

Iron and silicate regulation of new and export production in the equatorial Pacific: A physical-biological model study

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[1] Based on a physical-biological model with monthly mean forcing, numerical experiments are conducted to examine the effects of iron and silicate availability on phytoplankton growth in the equatorial Pacific. The effects of elevated iron are realized in terms of increasing the phytoplankton light acclimation efficiency (α) and decreasing the molar ratio Si/N of diatom uptake. The increase of α (decrease of Si/N) would release the iron stress to phytoplankton growth in the equatorial Pacific thus support higher organic production, which tends to drive the system into nitrate depletion. However, the biogenic silica (BSi) production remains largely unchanged due to the reduction of Si removal for unit production of organic nitrogen by diatoms. As a result, the BSi production is lower than the new production and the $\text{Si}(\text{OH})_4$ is higher than the NO_3^- , which is consistent with conditions during glacial periods as inferred from the geological records but opposite to the conditions in the modern equatorial Pacific. The numerical experiments suggest that, if other conditions stay the same, low NO_3^- concentration during glacial periods may prevent diatoms from out-growing small phytoplankton in the equatorial Pacific. **INDEX TERMS:** 4231 Oceanography: General: Equatorial oceanography; 4255 Oceanography: General: Numerical modeling; 4845 Oceanography: Biological and Chemical: Nutrients and nutrient cycling; 4267 Oceanography: General: Paleooceanography. **Citation:** Jiang, M. S., and F. Chai (2004), Iron and silicate regulation of new and export production in the equatorial Pacific: A physical-biological model study, *Geophys. Res. Lett.*, *31*, L07307, doi:10.1029/2003GL018598.

1. Introduction

[2] Only in recent years have scientists realized that iron and silicate could have complex interactions in regulating phytoplankton productivity in the high nutrient low chlorophyll (HNLC) regions. Both iron [Martin and Fitzwater, 1988] and silicate [Dugdale and Wilkerson, 1998] can limit phytoplankton growth, but the interactions between these two elements are yet largely unknown. The in-situ incubation experiments in HNLC areas demonstrated that additional iron could significantly decrease the silicate/nitrate (Si/N) uptake ratio by diatoms [Takeda, 1998; Hutchins and Bruland, 1998; Franck et al., 2000]. On the other hand, a high Si/N uptake ratio, created by a low ambient iron

concentration, tends to drive the surface water into silicate limitation. With higher iron concentration during glacial periods in the Southern Ocean, it would reduce the silica requirement by diatoms and result in excess silicate in the surface layer and higher biological productivity [Brzezinski et al., 2002; Matsumoto et al., 2002]. If this hypothesis holds, surface nitrate in the Southern Ocean could be completely depleted while excess $\text{Si}(\text{OH})_4$ could leak into low latitudes [Matsumoto et al., 2002].

[3] Geological records have not been conclusive on how biological productivity might change during glacial periods in the equatorial Pacific. Sediment records have indicated an enhancement of biological productivity in this region [Pederson, 1983; Paytan et al., 1996]. However, Loubere [2000] reconstructed the benthic foraminiferal records, which suggested a reduction in productivity. On the other hand, the siliceous sedimentary materials were more or less stable during glacial periods in the equatorial Pacific [Berger and Herguera, 1992], which suggests little change in biogenic silica (BSi) export. The changes of diatom preferential uptake between Si and N may explain, to a certain degree, the decoupling of BSi and carbon records in the sediments [Ragueneau et al., 2000].

[4] In this communication, a physical-biological model is used to investigate the coupling between iron and silicate limitation on the phytoplankton productivity in the equatorial Pacific. Particularly, the organic and BSi production are simulated and compared under the conditions of modern ocean and during glacial periods. The implications are also discussed.

2. Model Description and Design of Numerical Experiments

[5] The numerical model is a physical-biological model specially designed for the equatorial Pacific Ocean, which couples a biological model [CoSINE, Chai et al., 2002] with the NCAR Climate Ocean Model (NCOM) [Li et al., 2001; Jiang et al., 2003]. The biological model is based on the one-dimensional (1-D) model developed by Chai et al. [2002], which has ten components representing two sizes of phytoplankton (small phytoplankton and diatoms), dissolved silicic acid (silicate; $\text{Si}(\text{OH})_4$), nitrate (NO_3^-) and ammonium (NH_4^+), two zooplankton and two detritus components. More details can be found in Chai et al. [2003] and Jiang et al. [2003].

[6] The effects of ambient iron concentration on the phytoplankton growth are expressed in the phytoplankton

Table 1. The Initial Slope of P-I Curve α (Unit: $[(\text{Wm}^{-2}) \text{ day}]^{-1}$) and Si/N Uptake Ratio by Diatoms for the Numerical Experiments

Group BOTH: Both α and Si/N ratios vary					
Si/N	4	2	1.5	1	0.5
α	0.00625	0.0125	0.025	0.05	0.1
Group Fix-Fe: Change Si/N ratio only ($\alpha = 0.025$)					
Si/N	4	2	1.5	1	0.5
Group Fix-Si/N: Change α only (Si/N = 1.5)					
α	0.00625	0.0125	0.025	0.05	0.1

light acclimation efficiency (α), which is the initial slope of P-I curve [Platt *et al.*, 1980], and the diatom Si/N uptake ratio with N uptake including both NO_3 and NH_4 uptakes. In situ iron incubations have shown that additional iron increases the phytoplankton maximum growth rates [De La Rocha *et al.*, 2000]. Measurements of phytoplankton photosynthesis in the equatorial Pacific and simulations with a P-I model [Lindley *et al.*, 1995] showed that additional iron would increase the phytoplankton growth through an increase of α . On the other hand, diatoms can adjust to iron-deplete conditions by increasing their Si/N uptake ratio [Takeda, 1998; Hutchins and Bruland, 1998]. Assuming a roughly linear relationship between ambient Fe concentration and α , we construct a group of α and Si/N uptake ratios by diatoms with a relationship similar to the empirical relationship between Fe and Si/N observed in the Southern Ocean [Franck *et al.*, 2000] (Table 1, group BOTH). The combinations of $\alpha = 0.025$ $[(\text{Wm}^{-2}) \text{ day}]^{-1}$ and Si/N = 1.5, $\alpha = 0.05$ and Si/N = 1 are used to represent nutrient and productivity conditions of modern ocean and glacial periods, respectively. In these five experiments, both Si/N and α vary at the same time. The Si uptake of diatom equals to the product of Si/N ratio and total N uptake. We also conduct two other groups of experiments, which fix α (Fix-Fe) and Si/N (Fix-Si/N), respectively. All of the analyses are focused on the eastern part of the equatorial upwelling zone (EUZ), which is divided into two boxes: central equatorial Pacific (CEP) (2°N – 2°S , 180°W – 135°W) and eastern equatorial Pacific (EEP) (2°N – 2°S , 135°W – 90°W). All variables presented below are averaged values over the boxes of CEP, EEP or whole area (CEP+EEP). For nutrients and biomass, only surface values are presented.

3. Results and Discussion

[7] In the experiments for group Fix-Si/N (Si/N = 1.5) diatom biomass in the EEP decreases and silicate accumulates in response to the decrease of α (not shown), which suggests that iron is the most limiting factor in controlling diatom production. By comparison, the diatom biomass in the CEP does not decrease monotonically with the decrease of α (Figure 1). Enhanced diatom biomass under the lower α conditions is a result of a substantial increase of $\text{Si}(\text{OH})_4$ concentration in the CEP because the photosynthesis efficiency is reduced and the NO_3 concentration already increases to $\geq 4.7 \text{ mmol m}^{-3}$ at $\alpha = 0.025$. The elevated $\text{Si}(\text{OH})_4$ concentration in the CEP is primarily due to westward transport of excessive $\text{Si}(\text{OH})_4$ from the EEP via the south equatorial current (SEC) [Jiang *et al.*, 2003]. This indicates a potential $\text{Si}(\text{OH})_4$ limitation to diatom

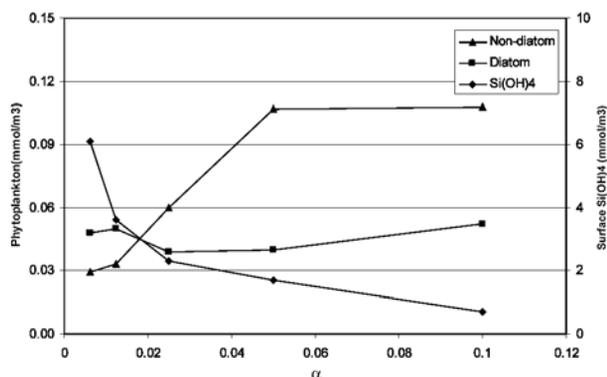


Figure 1. Surface phytoplankton biomass (mmol m^{-3}) and $\text{Si}(\text{OH})_4$ (mmol m^{-3}) in the CEP for the group Fix-Si/N experiments (Si/N = 1.5).

growth in the CEP under the current iron condition, which is consistent with suggestion by a recent field Si enrichment experiment conducted at 180° using ^{32}Si as a tracer [Leynaert *et al.*, 2001]. As expected, the iron controls the growth of small phytoplankton for the entire equatorial Pacific such that the non-diatom phytoplankton biomass increases with the increase of α in both the CEP (Figure 1) and EEP (not shown).

[8] Comparatively, the model simulations for the group Fix-Fe ($\alpha = 0.025$) show that when Si/N decreases from 4 to 0.5, the surface $\text{Si}(\text{OH})_4$ concentration within the CEP and EEP increases 4-fold while NO_3 remains unchanged (Figure 2). As a consequence, the diatom new production triples, while the new production of non-diatom phytoplankton decreases about 35% (Figure 2). The reduction of new production by non-diatom phytoplankton is caused by increasing inhibition of ammonium, which has increasing concentrations from 0.11 to 0.15 mmol m^{-3} in response to more ammonia released by meso-zooplankton population. This result is consistent with the suggestion that the ambient concentration of $\text{Si}(\text{OH})_4$ determines the percentage of diatom production in the total new production in the equatorial Pacific if Fe condition is fixed [Chai *et al.*, 2002; Dugdale *et al.*, 2002a].

[9] Now, we present the results from the group BOTH experiments. The $\text{Si}(\text{OH})_4$ concentration in both the CEP and EEP remains largely unchanged, while the NO_3 con-

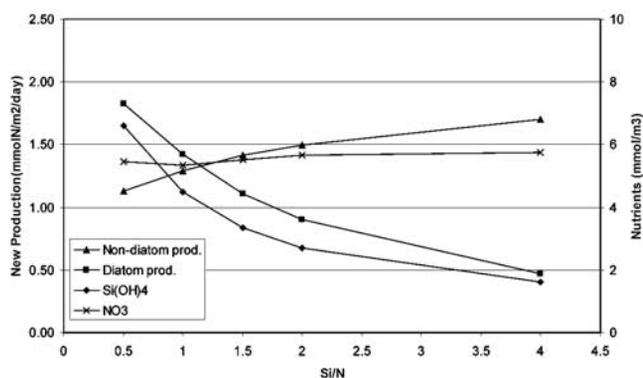


Figure 2. Diatom and non-diatom production ($\text{mmol m}^{-2} \text{ day}^{-1}$) and surface nutrients (mmol m^{-3}) in the CEP+EEP for the group Fix-Fe experiments ($\alpha = 0.025$).

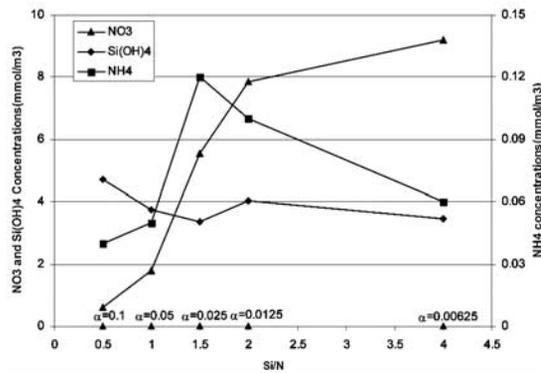


Figure 3. Surface nutrient concentrations (mmol m^{-3}) in the CEP+EEP for the group BOTH experiments. The value of α for each Si/N is shown on top of the x axis (see Table 1).

centration decreases dramatically in response to the increase of iron (α) and decrease of the Si/N uptake ratio (Figure 3). The NO_3 depletion under the high uptake condition is similar to the iron enrichment experiments in the Southern Ocean, in which a switch from Si(OH)_4 to NO_3 depletion was reported when 1 nM Fe was added to the high-nutrient waters [Franck *et al.*, 2000; Brzezinski *et al.*, 2002]. The NH_4 concentration increases at first due to the increasing sources of organic material, reaches peak at $\alpha = 0.025$ ($\text{Si/N} = 1.5$) and then declines due to enhanced NH_4 consumption by phytoplankton when α further increases (Figure 3). The diatom biomass increases dramatically from 0.037 to $0.054 \text{ mmol m}^{-3}$ when α increases from 0.00625 to 0.0125 , then increases slightly when α further increases. The biomass of non-diatom phytoplankton increases from 0.023 to $0.235 \text{ mmol m}^{-3}$, roughly doubles for each successive experiment.

[10] The new production by both diatom and non-diatom increase steadily in response to the increase of α and decrease of Si/N, as compared to the relatively constant BSi production (Figure 4). The peak of ammonium inhibition on NO_3 uptake by small phytoplankton [Chai *et al.*, 2002] at $\alpha = 0.025$ expected from maximum NH_4 concentration is not enough to offset the dramatic change of production induced by factor α . Franck *et al.* [2000] also observed 2–7 times greater NO_3 uptake in the Southern Ocean, which was overall stronger than the increase of Si uptake rates. As a result, they found that the Si/N uptake ratio by the phytoplankton community was 2–5 times reduced, which is consistent with our modeled ratio reduction of BSi production to N production (Figure 4). Under the high iron conditions, the high new production along with low NO_3 indicates that the NO_3 is not limiting the phytoplankton growth in the range of α tested, which may be explained by a fast recycling of nitrogen [Jiang *et al.*, 2003]. The BSi production shows a peak at $\alpha = 0.025$ ($\text{Si/N} = 1.5$) and decreases on both sides. Clearly this is largely due to the change of BSi production associated with NH_4 uptake (Figure 4), which has similar shape with NH_4 concentration and contrasts to the approximately constant BSi production contributed by NO_3 uptake. This peak of BSi production at a medium value of α is consistent with the drop of surface Si(OH)_4 seen in Figure 3. The organic nitrogen export and the BSi export (not shown) show

similar patterns to that of the new production and the BSi production, respectively, which suggests that same amount of BSi export would correspond to more organic nitrogen export under the high α and low Si/N conditions. Overall, the model shows contrasting results of nutrients, new and export production in the equatorial Pacific under the modern ($\alpha = 0.025$, $\text{Si/N} = 1.5$) and glacial conditions ($\alpha = 0.05$, $\text{Si/N} = 1.0$). As a result, the Si/N ratio in the export production (defined as BSi Export/N export) reduces from 2.3 of current value to 1.0 during glacial periods.

[11] The relatively stable Si(OH)_4 concentration and BSi production can be explained using the product of Si/N ratio and the uptake rates of N by diatoms. The increase of organic production by diatoms is driven by the increasing photosynthesis efficiency, though the decreasing NO_3 may restrict the incorporation of nitrogen. The changes of NH_4 concentration also affect the N removal by diatoms. The net result of these is the increasing organic production, which corresponds to a stable BSi production due to the reduced Si removal for unit organic production by diatoms. Comparatively, the increase of α in the experiments of Fix-Si/N drives the organic production and BSi production to higher values simultaneously without compensation from the reduction of Si/N uptake ratio, which leads to the depletion of both NO_3 and Si(OH)_4 . In the experiments of Fix-Fe, reduction of Si/N uptake ratio by diatom alone favors higher Si(OH)_4 concentration and diatom production, while the growth of non-diatom phytoplankton is increasingly inhibited by ammonia [Chai *et al.*, 2002]. The net effect is that the BSi production decreases linearly from $2.0 \text{ mmolSi m}^{-2} \text{ day}^{-1}$ to $0.9 \text{ mmolSi m}^{-2} \text{ day}^{-1}$. The latter two scenarios clearly differ from the BOTH experiments.

[12] It is worth noting that the diatom and non-diatom phytoplankton production increase in a similar proportion in association with the increase of α (Figure 4), while non-diatom biomass is much higher than diatom biomass at high α . This suggests that diatoms are unable to dominate the total production even under an Fe-replete condition in the equatorial Pacific. We offer two reasons. First, the dominance of diatoms observed during the iron fertilization experiments only occurs in the initial phase of the iron injections, which usually lasts about 7–10 days [e.g., Coale

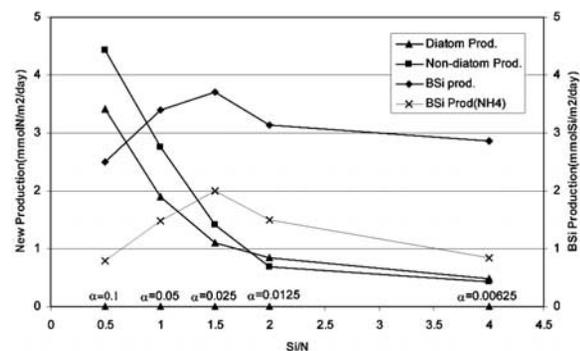


Figure 4. New production ($\text{mmolN m}^{-2} \text{ day}^{-1}$) of phytoplankton and BSi production ($\text{mmolSi m}^{-2} \text{ day}^{-1}$) in the CEP+EEP for the group BOTH experiments. Also shown is the contribution of BSi production by ammonium uptake (crosses). The value of α for each Si/N is shown on top of the x-axis (see Table 1).

et al., 1996; Boyd et al., 2000]. After this short, transient period, other limiting factors such as nutrients, grazing, and sinking, start to control the diatom growth such that the diatom biomass decreases rapidly. In the current experiments, the monthly climatological forcing produces a quasi-steady state condition, in which meso-zooplankton grazing places a strong control on the diatom abundances, and increases the grazing pressure corresponding to the elevated organic production under the high α conditions. Secondly, the low NO_3 condition at high α end might restrict the diatoms growth but have less influence on the growth of small phytoplankton, which has low half-saturation constants for both NO_3 and NH_4 uptakes.

[13] Many geological records indicate enhanced productivity and increase of organic material export during glacial periods [e.g., Pederson et al., 1983; Paytan et al., 1996], which are consistent with our increased production of organic nitrogen if C:N ratios in the sediments do not have significant changes over glacial/interglacial cycles (Figure 4). The sediment records in the Southern Ocean indicates a diminished $\text{Si}(\text{OH})_4$ utilization and an increased NO_3 utilization thus reduced Si/N ratios during three glacial periods [Brzezinski et al., 2002], which agrees with the reduced Si/N ratios in the modeled export. Furthermore, the relatively constant opal production simulated here is supported by the observations that the siliceous sedimentary materials were more or less stable during glacial periods in both the equatorial Pacific and the Southern Ocean [Berger and Herguera, 1992; Kumar et al., 1995].

[14] Very low surface nitrate simulated seems to contradict with lighter ^{15}N records in the cores in the eastern equatorial Pacific during the last glacial maximum (LGM) [Farrell et al., 1995], which suggests higher nitrate concentration near the surface. Farrell et al. [1995] attributed low ^{15}N at the LGM to a NO_3 supply to the euphotic zone that was higher even than the elevated LGM productivity. Recent evidence of foraminifera suggests that a stronger SEC during glacial periods has resulted in 5°C lower SST in the SEC but only 1°C on the equator, creating a stronger meridional SST gradient [Martínez et al., 2003]. This indicates a stronger nitrate transport from Peru upwelling regions to the equatorial Pacific. On the other hand, model results and observations in the Southern Ocean indicate low surface dissolved inorganic nitrogen (DIN) during glacial periods [Brzezinski et al., 2002; Matsumoto et al., 2002]. This may lead to further reduction of DIN in the equatorial Pacific because Southern Ocean is one of the two major nutrient sources to the equatorial Under Current [Toggweiler and Carson, 1995; Dugdale et al., 2002b]. More research is required to resolve these contradicting evidences about the surface DIN concentrations during glacial periods.

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