2. AVAILABILITY OF PHOSPHORUS TO AQUATIC PLANTS

A brief review of the forms of phosphorus in freshwater and their availability for plant growth is necessary to put into context the relevance of phosphate water column standards.

2.1 Forms of phosphorus

Phosphorus is routinely measured as either the Soluble Reactive fraction (SRP), a measure of orthophosphate, or as Total Phosphorus (TP). The actual measurement of phosphorus in aquatic samples is usually undertaken using the molybdenum blue method (SCA 1981). Six phosphorus determinands can be measured directly by analysis, and a further nine determinands can be calculated from these six basic results (Table 2.1 and Figure 2.1).

Table 2.1 **Phosphorus determinands determined directly by analysis and by subsequent calculation** (after SCA, 1981).

Determinands obtained by direct analysis	**Determinands derived by calculation**
Total reactive phosphorus (approx. equates to Total orthophosphate) (TRP)	Particulate orthophosphate (PRP) (PRP)=(TRP - DRP)
Filtrable reactive phosphorus (approx. equates to Dissolved orthophosphate) (DRP) or (SRP)	Particulate inorganic phosphate (PIP) (PIP)=(TIP - DIP)
Total reactive and hydrolysable phosphorus (approx. equates to Total inorganic phosphate) (TIP)	Total condensed phosphate (TCP) (TCP)=(TIP - TRP)
Filtrable reactive and hydrolysable phosphorus (approx. equates to dissolved inorganic phosphate) (DIP)	Dissolved condensed phosphate (DCP) (DCP)=(DIP - DRP)
Total phosphorus (approx. equates to total phosphate) (TP)	Particulate condensed phosphate (PCP) (PCP)=(TIP + DRP - TRP - DIP)
Total filterable phosphorus (approx. equates to total dissolved phosphate (TDP)	Total particulate phosphate (TPP) (TPP)=(TP - TDP)
	Total organic phosphate (TOP) (TOP)=(TP - TIP)
	Dissolved organic phosphate (DOP) (DOP)=(TDP - DIP)
	Particulate organic phosphate (POP) (POP)=(TP + DIP - TIP - TDP)

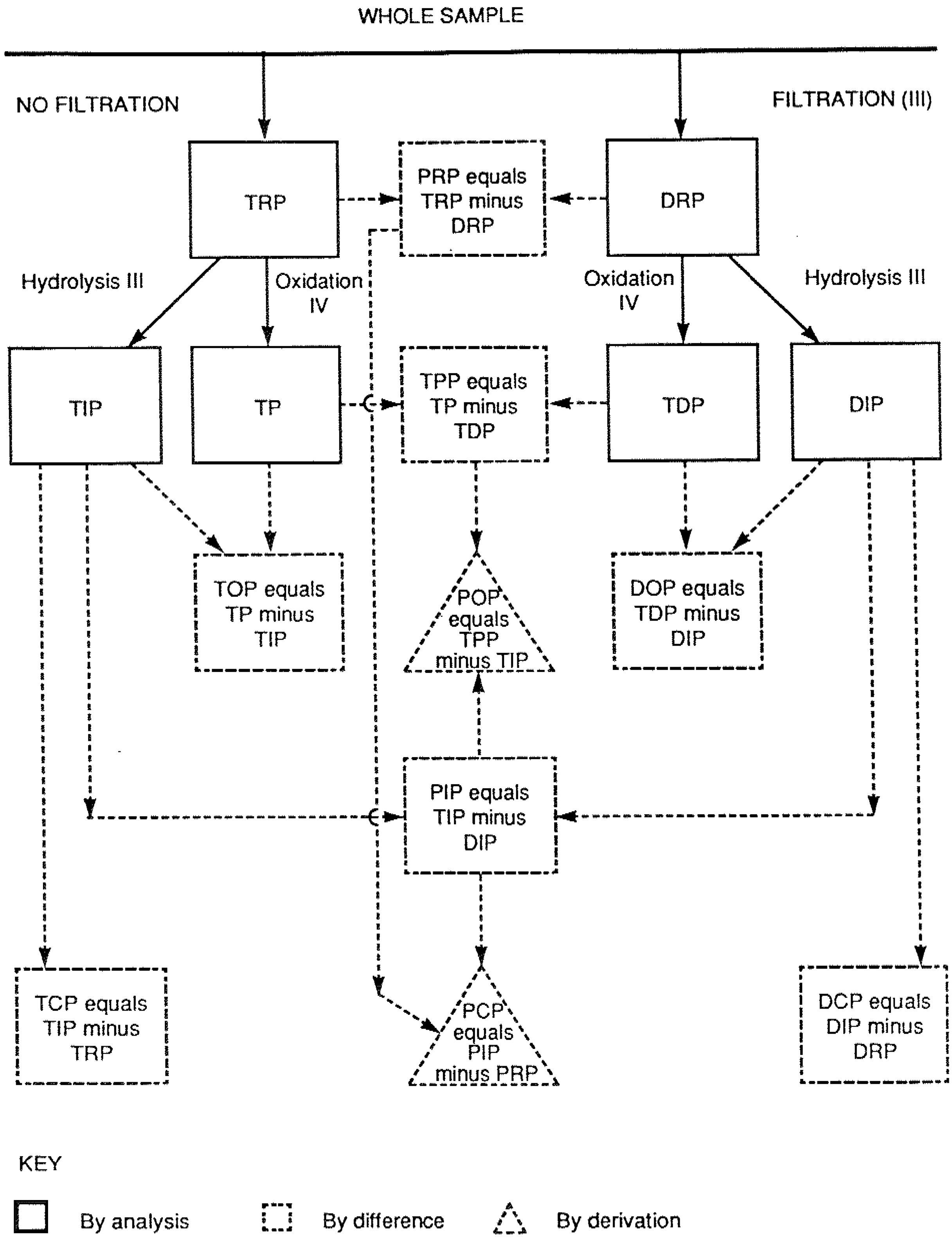
Most regulatory authorities and water utilities measure SRP (also called Dissolved Reactive Phosphorus, DRP), although a smaller number also measure TP. Both SRP and TP are of use as measures of trophic potential in freshwaters, but for different reasons. SRP is widely used as a measure of the orthophosphate (free phosphate ions) present in the water sample, but the conditions for analysis of aquatic samples also break down simple organic phosphates. As such, the SRP value for a given aqueous sample is likely to be greater than the actual orthophosphate content, and it is wrong to assume that all SRP is bioavailable, since the molybdenum blue method fails to distinguish between truly dissolved (available) and colloidal (unavailable) forms of phosphorus (Rigler 1968). Nevertheless, SRP gives a closer estimate of bioavailable phosphorus than any other phosphorus determinand. The situation is made more complex by the fact that some algae can produce alkaline phosphatases and thereby utilise some forms of dissolved organic phosphorus.

The relative unpopularity of TP for monitoring fresh waters is due largely to its greater expense, since its analysis involves a costly extra digestion step when compared to SRP. It is a valuable determinand in the monitoring of trophic status, since it gives a better indication of the potential for accumulation of phosphorus in sediments, which is an important nutrient source in both still and flowing waters. TP is most popular in lake monitoring, as much of the bioavailable phosphorus is locked inside phytoplankton cells at any one time. In addition, winter levels of TP give a good indication of the amount of water column phosphorus that will be bioavailable in the following summer (eg Dillon and Rigler 1974, OECD 1982). In rivers, however, the much shorter residence times do not lend themselves to this type of approach, and the utility of TP is essentially restricted to indicating likely sedimentary phosphorus levels; even this use is subject to uncertainty, since current velocity ultimately dictates whether a significant phosphorus reservoir accumulates (see Section 2.4).

Within the context of this report, phosphorus concentrations are cited wherever possible as either SRP or TP, with values cited as the phosphorus (P) content rather than phosphate (PO_4). The importance of standardising the latter cannot be stressed enough, since phosphate concentrations quoted as PO_4 will appear around three times higher than those quoted as P; ie 10 µg/l as PO_4 is about 3 µg/l as P. Owing to its imprecise analytical meaning, the term "orthophosphate" has largely been replaced by SRP. However, on some occasions the original literature is so vague with regard to what determinand was analysed that loose terms such as "phosphate" are retained.

The level of detection achievable by the molybdenum blue method is suitable for most nature conservation purposes, but only providing the drawbacks of the method are appreciated. Depending on the laboratory undertaking the analysis, this level of detection may not be suitable for monitoring oligotrophic waters, since the limit of detection in UK laboratories varies between 2 and 20 µg P l^{-1}. Karl and Tien (1992) have recently made a modification to the standard molybdenum blue analytical technique involving the removal of phosphorus from solution by the formation of brucite [$Mg(OH)_2$], which they claim allows dissolved phosphorus to be reliably measured to a concentration of 0.031 µg l^{-1} SRP (1 nM SRP).

A significant proportion of the phosphorus within an aquatic system may be bound up as insoluble particulate matter which falls to the benthos. Much of



• For abbreviations see Table 2.1. Pretreatment procedure numbers in Roman type

Figure 2.1 Relationship between phosphorus determinations (after SCA 1981)

this sedimentary phosphorus may be organic, with the organic fraction increasing with increasing eutrophication. Weimer and Armstrong (1979) reported that up to 70% of phosphorus in lake sediments may be organic. Much of the organic phosphorus in sediments may have been derived from plants and algae themselves.

Organic matter laid down in the sediment may later be mineralised to a biologically available form. The release of SRP from sediments is greatly increased at low dissolved oxygen levels/low redox potentials. This bioavailable phosphorus is released into the interstitial water, where concentrations may be orders of magnitude higher than in the overlying water column, and it is this phosphorus which provides by far the largest source of phosphorus taken by many rooted macrophytes. It is also therefore important when considering phosphorus in sediments to take into account the fraction held in the interstitial water.

2.2 Sources of phosphorus

Phosphates are derived naturally from: (i) weathering of catchment soils containing phosphatic minerals; and (ii) from atmospheric deposition, either biological (pollen, etc) or lithologic (mineral dust) in origin. However, in many lakes and watercourses, the majority of the phosphorus can be attributed directly to man's activities; so-called "cultural eutrophication". In this report, such artificial enrichment is termed "eutrophication" and enrichment occurring through natural processes is termed "natural eutrophication".

Every watercourse and waterbody has a different nutrient budget, with attention recently having been focused on sewage treatment effluent by the Urban Wastewater Treatment Directive (91/2711 EEC). Sewage effluent is estimated to account for about half of the UK phosphorus budget: for example, the Soap and Detergent Industry Association (SDIA) calculated that of the 105 000 tonnes TP/annum which is output to surface waters, sewage effluent accounts for 56 000 tonnes (53%, see Table 2.2). However, this value will differ dramatically from one catchment to another: in heavily populated lowland areas this proportion is likely to be higher, while in sparsely populated upland areas this proportion will be lower (as will the total phosphorus budget for similar-sized catchments). Biologically treated sewage from sewage treatment works is a major source of phosphorus in some rivers. Daily *per capita* contributions of SRP in sewage have been estimated at around 2 g (Smith 1976, Oborne *et al.* 1980). Sewage treatment works can constitute a large proportion of river flow; Hayes *et al.* (1984) reported that, under base flow conditions, the Anglian rivers that are used for public supply can contain up to 60 per cent effluent.

Table 2.2 Estimated UK phosphorus budget (after SDIA, 1989).

Phosphorus usage (tonnes annum^{-1})		**Phosphorus output to surface waters (tonnes annum^{-1})**	
Industrial uses	10 000	Direct industrial discharges	3 000
Detergents/Cleaners	35 000	Sewage Effluent	56 000
Food additives	5 000	Manure/Slurry	26 000
Feed supplement	60 000	Silage losses	2 000
Fertiliser	190 000	Soil runoff	18 000
Total	300 000		105 000

The EC Urban Wastewater Treatment Directive states that the effluent from some sewage treatment works will have to contain no more than 1 mg TP l^{-1}. As an example of the scale of reduction of the phosphorus input to rivers that this could account for, reducing the phosphorus content of the ten major STWs discharging into Lough Neagh from 8-12 mg TP l^{-1} to <2 mg TP l^{-1} accounted for a 75-80% reduction in sewage-derived phosphorus (Rendle 1990).

Nutrient export from livestock and arable farming depends greatly on farm management practices, soil, meteorology and catchment morphology. This being the case, nutrient export from different catchments with the same land use can vary by orders of magnitude. For example, runoff from pasture is reported to be in the range 0.05-4.90 kg P ha^{-1} yr^{-1}, while the range given for animal feedlots is 10-795 kg P ha^{-1} yr^{-1} (EPA 1980, Loehr *et al.* 1989). Various national estimates of the contribution made by agriculture to phosphorus inputs into freshwater have been made, including: 44% (SDIA 1989), 43% (Morse (1993) and 36% (Withers 1993). The latter estimate distinguishes between agricultural point sources (20%) and non-point sources (16%). As with sewage-derived phosphorus, the contribution of agriculture within any one catchment will vary depending upon land use. For many catchments, it may be that significant reductions in phosphorus loadings would not be achievable without addressing agricultural sources.

Using a value of 13 µg TP l^{-1} for the phosphorus in rainfall, this equates to an annual phosphorus load similar to the amount discharged directly by industry. However, the proportion of atmospheric phosphorus deposited with rainfall varies greatly - Cawse *et al.* (1989) found this "wet" phosphorus to comprise between 2.3 and 100% of the total amount of atmospheric phosphorus deposited at a number of sites throughout Wales.

2.3 Bioavailability

As stated above, only a part of the phosphorus measured in a sample will be available for uptake from the water column by plants. While SRP gives an indication of what this fraction is, a more certain way of finding out is to undertake bioassays, usually employing algae because of their rapid growth rates compared to macrophytes. However, the results obtained from such tests indicate only what fraction of the phosphorus was bioavailable when the assay was being undertaken; since phosphorus speciation is dynamic, the bioavailability of phosphorus is likely to change. The most obvious example of this is phosphorus dissolution from previously non-bioavailable sediment particles, which increases as dissolved phosphorus is utilised. Estimates of the bioavailability of phosphorus from different sources are given in Table 2.3. Thus, assuming a biological availability of phosphorus of 100% for orthophosphate, the availability of phosphorus from different source varies quite considerably.

Table 2.3 **Bioavailability of different sources of phosphorus** (after Berg, 1989).

Source	**Bioavailability** (% of total)	**Notes**
(Orthophosphate	100	)
Runoff from cereal fields	35	1
Farmyard slurry	60	2
Glaciated deposits	10	1
Manure seepages	75	2
Silo seepages	60	3
Raw sewage	50	
Chemically treated sewage	20	4
Detergents	70	
Phosphorus in rainfall	45	5

Notes:

1 The amount of phosphorus per unit weight increases sharply with decreasing particle size (Viner 1982, 1984, 1988) and extractable iron.

2 Estimates for different types of manure vary considerably, but most place the phosphorus content within the 0.1-1.0% (w/w) range (ADAS 1986).

3 Silage is not usually considered to be a source of eutrophication problems in UK rivers, largely because its role in diminishing this aspect of water quality is minor in relation to the ecological damage caused by its extremely high BOD. However, Table 2.2 shows silage to be a similar sized source to direct industrial discharges.

4 Chemical treatment is used to remove phosphorus. This figure will vary depending upon the flocculant used and the quality of the final effluent produced. Biological methods of phosphorus removal in sewage treatment are likely to replace chemical treatment at larger STWs in the coming years because of the financial advantages.

5 This may only account for a relatively small proportion of the total atmospheric phosphorus deposition. The "dry" phosphorus which is deposited is largely unavailable.

2.4 Sediment-water phosphorus cycling

The vast majority of work in this area has been undertaken in lentic waters and a considerable amount of information has been accumulated, perhaps the most prestigious study being that documented by Sas (1989, 1990). This work analysed data from 18 European lake restoration projects in waterbodies of differing sizes (0.03-503 km^2 surface area). In shallow waterbodies, the amount of phosphorus in sediment surface layers (0-15 cm deep) was critical to phosphorus release: for sediments containing >1 mg P g^{-1} dry weight, up to 5 years of net phosphorus release from the sediment is likely to occur following a large reduction in external nutrient loading. However, in deep lakes, the phosphorus content of sediment rarely exceeded this critical value, presumably because phosphorus sedimentation in such lakes was associated with a large influx of mineral material.

It appears that a large proportion of internal loading in shallow waters may be due to wind-generated waves, which disturb the sediment surface and so mix phosphorus-rich interstitial water into the water column. Deep-lake restoration projects would therefore appear to be less affected by internal phosphorus loading than shallow lakes; however, deeper lakes are prone to stratification, resulting in hypolimnetic deoxygenation and lower sediment redox potential (E_h), which stimulates phosphorus release from sediments.

All lake trophic status models take account of phosphorus sedimentation and subsequent nutrient release. This is usually in the form of either a separate sub-model when specific waterbodies are being modelled (Somlyódy and van Straten 1986), or in the case of empirical statistical models (eg OECD 1982), a factor which is accounted for by considering the residence time of the waterbody.

Empirical models take account only of long-term trends and assume a steady-state with regard to phosphorus loading/recycling etc, so year-to-year variation is not accounted for *per se*, only in terms of confidence limits. The 95% confidence limits for the OECD model are wide, even when anomalous "flyers" are excluded from the regressions - approximately an order of magnitude for the chlorophyll-a/in-lake phosphorus concentration relationship, and 6-fold for the feeder stream/in-lake phosphorus relationship. Models developed for single lakes are likely to be more accurate, and only these can take account of factors which are specific to given lakes, so allowing the prediction of when and to what extent net phosphorus deposition and sediment release will occur.

In lakes, the length of time over which phosphorus enrichment has occurred as well as the extent of enrichment appears to be important. For example, the experimental manipulation of Swedish oligotrophic lakes allowed them to revert to pre-enrichment algal biomass within a year (Holmgren 1984). However, the recovery of Lake Vesijärvi, Finland (which had received sewage effluent for over 50 years), took place very slowly due to the persistent phosphorus release from the sediment (Keto 1982).

It is unlikely that a similar rule of thumb to Sas's internal loading-sediment phosphorus content relationship for lakes will exist for rivers. This is because of the enormous differences that exist both between and within single rivers in terms of water velocity and sediment deposition/suspension. Water velocity probably has a greater overall control on sediment chemistry, by controlling the rate and size of particle deposition/suspension, than any other factor within the confines of the river. This is because the coarser sediments associated with fast-flowing rivers have less capacity for phosphorus storage, thereby minimising the size of the sedimentary phosphorus reservoir. In addition to this, the faster flowing a stretch of river is, the more likely it is to be well oxygenated, thus reducing the likelihood of low oxygen levels at the sediment-water interface and consequent enhanced phosphorus release.

Phosphorus dynamics in small rivers tend to be dominated by a few heavy rainfall/snowmelt events per year, because spate conditions are associated with high levels of sediment resuspension as well as increased nutrient runoff from the catchment. While a similar pattern occurs in larger rivers, it is less dramatic, but still gives rise to skewed frequency histograms for phosphorus levels (eg Figure 2.2). The pattern of phosphorus inputs to a river can also vary greatly depending upon the activities undertaken in the catchment and the prevaling climatic conditions (Figure 2.3). Phosphorus concentrations in rivers receiving sewage effluent tend to be inversely related to river flow (Edwards 1973, Oborne *et al.* 1980), whilst more rural catchments may conversely exhibit positive correlations associated with agricultural run-off. The phosphorus load entering Lough Neagh in "dry" years is approximately half the amount that enters during "wet" years (Rendle 1990), with phosphorus concentrations (not taking into account the increased flow) varying by more than an order of magnitude from day to day.

Apart from physico-chemical factors such as current velocity and substrate type, biotic factors also affect phosphorus cycling. Jupp and Spence (1977) considered that submerged macrophytes and other organisms may play an important role in the release of phosphorus from sediments, particularly where the sediments have an oxidised layer and release from undisturbed underlying anaerobic sediments can only follow the activity of organisms such as benthic bacteria (eg through physical action of methane release), burrowing invertebrates and rooted plants. The evidence for excretion by plants is somewhat contradictory. DeMarte and Hartman (1974) demonstrated using autoradiography that phosphorus absorbed by roots can be translocated to the shoot system and some may be released to the surrounding water, and particularly so when the plant shoots were damaged. Barko and Smart (1980) considered that phosphorus released from the submerged *Egeria densa*, *Elodea nutallii* (previously *Hydrilla verticillata*) and *Myriophyllum spicatum* was principally through tissue decay, although some excretion also occurred. Welsh and Denny (1979) found no evidence of excretion by *Potamogeton pectinatus* and *P. crispus*.

In rivers, the presence of plants will reduce the mixing effects of wind and current action, which may have the effect of either reducing or increasing phosphorus cycling. During the growing season, plants can prevent the resuspension of particulates which might otherwise contribute phosphorus to the water column. In contrast, they can encourage the development of still water zones in which an anaerobic sediment layer can become established, resulting in phosphorus release.

In lakes, macrophytes themselves may contain a substantial part of the phosphorus that would otherwise be available in the water column. Blindow (1992) considered that charophytes can produce reductions in available phosphorus through uptake into dense plant stands and/or co-precipitation with

$CaCO_3$ during photosynthesis. Owing to the faster replenishment of water column nutrients in river systems, this phenomenon is of less importance. In lakes and slow-flowing rivers, plant-bound P is subsequently incorporated into the organic fraction of sediment P and can subsequently contribute to internal loading. In faster-flowing rivers, much of this phosphorus is carried downstream and out of the system as plant material breaks away, particularly during autumn spates.

2.5 Nutrient limitation in plants

If nutrient limitation occurs in freshwater systems it tends to be caused by phosphorus limitation. However, nitrogen may become limiting in some cases, for instance in the summer when denitrification processes occur at a high rate. The nitrogen:phosphorus ratios derived from water quality data for rivers are generally high (>15), particularly in upper reaches (>20), in relation to the ratios found in aquatic plants of around 10, thus supporting the hypothesis of phosphorus limitation. Lower ratios (<10) may occur where there is phosphorus enrichment from sewage works and generally high concentrations of both N and P. Increased plant (macrophytes and algae) growth and biomass may be expected as a direct effect of phosphorus enrichment in a phosphorus-limited system.

Further supporting evidence of phosphorus limitation comes from a variety of studies, eg Gerloff and Krombholz (1966) and Duarte (1992). Gerloff and Krombholz (1966) calculated that the "critical level" of phosphorus and nitrogen in plant tissues were 1.3 mg g^{-1} and 13 mg g^{-1} respectively. A variety of plant species were collected from a number of lakes during periods of heaviest plant growth. Phosphorus, rather than nitrogen, was found at times to be below the critical concentration of analysed plant tissues, suggesting that phosphorus was more likely to limit macrophyte growth than was nitrogen. Duarte (1992) examined the patterns of nutrient concentration across a number of species of aquatic plants, including phytoplankton, macroalgae and freshwater macrophytes. There was a tendency towards higher concentrations of N and P (relative to C) in phytoplankton compared to that of macrophytes. This was interpreted as reflecting a greater degree of N and P limitation of growth in macrophyte populations rather than an intrinsic difference in their chemical composition relative to phytoplankton.

Macrophyte growth and nutrient uptake kinetics can be described in terms of the half-saturation coefficient (K_S). For phosphorus uptake, K_S is the external concentration required for an organism to achieve half its maximum growth rate when all other resources are available in excess. Growth rate/nutrient concentration relationships follow Michaelis-Menten enzyme kinetics and are asymptotic, so the nutrient values at which maximal growth rates are approached are considerably greater than twice K_S (Figure 2.4). A more detailed explanation of growth kinetics (as applied to phytoplankton) is given by Reynolds (1984).

Providing phosphorus is in excess of K_S, under natural riverine conditions, the growth rate is more likely to be limited by another factor such as light availability, supply of another nutrient, etc. Little information on phosphorus K_S values for aquatic macrophytes and filamentous algae was found in the literature. However, Cartwright *et al.* (1993) summarised information on concentrations limiting the growth of *Cladophora*, an important nuisance alga in

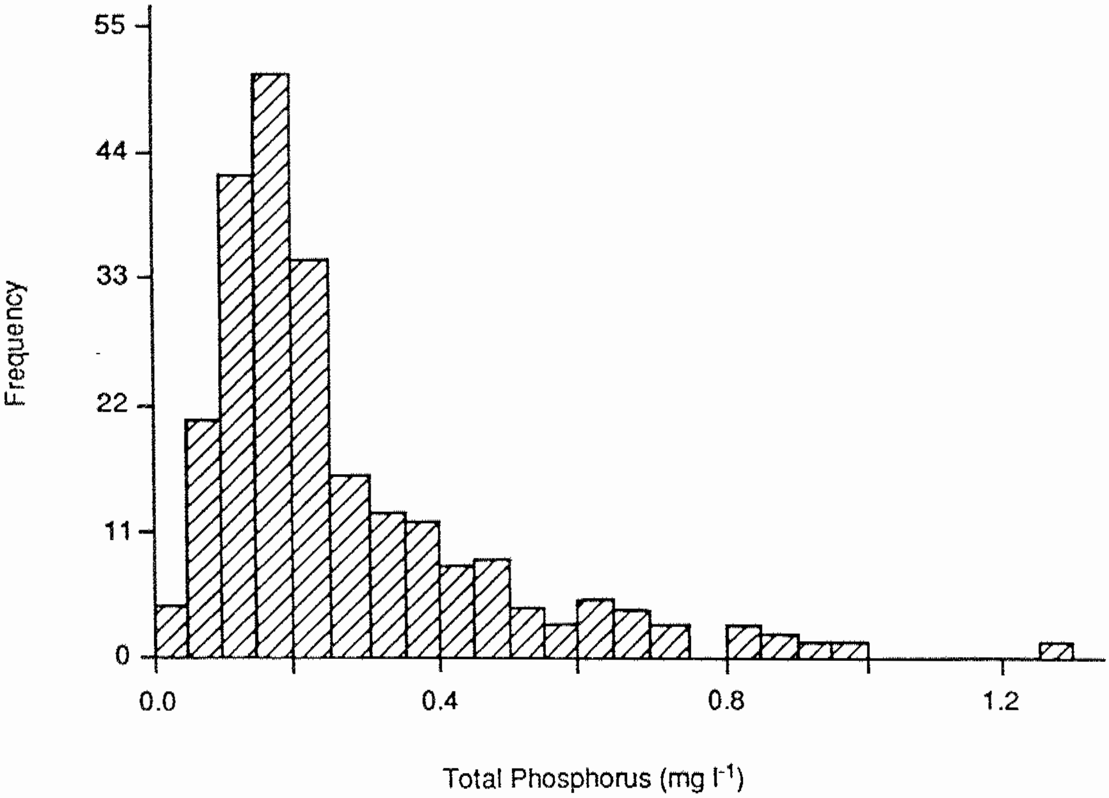


Figure 2.2 **Total phosphorus in Rivers. Data for Six Mile Water at Castle Farm Bridge, Northern Ireland (1975-1986) (after Parr and Clarke 1992)**

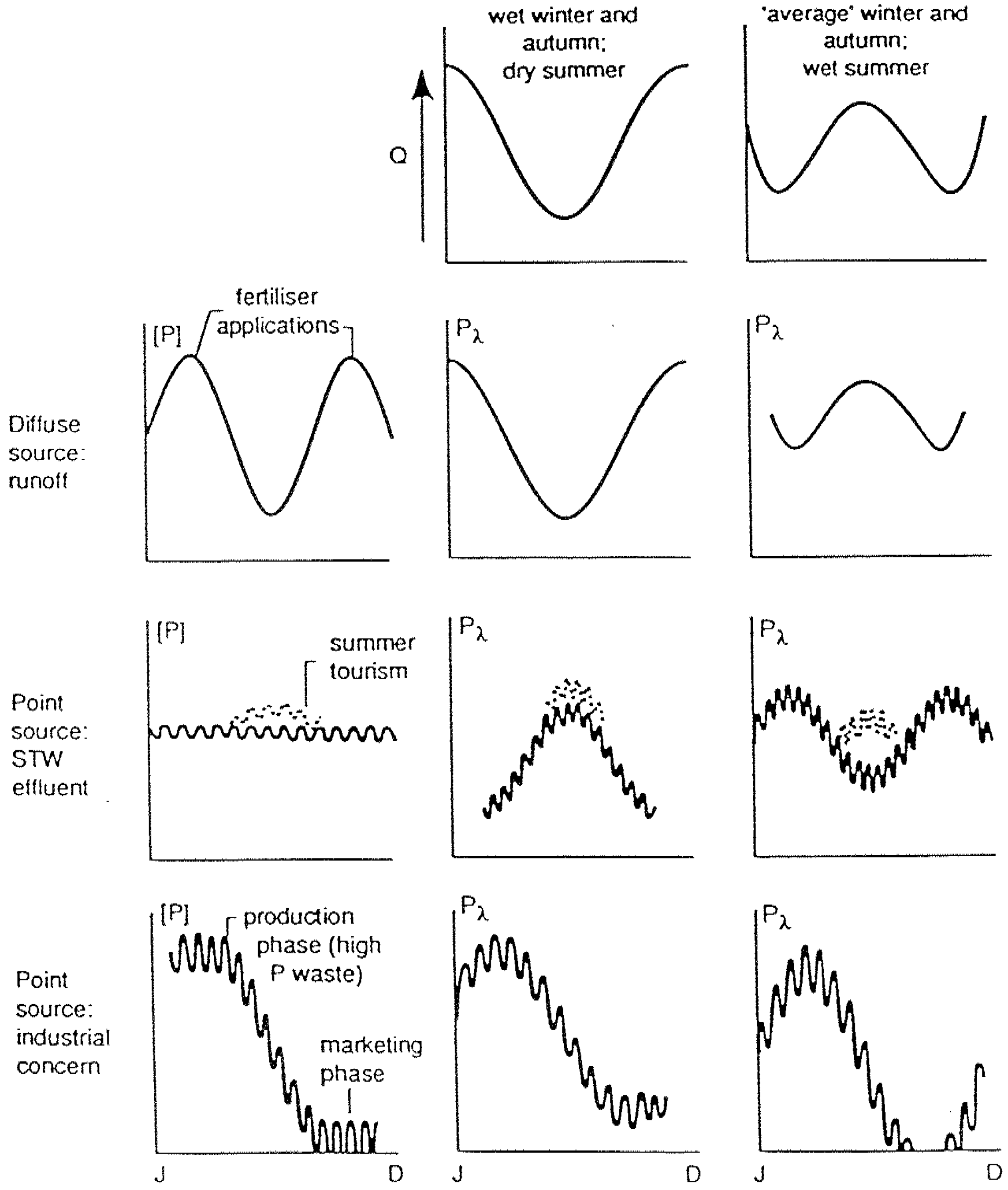


Figure 2.3 **Seasonal patterns in phosphorus. Phosphorus loads ([P]) from three different sources and the likely fluctuations in phosphorus levels (Pλ) in a receiving stream, under two contrasting flow (weather) regimes (Q) (after Johnson *et al.* 1992)**

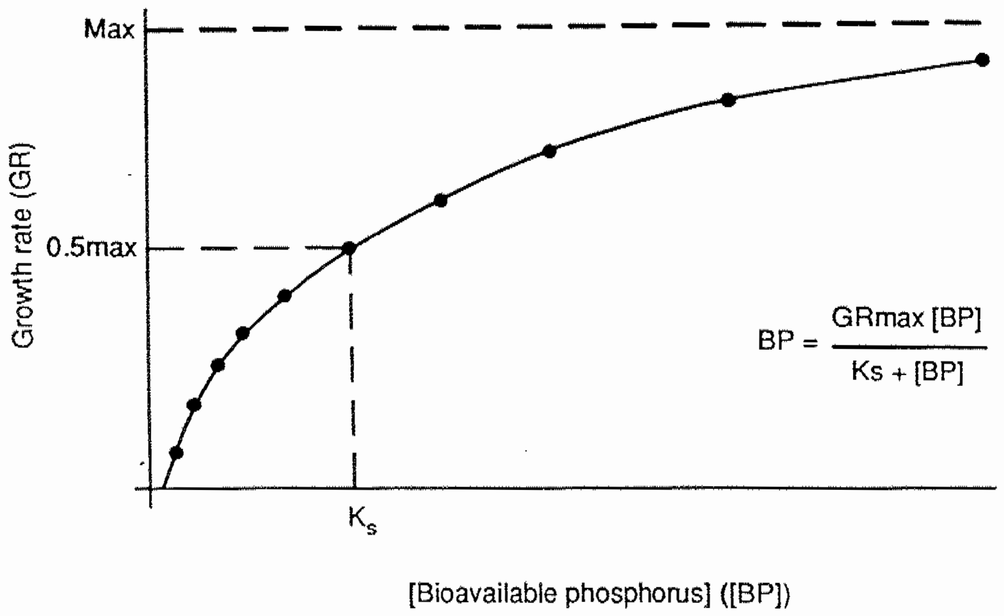


Figure 2.4 The dependence of macrophyte growth kinetics on external phosphorus availability

riverine systems. Estimates from different authors included 14 µg l^{-1} SRP, 20 µg l^{-1} TP and 60 µg l^{-1} TP. It is likely that phosphorus K_S values for different macrophyte and filamentous algal species cover a wide range of concentrations. As an example of the variability within a large taxonomic group, recorded phosphorus K_S values for freshwater phytoplankton fall within the range 0.011-0.364 mg l^{-1} SRP (Reynolds 1984). For many rooted macrophytes, sedimentary K_s values will normally be more appropriate than water column values (see Section 2.6).

2.6 Uptake mechanisms used by aquatic plants

The uptake of phosphorus is fundamental to the growth of macrophytes and the ability of plants to utilise phosphorus from different sources may determine the success of a species and consequently the nature of plant communities. The sources of nutrients are obvious for plants of certain growth forms, eg detached floating species such as *Lemna* must obtain nutrients from the water column, there being no contact with the substrate. Most rooted species could in theory obtain nutrients from both water and substrate, but emergents in riparian habitats must obtain nutrients solely from the soil. A number of studies have been conducted to identify the nutrient sources used by aquatic plants, and particularly by those species with the option of uptake from either the substrate or the water column.

Peltier and Welch (1969) investigated factors affecting the growth of rooted aquatic plants in the Holston River, USA, and concluded that the growth of *P. pectinatus* was little influenced by nutrients in the water, which were at concentrations ranging upwards from 0.03 mg l^{-1} SRP, and that other factors were important such as nutrients in the sediments, water depth and turbidity.

Denny (1972) discussed the relative importance of different sources of phosphorus to different plant groups (eg submerged, floating-leaved and emergent macrophytes). Supported by evidence from laboratory experiments with *Potamogeton* spp, *Vallisneria aethiopica*, *Elodea nutallii* and *Ceratophyllum demersum*, the author suggested that there is an increasing dependency in nutrient absorption potential via shoots with both the extent of submergence of the plant form and with the simplicity of its anatomy. Conversely, there is a decreasing dependence on nutrient absorption potential via roots. Thus, the emergent *Phragmites australis* would absorb nutrients entirely through roots, and the submerged rootless *Ceratophyllum demersum* through shoots. Intermediate plant forms, such as the *Potomageton* spp studied and *Vallisneria*, were considered to utilise both roots and shoots for nutrient absorption to varying degrees. The extent of submergence was also considered to be negatively related to factors of direct substrate effect (ie the mud/sand growth rate ratio, the root/shoot ratio on poor substrate and the extent of vascular differentiation).

DeMarte and Hartman (1974) used autoradiographs and radioactivity measurements to produce direct evidence that phosphorus (as phosphoric acid with ^{32}P) was absorbed by both the roots and shoots of the submerged macrophyte *Myriophyllum exalbescens* prior to translocation around the plant. Changing the substrate type (sand or "muck") did not significantly change the amount of ^{32}P absorbed by roots. Gentner (1977) similarly studied the uptake and transport of ^{32}P in *Vallisneria spiralis*. Phosphate was found to be taken up equally by roots and shoots, with transport occurring principally in the direction of shoots to roots. Phosphate was found to be excreted more readily from the roots than from the shoots. Jana and Choudhuri (1983) demonstrated the transport of ^{32}P from roots to shoots in *Potamogeton pectinatus*, *Vallisneria spiralis* and *Elodea nutallii*, and similarly root-shoot transport in *Potamogeton pectinatus* was demonstrated by Welsh and Denny (1979).

Barko and Smart (1980) demonstrated that *Egeria densa*, *Elodea nutallii* and *Myriophyllum spicatum* were able to derive their phosphorus exclusively from sediments, despite their having only minor root systems on a biomass basis. Bole and Allan (1978) found that *Myriophyllum spicatum* and *Elodea nutallii* took up most of their phosphorus from the sediment when the overlying water contained 0.015 mg l^{-1} SRP. *Myriophyllum* also continued to largely use the sediment as a source of phosphorus at water concentrations of 0.5 mg l^{-1} SRP. However, at a water concentration of 2.0 mg l^{-1} SRP, the majority of uptake occurred from the water column.

Myriophyllum spicatum plants grown in laboratory culture have been estimated as obtaining over 90% of both nitrogen and phosphorus from the sediment, when the sediment concentration was 0.7 mg g^{-1} (dry weight) and the concentration in overlying water was 0.046 mg l^{-1} (as 0.2 mg l^{-1} KH_2PO_4) (Hoffman *et al.* 1984). A reduction in sediment phosphorus concentration from 0.7 to 0.2 mg g^{-1} resulted in a 74% reduction in growth.

The concentrations of sediment-based materials have been found to have an influence on community structure, as might be expected from their effects on individual species. Chambers (1987) observed changes in lake community composition with increasing sediment fertility, associated with an increase in the proportion of total plant biomass attributable to canopy-producing or erect growth forms (eg canopy-producing, *Myriophyllum spicatum*; erect, *Potamogeton lucens*, *P. perfoliatus*) and a decrease in the rosette and bottom-dwelling forms (eg rosette, *Vallisneria americana*; bottom-dwelling, Characeae). These observations were supported by experimental evidence (Chambers and Kalff 1987), which demonstrated that both sediment composition and irradiance influenced the biomass and morphology of *P. praelongus*, *Vallisneria americana* and *P. robbinsii*. In examining the relative importance of irradiance and sediment fertility, the authors found that the biomass of the erect *P. praelongus* was primarily determined by sediment composition, the biomass of the bottom-dwelling *P. robbinsii* was largely determined by irradiance, and the intermediate, rosette form, *Vallisneria americana* showed an intermediate response.

Chambers *et al.* (1989) demonstrated that in riverine conditions *Potamogeton crispus* obtained most of its nutrients through the roots, when sediment concentrations ranged from 0.26 to 0.60 mg g^{-1} Total Phosphorus and water column concentrations ranged from 0.010 to 0.075 mg l^{-1} SRP.

Haslam (1978) suggested that the amount of cuticle on submerged plants may be important in determining the extent of nutrient uptake from the surrounding water. The author presented lists of species with different amounts of cuticle, eg *Ceratophyllum demersum* and *Elodea canadensis* leaves had "very little or negligible cuticle", the stems of both species had "little cuticle" and *Nuphar lutea* floating leaves had "more cuticle".

Haslam (1978) also pointed out that fragments of plants such as *Apium nodiflorum*, *Myriophyllum spicatum*, and *Ranunculus* spp may survive for some time by taking up nutrients from the surrounding water, but may only thrive when they become anchored. The higher concentrations of nutrients required by some plants for effective shoot, rather than root, uptake may be more likely to produce inhibitory effects resulting from the stimulation of algal growth (Barko and Smart 1986).

Attempts have been made to relate the extent of nutrient uptake to concentrations in the environment by measuring concentrations of nutrients in plant tissues. Ho (1979) recorded significant positive correlations between concentrations of nitrogen and phosphorus in the water column and those in plant tissues in studies on *Potamogeton pectinatus*, the dominant macrophyte in a sewage effluent enriched Scottish loch. Water samples typically had concentrations of between 0.8 and 1.0 mg l^{-1} SRP. However, Owens and Edwards (1961) and Ladle and Casey (1971) found that neither tissue nutrient concentrations nor aquatic macrophyte biomass were correlated with open-water concentrations. It is likely that the availability of nutrients and uptake mechanisms available to a plant will determine such relationships.