Greenhouse effect of the past and plant evolution

It is generally assumed that variations in the atmospheric CO_2 produced alternatively, the Ice Age and the greenhouse state on the earth. In the past, two greenhouse effects are mostly recognized: (i) Ordovician–Devonian and (ii) Jurassic–Cretaceous. In the first greenhouse state, bryophytes, pteridophytes, gymnosperms and some other plant groups evolved; in the second angiosperms appeared. The evolution of marine animal life was also analysed in relation to plants; it was revealed that evolution of plant life is generally inversely proportional to animal life.

Greenhouse effect is a phenomenon by which carbon dioxide (CO_2), water vapour (H_2O), atmospheric methane (CH_4), nitrous oxide (N_2O), ozone (O_3), and aerosols trap more heat from the sun, causing the earth to get warmer. It was Arrhenius who first introduced the 'hot house theory' later known as 'greenhouse theory' to model quantitatively the effect of changes in the concentration of atmospheric CO_2 on climate[1]. According to an estimate, the atmospheric concentration of CO_2 has increased from 280 ppm in 1750 to 367 ppm in 1999, atmospheric methane by 150% and nitrous oxide by 16%. In 1985, scientists at Villach in Austria concluded that due to this effect the earth has already warmed slightly and if this process is continued then by 2030, the earth's temperature may rise by 1.5–4.5°C (ref. 2). They also predicted that if the increase were on the higher side then the sea level could rise by 25–140 cm, sufficient to flood the major cities and the low lands like Bangladesh and the Nile delta. This increase in temperature could also radically disturb the world's delicate agricultural systems, dry out the tropical rain forests and disrupt marine food chains.

During the last Ice Age, the atmosphere contained much less carbon dioxide than the present. The end of the Ice Age was ushered by the marked rise of temperature and CO_2. It is advocated that the earth's climate in the past changed only between two states – the 'greenhouse state' characterized by increased carbon dioxide content and the 'icehouse state' where the amount of carbon dioxide appreciably decreased[3]. The occurrence of Palaeogene glaciation in Antarctica is attributed to the declining atmospheric CO_2 (ref. 4).

However, many have challenged this contention and even argued that the 'greenhouse theory' is a fallacy[5-7].

That the climate of the earth is ever changing is evidenced by the facts that in the distant past there were several Ice Ages and greenhouse stages. The earliest Ice Age is known from the Neoproterozoic rocks about 750 million years old in Namibia. Palaeomagnetic evidence indicates that ice reached almost to the equator leading to the 'snowball earth' hypothesis[8-10]. Since the earth was totally covered by ice, biological activity collapsed for millions of years only to reactivate when subaerial volcanic outgassing raised atmospheric CO_2 enormously[8-10]. However, experiments on the Neoproterozoic climate point out that a low latitude sea ice distribution cannot be sustained[11].

The icehouse state has marked gradients in latitudinal temperature, low mean ocean temperature, turbulent oceanic convention, oceans with good amount of oxygen and a tendency to accumulate ice sheets in low land and water. The greenhouse state, on the other hand, is characterized by low gradients in latitudinal temperature, sluggish oceanic circulation, hot polar regions, high average ocean temperature, depletion in oxygen in sea water and absence of ice sheets in sea and lowland[3]. The greenhouse state is also associated with volcanism and sea level rise. Engel and Engel[12] have shown two major peaks of volcanic activity – the older one persisting through Late Cambrian to Late Devonian and the younger one in the Late Jurassic–Cretaceous. Similarly, Hallam[13] and Vail et al.[14] have also shown two major sea level rises – one in the Late Cambrian–Late Devonian and the other during Jurassic–Cretaceous. A model for variation of carbon dioxide in the air throughout the ages suggested that CO_2 concentration was very low during most of the Ice Ages, e.g. in Late Precambrian, Late Palaeozoic, Oligocene–Neogene. A higher amount of carbon dioxide is contemplated during the greenhouse stages, e.g. Late Cambrian–Devonian and Jurassic–Eocene[3,15].

The first major adaptive radiation of plants onto land occurred sometime in the middle of Ordovician (Llanvirnian–Llandeilan). The obligate spore tetrads of these plants are found in abundance in

the fossil state. These plants were in dominance from mid-Ordovician to about mid-late Early Silurian. The close similarity of the fossil tetrads with the obligate spore tetrads produced by some extant hepatics and mosses (bryophytes) suggests the presence of nonvascular plants[16].

The second major adaptive radiation of the land plants started with the replacement of spore tetrad assemblage by the single trilete spores in the mid-late Early Silurian[16]. These trilete spores resemble the spore-producing vascular cryptogams (pteridophytes) of the present day. The simple, smooth-walled trilete spores gradually gave rise to variously ornamented forms with different laesurae morphologies by the mid-late Silurian. The interval from the mid-Ordovician to the mid-late Early Silurian is hypothesized to be one of rapid colonization by the pioneer populations with limited genetic diversity, an eco-physiological tolerance to desiccation and a short vegetative life cycle. The second phase of evolution ushered in the mid-late Early Silurian and continued up to Pridoli (Early Devonian) and this coincides with the appearance of vascular plant megafossils. This period was one of the major establishments of large population of varied plants exploiting a broad spectrum of ecological niceties that have very few megafossil records.

During the Devonian, modern aspects of plant life were attained. The first appearance of various anatomical features, vegetative morphologies and reproductive structures of the Devonian fossil plants were: tracheids with annular thickenings, stoma with apparently interconnected guard cells, stele with xylem of elliptical cross section with exarch protoxylem, polystele, secondary xylem, equal dichotomy, overtopping, vascularized microphylls, expanded leaf base, leaf abscission, terminal, lateral and fusiform sporangia, with morphologically distinct spores of two sizes, sporangia with mega and microspores, megaspore tetrad, radiospermic and platyspermic seeds. Some of the Devonian plants also gained height for the first time and to hold the plants fast on the ground an effective root system was also developed.

A phylogeny of Late Silurian and Devonian vascular plants depicts that the
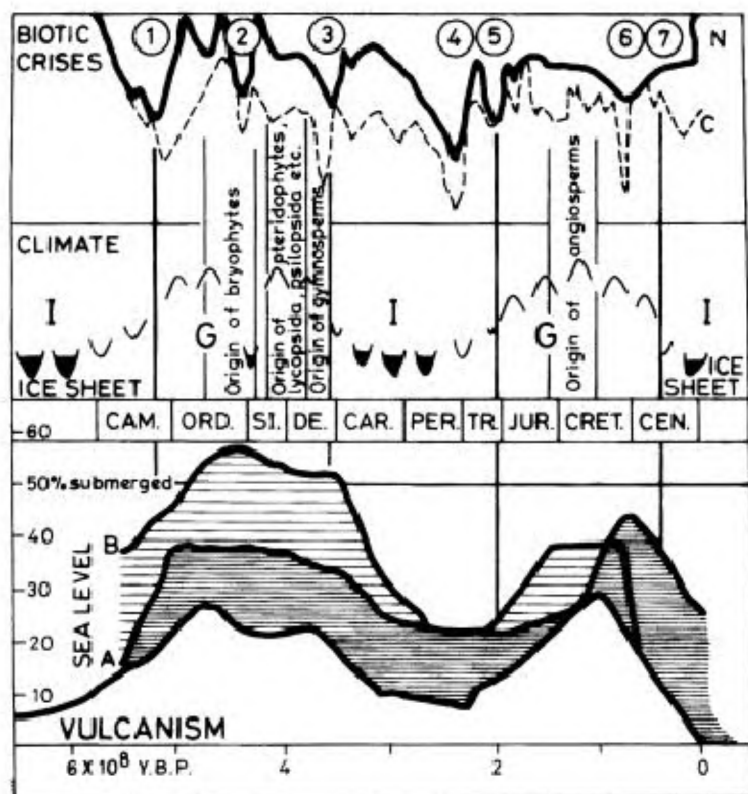
Figure 1. Biotic crises, climatic fluctuations, sea level changes, volcanism and plant evolution in the Phanerozoic. The biotic crises show the number of marine animal families declined [after Newell (N) and Cutbill (C)]. Climate of the past is divided into Ice Age stage (I) and Greenhouse stage (G). Sea level changes in the different periods are plotted following Vial et al. (A) and Hallam (B). Volcanism is shown from American granite emplacement (after Engel and Engel). The origin of different plant groups is plotted from the present studies. Note that all the plant groups evolved in the Greenhouse stages and are associated with sea level rise and intensive volcanism. In majority of cases when the plant groups evolved, marine animal families declined. This figure is adapted after Fischer (1981) with modifications.

major groups of plants, viz. Barinophytales, Lycopsida, Zosetrophyllales, Psilopsida, Trimerophytales, Progymnospermopsida, Pteropsida and Cladoxylales evolved during these periods[17]. In the Late Devonian (Famisian) Pteridospermales?, Cycadopsida, Coenopteridales and Sphenopsida also evolved. The discovery of *Archaeosperma arnoldi* – a cupulate seed from the Late Devonian of North America and *Spermolithus* – a platyspermic seed also from the Late Devonian points to the origin of gymnosperms during this time[18,19].

The greenhouse effect reappeared during the Jurassic–Cretaceous to usher the origin of angiosperms (Figure 1). A number of peculiar leaf impressions have often been claimed as early angiosperms, e.g. *Furcula* from Rhaetic of Greenland, *Sanmiguelia lewisi* from the Middle Triassic of USA, *Fraxinopsis* from the Rhaetic of Argentina, *Phyllites* from the Jurassic of Yorkshire and *Propalmophyllum liassicus* from the Lias of northern France[20–25].

However, Pant and Kidwai[26] remarked that the attribution of either of these fossils to angiosperms is uncertain because external morphology alone is not sufficient to claim the affiliation. *Archaefructus liaoningensis* and *A. sinensis* reported from Yixian Formation of western Liaoning, China is Upper Jurassic/Lower Cretaceous in age. According to the authors these plants are a sister clade to all angiosperms; they are aquatic in habit, the reproductive axes lack petals and sepals and bear stamens in pairs below the conduplicate carpels[27].

However, unmistakable angiospermic pollen, viz. *Clavatipollenites hughesii* was recorded from the Late Barremian to Aptian strata of England and *Tricolpites albiensis* from the Albian of England[28]. Walker and Walker[29] recorded as many as 22 monocot types of pollen from the Potomac Group (Barremian) of North America. The diversity of the angiosperm pollen in Barremian indicates that the

angiosperms should have evolved earlier. Many characters were again introduced for the first time in angiosperms. These are broad, reticulate, veined leaves, eight nucleate embryo sac, double fertilization, sieve tubes and companion cells originating from the same mother cell and above all, the flower containing stamens and carpels[30,31].

Newell studied the revolutions in the history of life based on mass extinction of marine animals and outlined seven animal crises. These are the Cambrian–Ordovician crisis, the Ordovician–Silurian crisis, the Late Devonian crisis, the Permo–Triassic crisis, the Triassic–Jurassic crisis, the Cretaceous–Teritary crisis and the Late Eocene–Oligocene crisis[32]. Sepkoski[33], however, advocated five major crises, viz. the Late Ordovician, the Late Devonian, the Late Permian, the Late Triassic and the Late Cretaceous. In the Late Ordovician 22%, in the Devonian 21%, in the Late Permian 50%, in the Late Triassic 20% and in the Late Cretaceous 15% of the families were eliminated[33].

Fischer related all these crises due to the change from icehouse state to greenhouse state[34]. Most of the crises mentioned earlier happened during the greenhouse state except the Permo–Triassic crisis. In the first greenhouse state, i.e. from Ordovician–Devonian, the bryophytes, pteridophytes, gymnosperms and many other forms evolved. In the second greenhouse state, the angiosperms evolved. So it seems that when plants evolved and flourished, the marine animals faced hardship and extinction.

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Estimating terrestrial net primary productivity over India using satellite data

Net primary productivity (NPP) is the fundamental process in biosphere functioning and is needed for assessing the carbon balance at regional and global scales. Changes in NPP could arise due to anthropogenic effects and climate change, and directly affect human and animal food supplies. Terrestrial NPP is one of the most-modeled ecological processes with models that differ markedly in approach and complexity, often yielding comparable global estimates[1]. With the availability of space-based Remote Sensing (RS) measurements providing global coverage with nearly daily sampling and techniques to estimate absorbed photosynthetically active radiation (APAR), the use of RS data has become the most preferred technique for estimating global NPP[2].

The terrestrial NPP of India, its quantum, spatial variability, and distribution across seasons is not well understood.

Some preliminary estimates have been made as part of terrestrial carbon cycle assessment, viz. 1.24 PgCa^{-1} [Pg = 10^{15} g] for 1980 (ref. 3), and 1.32–1.59 PgCa^{-1} for mid-eighties[4]. Recently, SPOT-VEGETATION data in the form of 10-day global NDVI (Normalized Difference Vegetation Index) composites have been used with C-Fix model to compute PAR and NPP at 1 km scale (http://www.geosuccess.net). These NPP outputs from the C-Fix model have been used for arriving at country-wise estimates of African and European continents and also validated by comparing the model outputs with field measurements for two Euroflux test sites[5,6]. The C-Fix model calculates NPP by simulating carbon exchange using the following equation[7]:

NPP = uptake of carbon by photosynthesis – autotrophic respiration losses by vegetation

$$= S*c*\text{fAPAR}*\varepsilon*\text{p}(T)*\text{CO}_2\text{fert}*(1 - r)$$
$$(\text{mgC/m}^2/\text{day}), \qquad (1)$$

where S is the daily incoming global solar radiation [MJ/m^2/d]; c is the climatic efficiency 0.48, fAPAR is the fraction of adsorbed PAR estimated from RS-based NDVI, ε is the photosynthetic efficiency 1.10 [gC/MJ(APAR)], p(T) is normalized temperature dependency factor (value between 0 and 1), and CO$_2$ fert is normalized CO$_2$ fertilization factor (dimensionless), and r is the fraction of assimilated photosynthates consumed by autotrophic respiration; modeled as simple linear function of daily mean air temperature.

We report here estimates of monthly net C fixation and net primary productivity over India and its eight regions, using SPOT-VEGETATION 10-day NPP composites, and comparing the monthly patterns of NPP and NDVI. Although many studies use calendar year for reporting