission could be stimulated by the threshold number of pollen grains and mediated by a growth regulator synthesized by either the pollen grains

or the style²⁶. The stochasticity in such a process can also bring out variations in petal-drop response.

It is possible that in self-compatible species with multi-ovulated, short-lived flowers like *Momordica*, genotype-specific induction of flower senescence may constitute an important aspect of plant reproductive biology, especially in the light of sexual selection. To evaluate the importance of these effects on pollination dynamics and fitness consequences, detailed field studies are however necessary.

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ACKNOWLEDGEMENTS. We thank the Department of Science and Technology, Govt. of India for the financial support and Drs K. N. Ganeshaiyah and R. Uma Shaanker, University of Agricultural Sciences, Bangalore, for their valuable suggestions to improve the manuscript. We also thank ANUTECH Pvt Ltd, Australia, for their help in literature search on petal abscission and the anonymous referee for several interesting suggestions and comments.

Received 2 February 2001; revised accepted 25 September 2001

High biological productivity in the central Arabian Sea during the summer monsoon driven by Ekman pumping and lateral advection

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Open oceans are generally oligotrophic and support less biological production. Results from the central Arabian Sea show that it may be an exception to this. We provide the observational evidence of fairly high biological production (up to $1700 \text{ mg C m}^{-2} \text{ d}^{-1}$) in the central Arabian Sea, along 64°E , during the summer monsoons of 1995 and 1996. The reasons for the observed high biological production, comparable to that from the traditionally well-known Somali upwelling region, were examined in light of the physical forcing and prevailing chemical fields. In the northern part of the central Arabian Sea, north of the axis of the Findlater Jet, upward Ekman pumping and entrainment driven by basin-wide winds along with advection of upwelled waters from the coastal region of Arabia supply nutrients to the upper layers. In the southern part, production is supported by nutrients advected from the Somali upwelling region.

CONVENTIONAL understanding of the Arabian Sea productivity, largely based on observations from the International Indian Ocean Expedition^{1,2} (IIOE, 1959–65) and the Indian Ocean Experiment³ (INDOEX, 1979), is that upwelling occurring along continental margins of Somalia, Arabia, and to a lesser extent, along the southwest coast of India during the summer (south-west) monsoon (ca. June–September) leads to high primary production. The general picture which emerged out of these studies was that during summer, the open waters of the Arabian Sea are oligotrophic (nutrient-depleted) and surface chlorophyll-*a* typically ranges from 0.1 to 0.5 mg m^{-3} , while primary productivity ranges from 100 to $500 \text{ mg C m}^{-2} \text{ d}^{-1}$ (refs 1, 2, 4). The lower ranges of these values are usually from the southern and eastern areas (ca. south of 15°N ; east of 67°E). Subsequently, Pant⁵ and Bansa⁶ also arrived at similar conclusions. However, satellite imageries⁷ have shown higher surface pigment concentrations (>0.5 and up to 2 mg m^{-3}) over larger areas up to 10°N . In the present study, we show that high production indeed occurs in the open (central) Arabian Sea, at least westward of 64°E , during

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