Patterns of Primary Terrestrial and Ecosystems Function

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Introduction
The net primary productivity (NPP) of the world has been estimated to be $172 \times 10^9$ t yr$^{-1}$ (Whittaker et al. 1975). Of this, the land communities are much more productive than the ocean ones because of a more complex community structure on land that supports extensive leaf surface for photosynthesis and better nutrient retention abilities. This is in spite of the more efficient production per unit chlorophyll, in the marine environment. According to Rodin et al. (1975), tropical belt produces 60% subtropics 20% sub-boreal 10% boreal 9% and polar 0.8% of NPP. Forests constitute 49% NPP of the land while that of the oceans is estimated at $4.7 = 7.2 \times 10^{10}$ t yr$^{-1}$.

The major emphasis of the primary productivity studies should be: (i) to make an assessment of NPP of a given ecosystem type and relate it to environmental variables and develop predictive models, (ii) to make comparative assessment of NPP of different ecosystem types and develop productivity maps (Leith 1975) for better land management, and (iii) to understand light interception strategies of plant communities (Madgwick 1970, Ramakrishnan et al. 1982) for better management of our natural resources. However, these objectives are far from realized in this country though scattered attempts have been made to conduct studies in the area of production ecology (Misra & Singh 1971, Tewary & Singh 1981).

Forest Productivity
Net primary productivity studies on forest ecosystems and mainly restricted to deciduous forests and a few plantations (Golley & Golley 1972, Singh & Mishra 1978). The major emphasis in all these studies has been on quantifying NPP and discussing the data in relation to productivity values available from similar or diverse climatic zones in India or elsewhere where studies are mainly concerned with leaf litter fall which gives an indirect measure of NPP. This has often been related to seasonal parameters such as moisture and temperature. However, little has been done to relate productivity to successional status, though Golley (1972) tried to have a synthesized summary for deciduous forests and Ramakrishnan and co-workers (Singh & Ramakrishnan 1982, Tokyo & Ramakrishnan 1983a; Mishra & Ramakrishnan 1983c) addressed themselves to this aspect of productivity changes in the humid forests of the north-eastern India. Further, no serious attempt has been made to relate productivity and related nutrient cycling aspects to applications such as land management as has been attempted by our group in the north-eastern hill region, under the slash and burn agriculture (Jhum) system of land use (Ramakrishnan 1980, Ramakrishnan & Toky 1978, 1981, Ramakrishnan et al. 1981a, b, Mishra & Ramakrishnan 1981, 1983a, b, c, Toky & Ramakrishnan 1981 a, b, 1983a, b). Relationship between canopy architecture of individual trees/communities and productivity which has so much relevance from an applied angle has also not been attempted except in the humid forests of the north-eastern India (Shukla 1981, 1983, Ramakrishnan et al. 1982, Boojh & Ramakrishnan 1982a, b, 1983a, b). Ramakrishnan unpublished.

Net Primary Productivity of Forest Types
Much of the information on productivity of forests is based on natural or plantation deciduous forest types from north-western parts of India. Even here, the values are based on litter fall in the forest. The litter production in these deciduous forest types ranges between 4 and 11 tons$^{-1}$ yr$^{-1}$. Many of these values are closer to the average of 10.9 t ha$^{-1}$ worked out by Bray and Gorham (1964) though somewhat lower. However, the very low values of 4.04 t ha$^{-1}$ yr$^{-1}$ reported for deciduous forests of the semi-arid zone in Rajasthan is understandable in view of the extreme climatic limitations. If litter production is about $1/3$ of the total NPP (Bray & Gorham 1964), the NPP would be around 23.4–33.0 t ha$^{-1}$ yr$^{-1}$ for the deciduous forests of Uttar

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Pradesh and about 12 t ha\(^{-1}\) yr\(^{-1}\) for the semiarid deciduous forests. The values obtained for Shorea robusta forests of Madhya Pradesh (Pandey et al. 1970, 1972) and dry deciduous forests near Ujjain (Kotwal & Mall 1977) also point to production values similar to that for Uttar Pradesh.

Only a few studies are available on the subtropical montane forests of the Himalayas. Even here the NPP values is often worked out indirectly based on the litter fall as in the case of an oak-conifer forest in Nainital, Himalayas (Pandey & Singh 1981). The litter production here was 6 t ha\(^{-1}\) yr\(^{-1}\) of which 5.5 t ha\(^{-1}\) yr\(^{-1}\) was due to tree litter.

In the Nainital Himalayas, Chaturvedi and Singh (1982) studied the biomass and productivity of Pinus roxburghii over a range of 16–128 years of age. The cumulative dry matter produced by a sample tree within its life time was much greater than the respective current biomass. The largest proportion of the production in this species was attributable to the tree crown and fine roots while the largest biomass resided in the bole. This species attained maximum current biomass increment at the age of 39 years. For this species, the mean annual production increased with age except for bole and root system where it first increased and then attained a plateau.

A comprehensive study of the productivity of khasi pine (Pinus kesiya) is available from Meghalaya (Das 1980, Ramakrishnan & Das 1983). The mean annual productivity increased with the age of the stand. However, the NPP reached a peak in a 5–7-year-old stand after which there was a decline. The net assimilation rate followed a similar trend with a peak value of 5.0 in a 5–7-year-old stand (table 2).

The biomass and productivity studies on Pinus Kesiya revealed that it has a fast rate of dry matter accumulation. This species could be compared with P. radiata and P. caribaea which were reported as the two fast growing pine species of the world (Egujobi 1975, Madgwick, et al. 1977) P. radiata of comparable age from New Zealand accumulated about 317×10\(^3\) kg ha\(^{-1}\) for P. kesiya. The needle biomass P. kesiya was much lower than that of other species, like P. radiata and P. densiflora in Japan (Satoo 1968). The higher needle biomass in the latter two species could be due to the needles of several years being retained on the canopy compared to P. kesiya where the three flushes of needles are retained for less than a year. The non-green/green biomass ratio for a 7-year stand of P. kesiya works out to 13.34 compared to 6.48 and 7.44 for P. radiata and P. caribaea respectively, of the same age. The NPP was 14.4 t ha\(^{-1}\) yr\(^{-1}\) for a 12-year stand of P. radiata (Forrest & Ovington 1970) and 15 t ha\(^{-1}\) yr\(^{-1}\) for a 15-year stand of P. densiflora (Satoo 1968), and 22-year stands of P. kesiya. It was 20 t ha\(^{-1}\) yr\(^{-1}\) and 30 t ha\(^{-1}\) yr\(^{-1}\) for the 7 year respectively. Higher productivity of P. kesiya was related to the high photosynthetic efficiency of the needles under a high light regime with a net assimilation rate of 4.08 t per t needle yr\(^{-1}\) as compared to 3.21 t t\(^{-1}\) reported for P. densiflora (Satoo 1968). The high net assimilation rate (NAR) is due to the prolonged photosynthetic activity of needles which are produced in three flushes during the year. This coupled with a faster turnover rate of needles may contribute towards higher production efficiency of this species. More studies of this kind are needed at specific and sub-specific level for a proper understanding of our indigenous tree resources.

**Succession and Forest Productivity**

As discussed earlier, while several scattered studies on productivity of different forest ecosystem types are available, no major attempt has been made to relate any of these studies with the successional status of the community since the latter is a significant unifying concept in ecological thoughts (Clements 1916). One such comprehensive study available is for the aggrading northern hardwood ecosystem of the Hubbard Brook in the United States where Bormann and Likens (1979) have examined the recovery of primary production and how this compares with that prior to disturbance in the form of clear-cutting.

The secondary successional patterns (Ramakrishnan et al. 1981a, b, Toky & Ramakrishnan 1983a) and the array of growth and allocation strategies of herbs (Saxena 1981, Saxena & Ramakrishnan 1982, 1983a, b) shrubs (P S Ramakrishnan unpublished) and trees discussed separately (Ramakrishnan et al. 1982, Mishra & Ramakrishnan 1983c), and the biomass and primary productivity changes in communities that come up after clearcutting of forested ecosystem for slash and burn agriculture (Jhum) in north-eastern India represent a comprehensive study of its kind for this country. In fact, more studies from different ecological regions of the country would help in bringing out the much needed information for tropical forests and also help in developing ecologically sound programmes of forest landscape management.

Clear-cutting of the community type for cropping under jhum would depend upon the jhum cycle (the intervening fallow period before the same site is again cropped). If it is a long cycle of 20 years or more then it is a forest community that is clear-cut; if it is a short cycle of 5 years or less then it is a herbaceous community that is slashed (Ramakrishnan et al. 1981a, Toky & Ramakrishnan 1983a). However, the speed with which the ecosystem would re-establish maximum biotic regulation over energy flow, hydrology and bio-geochemistry (Ramakrishnan & Toky 1981, Toky & Ramakrishnan 1981b, 1983a, b) would depend upon the rapidity with which biomass and primary productivity recover. The following account concerns itself with photosynthetic efficiency and early growth strategies of successional herbaceous communities up to 5 years or
so of re-growth and the biomass and NPP during secondary succession up to 20 years of ecosystem development, with some comparisons with a 50-year-old forest at lower elevations of Meghalaya. What is discussed here generally holds true for secondary succession after Jhum in the high elevations of Meghalaya (Mishra & Ramakrishnan 1983c).

Growth and allocation Strategy of Early Successional Herbaceous Communities

Under jhum, when a forest is converted to cultivable land, not only is its original vegetation destroyed but the site is subject to continuing perturbations due to fire (Ramakrishnan & Toky 1981, Mishra & Ramakrishnan 1983b), introduction of a variety of crops (Toky & Ramakrishnan 1981a, Mishra & Ramakrishnan 1981), successive weeding, and disturbance to the soil at the time of crop harvest (Toky & Ramakrishnan 1981b, Mishra & Ramakrishnan 1983a). This results in a progressive reduction in species diversity in the developing ecosystem subsequent to jhum. The first five years of fallow development bring predominantly a weedy community consisting of species such as Eupatorium odoratum, Imperata cylindrica and a host of others (Toky & Ramakrishnan 1983a).

A variety of strategies are adopted by these early successional species of clear-cut jhum sites, among which stump, root and rhizome sprouts and invasion through seeds are common. As for the weedy species of the first five years of secondary succession in the north-eastern hill region, a useful strategy should be to capitalize upon the resources of an enriched stabstratum which is transient (Ramakrishnan & Toky 1981) and make adequate growth as quickly as possible. The depletion of nutrients is rapid in these systems due to rapid uptake by the community and this is accentuated due to initially high run-off and infiltration losses (Toky & Ramakrishnan, 1981b; Mishra & Ramakrishnan, 1983a). Besides, nitrogen is low to start with owing to volatilization during the burn (Ramakrishnan & Toky 1981). The weed species establishing in such environments have two contrasting sets of strategies: (i) establishment from seeds vs establishment from vegetative sprouts, and (ii) $C_3$ vs $C_4$ photosynthetic pathway.

The reproductive effort of early successional species whether through seed reproduction as in Eupatorium odoratum or through vegetative reproduction as in Imperata cylindrica is maximum while late successional species allocate more of photosynthetic and nutrients for vegetative growth at the expense of reproductive effort. Even within the same species of Eupatorium odoratum allocation of nutrients and photosynthates to the reproductive effort declined with the age of the fallow (Saxena & Ramakrishnan 1983c). Such a differential strategy is an adaption to the unpredictable environment for the early successional weeds and to the more predictable but competitive environment of the late successional herbs (saxena & Ramakrishnan 1981).

In a comprehensive study on the $C_3$ vs $C_4$ strategy in successional communities, it was found that $C_4$ herbaceous plants tended to dominate in early successional environments both in terms of the number of species, number of individuals and biomass contribution compared to late successional environment which is to be expected as the former environment is characterized by open high light intensity and drier environment (Saxena 1981).

The survival of Eupatorium odoratum, a $C_3$ species is ensured through rapid growth rate and allocation of many resources (resources include photosynthesize and nutrients) to the shoot system and heavy seed reproduction. Since $C_4$ species like Imperata cylindrica and Thysanolaena maxima allocate more resources to the vegetative organs of regeneration, the sprouting species are expected to have less allocation to sexual reproduction as compared to non-sprouting ones. This was found to be true (Saxena & Ramakrishnan 1983a). However, is species that regenerate mainly through vegetative means, the small number of new recruits which may arise from seeds are very important in maintaining genetic diversity.

The $C_3$ strategists like Eupatorium odoratum had much higher relative growth rate and NAR than the $C_4$ strategists like Thysanolaena maxima and Imperata cylindrica (Wilson 1967). This may be due to the higher leaf area ratio in $C_3$ species, which expresses the proportion of photosynthetic surface to respiratory mass and the available light interception surface, which is more critical for comparing the productive potentials of $C_3$ and $C_4$ plants (Caldwell 1974) rather than photosynthesis per unit leaf area (Black et al. 1969). The large potential advantage of the $C_4$ species is progressively attended while moving from microscopic to macroscopic parameters and there remains no apparent difference between the two photosynthetic pathways when each species grows in its own preferred environment (Gifford 1974).

The soil nutrient status is in a state of flux after slash and burn and such a site is colonized by $C_3$ and $C_4$ plants, though the latter predominate. The $C_3$ species with a large uptake and utilization of nutrients for a given dry matter yield are suited to occupy nutrient rich microsites while the $C_4$ species with a lower uptake and higher efficiency of utilization of nutrients can successfully colonize nutrient poor microsites. The $C_4$ species with a higher efficiency in nutrient-uptake efficiency may be a case of parallel evolution with the $C_4$ strategy developed under the generally nutrient-poor status of the tropical environment (Black 1971, Brown 1978) where efficient uptake of nutrients could be important for survival. This niché differentiation of $C_3$ and $C_4$ species may ensure their co-existence in the post-burn environment. Placed in the light of C-S-R strategy of Grime (1979) the non-sprouters have a ruderal (R) strategy while the sprouting species exhibit competitive (C) strategy. These two contrasting strategies along
with the differential uptake and use associated with \( \text{C}_3/\text{C}_4 \) strategies may help in the apparent co-existence of these in the same site after slash and burn (Saxena & Ramakrishnan 1983a, b).

**Biomass and Productivity**

A remarkably linear relationship was observed at low elevations of Meghalaya after slash and burn agriculture (Toky & Ramakrishnan 1983a) up to a period of 20-year succession age not only with respect to community structure but also with respect to functional aspects such as litter production and NPP, as a whole, which is due to drastic changes in the community composition from weedy herbaceous species in the initial stages to bamboos and other true species subsequently.

The relatively higher values of litter production in secondary successional communities started with 0.1 kg m\(^{-2}\) yr\(^{-1}\) in a one-year-old successional fallow and gradually reached a maximal value of 1.0 kg m\(^{-2}\) yr\(^{-1}\) in a 20-year-old forest. As compared to this, it was only 0.55 kg m\(^{-2}\) yr\(^{-1}\) in a 50-year-old forest in the same area (Singh & Ramakrishnan 1982). This is due to the fast developing vegetation during the early successional phase and the subsequent faster turnover of the biomass. Further, in the early phases of succession bamboo species like *Dendrocalamus hamiltonii* and many tree species are deciduous compared compared to more evergreen elements in an older stand.

A sharp and linear increase in the aboveground biomass with age to 20 years was noted, starting with 0.5 kg m\(^{-2}\) in a one-year-old stand and reaching 15 kg m\(^{-2}\) in a 20-year-old forest. The community also showed linear increase in NPP up to 20 years. This may be based upon the growth response of the exploitative species utilizing available resources after slash and burn, accelerated decomposition of the forest floor organic matter and favourable conditions of radiant energy. The rapid increase of NPP (table 3) after 5 years may be due to a shift in community structure from a predominantly herbaceous one to community with fastgrowing bamboo (*Dendrocalamus hamiltonii*) and other shade intolerant species. The rate of production in a 20-year-old forest is higher than in a 50-year-old stand based on litter production values in the latter (assuming that litter production represents \(1/3\) of NPP). Thus, the NPP in a 50-year-old forest is only 1.65 kg m\(^{-2}\) yr\(^{-1}\).

**Early versus Late Successional Trees**

Three early successional species namely, *Alnus nepalensis*, *Schima khasiana* and *S. wallichii* and three late successional species namely, *Machilus kingii*, *Quercus dealbata* and *Q. griffithii* are from the high elevation subtropical montane forests of Meghalaya (Boojh & Ramakrishnan 1982a,b,c,d, 1983) and in part from the basis for this account. From lower elevation sub-tropical humid forest of Meghalaya, two early successional *Duabanga sonneratiioides* and *Anthocephalus kadamba* and two late successional *Dillenia pentagyna* and *Artocarpus chaplasha* were considered (Shukla 1981). Further generalizations on biomass allocation pattern and productivity of trees based on their successional status were done on the basis of the work on an additional six early successional, seven late successional and nine mid-successional tree species (Shukla & Ramakrishnan 1983). The categorization of the species into early, mid and late successional trees is based on their relative status in the forest community and their shade tolerance/intolerance attributes. Thus, while the early successional species are light-demanders, the late successional ones are shade-tolerants and the midsuccesional ones are intermediate between the two.

**Extension Growth and Architecture**

The early successional trees, in general, showed the following growth characteristics of adaptive value to capitalise upon the high light environment of the forest. They showed prolonged and faster extension growth and leaf production, shorter dormancy phase and syleptic branching. In contrast, late successional had shorter period of slow extension growth, longer...
dormancy phase and proleptic branch production. The sparse branch arrangement of early successional facilitate better leaf exposure and light penetration through different canopy layers. This along with longer growth period partly account for faster growth rate of these species. The early successional had more acute placement of branches under forest grown conditions when compared with late successional under similar conditions. This helps in putting up the canopy as light as possible. The late successional under similar conditions show more horizontally oriented branches in order to maximize on photosynthesis under low light regimes. Besides, the production and contribution of the first order branches to the total framework work of the branch complex was much higher in early successional species than in late successional ones.

The architectural models of trees as conceived on purely morphological considerations (Halle et al. 1978) have no relation with adaptation to different light regimes in a community. However, the finer architectural development patterns do have adaptational overtones as shown by us. Thus, intrinsic growth rhythms are more in early successional trees than in late successional ones. Branch production through syllepsis in early successional is a mechanism to deploy an extensive branching system to avoid shade due to overlap of leaves from the parent shoot which is further helped by plagiotropism and hypopodium often developed in sylleptic branches. This growth pattern with heavy shoot tip abortion in the first and second order branches of the lower canopy positions helps in the development of an excurrent crown form in early successional trees. On the other hand, the production of proleptic first and second order branches in the late successional species over a brief period of time with greater emphasis being placed on production and extension of second order branches helps in developing a broader tree crown where the leaves are placed more peripherally to maximize photosynthesis under the shade of the forest canopy.

Bifurcation ratio (Rb) has often been used as an index of branch organization. According to Whitney (1976), based on his study on temperate deciduous trees, the early successional species should have a higher Rb value in view of the fact that the first order branches are vertically placed with less forking. This generalization, based on inadequate data from a range of ecological conditions, is contrary to our own observations where the contribution of first order branches to the total framework of branch system of early successional was very high. In view of the variability observed in the bifurcation ratio, depending upon the species and the environment in which it grows, it cannot be used for obtaining ecological generalizations on tree growth and adaptation (Boojh & Ramakrishnan 1982c).

**Leaf Dynamics**

Our studies on leaf demography and dynamics of humid forests at low (Shukla 1981) and high elevations (Boojh & Ramakrishnan 1982b) suggest the following broad generalizations.

The dynamics of leaf population of early and late successional species indicates the potentials that enable them to perform their role in the ecological niche they occupy in the forest. Early successional through extended period of leaf production have a large photosynthetic area to exploit effectively temporary conditions of resources availability which follow disturbance. The high turnover rates of leaves may be associated with the tendency of these species to achieve fast growth by always placing their leaves in a favourable light environment. Studies on some tropical trees suggest that the rapid growth of early successional species does not lie in particularly efficient energy conversion but rather in their capacity for unrestricted leaf production (Coombe & Hadfield 1962). Late successional species which have a brief leaf production and with determinate growth strategy for the high elevation montane species, have evolved this strategy for the high elevation montane species, have evolved this strategy to suit the competitive late successional environment.

Leaves change their activity with age; in particular their photosynthetic activity rises to a plateau and then declines. Hence the population of leaves that constitute a canopy should have a function determined by the age structure and age-specific photosynthetic activity of the leaves. Thus, apart from having leaves of younger age groups, early successional trees have fewer age groups as mutual shading of a large number of categories would reduce their performance. The late successional species being shade adapted pack leaves of various age groups in their crown, and this is more pronounced in the forest-grown trees of this category.

For early successional species, the net population size was greater during the favourable growing season. They showed greater fluxes of births and deaths than late successional species. These have, thus, developed a competitive attribute in the form of large leaf population and an extended period of photosynthetic activity. In late successional species, the lower flux of leaf modules, especially in forest grown situations, can be attributed to their rapid adjustment in growth in response to local depletion in resources arising during competition.

**Biomass Allocation and Productivity**

The early successional and late successional species differ significantly with respect to biomass allocation pattern and productivity (Shukla 1981). The former allocate more to the shoot system at the expense of the root system in order to put up the canopy as high as possible for exploiting the high light energy
environment in early successional communities. Further early successional species had major biomass of the root system in surface layers of the soil profile which though would provide only weak physical support would give enough absorptive system to exploit the short term increase in nutrient availability associated with disturbed sites. On the other hand, more uniform distribution of root system through deeper depths of the soil profile in late successional species and yet with more root biomass in deeper layers of the soil would be helpful in drawing nutrients from these layers over a longer period of time.

The allocation to the bole compartment in early successional species is much higher than in late successional ones. This along with greater clean bole length of the former (due to faster self-pruning of the lower branches) helps in the vertical upward movement of the crown for maximum exploitation of high light intensity by a larger and deeper crown with a higher leaf area index.

Both biomass and productivity for early successional was higher than that for late successions due to faster growth rate, larger leaf area and faster turnover rates for the leaves, compared to late successional. However, this difference between the two categories was more obvious with respect to shoot productivity alone. When a range of age classes up to seven years was compared for the two categories, the NPP for early successional species was steeper up to 5 years followed by a decline, while the late successional species showed exponential growth throughout, which is in agreement with the observations of Leburn and Gilbert (1954) for tropical forest pioneers in Zaire.

The author considered the growth strategies of trees related to productivity at some length as it was felt that this kind of research on tropical trees has considerable importance for a country like ours where forest management has yet to be based on firm scientific footing. Apart from the academic value of this kind of work for tropical trees about the growth characteristics of which we know so little, such an approach for different tree species from diverse ecological zones of the country has much value for exploiting indigenous tree species for mixed forestry management and for agro-forestry systems with a view of optimizing biomass production (Ramakrishnan et al. 1982). In fact, as next step, such studies at the sub-specific level as was done by us for Schima wallichii populations from different altitudes in Meghalaya and in the case of Schima khasiana (Boojh & Ramakrishnan, 1982d, 1983) would help in identifying faster growing ecologic races as was possible in the former species.

Grassland Productivity

An understanding of the productivity of grasslands from diverse climatic zones of the country and under varied levels of biotic pressures is important to formulate land use and grazing strategies. While this problem has received considerable emphasis for the temperate zone grasslands, much less is known for the tropics and subtropics. However, there is a growing awareness of the need to formulate grazing strategies which would allow maximum and herbage use without deterioration of the land (Swatzman & Singh 1974, Whyte 1977, Singh & Joshi 1979b, Singh et al. 1979).

In the tropics, very often the grasslands are created and maintained due to a complex of biotic pressures like grazing, fire, shifting agriculture and clear-cutting of forests. This is particularly true for the Indian subcontinent where the grasslands represent successional communities stabilized under biotic disturbances (Raman & Verma 1963) or are conversions from forests that are maintained due to fire (Whyte 1977) as in the Western Ghats (Bharucha & Shankarnarayan 1958).

Productivity Patterns

Much of the published reports on NPP of Indian grasslands based on periodic harvests of aboveground replicate samples, often belowground productivity is ignored. However, for comparisons an estimated value of 40% (Varshney 1972) has been added up to the data presented in table 5 make comparisons valid, though others have reported a lower (32% of the total) for a grassland at Kurukshetra (Singh & Yadava 1974) and as much as 52% of the total for a grassland at Varanasi (Choudhury 1972). The grasslands considered here range from short, sparse herbaceous communities with clearly visible bare soil to tall and dense ones. NPP of grasslands varied depending upon the soil, the total annual rainfall and its seasonal distribution. A prolonged dry period of up to 9 months greatly restricts the growing season and consequently the productivity. Thus, NPP may be reduced by half during winter season and even more during the summer season compared to that during the monsoon season (Singh & Yadava 1974). Inspite of this, many moderately grazed tropical grasslands have a better efficiency of energy capture compared to many temperate grassland types (Leith 1975).

A wide range of NPP is reported (180-3810 g m⁻² yr⁻¹) for different grassland types. A very low value of 40 g m⁻² yr⁻¹ for desert grassland at Jodhpur was reported by Gupta et al. (1972) for a dry year in which the annual rainfall totalled only 927mm. On sites with 700-1000mm of annual rainfall total NPP ranged from 650 to 3810 g m⁻² yr⁻¹ within this narrow range of rainfall and this may be due either to one or a combination of factors including rainfall periodicity, evapotranspiration rate, soil permeability, fertility, species characteristics and grazing pressure (Murphy 1975). The maximum value of 3810 g m⁻² yr⁻¹ was measured in a Heteropogon contortus dominated grassland near Varanasi receiving over 1000mm of
annual rainfall. Murphy (1975) has shown a relationship between the total annual rainfall and the total NPP for tropical grasslands in India, Australia and Africa. Singh and Joshi (1979b), however, suggest that the NPP is more influenced by botanical composition than by environmental parameters such as rainfall; though one may argue that the former is a function of the latter. Considering a number of grassland types of varied degrees of disturbance, Singh and Misra (1969) conclude that species diversity increases production efficiency of the system while dominance makes the system stable.

The most comprehensive account on grassland productivity is provided by Singh and co-workers at Kurukshatra (Singh & Yadava, 1974. Singh & Joshi 1979a). The results on seasonality obtained by them could be considered to generalize the pattern under monsoonic climate. NPP of the aboveground parts was maximum during the rainy season of June-September and minimum during the dry winter season. According to them the higher aboveground production during the summer season as compared to the winter seems to be associated with a greater rainfall during the summer. On the other hand, belowground NPP as well as production rate were maximum during the winter season and minimum during the rainy season; this being intermediate during the summer. According to them, low temperature and xeric conditions during winter favour the belowground production. While the effect of dry conditions on promoting belowground production is well known, they suggest that lower temperature may promote downward translocation of the assimilates with lower respiratory loss. The turnover rate for the belowground biomass (belowground NPP maximum belowground biomass) suggested that the biomass replacement was maximum during winter (67%), minimum during rainy season (14%) and about 26% during the summer. The roots of the annuals and perennials die at the end of the rainy season, new root growth occurring chiefly during winter and for some species may also be during the summer season; maximum root biomass per unit area was during the rainy season. The high annual turnover rate of 0.97 is indicative of the high dynamic nature of the belowground parts and that most of it is replaced each year. Compared to this, the turnover values for a temperate grassland ranged from 0.19 to 0.68; the belowground net productivity was much lower (104–1699 g m⁻² yr⁻¹), though the belowground biomass was very high (2540 g m⁻²) indicating a low rate of replacement (Sims & Singh 1971).

Golley (1972) made a comparison of NPP of grasslands with forest types (tables 1 and 4) and suggested that this equaled or exceeded that of forest types in a given area. Thus, the net productivity of 1550 g m⁻² yr⁻¹ for a tropical deciduous forest at Varanasi (Misra 1972) was lower than that reported for grassland in the same area (which may go up to 3810 g m⁻² yr⁻¹) (Amvasth et al. 1972).

The reasons for equal or even higher NPP productivity of tropical grasslands compared to forest types in the same area or even a generally higher level of productivity compared to temperate grasslands may be two-fold: (i) It is well known that during succession, NPP usually reaches a maximum (Toky & Ramakrishnan 1983a, Singh & Ramakrishnan 1982) at some point before the climax or steady state is attained. Grasslands in India, representing a seral stage leading to a climax forest, may be at that point when productivity reaches its maximum; (ii) the C₄ photosynthetic strategy of many tropical grasses permits higher productivity under conditions of water stress and higher temperature conditions. The prolonged drought for a major part of the year under a monsoonic climate and brief spells of drought even during the monsoon and higher temperatures for a major part of the year are the conditions under which our grasslands are developed. The significance of this strategy in a successional community in north-east India has been considered in detail by Saxena and Ramakrishnan (1983a, d) and showed that C₄ strategy is better suited for early successional open communities and that these communities show higher numbers and biomass for this category of species compared to that met with in late successional herbaceous communities of a closed environment.

Productivity and Grassland Management
Tropical grasslands need to be managed more effectively to maintain soil fertility, prevent soil erosion and above all to provide sustained yield for livestock maintenance. The task is to evolve a strategy for grazing intensity and duration to remove excess production which would otherwise contribute to the successional process leading towards a forest. Further, under a monsoonic climate, aboveground productivity is low during the drier parts of the year. These considerations make tropical grassland management distinct from those climax types of the temperate climate.

In a well-managed temperate grassland, about 40% of NPP may be recovered before the grassland starts deteriorating. However, with so much variation in climate, soil and biotic pressure under which Indian grasslands are developed, it is difficult to have an approximation: this is particularly true when the productivity and biomass allocation between the aboveground and belowground parts are different from temperate grasslands (Singh & Yadava 1974). Only scant attention has, however, been paid to develop models for formulating grazing strategies for our grasslands.

One of the few attempts made to predict and formulate grazing strategies for maximum herbage utilization is that of Swartzman and Singh (1974) for
grasslands at Varanasi. Their model is based on
incomplete though relatively larger data base for these
glossland types and simulating successions on an alluvial
glossland, though such a model is partly based on
conjecture, simplified assumptions and on arbitrary
determination of objectives, as the authors themselves
suggest. For a 12 year period, they suggest 5 years of
moderate grazing gollowed by a year of light grazing
and then 6 more years of moderate grazing. The poor
data base raises questions such as the balance between
legumes and non-legumes, which prolonged moderate
grazing is suggested to adversely affect.

Recently, Kumar and Joshi (1980) examined the
effect of grazing and site differences on energy caput-
ture by semi-arid glossland communities and found
maximum efficiency in exclosures and in moderately
grazed communities. The energy capture by Cenchrus
ciliaris pastures under various defoliation stresses has
been discussed by Shankar et al. (1976). While many of
these studies pertain to isolated observations on one or
more components of the glossland ecosystem, more
comprehensive studies on productivity as part of the
ecosystem function should be undertaken so that the
information obtained by this holistic approach could be
applied for developing strategies for glossland man-
gement.

Aquatic Productivity

Inland Aquatic Systems

Photosynthetic fixation of carbon in inland aquatic
systems may occur through phytoplankton, macro-
phytes and periphyton. However, the information on
the productivity of the latter two groups of organisms is
meagre. Yet productivity by macrophytes may be
significant in fertile sites and in shallow waters (West-
lake 1966, Likens 1975). In fact, very few studies are
available in the literature of complete production
analysis of freshwater systems of the kind available for
Lawrence lake, Michigan and Mirror lake, New Hamp-
shire, U.S.A. (quoted by Likens 1975). Such a com-
plete budget analysis for organic carbon fluxes through
freshwater systems is not available for freshwater systems
not available for freshwater bodies in India.

While many papers have been published on descript-
tive limnology and aquatic weeds (Varshney & Rzoska
1976), a functional aspect of the aquatic ecosystem such
as productivity has received little attention in this
country. Much of the information available is rather
fragmentary. The available information, to date, on
inland aquatic production was summarized by Golley
(1972). Ganapatia (1972) considered different aquatic
systems and showed that the productivity of temple
ponds and lagoons to be highly productive, with rivers
and estuaries least productive, though such high annual
rates for fish ponds and lagoons as calculated from daily
rates seem to be overestimates.

The lake systems of Kashmir Himalayas has received
relatively greater attention from the point of view of
phytoplankton production (Kaul et al. 1978a, Khan &
lake in the Kashmir Himalayas, Khan and Zutshi
(1980) reported a productivity range of 90 to 100 g C
m⁻² yr⁻¹ for this mesotrophic water body and suggested
that it compared with the reported value of 104 g C m⁻²
yr⁻¹ for a similar lake in Sweden, though such a
comparison between two lakes from two diverse
geographical zones is perhaps not realistic.

A few studies on freshwater systems in this country
are related to pollution problem using phytoplankton
productivity as an indicator (Zutshi 1981). Majority of
aquatic habitats in the country witness three processes
such as eutrophication, pollution and saprotrophication
running parallel to one another at differing paces.
While they are hardly distinguishable on the basis of
water chemistry, biological methods of assessing water
quality is more relevant her and yet has not received as
much attention as it deserves. Sreenivasan (1963)
showed correlation between lake typology in southern
India and primary organic production. He suggested
that the Kodoikanal lake is oligotrophic with low
productivity and a dominance of desmide while Yar-
cand like is entrophic with high productivity and a
bloom of Microcystis aeruginosa. More recently,
Zutshi et al. (1980) compared the limnology of nine
lakes of Jammu and Kashmir Himalayas and showed
that lakes with low fertility level had a phytoplankton
of diatoms and chlorophyceae chiefly contributing to
productivity whereas in eutrophic lakes cyanophyceae
predominate.

The information available on macrophyte productivity
is even more meagre. Sahai and Sinha (1976)
compared the productivity of a few selected macro-
phytes in polluted and nonpolluted regions of a lake of
eastern U.P. and concluded that productivity could be
31 to 93% less in the polluted areas for some of the
species studied. Again working near Varanasi in
eastern U.P., Ambasht and Ram (1976) suggested
three types of productivity profiles for selected macro-
phytes: (i) an upright triangle type for species whose
photosynthetic biomass is concentrated just above the
basal layer of water like Oryza rufipogon, Eleocharis
plantaginosa and Vallisneria spiralis; (ii) the inverted
triangle type for other submerged species such as
Hydrilla verticillata and Najas graminea whose pho-
tosynthetic biomass is greatest at depths of 20 to 40cm
and (iii) the flag type represented by floating species of
Nymphaeaceae and Pontederiaceae, Kaul et al. (1978b)
gave a range of 4.25 to 17.5 g m⁻² day⁻¹ for emergent
macrophytes of some Kashmir lakes depending upon
the species and consider that this community contrib-
uted about 50% of the total biomass of macrophytes.
Marine ecosystem

While much of the information on marine productivity on a global basis has been summarised by Bunt (1975) and the estimate for total oceanic primary production is placed at \(23 \times 10^9\) metric tons C\(^{-}\) yr\(^{-}\) we ought to have detailed information for different zones along the coastal areas of the country which is totally lacking. A few studies available represent only a segment of the ecosystem and report only productivity values of a given ecosystem (Prasad & Nair 1963) without linking it to ecosystem properties. Quasim (1979) has demonstrated the role of detritus in nutrient cycling in Indian coastal waters and as a food for fish and invertebrates.

Gopal et al. (1978) reviewed the primary productivity patterns for the macrophyte communities in Indian fresh waters and apart from synthesizing the value ranges for production as 7.2 to 7796mg cm\(^{-2}\) day\(^{-2}\) could conclude that the upper limits of production are amongst the highest reported from any where. More recently, Gopal (1987) has looked at the productivity of a single species, Eichhornia crassipes, and showed how productivity varies depending upon geographical location, of nutrient load in the water body and the harvesting regime.

Conclusions

While some excellent studies on selected ecosystem types are available, much of what is available in the Indian ecological literature on productivity of different ecosystem types such as a forest, grassland or aquatic system are often fragmentary. Traditional Agroecosystems are least studied from an ecological view point (Mitchell 1979) though some agronomic studies on these and other intensely managed agroecosystems are extensive. On others, such as marine, marsh and swamp, mangrove and desert ecosystem types, little is known. Future studies on productivity of different ecosystems should be addressed to problems of the sub-continent such as climatic patterns related to latitude, community succession, fragility to perturbations and that related to functional attributes at the level of the community and ecosystem. The individual approach to productivity may be related to photosynthetic efficiencies and growth strategies such as canopy architecture. Population approach may also be related to canopy structure related to numbers in pure and mixed stands (Ramakrishnan 1972, Ramakrishnan & Kumar 1971a, b, Monsi et al. 1973). The ultimate objective should be better management of our ecosystem types for the benefit of man.

References


---- Maurya A N and Singh U N 1972 Primary production and turnover in certain protected grasslands of Varanasi, India; in Tropical Ecology with an Emphasis on Organic Production pp 43-50 eds P M Golley and F B Golley (Georgia: Univ. of George)


Bharucha F R and Shankarnarayan K A 1958 Studies on the grasslands of the Western Ghats India; J. Ecol. 46 681-705


---- Chen T M and Brown R H 1969 Biochemical basis for plant competition; Weed Sci. 17 328-344


---- and ---- 1982b Growth strategy of trees related to successional status II. Leaf dynamics; Forest Ecol. Manage. 4 375-386

---- and ---- 1982c On bifurcation ratio in Schima species; Curr. Sci. 51 436-437

---- and ---- 1982d Growth and architecture of two altitudinal populations of Schima wallichii; Proc. Indian natn. Sci. Acad. B48 534-545

---- and ---- 1983 The growth pattern of two species of Schima; Biotropica 15 142-147

Borchert R and Slade N A 1981 Bifurcation ratios and the adaptive geometry of trees; Bot. Gaz. 142 394-401

Bormann F H and Likens G E 1979 Pattern and Process in a Forested Ecosystem (New York: Springer-Verlag)


Brown R H 1978 A Difference in nitrogen use efficiency in C\(_3\) and C\(_4\) plants and its implication in adaption and evolution; Crop. Sci. 18 43-48

Bunt J S 1975 Primary productivity of marine ecosystems; in Primary Productivity of the Biosphere eds H Leith and RH Whitaker (New York: Springer-Verlag)

Caldwell M M 1974 Carbon balance and productivity of two cool desert communities dominated by shrubs possessing C\(_3\) and C\(_4\) photosynthesis; Proc. 1st Internat. Conf. Ecol. 52-56

Chowdhary V B 1972 Seasonal variation in standing crop and net above ground production in Dichanthium annulatum grassland at Varanasi; in Tropical Ecology with Emphasis on Organic Production pp 51-57 eds P M Golley and F B Golley (Athens: Univ. of Georgia)

Chaturvedi O P and Singh J S 1982 Total biomass production of Pinus vexburghii trees growing in all aged natural forest; Can. J. Forest Res. 12 632-640

Coome D E and Hadfield W 1962 An analysis of growth of Musanga cecropioides; J. Ecol. 50 221-234

Clements F E 1916 Plant Succession (Washington: Carnegie Inst.)

Ekanoboji J K 1975 Dry matter production by an immature stand of Pinus caribocca in Nigeria; Oikos 26 80-85

Forrest W G and Ovington J D 1970 Organic matter changes in an age series of Pinus radiata Plantations; J. appl. Ecol. 7 177-186

Ganapati S V 1972 Organic production in seven types of aquatic ecosystems in India; in Tropical Ecology with an Emphasis on Organic Production pp 313-351 (Georgia: Univ of Georgia)

Garg R K and Vyus L N 1973 Litter production in a deciduous forest near Udaipur (South Rajasthan), India, in Tropical Ecological systems pp 131-135 eds F B Golley and E Medina (New York: Springer-Verlag)

Gifford R M 1974 A comparison of potential photosynthesis, productivity and yield of plant species with differing photosynthesis mechanisms; Austr. J. Pl. Physiol. 1 107-117

Golley F B 1972 Summary in Tropical Ecology with an Emphasis on Organic Production pp 407-413 eds PM Golley and F B Golley (Athens: Georgia Univ. of Georgia)

Golley P M and Golley F B (eds) 1972 Tropical Ecology with an Emphasis on Organic Production (Georgia: Univ of Georgia)

Gopal B 1987 Water Hyacinth (Amsterdam: Elsevier)


Khan M A and Zutshi D P 1980 Contribution to high altitude limnology of the Himalayan system. 1. Limnology and primary productivity of the plankton community of Nilmag lake, Kashmir; Hydrobiologia 75 103-112

Kotwal P C and Mall L P 1977 Litter production and disappearance in tropical dry deciduous forests near Ujjain; Ann. Arid Zone 16 111-116

Kozlowski T T 1964 Shoot growth in woody plants; Bot. Rev. 30 335-392

Kumar A and Joshi M C 1980 Grazing and site difference affecting energy storage and energy conserving efficiency in grassland communities at Pilani, Rajasthan, India; Trop. Ecol. 21 1-8

Lebrun J and Gilbert G 1954 Une classification écologique des forêts du Congo; INEAC Bbursel Publ. 63 1-89


Likens G E 1975 Primary production of inland aquatic ecosystems; in Primary Productivity of the Biosphere pp. 185-202 eds H Leith and R H Whittaker (New York: Springer-Verlag)

Madwick H A J 1970 Biomass and productivity models of forest canopies; in Analysis of Temperate Forest Ecosystems pp 47-54 ed. D E Reichle (New York: Springer-Verlag)

Marks P L 1975 On the relation between extension growth and successional status of deciduous trees of the north-eastern United States; Bull. Torrey Bot. Club. 102 172-177


—- and —- 1983 Slash and burn agriculture at higher elevations in north-eastern India. I. Sediment, water and nutrient losses; Agric. Ecosyst. Environ. 9 69-82

—- and —- 1983b Slash and burn agriculture at higher elevations in north-eastern India. II. Soil fertility changes; Agric. Ecosyst. Environ. 9 83-96

—- and —- 1983d Secondary succession subsequent to slash and burn agriculture at higher elevations of north-east India. I. Species diversity, biomass and litter production; Acta Oecologia. Oecol. Appl. 4 97-107

Misra R 1972 A comparative study of net primary productivity of dry deciduous forest and grassland of Varanasi, India; in Tropical Ecology with an Emphasis on Organic Production pp 279-293 eds M Golley and F B Golley (Athens Georgia: Georgia)


Mitchell R 1979 The Analysis of Indian Agрогeосystems; (New Delhi: Interprint)


Murphy P G 1975 Net primary productivity in tropical terrestrial ecosystems; in Primary Productivity of the Biosphere eds H Leith and R H Whittaker (Berlin: Springer-Verlag)

Pandey U and Singh J S 1981 A quantitative study of the forest floor, litter fall and nutrient return in oak-conifer forest in Himalaya. II. Pattern of litter fall and nutrient return; Acta Oecologia Oecol. Generals 2 83-89

Pandeya S C, Sharma S C and Pandit R R 1970 Dry matter production relations of sal (Shorea robusta Gaertn.) in the reserve forest communities in river Narmada catchment area; J. Indian Bot. Soc. (Jubilee Vol.) A50 601-660

—- and —- 1972 Biomass and production relations of teak (Tectona grandis Linn.) in natural reserve forests in Central India; in Tropical Ecology with an Emphasis on Organic Production pp. 201-216 eds P M Golley and F B Golley (Athens: Univ. of Georgia)
etasad R R and Nair P V R 1963 Studies on organic production in Gulf of Manar, J. marine Biol. Assoc. S 1-26
Quasim S Z 1979 Primary production in some tropical environments; in Marine Production Mechanisms pp. 31-64
Ramakrishnan P S 1972 Individual adaptation and its significance in population dynamics; in Biology of Land Plants pp. 344-355 eds V Puri et al. (Sanita Prakashan)
—1978 Observations on biological aspects of productivity of forest ecosystems; in Glimpses of Ecology pp 194-199
(President R Mishra Commemoration Vol.) (Jaipur: International Scientific Publications)
—1980 Ecological impact of jhum (slash and burn agriculture) on forested ecosystem of north-eastern India; INSA Newsletter 60 3-7
—and—Kumar S 1971a Productivity and plasticity of wheat and Cynodon dactylon (L.) Pers. in pure and mixed stands; J. Appl. Ecol. 8 85-98
—and—1971b Mortality, plasticity and productivity of interferring model population of maize and Cynodon dactylon (L.) Pers.: J. Indian Bot. Soc. 50 321-331
—and—Toky O P 1978 Preliminary observations on the impact of jhum (shifting agriculture) on the forested ecosystem; in Resources, Development and Environme in the Himalayan Region pp. 343-354 (New Delhi: Dept. Sci. Technology, Govt. of India)
—and—1981 Soil nutrient status of hill agro-ecosystems and recovery pattern after slash and burn agriculture (Jhum) in north-eastern India; Pl. Soil 60 41-64
—Shukla R P and Boojh R 1982 Growth Strategies of trees and their application to forest management; Curr. Sci. 51 448-455
Rao, Subba B K, Dabral B G and Pande S K 1972 Litter production in forest plantation of Chir (Pinus roxburghii), Teak (Tectona grandis) and Sal (Shorea robusta) of New Forest, Dehra Dun; in Tropical Ecology with an Ephasis on Organic Production pp. 235-243 eds P M Golley and F B Golley (Athens: Univ. of Georgia)
Rodin L E, Bazilevich N I and Rozov N N 1975 Productivity of the world’s main ecosystems; in Productivity of World Ecosystems pp. 13-62 eds D E Reichele, J F Franklin and D W Goodall (Washington: National Academy of Sciences)
Sahai R and Sinha A B 1976 Productivity of submerged macrophytes in polluted and non-polluted regions of the entropic lake, Ramgarh (U.P.); in Aquatic Weeds in South East Asia pp 131-140 eds C K Varshney and J Rizoska (Hague: Dr. W Junk B V)
—and Ramakrishana P S 1982 Reproductive efficiency of secondary successional herbaceous populations subsequent to slash and burn of subtropical humid forests in north-eastern India; Proc. Indian Acad. Sci. (Plant Sci.) 91 61-68
—and—1983a Growth and allocation strategies of some perennial weeds of slash and burn agriculture (Jhum) in north-eastern India; Can. J. Bot. 61 1300-1308
—and—1983c Growth and patterns of resource allocation in Opatorium odoratum L. in the secondary successional environments following slash and burn agriculture (Jhum). Weed Res. 24 (In Press)
Shankar V, Shankaranarayan K A and Rai P 1976 Comparative study of potential growth and regrowth under various defoliation stresses in ragine grasses. II. Cenchrus ciliaris Vahl; For. Res. 1 99-105
Shukla R P 1981 Studies on Adaptive Strategy of a Few Selected Tree Species in North-Eastern India; Ph.D. Thesis (Shillong: North-Eastern Hill Univ.)
Singh J S and Joshi M C 1979a Primary productivity; in Grassland Ecosystems of the World pp. 197-128 ed RT Copland (Cambridge: Cambridge Univ. Press)
—and—Yadava P S 1974 Seasonal variation in composition, plant biomass, and net primary productivity of a tropical grassland at Kurukshetra. India; Eco Monogr. 44 351-376
—and—Misra R 1978 MAB report on structure and functioning of natural, modified and silvicultural ecosystems of eastern Uttar Pradesh (Varanasi: Banaras Hindu Univ.)
Sreenivasan A 1963 Primary production in three upland lakes of Madras State. India; Curr. Sci. 32 130-131
Swatzman G L and Singh J S 1974 A dynamic programming approach to optimal grazing strategies using a succession model for a tropical grassland; *J. appl. Ecol.* **11** 537-548
Tokyo O P and Ramakrishnan P S 1981a Cropping and yields in agricultural systems of the north-eastern hill region of India; *Agro Ecosystems* **7** 11-25
—— and —— 1981b Runoff and infiltration losses related to shifting agriculture (Jhum) in north-eastern India; *Environ. Conserv.* **8** 313-322
—— and —— 1983 A secondary succession following slash and burn agriculture in north eastern India. I. Biomass, litterfall and productivity; *J. Ecol.* **71** (in press)
—— and —— 1983b Secondary succession following slash and burn agriculture in north-eastern India. II. Nutrient cycling; *J. Ecol* **71** in press
Varashney C K 1972 Productivity of Delhi grasslands; in: *Tropical Ecology with an Emphasis on Organic Production* pp. 27-42 eds PM Golley and FB Golley (Georgia: Univ. of Georgia)
—— and Rzoska J (eds) 1976 *Aquatic Weeds in South East Asia* (The Hague: Dr. W Junk B V Publ.)
Westlake D F 1966 some basic data for investigations of the productivity of aquatic macrophytes; in *Primary productivity in Aquatic Environments* ed. C R Goldman; *Mem. 1st Int. Idrobiol.* **18** (suppl.) pp. 229-248 (Berkeley: California Univ. Press)
Whitney G G 1976 The bifurcation ratio as an indicator of adaptive strategy in woody plant species; *Bull. Torrey Bot. Clubs* **103** 76-72
Whyte R O 1977 Analysis and ecological management of tropical grazing lands; in *Handbook of Vegetation Science* Part XIII. *Application of Vegetation Science to Grassland Husbandry* pp 3-121 ed. W Krause (The Hague: Dr. W Junk B V. Publ.)