CHAPTER 7

DISCUSSION
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On the basis of duration and depth of water in the various wetlands under study, Kalamplora and Tullamulla are of temporary-shallow type while those of Kranchu and floating-islands belong to permanent shallow-type. In both these types the height of the water-level during the growing period does not exceed 75 cm. In the temporary-deep type wetland of Shalbogh and the permanent-deep type wetlands of Hokersar and Narkora, the water depth, however, exceeds the above mentioned limit. The permanence, according to Steward and Kantrud (1972) is a measure of the extent to which surface water persists at a given site and is, together with the relative height of water-level, determined by the
interaction of such hydrological factors as the amount of water brought in by the feeding channels and the situation of the overflow channel. The temporary wetlands, located in the flood plain of the rivers, have their basins and overflow channels in level with the emergent zone, and with the general decline in the water-level during autumn and winter months, the substratum in these wetland types gets exposed due to the severance of connection with the water-shed (rivers). On the other hand, the permanence of water at Hokersar and Kranchu is maintained, because of their location at the end point of the drainage system, as both the wetland types do not possess any well defined outlet late in the growing season. At Narkora, where the overflow channel is sufficiently above the basin surface, the water supply during the winter months is maintained by the seepage water oozing out of the springs spread over its bed.

The annual amplitude of water level fluctuations, in general, depicts an increase during spring against a fall during autumn in all the wetlands except the one at Kranchu. The increase in spring is the result of liberation of winter precipitation in the catchment areas as the snow melts. The meltwater from the higher regions being carried into the wetlands by the feeding channels or into the rivers, wherefrom the feeding channels arise. The wetland at Kranchu is peculiar in sustaining an increased water depth towards the end of summer and a low level in June as a result of the diversion of feeding channels towards the agricultural fields from time to time. The rhythmic fluctuations in water-level during the course of one solar year (ecoperiod) and the frequency and
amplitude of fluctuations in addition to the height of water-level preserved during a certain time interval (ecophase) have been distinguished into three ecophase sequences viz. i) Hydro-littoral sequence of ecophases, characterized by stabilized water-level, ii) Littoral-terrestrial sequence of ecophases, with a distinct fall of water-level or with its complete disappearance and iii) Terrestrial-littoral sequence of ecophases with a distinct rise of water-level, by Hejny (1960, 1971). These three ecophase sequences at the wetlands of Malangpora, Tullamullu and Shalbogh last from May-August, August-March and March-May; while at Krianchu they last from November-March, March-July and July-November respectively. A single ecophase of hydro-littoral with relatively little water level fluctuations can be said to prevail at Harora and Hokersat wetlands. The floating-islands composed of the light weight of a network of roots and rhizomes show a rise and fall in accordance with the oscillations of the water-level underneath, with this type of mobility preventing their inundation for the major part of the year. The buoyancy, of course, is no use to ward off submergence during heavy rains and the associated high water level. The water rising through the capillary spaces inbetween the tangled masses, thus, records a rise of a few centimeters early in the growing season.

The surface water temperature at the various wetland sites changed in a similar pattern as the air temperatures during the course of the solar year. The relatively lower water temperatures as compared to the mean air temperature at
Tullamulla and Shalbogh during March-October (3.4°C and 4.77°C lower at the two sites respectively) were due to the impact of the cold water brought into the wetland sites by the tributaries of the River Sind. The annual cycle of oxygen, however, depicted an inverse relationship with the thermal cycle. The higher values recorded in the permanent wetland types both during winter and spring, and in temporary wetland types early in the growing period, were followed by a fall towards the summer. According to Edberg and Hofstein (1973) the oxygen consumption depends both on the rate at which oxygen is transported down into the sediments and the rate at which reduced substances are conveyed up into the water, while according to Alsterberg (1922) intense decomposition processes in the sediments can give rise to oxygen free conditions in the overlying water. In shallow wetlands, because of relatively small volume of water in relation to the area of contact with sediments, oxygen consumption is fast and as such low oxygen concentrations falling even below 3 mg/l are detected during summer. The higher mean annual content of oxygen at Tullamulla as compared to Malangpora is due to continuous replenishment of water by cold water of the feeding channels at the former site against the almost stagnant conditions at the latter site. In the deeper wetlands, on the other hand, the higher mean annual values prevail on account of larger volume of water, slower diffusion and lower consumption during winter months at the permanent wetland sites.

The waters, in general, are alkaline, with pH ranging
between 7.1 - 9.4. The pH depending upon the amount of carbonates of calcium and magnesium and the carbon dioxide tension in water is very much influenced by the photosynthetic activity of aquatic macrophytes. The increased photosynthetic activity resulting in greater utility of carbon dioxide during summer is, thus, responsible for the higher pH values as has also been observed by Nasser and Dutta Munshi (1974) and Otsuki and Wetzel (1974). The lower values for pH prevalent in spring and autumn are, on the other hand, obviously due to the increased decomposition under the retarded water-level during these seasons.

The alkalinity is principally due to bicarbonate ions and the waters fall within the hard water type as per classification of Boyle (1945). It depicts a marked seasonal variation, the values increasing towards autumn and winter and showing a decrease towards summer. The decrease in alkalinity during summer associated with an increase both in pH and temperature is, according to Wetzel (1960, 1973) largely biogenic in origin and a result of photosynthetic utilization and induced precipitation of carbon sources. A seasonal trend similar to that of alkalinity was observed for conductivity which is assumed to be due to two most dominant ions viz. bicarbonates and calcium (Wetzel, 1973, Otsuki and Wetzel, 1974). The specific conductance in the temporary wetlands showed drastic changes as the salt concentration kept on increasing or decreasing alternately as a result of increased or decreased, due to losses caused by evapo-transpiration, water depth. The mean specific conductance of the wetland waters, however, increased in progression from Hokersar (284 μS/25°C) to
Shalbogh \((294 \text{ uS/25°C})\) to floating-islands \((310 \text{ uS/25°C})\) to Tullamulla \((378 \text{ uS/25°C})\) to Narkora \((385 \text{ uS/25°C})\) to Malangpora \((434 \text{ uS/25°C})\) and to Kranchu \((619 \text{ uS/25°C})\), revealing the increased water depth together with the presence of effective means for the removal of accumulated salts through the outflow waters to be limiting to the build up of soluble salts. The higher mean conductivity at Tullamulla and Shalbogh wetland basins as compared to the inflowing tributary streams can be explained on the presumption that some particulate inorganic matter dissolves after entering the wetlands.

The average annual values of calcium, ranging between \(27-38 \text{ mg/l}\) except at Shalbogh site \((24 \text{ mg/l})\) would put them in the 'calcium rich' types of Ohle \((1934)\). However, the calcium content in all the wetlands during summer falls below \(25 \text{ mg/l}\) - the border area between 'calcium rich' and 'calcium medium' types - as the decalcification, under increased atmospheric temperature and biological activity during this season takes place due to the formation of insoluble \(\text{CaCO}_3\). Letzel \((1974)\), while studying a marl lake in Michigan arrived at similar conclusions besides obtaining a linear correspondence of observed differences between vernal value of calcium and total alkalinity. The lack of any such proportionality between the two parameters in the present study can, however, be attributed to the high decomposition of organic matter in the wetland basins. During this process, the H-ions formed by the oxidation of carbohydrates exchange with adsorbed cations to release equivalent amount of bicarbonate ions \((\text{Johnson}, 1975)\). And because of this increased
supply of bicarbonates, the depletion of alkalinity during summer months is disproportionate to that of decalcification.

Magnesium, in contrast to calcium, depicted an inconsistent trend in the various wetland sites with somewhat higher values prevailing both in spring and autumn. The same was true for sodium, while potassium, on the other hand, showed a definite seasonal trend by way of an increase in autumn and decrease in summer, the increased concentration during July-August being the result of the flushing in of the mineral from the surrounding lands.

The cation progression for the wetland sites, in general, is very much in accordance with Fother's (1949) generalized scheme of \( \text{Ca} > \text{Mg} > \text{Na} > \text{K} \) for the freshwaters, resulting in extremely low monovalent : divalent ratio. And the combination of extremely high divalent cation concentrations, low monovalent : divalent cation ratios, high carbonate anionic levels and high pH are the characteristics of hard water fresh water bodies, creating extremely unsatisfactory osmotic conditions for the assimilation of nutrients (Wetzel, 1973).

The natural loading of phosphorus in aquatic bodies originates from the inputs from the sediments and the drainage basin while the losses occur through the precipitation and adsorption with sediments and the biological activity in water column. Evidences from the existent literature concerning the role of sediments in controlling the \( \text{PO}_4 \) concentration in waters show the latter to be sort of "stores" where phosphorus is accumulated or from which it is released according to the various physico-chemical factors (Mortimer,
1941, 42; Hutchinson, 1959; Stumm and Morgan, 1970). The substantiating data from these studies indicate the bottom sediments having specific properties as regards the buffering of $P_{O_4}$ concentration in water. Such a phosphate buffering by bottom sediments has been opined to depend upon its concentration in the water (Kufel, 1976), pH (MacPherson et al., 1958; Kufel, 1977), sediment structure (Kufel, 1976, 77), sorption with iron and aluminium compounds (Sukla et al., 1971; Harter, 1968) and the solubility products of some phosphate salts such as hydroxyapatite $[Ca_5(Po_4)_3(OH)]$, calcium phosphate $[Ca_3(Po_4)_2]$ and ferric phosphate etc. (Hepher, 1958; Golterman, 1973). Lee (1970), however, does not contribute to the control of phosphate concentration by a particular insoluble salt since i) sediments consist mainly of amorphous material and it is doubtful to find any defined mineralogical species and ii) many natural waters contain calcium and phosphate in concentrations greatly exceeding solubility product. The content of $P_{O_4}$ in water is also mediated by the rooted macrophytes, which by absorption during growth and subsequent release upon decomposition represent a contribution from the sediments (Boyd, 1970).

The variation in the $P_{O_4}$-P concentrations in the waters of the wetlands under study are likely to be a function of the drainage basin; as the higher mean concentrations are observed in the wetlands which are in the immediate vicinity of the agricultural lands. Such a pattern at Malangpora and Narkora is associated with an increase in $P_{O_4}$-P concentration during rains (July-August) when the nutrients get leached from the surrounding lands. The decline in its concentration
from spring to late summer can, however, be attributed to the biological assimilation and to its coprecipitation with the inorganic compounds, as has also been reported by Akira and Wetzel (1972) and Einsele (1938). The coprecipitation rate of phosphorus has experimentally been shown to be dependent upon CaCO₃ solubility and temperature up to pH 9 by Ostuki and Wetzel (1972) and both the conditions for the depletion of phosphate-phosphorus, prevail within the wetland waters under study during the summer months.

Nitrate-nitrogen is the most abundant nitrogen source in these wetlands, though its leaching due to the lack of nitrate-nitrogen complexes and high solubility is well known (Mackenthun and Ingram, 1967). The increasing nitrate-nitrogen concentrations towards winter and spring may be attributed to the combined result of nitrification at the mud-water interface and the vigorous stirring of wetland waters which eliminate any type of limitations for oxygen diffusion. Chen, Keeney and Konard (1972) opined the sediments not adding any appreciable amounts of nitrate-nitrogen to water except in well oxidized stirred situations such as might be occurring in shallow areas of the wetlands under study. Increased standing crops of autotrophic organisms by uptake and accumulation in their body (Symous et al, 1964; Cushing, 1964) are apparently causative for the decreased concentrations of nitrate-nitrogen during summer.

Nitrite-nitrogen and ammonical-nitrogen seem to have an insignificant role in comparison to nitrate-nitrogen which is the main source of nitrogen in the present study sites. The
low amounts of nitrite-nitrogen detected are in conformity with the tendency for rapid transition between nitrate-ammonia and molecular nitrogen. Nitrites, under such conditions, have a very short residence time in water (Alexander and Barsdate, 1971); while the losses of ammonical-nitrogen also occur through their immediate utilization by plankton and other plants without the consumption of any extra-energy for chemical reduction (Dugdale and Dugdale, 1965; Procházkova et al., 1970, 75) or through "adsorption" to some extent (Lee, 1970; Dolejskova and Kover, 1971).

The nutrient levels appear to be biologically mediated and as a result high levels of nutrients occur due to the mineralization of previous year's dead organic matter during spring and autumn. The periodic drying and flooding have been thought to renew the habitat and in consequence enrich it in minerals by Pięczynska (1975), and this fact is clearly illustrated by the unusual water-level fluctuations at Kranču where the increased mineral concentration in June, when the water-level is at its minimum, decreases from July onwards after the habitat gets flooded. The phenomenon is further supported by the observations made in other wetland sites that were studied for comparison purposes, where with no fall in the water-level in June, the mineral concentration from May-July did not show any such increase at all. This obviously is in conformity with the view that the increased aerobic decomposition of organics is caused by a drop in the water-level (Mønsjo, 1969) and is further substantiated by the relatively much more increase in the salt content of the temporary wetlands as compared to the permanent ones towards ending summer. In the temporary wetlands, the exposure and
eration of the dead macrophytes, left on the mud surface during the drawdown speeds up leaching and decomposition (Cook and Powers 1958; Kadlac 1962; Harris and Marshall 1963); with the subsequent flooding bringing about mineralization and solution of the nutrients, and thus releasing them back into the cycle in an available form.

The thus increased mineral content, in addition to that brought in by the feeding channels, form the initial supply for the next growing season. The low level of minerals prevalent in this season is, however, concomitant with an increase in the biological activity as is reflected by an increase in the macrophytic biomass. These macrophytes accumulate nutrients in excess of their demand, a phenomenon described as 'luxury' uptake by Gerloff and Kantihalz (1966).

The amounts of phosphorus in the macrophytic communities represent a large pool of phosphorus unavailable to other organisms and pathways (Twilley, 1976). These and the interrelated phenomena like the amount of soluble salts in the soil available for solution by ground water, the concentration of ground water, the permeability of the soil, the height of the water table and the topographical position of the wetlands etc., as outlined by Driver and Peden (1977), have a profound influence upon the water chemistry of the wetlands.

The substrate analyses indicate the particle size of the wetland sediments to depend upon the inflow of the eroded material brought in by the feeding channels. Both the Shalbogh and Tullamulla wetlands, fed by the swiftly flowing tributaries of the River Sind, showed the highest content of sand while the silt and fine sand were almost equally predominant at the Hokersar and Narkora sites, fed by the relatively slow
flowing off-shoots of the Flood Channel and the Doodganga River respectively. In the two wetlands of Kranchu and Malangpora, receiving runn-off waters from the agricultural fields and being normally cut off from the River Jhuleum, the sediments are mainly clayey. The floating-island soils, mainly composed of the underground parts of the plants, are highly organic. Studies pertaining to bottom sediments, elsewhere, point to their diverse character depending upon depth and distance from shore (Entz et al, 1963; Bernatowicz and Zachwieja, 1966; Hart et al, 1976). Because of the differential settling rates of the various particle size classes sedimentation leads to the development of distinct zones of sand, silt and clay with increasing depth (Mortimer, 1949; Tadajeswaki, 1966; Frink, 1969). In the wetlands under study, due to their narrowness and shallowness, any horizontal banding of sediments as such is absent though the coarser particles are usually encountered towards the margins, as has been reported for many oxbow lakes of the Pembina River valley in Canada (Van Der Valk and Bliss, 1971).

Several workers have used organic carbon : kjeldhal nitrogen ratio as an aid for deciding the nature of the source of sediments. Thus, ratios in the range of 7-11 have been suggested as indicative of soils carried into the water by surface run-off (Hendricks and Silvey, 1973). Since both the maximum and the minimum ratios in the present study sites far exceed these values, the heavy additions of organic matter due to auto-trophs appear to be far greater than the additions from other sources. The other plausible explanation for higher C : N ratio in these wetland sediments would be the
highly efficient bacterial decomposition of organic nitrogen compounds as has also been suggested by Hart et al. (1976) for lake Mulwala sediments.

The diversity in the sediment types coupled with the varied types of allochthonous material brought in by run-off and/or the feeding channels from the catchment result in considerable differences in chemical composition at various sites. The analyses, however, showed calcium to be the main mineral component of the investigated bottom sediments, because of the presence of lacustrine deposits both within and around all the wetland sites. Besides, calcium is also brought into sediments as a result of biological decalcification of water and the decomposition of plant and animal organisms. Overliming has been shown to bring about toxic effects on growth and development of plants (Daubenmire, 1947); while according to Joestels (1944), Rich et al. (1971) and Wetzel (1960, 66) such situations provide unfavourable chemical milieu for many macrophytes, resulting in relatively low species diversity.

The ratios of total to exchangeable mineral content indicate large amounts of nutrients to be in non-available form. Large quantities of calcium, phosphorus and organic matter according to Akira and Wetzel (1972) and Norvell (1974) are held in insoluble CaCO$_3$ molecules. Similarly, clay fraction (Jitts, 1959; Harter, 1968; Li et al. 1972) and humic-chelate complexes of iron and aluminium (Jackson and Schindler, 1975) have been opined to be quite important in binding phosphorus. The ratios of total to exchangeable mineral concentration would also very much indicate the plant species under mo
rich sediment situations suffering indirectly from a
decrease in the availability of phosphorus, organic matter
and possibly iron as well, as has been reported earlier by
Mortimer (1941, 42), Einsele (1938) and Kufel (1976 a).

In his studies on some lochs of Scotland, Spence (1967)
failed to observe any definite relationship between the soil
type and macrophytic distribution, though the submerged
aquatic plants showed better growth on soils rich in organic
matter. Similarly Wilson (1941) found that many aquatics did
not show any marked preference for any particular substrate
though some showed a distribution which could be correlated
with substrate conditions. During the course of present
investigations the silty sediments of Hokersar and Narkora
appeared to be conducive for the colonization of floating-leaf
species and non-conducive for the establishment of submerged
forms. The highly thickened rhizome system of Nymphaea
stellata, at Narkora, reduces the probability of its getting
uprooted under biotic interference in soft sediments while
the continued growth of the rhizome and subsequent decay of
its older portions is an effective asexual mechanism in its
colonization leading to the monospecific communities so
characteristic of this biotope.

The widely ranging mineral content of the sediments under
the various plant communities points to a wide ecological
amplitude of the species concerned. The free movement of
water together with the mixed nature of the sediments,
containing organic matter in the various stages of
decomposition and the absence of horizontal sedimentary
stratification eliminates any possible correlation between
plant distribution and substrate characteristics. However, higher mean values for organic matter are obtained under the floating-island communities and *Phalaris arundinacea* communities against the least for *Trapa bispinosa* and *Sparganium erectum* communities which instead show higher silica content in their substratum. In general, the higher values of nitrogen are usually associated with higher organic matter content.

Temperature is of fundamental significance in determining the development of vegetation, other things being equal, higher water temperatures result in the increased growth rate of plants (Jenkin, 1942). The delayed vegetal growth at Shalbogh and Tullamulla is probably the consequence of low temperatures prevailing in these wetlands for quite sometime in the beginning of the growing season. The rise in the atmospheric temperature in the subsequent months, however, greatly influences both the vegetational and the phasic development of the plants. The development of a large number of plant species during summer and the death of all the aboveground shoots during winter in all the study sites is more an impact of temperature than anything else.

The hydrological factor represents the chief milieu of conditions governing the occurrence and growth of various plant species and their associations in wetland habitats. With regard to the distribution of plant species, Bellrose, (1941) stated that marsh plants usually thrive on moist soil or in water not more than 18 inches to 4 feet deep. The growth of emergents in depths greater than normal involves the need of extra-energy for their reaching the surface and
if this added energy demand is great enough it could conveniently prove fatal in itself or weaken the plants to the point where other environmental factors would produce a die back (Millar, 1973). Laing (1941), from his experiments, concluded that the adaptation of the different species of semi-submerged water plants to various depths of water is at least partly due to different oxygen requirements for maximum growth of the young shoots. This was associated with the observation that the plants flourishing in comparatively shallow waters were also to be found growing on well aerated muddy shores partly inundated in early part of the season. Similarly, Haslam (1973), while reviewing the biology of Phragmites communis, noted the aeration in this species occurring through the standing shoots and if ice or waves removed the reed in autumn, the species showed only a limited growth. Flooding, according to Haslam (1969 a) impedes the aeration of both the rhizomes and roots while according to Rodescu et al. (1965) it also decreases the bud formation. McDonald (1955) attributed a die back of Typha latifolia in lake Erie marshes to lack of oxygen, as a result of submergence of the dominant shoots throughout the winter. Sculthorpe (1967) described the occurrence of a transport pathway of gases from leaves to roots and rhizomes and ascribed the survival of the below-ground structures under reduced conditions in sediments to such mechanisms.

Amongst the wetlands studied, the tall-growing emergents were sparsely distributed at Narkora. The prevalent depth conditions, favouring little potential competitors should have resulted in the establishment of monodominant stands of
these species at this site as is said to have been the case in regard to *Phragmites communis* during sometime past. The dwindling of this tall-growing emergent is due to increased harvesting in recent years which must have left hardly any aboveground shoots above the water-level for the aeration of the underground parts. It is undoubtedly the need for oxygen that ultimately must have led to its decline. The few shoots of the species confined to a few shallow and protected areas have, however, remained unaffected. In another deep and permanent wetland of Hokersar, *Phragmites communis* occurs in tall and robust stands due to the absence of any harvesting at this site, which leaves enough of autumn shoots for the aeration of the underground parts. The restriction of the species to isolated stands is, however, an effect of the unfavourable water depth. At Kranchu also the emergent beds survive in absence of any biotic interference while in the temporary wetlands of Malangpora and Tullamulla, the harvesting of shoots late in the growing season has no effect in the successful colonization of the plant species as the stubble, though short, remains in direct contact with air during winter months.

The general changes in vegetation under the varying water regimes are well recognized (Evans and Black, 1956) Leitch, 1960, Steward and Kantrude, 1971). The violent fluctuations in water-level, both within and between seasons, create an extremely unstable environment for plant growth. The unusual fluctuations in the water-level during the optimum growth period at Kranchu resulted in a decrease both in the frequency and the density of the floating leaved and
submerged species against an increase in the number and presence of the emergents, resulting in the intense competition among the plant species. The constancy in the water-level during the optimum growth period at other wetlands, on the other hand, was highly conducive for the completion of the various biological processes. At Malangpora and Narkora, fall in water level in the late growing period was accompanied by an increase in the number and density of *Polygonum hydropiper* at the former site and the colonization of *Scirpus-palustris-Hydrilla quadrifoliata* community on the exposed margins at the latter site. According to Segal (1971) it is the presence or absence of the drying period rather than the degree of fluctuation that determines the performance of certain growth forms; while most of the other classificatory systems (Hayden, 1943; Bach, 1950; Nord et al. 1951; Martin et al., 1953; Shaw and Fredine, 1956; Evans and Black, 1956; Mason, 1957; Adam and Zoltai, 1969; Stewart and Kantrud, 1971; Zoltai et al. 1975 and Miller, 1976) seem to be based upon two unifying concepts of (i) water permanence being a key factor in wetland classification and (ii) vegetation being used as an index of water permanence. In the temporary wetlands, the dry period during winter does not appear to affect the vegetation in any way during the subsequent growing phase. The shoots of the emergent species sprout early in spring, before the water-level is much above the ground level. In these habitats, the variation in the plant composition is determined not by the mean water-level but rather by the mean high water-level during the vegetative period, as is
evidenced by differential vegetal structure in the wetland sites under the present investigation. In the shallow wetlands especially those of Malangpora, Tullamulla and floating-islands, several species usually occur together resulting in a complex physiognomic structure comprising an over-storey of less dense tall-growing emergents, a moderately dense intermediate tier of low-growing emergents, a low very dense under-storey of ground-layer species besides the sparse growth of floating-leaf and submerged tiers. The low water-level associated with less of annual fluctuations probably brings about somewhat greater differentiation than can occur under conditions of a widely fluctuating water-level (at Shalbogh and Kranchu) or under increased water depths (at Hokersar and Narkora) as has been observed earlier by Toorn (1972) in his studies on Phragmites communis.

With an increase in water depth, the tall-growing emergents covering large areas at Shalbogh, become etioliated and are subsequently replaced by the floating-leaf species having an adaptive connection between deep water and germination requirements (Spence, 1967). Thus, the deep and permanent wetlands of Hokersar and Narkora, predominantly covered by floating-leaf types, are structurally significantly less complex with only a few species /m². Besides, the plant communities at these sites show an overwhelming dominance of a single species only. All the three conditions according to Monk (1967), Auclair and Goff (1971) and Van Der Valk (1975) are indicative of harsh environment prevailing in these sites.

Though a number of factors are known to affect the growth and distribution of the submerged plant species (Ruttner, 1963; Sculthorpe, 1967; Westlake, 1973) water depth
(Swindale and Curtis, 1957; Spence, 1967), turbidity
(Robel, 1961), floods (Edwards, 1969) and drawdown (Kadlec,
1962, Nichols, 1974) have often been considered as important
factors. In the present study, the poor growth of this life
form appears to be due to low water depth at Malangpora and
Tullamulla and drawdown during June–July at Kranchu, since
the plants depend upon water for mechanical support. In the
deeper wetlands of Hokersar and Narkora high water turbidity
(secchi disc reading 0–15 cm), due to heavy load of silt
brought in by the feeding channels, and the thick cover of
the floating-leaf species, allowing very little light to pass
through, are the chief causative factors for the suppression
of submerged types, as was also concluded earlier by Clayworth
the paucity of submerged forms in some South African rivers
to the frequency of flash floods and the resultant silt
deposition and silting according to Van Der Valk and Bliss
(1971) not only reduces the light to the limiting level but
also results in burying the submerged growth especially during
floods. However, the presence of Myriophyllum spicatum and
Ceratophyllum demersum as common under-storey species in
some deep growing emergent and floating-leaf associations
is probably due to their tolerance of low light intensities
as has also been observed by Wilson (1941) with regard to
some Wisconsin lakes.

The present investigation has revealed the tall-growing
emergent communities to contain the highest standing crop of
all other wetland plant communities. A high standing crop in
the range of 1500 - 4500 g/m² has also been reported by Penfound (1956), Pearsall and Gorham (1956), Seidel (1959), Bray and Chivvi (1965), Buttery and Lambert (1965), Stake (1967), Bernatowicz et.al (1968), Kučet et.al (1969) Boyd (1969), Bjork (1967), Kuč (1971), Korelya - Kova (1971), Imhef and Burian (1972) Dykyjova (1971), Dykyjova and Ondak (1973), and Koul et.al (1971). The maximum standing crop evinced for Typha angustata and Phragmites communis communities in the wetlands is, however, greater than in the communities of Phalaris arundinacea, Scirpus lacustris, Sparganium erectum and Acorus calamus. The standing crop values in P. arundinacea community, comparable to those of Husák and Hejny (1973) and Kroška (1976), are nearly three times the values obtained earlier by Petrik (1972).

The presence of tall shoots and a greater number of vertical tiers viz. submerged, floating-leaf, ground-layer species and low-growing emergents, greatly enhance the community, standing crop. In the sedge-meadow and floating-leaf communities, however, only two or three tiers of plant species enter into the structure of these plant communities. Bray (1960) and Van Der Valk and Bliss (1971) also obtained an increase in the chlorophyll content with an increase in shoot height, while Saeki and Kuroiwa (1959); Saeki (1960), Monsi (1960), Jahnki and Lawrence (1965) and Tooming (1967) attributed this increase in standing crop and hence the production of a community with increasing height and structure, to the greater chances of light entering the community being intercepted.
The photosynthetic capacity of plant cover and its relationship to photosynthetic production per unit area are strongly influenced by the mode of display of phytomass within vertical light gradients (Talling, 1975). According to Watson (1974) the maximum rate of production is attained if a high portion of the assimilates is ploughed back into the leaf tissue and the 'expenditure' of dry matter on the rest of the plant (stem, petiole, root etc.) is not more than that is required to support the leaves in an efficient arrangement and supply them with minerals and water. In the present investigation, the highest standing crop/shoot in Typha angustata appears to be linked with the presence of vertically oriented ribbon like leaves. The leaves are moved by the feeblest air motion and thus the shading of any spot in the lower layers of the stand never continues for long. Besides, the vertical leaves not only avoid heating (Palmer, 1941) but also minimize leaf area index as both the leaf surfaces are almost equally illuminated. In Phragmites communis the broad and thin leaves achieve a rather planophilous inclination in a fully developed stand during the later phases of growth when the increased shading of the lower canopy layers promotes the senescence of the leaves lower below. Since, new leaves are continuously formed at the shoot tip, much of the assimilates are used in the build-up of the non-photosynthetic tissues by increases in shoot height. These conclusions, similar to those drawn by Kvet et al (1969) in regard to the reedswamp stand is South Moravia, are probably responsible for the high aggressive power of the species, as only few species can
outcompete under intense shade of the lower strata. *Scirpus lacustris* shoots which fail to colonize the shallower sites, probably because of competition, have developed maximum adaptation to deep water and wave action by the loss of flat assimilatory organs resulting in the simplest possible stand structure allowing maximum light to pass to the deeper strata (Dykyjova and Ondak, 1971).

Bray et al. (1959), Pilot (1967) and Jakrlova (1967) estimated a standing crop of 400-550 g/m² for the various meadow communities. In their studies on *Carex* dominated communities Mosénsojo (1969), Auclair et al. (1976a), Pearsall and Gorham (1956) and Getz (1960) obtained standing crops to the tune of 840 g/m², 807 g/m², 420 g/m² and 465 g/m² respectively, while Auclair et al. (1976b) recorded an average standing crop of 845 g/m² for a *Scirpus-Equisetum* wetland community at South Quebec. Most of these studies report on monospecific assemblages. The values obtained for the various sedge-meadow associations (1087-1432 g/m²) in the present investigation are comparable to those of *Carex* communities of Bernard (1973), Bernard and MacDonald (1974) and the mixed emergent community dominated by *Zizania aquatica* of Jervis (1969), falling strictly within the range of 400-1470 g/m² as reported by Gorham (1974).

For a wetland at Northern Iowa, USA; Van Der Valk (1976) postulated the low standing crop of the sedge-meadow zone to be due either to i) greater environmental stress or ii) inherently low productive nature of the constituent species. In the present study, the major environmental factors of soil and water do not, however, show much variation from the more productive reed-swamp communities of the corresponding sites, nor should
the presence of a greater number of species/m² and the domination by more than one species be indicative of any factor/s being limiting (See Van Der Valk, 1975; Monk, 1967; Auclair and Goff, 1971). Thus, the only plausible explanation would seem to lie in the assumption that the low standing crop of the sedge-meadow associations is a reflection of the different floristic composition. Relative to the tall-growing emergents, these species invariably showed very low standing crops in their ecologically optimum conditions i.e. the environmental conditions under which a particular species showed greatest abundance. Besides, the high species diversity in these communities by lowering the physiological optimum growing conditions through competition would still be causative for the low standing crop values, as has also been observed by Williams (1964), Whiteside and Harnsworth (1967), Leigh (1968), McNaughton (1968), Mellinger and McNaughton (1975) and Auclair et al. (1976 a). Whittaker (1972) and Horn (1975) did not, however, find any obligate relationship between the species diversity and standing crop.

Among the floating-leaf associations, the maximum standing crop obtained for Trapa communities is lesser than the value of 1055 g/m² reported by Ambasht (1971) for a pond in Benaras. These communities, because of the presence of a hard edible heavier nut, show higher standing crop as compared to Nymphoides peltatum and Nymphaea stellata communities under present investigation. The standing crop values for the latter two communities are, however, comparable to the values obtained for similar community types of the
8x-bow lakes in Central Alberta (Van Der Valk and Bliss, 1971)
and the valley lakes of Kashmir (Kaul et al, 1971), but higher
than those reported for *Nymphaea stellata* communities of
Minnesota (110 g/m²) by Bray (1960). The standing crop in the
floating-leaf communities is the lowest of all other
communities investigated, the causative factor being the
shading, by the flat leaves present on the water surface, of
a large phytomass suspended vertically in the water column.
The respiration of this poorly illuminated part at the cost
of the food material synthesized by the upper parts of leaves
only, greatly depresses the net photosynthesis of these
communities (Westlake, 1963).

The present study reveals the annual primary production
being mainly dominated by the tall-growing emergent species.
The maximum and minimum primary production values at Shalbogh
and Narkora wetland sites correspond to the high and low
importance values of the tall-growing emergent tier at these
two wetland sites. The generalizations, in regard to increased
primary production from meadow to tall-growing emergents and
decreased primary production from the tall-growing emergents
to floating-leaf types as drawn earlier by Penfound (1956)
and Westlake (1963) are very much strengthened by the results
obtained during the course of the present investigations. The
changes in the wetland production are significantly related
to increased importance values of tall-growing emergents
against the decreased importance values of the sedge-meadow
and floating-leaf species at the various sites; a trend
similar to that observed by Van Der Valk and Bliss (1971)
in their studies on hydaphy succession and primary production
of a number of ox-bow lakes in Alberta, but dissimilar to that observed by Bray (1960) in central Minnesota.

The water-depth and duration of flooding have been shown as important controls on production by Moxnesjo (1969) and Walker and Wehrhahn (1971). Both the factors, by influencing the life-form and the species composition significantly, seem to have a profound impact on the primary production of the wetlands under the present investigation. The water-level fluctuations during the period of optimum growth at Kranchu have had an appreciable effect in lowering the standing crop of all the plant communities at this wetland site, in quite a contrast to the observations made earlier by Van Der Valk and Davis (1976). The drop in water-level during May-June, uncovered areas of submersed habitat, resulting in a harsh environment for the submersed and the floating-leaf species, and allowing for the addition of shoots of the same life form but different species in the various tall-growing emergent communities. In the competition, thus set in, both the dominant as well as the accessory species were put to a disadvantage, as was evinced by low standing crop values of the constituent species of the plant communities sustained at this wetland as compared to Tullamulla and Malangpora wetland sites, which do not suffer any fall in water depth during the period of optimum growth.

The role of water chemistry in determining the primary production in wetlands is highly doubtful as the water chemistry itself depends mostly on the seasonal fluctuations in water-level, the sediment buffer capacity, the rate of mineralization and to some extent on the nutrient content in the catchment. The presence of large beds of rooted macrophytes deriving nutrients mostly from the sediments, would also point to the insignificant control of water chemistry on macrophytic
production, as has also been opined by Boyd (1967) and Bernatowicz (1969).

The importance of sediments in governing the growth and production of macrophytes is well realized from a number of studies conducted since Pond (1905) reached the conclusion that the retarded growth of rooted plants was due to their inability to secure enough phosphorus and potassium (Pearsall, 1918, 1920, 1921, 1929; Misra, 1938; Moyle, 1945; Pearsall and Gorham, 1956; Gorham and Pearsall, 1956 etc.). All the wetlands are composed of nutrient rich sediments to which are added heavy quantities of organic matter in the various stages of decomposition. Such mixed sediments, because of the presence of higher nutrient content than either of the components, when occurring alone, are thought to be most productive (Roelofs, 1944). With their roots penetrating the deeper anaerobic layers of the substratum, where the release of iron, manganese and phosphorus is greatly facilitated, the various macrophytic species overcome the harsh environment of the marl bottoms (Martimer, 1941, 1942).

The total annual primary production is also greatly influenced by the interrelated factors of temperature and the rate of assimilation. Gorham (1974), Keefe (1972), and Pearsall and Newbould (1957) have demonstrated strong relationship between annual mean temperature or latitude, and production in Carex, Spartina and other types of wetland plants. In the present investigation the peak rate of production for Typha angustata, Phragmites communis and Scirpus lacustris was touched before the onset of high temperatures in July-August. The highest and lowest biomass values for a number of perennials, however, correspond to the high and low temperatures of summer
and spring. Such seasonal changes in photosynthetic activity were also recorded for *P. communis* by Burian (1971) who opined that the plant adapts itself to higher temperatures similar to arctic plants. The bimodal production curves obtained for *Eleocharis palustris*, *Juncus articulatus* and *Polygonum hydropiper*, on the other hand, reflect somewhat different basic growth patterns. These species show an increased number of shoots under low water-level and decreased temperature conditions as is reported for some cool season grasses by Evans et al. (1964); Bernard (1974) and for *Scirpus-Equisetum* and *Carex* dominated ecosystems by auclair et al. (1976 a,b).

On an overall basis, the environment in the wetlands is much conducive for the sustenance of highly productive stands, the main causative factor being the high nutrient level sustained by the flushing from the surrounding uplands. The essential minerals for growth are maintained in solution by the reducing conditions at the mud-water interface coupled with the high concentration of organic matter in soil and its decomposition. Tall-growing emergents are the most productive in comparison to other plant species for which production was estimated. The maximum yearly production for this life form at Shalbogh was 2943 g/m² compared with 1,200 and 3,000 g/m² for deciduous and coniferous forests respectively and 3,000 g/m² in both salt marsh and temperate perennial agricultural system (Westlake, 1963). Jarvis (1969) reported the emergent and sedge-meadow systems in New Jersey being 2.5 times more productive than the comparable terrestrial systems. The primary production due to phytoplankton and submerged macrophytes in Kashmir lakes and floating-leaf macrophytes at
Narkora and Hokersar wetland sites is, however, much less.

The change in annual production at the various wetlands is linked to the physical changes that occur in an area as a result of succession. With a decrease in water depth from deeper to the shallower wetlands new life forms become established, which leads to a sudden increase or decrease in annual production (Odum, 1960). An increase in production occurs, if a new life form invades an area that has become more conducive as a result of the shallowing. The emergents which replace the floating-leaf species in shallower situations are highly productive because, they, in most respects, have the best of both submerged and terrestrial worlds, in-as-much-as gaseous exchange of carbon dioxide and direct sunlight are concerned. The massive rhizomes in this life-form class provide enough of energy and nutrients for early rapid growth besides being a means of vegetative reproduction. This early rapid growth gives them an edge over the other competing species while the increased size and standing crop and the efficiency to utilize the available light and space with great economy enable them to store large quantities of energy, that befits them to fortify the unfavourable season more readily than the subdominant species.
SUMMARY

Seven wetland sites viz. Malangpora, Tullamulla, Kranchu, Shalbogh, Hokersar, Narkora and the floating-islands of the Dal and Anchar lakes in Kashmir were studied for assessing the structure, composition and production characteristics of the vegetation in relation to the environment. All the sites are saturated or covered with water for at least sometime of the year and are important both at the ecosystem level by serving as sinks during floods, and the component level for the valuable products derived from them.

The water-level fluctuations, excepting at Kranchu, are closely related to the precipitation received during the year. In Kranchu, the minimum depth obtains in June, while at
Hokersar the water-level during winter is manipulated by checking the outflow from late autumn onwards. The amplitude of fluctuations is, however, maximum at Shalbogh and minimum at Narkora wetlands.

The permanence and the height of the water-level during the growing season, determined, in turn, by the amount of water brought in by the feeding-channels and the situation of the overflow channel, justify the categorization of the wetlands into four basic types viz. (i) temporary and shallow (Malangpora and Tullamulla) type, (ii) temporary and deep (Shalbogh) type, (iii) permanent and shallow (Kranchu and floating islands) type, and (iv) permanent and deep (Hokersar and Narkora) type. The floating-islands composed of buoyant masses of underground portions of tall-growing emergent species, remain saturated as a result of soaking in of water from underneath and may be inundated for only a short period during rains and high water conditions.

The ionic concentration of waters changes seasonally in relation to the wetland volume. Generally, the salt content is maximum during spring and autumn months and minimum during summer. At Kranchu, on the other hand, the higher values of minerals during June are associated with the low water-level prevalent in the month. In general, the waters are alkaline (pH 7.1 - 9.4); the high alkalinity together with high divalent cation concentration and low monovalent : divalent cation ratios characterizing them as hard water marl types. Under the increased atmospheric temperatures of summer, much of calcium is possibly lost through the formation of an insoluble CaCO₃ precipitate, while the losses in phosphate-
phosphorus occur as a result of coprecipitation with CaCO₃.

The major sources of nutrients in these wetlands are i) the run-off from the surrounding agricultural fields which are under the cultural influence, ii) inputs from the drainage basin through the feeding channels, iii) the mineralization of the dead organic matter and iv) the returns from the sediments through the exchange at the mud-water interface.

The sediments in all the wetlands, under-study, are loamy except at floating-islands where a maximum content of organic matter is recorded. Due to the narrowness and shallowness of wetland habitats and the heavy additions of organic matter by autotrophs, the sediments are of mixed character and as such sufficiently high nutrient concentrations are maintained which preclude any limiting effects on macrophytic growth. Because of the marl character of the sediments, however, large quantities of minerals are held in non-exchangeable form.

Much of the variation is, thus, accounted in terms of the differential water-level at the various study sites. The low water-level associated with low amplitude of fluctuations is causative for well marked differentiation into tall-growing-emergents, low-growing emergents and the ground-layer species at floating islands, Malangpora and Tullamulla sites while this type of differentiation is not so well marked at Kranchu subject to greater fluctuations in water-level. Similarly, the heavy biotic interference at Narkora and the increased water depth at Hokersar prevent the aeration of the
underground parts and thus limit the growth of the tall-growing emergent species to a few isolated stands only, thus creating the niches for the floating-leaf species which attain the maximum cover. The failure of the submerged to form communities of their own is attributed to the low water depth associated with drawdown (as in shallow and temporary wetlands) and/or the little irradiance passing through the floating-leaf cover and the highly turbid waters of the deeper wetland habitats.

Amongst the twelve plant communities recognized on the basis of dominance in the uppermost tier, the highest standing crop values have been recorded for the reed-swamp species. The tall shoots, increased number of vertical tiers of plant species and the ability to utilize the available space and light with maximum efficiency and great economy are the main factors responsible for the high standing crop values of these plant communities. The large underground systems, containing large portions of the biomass enable them to present an effective cover and a rapid growth early in the growing season.

The Carex dominated communities, which are localized to the floating islands, are estimated to have the highest standing crop as compared to other sedge-meadow associations. The standing crop values in the associations are, however, much low than Typha angustata and Phragmites communis communities; due to their inherently low productive nature and high species diversity.

The floating-leaf communities depicted considerable variation in the standing crop values. Trapa communities
covering large areas in Hokersar, because of the presence of a hard edible heavier nut had higher standing crop than those of Nymphaoides peltatum and Nymphaea stellata communities. The low photosynthetic surface confined to the upper parts of a few leaves and the shading of those suspended vertically in the water column result in the lowest standing crop values (176 - 395 g/m²) in the group.

The seasonal curves of primary production show two peaks occurring in Eleocharis palustris, Polygonum hydropiper, and Juncus articulatus against a single peak in Typha angustata, Phragmites communis, Scirpus lacustris, S. palustris, Carex wollei, Carex rubigena and Cyperus serotinus. The daily production in these plant species showed close relationship to temperature, the peak rates being attained before the maximum summer temperatures are touched.

The annual production at the various wetland sites, under the present investigation, followed a definite pattern vis-à-vis the importance values of the various physiognomic forms. The increases in production from a low at floating-island sites, through Malangpora and Tullamulla, to a maximum at Shalbogh wetland very well correspond to a decrease in the importance value of both the ground-layer species and the low-growing emergents and an increase in the tall-growing emergent species. Similarly, the decrease in production from Shalbogh to Hokersar is associated with an increase in the importance value of the less productive floating-leaf types. The highest per hectare annual production by the floating-leaf species was registered for Hokersar (59.71 %) and Narkora (69.80 %) wetlands against a maximum of 95.75 %, 54.07 % and
77.04% by the tall-growing emergents at Shalbo, Tullamulla and floating-island sites respectively. The low-growing emergents and ground-layer species, on an average, contribute a maximum of 60.60% of the annual production/hectare at Malangpora wetland site.