Seasonality/aseasonality of aquatic macrophytes in Southern Hemisphere inland waters

Davis S. Mitchell[1] & Kevin H. Rogers[2]
[1] *CSIRO, Centre for Irrigation Research, Private Mail Bag, Griffith, NSW 2680 Australia;*
[2] *Department of Botany, University of Witwatersrand, 1 Jan Smuts Avenue, Johannesburg 2001, South Africa*

Keywords: limnology, aquatic macrophytes, seasonality, life-histories, Southern Hemisphere

Abstract

The term aseasonality is used in this paper to describe environmental conditions which either lack annual seasonal change or have periodicities of change which are longer or shorter than the seasons. Environmental factors act on plants either as stresses or disturbances and changes in environment can signal the onset of conditions which are favourable or unfavourable to plant growth and reproduction. Plant life-histories are thus adapted to these environmental factors and respond to them with both seasonal and aseasonal periodicities, depending on their manner of occurrence and effect on the plants. A review of pertinent studies from the Southern Hemisphere shows that plants of the same life-form (submerged, floating, emergent) might differ in the types of adaptation and response to environmental conditions according to latitude but that the periodicity of response could be seasonal or aseasonal regardless of latitude. The concept of seasonality versus aseasonality is therefore misleading and an oversimplification of the variety of periodicities with which the environment acts on plant genotypes. Limnological principles of the Northern Hemisphere are applicable to aquatic macrophytes in the Southern Hemisphere but there is a particular need for research into the effects of biotic variables and water level fluctuations on aquatic plants and communities in the latter.

Introduction

All plants exhibit periodicity of behaviour in their patterns of establishment, growth and reproduction and these are the result of progressive adaptation to the periodicity of change in environmental conditions. When the periodicity of behaviour follows the same regular annual pattern as seasonal changes in the external environment it can be considered seasonal. However, many environmental factors have different periodicities and predictability of occurrence, and for the purposes of this discussion can be considered aseasonal. Examples of such factors are the onset of night and day, the tidal cycle and the supposed long-term wet and dry cycles identified for southern Africa and Australia (Vines, 1977; Tyson & Dyer, 1978). Others such as the onset of disease or herbivory may occur seasonally or aseasonally.

This paper attempts to interpret the recorded adaptations and responses of aquatic macrophytes in terms of these environmental seasonal and aseasonal phenomena with particular reference to the Southern Hemisphere. Four general questions are addressed:

1. What is the basis of seasonal and aseasonal periodicity in environmental change?
2. What type of adaptation and response do the different seasonal and aseasonal components in the environment illicit in aquatic plants and plant communities?
3. What are the effects of factors which are normally seasonal in origin occurring out of season (e.g. discharges from impoundments during the dry season)?
4. Does seasonal behaviour of aquatic plants in the Southern Hemisphere differ from that in the Northern Hemisphere?

Hydrobiologia 125, 137–150 (1985).

The discussion is divided into two major sections. The first provides a general background to the different periodicities of change in the environment of plants and the way their life histories respond to conditions of their habitat. The second part is a review of examples which attempts to illustrate the response and adaptations of aquatic plants to seasonal and aseasonal phenomena.

Periodicity of change in environmental conditions

Seasonality

The seasons of the year result principally from the elliptical orbit of the earth around the sun and the constant inclination of the earth's axis to this orbit. Since the orbital movement is precise and predictable, so are the changes in day length, noon sun altitude and path-length of the sun's rays through the atmosphere which together establish the seasonal pattern. The duration of the seasons can thus be clearly defined (Rice, 1963; Table 1).

Man recognizes seasons more by differences in mean temperature, rainfall and consequent changes in the weather, than by the position of the earth in its orbit. These changes are, however, less predictable because a complex series of interactions between solar radiation, atmospheric gases, water vapour, the size of land and water masses and the topography of land surfaces cause large variability in weather conditions.

Plant genotypes are therefore exposed to and thus moulded by, a variety of selective pressures with a seasonal periodicity but because these vary in predictability from high (e.g. day length) to low (e.g. atmospheric temperature) probability of occurrence, we can expect plants to respond to them differently.

Aseasonality

The term aseasonality might be taken to mean a 'lack of' or 'without' seasons but clearly the rotation of the earth about the sun produces at least some seasonal change in day length, noon sun altitude and path-length of the sun's rays even in the equatorial regions. Thus some seasonality of environment occurs in these regions but the consequent annual changes in weather and climate are smaller than in temperate regions. The importance of these changes and their rôle as selective pressures on genotypes therefore arises and will be assessed in terms of plant behaviour in tropical environs later in the discussion.

There are a number of cyclical environmental phenomena which affect plant growth but which do not have a seasonal periodicity. The more obvious are diurnal and lunar cycles but those with a longer periodicity are less easy to recognize as they are subject to greater irregularity of intensity and timing. The most debated and topical of these phenomena are the long-term wet and dry 'cycles' proposed for Australia and southern Africa (Vines, 1977; Tyson & Dyer, 1978). The origins and predictability of these 'cycles' have been hotly debated (e.g. Troup, 1965; Wood & Lovett, 1974; Vines, 1977; Tyson & Dyer, 1978; Campbell & Gardiner, 1979; Nichols, 1981; King, 1973) but regular or not, aseasonal droughts, floods and hot or cold periods do occur on a longer time scale than the seasons and they do act as selective forces in the plant environment. Indeed, since these events are often severe, they may eliminate entire populations except for one or two exceptionally adapted individuals. This periodic screening of genotypes forms the basis of 'catastrophic' selection which is an important mechanism leading to adaptive traits and speciation in plants (Lewis, 1962; Stebbins, 1974).

Table 1. Duration of the seasons (Modified from Rice, 1963).

Northern Hemisphere	Southern Hemisphere	Length of season		Day of onset
		(Days)	(Hours)	
Spring	Autumn	92	20	March 21 equinox
Summer	Winter	93	14	June 21 solstice
Autumn	Spring	89	19	September 23 equinox
Winter	Summer	89	1	December 22 solstice

Disease and herbivory are two selective forces which often act aseasonally although it must be recognized that prevalence of such events may be higher during certain seasons and at certain stages of the plant life cycle (Stebbins, 1974). Unfortunately there have been very few studies of this nature on aquatic macrophytes in the Southern Hemisphere and so these aspects will not be considered further.

Life histories and plant response to environmental conditions

The relative uniformity of the aquatic, in contrast to the terrestrial, environment is held to encourage species with perennial life cycles and a predominance of asexual reproduction (Sculthorpe, 1967; Hutchinson, 1975). This may be true for the wet temperate and tropical latitudes but in semi-arid sub-tropical regions many aquatic macrophyte habitats experience alternate periods of wetting and drying which may be on short- (seasonal) or long- (aseasonal) term cycles. Annual growth patterns, desiccation resistant propagules and multiple regenerative adaptations (see below; Grime, 1979) may therefore be more the rule than exception in these habitats.

Unfortunately very few studies of aquatic macrophyte life cycles have been carried out under the umbrella of one of the conceptual frameworks which have been developed to describe plant life histories. As a result most information remains uncoordinated and dispersed, and it is difficult to formulate general principles on which to base this review. It is important for this discussion, however, to provide a background view of the way plants respond to environmental factors and to the types of adaptations which permit species to exploit different habitats.

The most significant work in the development of a holistic approach to the study of life cycles was that of MacArthur & Wilson (1967) who proposed the *r*/*K* concept of life histories. This work recognizes two types of organism at opposite ends of the evolutionary spectrum: (i) *K*-selected organisms which inhabit stable, non-fluctuating environments; they have a long life span and devote a small amount of energy to reproduction in order to produce few offspring with a high probability of survival, and (ii) *r*- selected species are considered opportunistic species which exploit fluctuating environments, have short life spans and expend a large amount of energy in producing many offspring.

Although very influential in the development of ideas on life-history adaptations the *r*/*K* concept has been found to present an oversimplified model (Whittaker & Goodman, 1979) which cannot provide a complete explanation of plant life-history phenomena. The main criticism is that it attempts to explain life-histories as the outcome of a single selection pressure (resource availability) and does not cater for the interactive manner in which many factors of the environment act. As a result, separate populations of the same species may occupy very different positions on the *r*-*K* continuum (Whittaker & Goodman, 1979) as may juvenile and adult components of one population (Stearns, 1976). More recent attempts to classify life-histories have tried to overcome these problems.

Calow & Townsend (1981) prefer the *a priori* testing of life-history adaptations on the basis of optimal use of limited resources. An organism's adaptations can be assessed by its ability to acquire resources and then partition them between maintenance, growth, storage, repair, defence and reproduction. However, our knowledge of how plants function in the multi-factorial environment is so limited that the optimal adaptations of a plant in any one habitat cannot be predicted *a priori* (Solbrig, 1981). While this does not detract from the scientific worth of this approach it does limit its applicability to studies orientated towards providing answers to immediate or short-term management problems. In such cases the *a posteriori* classification of life-history phenomena by Grime (1977, 1979) may prove to be more practical.

Grime (1979) defines 'strategies' as 'groupings of similar or analogous genetic characteristics which recur widely among species or populations and cause them to exhibit similarities in ecology'. He recognizes the need to consider different phases of the life cycles of the same organism, because even in the same habitat juvenile and mature stages may respond in different ways to the same selection force. Thus, he has proposed that plants have evolved three primary or vegetative adaptations (*C*, *R* and *S*) which operate in the mature or established phase of the life cycle and five regenerative adaptations for reproduction. Grime bases his model on the assumption that two sets of environmental conditions limit plant biomass in any one habitat; those which restrict production of biomass are termed 'stresses' while 'disturbances' effect the partial or total destruction of biomass in a productive environment. There are four permutations of high and low stress or disturbance but because severe stress would exclude recovery in a very disturbed habitat, only three are habitable (Grime, 1977, 1979). Thus, he considers that plants with three basic adaptations have evolved: *C* or competitive plants (low stress, low disturbance); *S* or stress-tolerant plants (high stress, low disturbance) and *R* or ruderal plants (low stress, high disturbance). Grime's regenerative adaptations are based on modes of reproduction and survival during the juvenile stage. These are; (i) Vegetative expansion, (ii) Seasonal regeneration, (iii) Persistent seed banks, (iv) Wind dispersal and (v) Persistent seedlings. However, individual species respond differently to particular selective forces of the environment (Menges & Waller, 1983). A flood may therefore stress some aquatic plants by reducing light penetration but act as a disturbance to others by causing physical destruction of biomass. Similarly a perennial species is adapted to seasonal drying out but desiccation of an annual may result in death (disturbance) of the plant or part thereof. The interpretation of stress and disturbance must therefore be based on each species' traits and adaptations assessed in relation to its particular habitat.

External environmental factors can also act in a third capacity, not considered by Grime, namely as 'signals'. Changes in the external environment often result in responses by plants which cannot simply be explained on the basis of biomass limitation by stress or disturbance; for example, the alternate drying and wetting of aquatic macrophyte seeds which is often required before germination can occur. Other signals may result when a stress or disturbance occurs, or is removed, but the significance of adaptation to signals lies in the fact that it regulates growth and dormancy to favourable and unfavourable periods respectively. Such adaptation is thus extremely important in promoting optimal use of resources by plants in both space and time or, in other words, promoting their ability to exploit favourable habitats (Howard-Williams & Ganf, 1981).

In the following review of examples we attempt to interpret aquatic plant responses to seasonal and aseasonal environmental change in terms of stress, disturbance and signals. To avoid a long, tedious list of examples, discussion is largely restricted: *Salvinia* and *Eichhornia* as examples of floating plants, *Typha* spp. as emergents and *Potamogeton crispus* L. as a submerged species.

Periodicity of response in aquatic plant reproductive cycles

The reproductive events of flowering, setting seed and the formation of hibernaculae or other propagules appear to have a largely seasonal cycle in rooted emergent and submerged plants, regardless of latitude, but in floating species they may be distinctly aseasonal.

The emergent *Typha* spp. flower at different times of the year in various habitats but with a seasonal periodicity. Thus, *Typha orientalis* Presl. and *Typha domingensis* Pers. in S.E. Australia flower in early summer (October/November) (Finlayson *et al.*, 1983) but *Typha latifolia* L. on the temperate highveld of South Africa (Rogers, 1982) flowers in mid-to late-summer (January) and *T. domingensis* on tropical Lake Chilwa (Howard-Williams, 1973) in mid-winter (July). Similarly, submerged species such as *P. crispus* (Rogers & Breen, 1980) and *Potamogeton pectinatus* L. (Howard-Williams, 1978) also show distinct seasonal reproductive cycles despite inhabiting hot sub-tropical and temperate climates respectively.

Few studies of aquatic plants in the Southern Hemisphere have elucidated the factors which act as signals for flowering and propagule production in emergent species. McNaughton (1966, 1975), however, has clearly demonstrated the importance of photoperiod and temperature change in growth and flowering of Northern Hemisphere *Typha* species and that these signals operate regardless of latitude. Vegetative reproduction by the formation of rhizomes also responds to photoperiod and temperature signals. A rise in temperature has been suggested as the signal for flowering and turion production in *P. crispus* (Waisel, 1971) but studies in both Japan (Kadono, 1984) and on the Pongolo River Floodplain in South Africa (Rogers & Breen, 1980) contradict this. In the latter habitat, propagule production is usually in winter and spring and

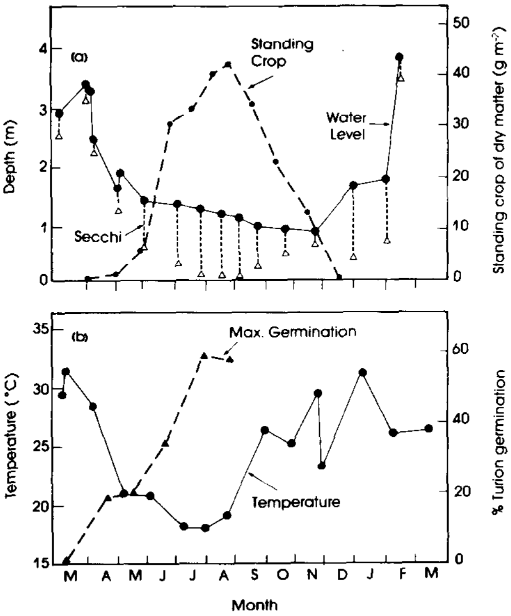

Fig. 1. Changes in *Potamogeton crispus* standing crop (1a) and turion germination (1b) in relation to water level (flooding) (1a), Secchi Disc depth (1a) and temperature (1b) on the Pongolo River Floodplain, South Africa. (After Rogers & Breen, 1980).

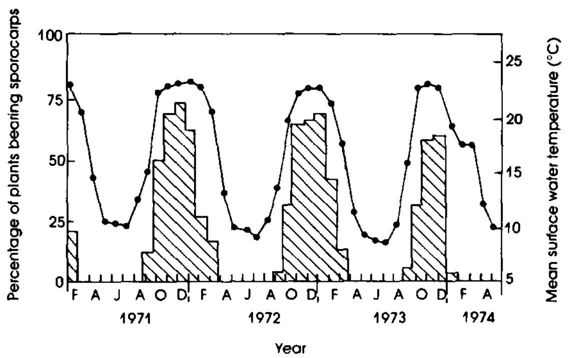

Fig. 2. The seasonal cycle of sporocarp production by *Azolla filiculoides* Lam. (histograms) in response to variations in mean monthly surface water temperature (-●-●-●-). (From Ashton, 1982).

is highly seasonal (Fig. 1), but does not occur in response to environmental conditions. Rather, individual plants have a short life-span (4-5 months) and, when grown out of season, reproduce at maturity regardless of the time of year (Rogers, 1984).

In contrast to rooted plants, floating species reproduce in response to both seasonal changes in the environment and changes in population density which may be aseasonal especially in the tropics. Thus, *Lemna* spp. respond to seasonal changes in photoperiod (Hillman, 1961) and *Azolla filiculoides* Lam. in the temperate regions of South Africa (Fig. 2) has a cycle of sporocarp production which correlates well with seasonal changes in water temperature (Ashton, 1982). *Eichhornia crassipes* (Mart.) Solms and *Salvinia molesta* D.S. Mitchell, however, seem to respond more to changes in density than temperature or photoperiod (Mitchell & Thomas, 1972). Both these species have a largely tropical and sub-tropical distribution where, although growing conditions change only slightly over an annual cycle, periodic flooding breaks up colonies and disperses the plants. Populations recover from such disturbance by rapid vegetative reproduction but as mats become more dense and competition for resources increases, the plants are stimulated to reproduce sexually. Presumably the limitation of one or other resource acts as the signal.

The marked tendency for asexual reproduction in aquatic macrophytes has resulted in the development of clonal populations or ecotypes (McNaughton, 1966; Hutchinson, 1975), which permit species to occupy widely differing habitats and to take advantage of locally favourable growing seasons. Many asexual reproductive organs, however, cannot survive dehydration and so in semi-arid regions desiccation-resistant propagules are a prerequisite for long-term survival. The production of seeds and fruits by most species provides a propagule with a tough outer covering which not only withstands desiccation but often requires it in order to break dormancy (Muencher, 1936; Teltscherova & Hejný, 1973). Even under wet conditions it may take several years to break the dormancy imposed by the thick coat (Hutchinson, 1975) with the result that large seed banks develop. This reduces the risk of local extinction during prolonged aseasonal dry periods.

The initiation of propagule germination is generally attributed to environmental signals such as day length, light, temperature and oxygen saturation (Hutchinson, 1975; Haller *et al.*, 1976; Weber & Nooden, 1976; Sastroutomo, 1980). The physiological basis of such stimulation is not well understood, but hormonal reactions similar to those of terrestrial seeds appear to be operative (Weber & Nooden, 1976).

This concept of regenerative adaptations becoming modified to promote the persistence of ecotypes in different habitats can be well illustrated by comparing reproduction of *P. crispus* in different southern and northern latitude habitats.

The literature on this cosmopolitan species is large (Sculthorpe, 1967; Hutchinson, 1975; Stuckey *et al.*, 1978; Stuckey, 1979; Rogers & Breen, 1980; Sastroutomo, 1980; Kadono, 1984) and confused, with much argument and contradiction about the times of reproduction and the importance of different reproductive structures. The many differences reported, however, appear to simply describe wide ecotypic differentiation. In general the species has a distinctly annual growth cycle and can be classified according to Grime (1979) as 'ruderal with multiple regenerative strategies'. The 'regenerative strategies' are 'seasonal regeneration' by means of turions, the formation of a 'persistent seed (achene) bank' and 'persistent seedlings' or young plants which can remain dormant over periods of poor light penetration (Stuckey *et al.*, 1978; Stukey, 1979; Rogers, 1984). However, the growing season differs from one habitat to the next as does the rôle of individual regenerative adaptations. The following examples illustrate this variability.

On the sub-tropical Pongolo River Floodplain in South Africa, frequent floods and concomitant poor light climate during summer (Fig. 1), create an unfavourable period for submerged plant growth but winter conditions are more suitable. Occasional droughts, however, do result in the lake habitats drying out with an aseasonal periodicity. *Potamogeton crispus* populations must, therefore, be adapted to seasonal reproduction which regulates plant establishment to winter and must also cope with aseasonal floods and occasional droughts (Rogers, 1984). Because the unfavourable summer light conditions vary in duration from 3–7 months, the autumnal decrease in temperature forms a more reliable signal of the forthcoming favourable winter period than does photoperiod. Thus, a drop in water temperature to 25 °C in autumn stimulates germination of turions ('seasonal regeneration') which increases until the winter minimum temperature of 15 °C (Rogers & Breen, 1980). Germination is thus staggered over a period of 3-4 months (April-July; Fig. 1), thereby increasing the chance of plant establishment if flooding is late and continues into autumn or winter. This chance is further increased by the ability of young plants to remain dormant for up to three months under poor light conditions ('persistent seedling strategy'). Achenes of *P. crispus* require drying and rewetting for germination and thus, during wet periods, the achene bank increases to several thousand m^{-2} but rewetting after a drought stimulates germination. This 'persistent seed bank strategy' is therefore an adaptation to ensure survival of long-term aseasonal drought conditions in this habitat.

In contrast to the above example, other populations of *P. crispus* respond to other signals which regulate growth and reproduction to favourable periods which occur at different times of the year. The most opposing example is of populations in north temperate ponds which freeze over in winter (Stuckey *et al.*, 1978; Stuckey, 1979). In these habitats growth occurs in spring or summer and survival over winter is either as turions (Sastroutomo, 1980) or dormant young plants which persist until the light climate improves with the spring thaw (Stuckey *et al.*, 1978). In the former instance turion germination is in response to changes in photoperiod and temperature in spring, while in the latter, turions appear to germinate in response to decreasing temperature in autumn as on the Pongolo Floodplain. Many of these temperate habitats do not experience severe drought and in the absence of this selection force, flowering is occasional (Hunt & Lutz, 1959) and no persistent achene bank develops. Thus, although entirely different seasonal and aseasonal environmental phenomena are experienced in these habitats, ecotypic differentiation of the different regenerative adaptations permits the species to survive over a wide latitudinal range.

The question of seasonality and aseasonality of aquatic plant reproductive cycles is therefore not a simple one. Plant responses in both production and germination of propagules depend on adaptations to conditions in their specific habitats, and responses to both seasonal and aseasonal changes in environment can be found in single species regardless of whether they occur in tropical or temperate regions. Furthermore, there is no evidence of a complete lack of seasonal response in tropical habitats.

Periodicity of response in the established phase

This part of the discussion deals with changes in the growth, biomass and productivity of aquatic plants in response to changes in environmental conditions. Measurements of biomass change of floating macrophytes are generally meaningless because they are affected by compaction due to wind and can change rapidly. Growth rate is, therefore, a better currency for measuring response of these plants and has been shown to be clearly seasonal in both *S. molesta* from tropical Lake Kariba (Mitchell & Tur, 1975) and *A. filiculoides* from the temperate highveld of South Africa (Ashton, 1982). Furthermore, it is important to distinguish between changes in biomass of the population as a whole, changes during growth and senescence of a single member of the population and changes during growth and senescence of a specific organ (e.g. leaf) of that member (Hopkins *et al.*, 1980).

These latter points are illustrated by studies of *Typha orientalis* (Mitchell & Chick, unpubl.; Fig. 3), *Potamogeton pectinatus* (Howard-Williams, 1978; Fig. 4) and *P. crispus* (Rogers & Breen, 1980; Fig. 1). Growth of *T. orientalis* leaves and rhizomes in S.E. Australia are both distinctly seasonal, but maximum biomass is reached at different times of the year. In contrast, root biomass shows no significant change over the annual cycle (Fig. 3). What this study does not show, however, is that the individual ramets from which new leaves arise each year may reach at least three years of age (Grace & Wetzel, 1981b) and so function on yet another time scale.

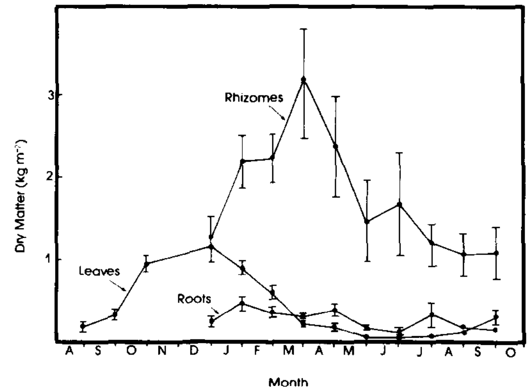

Fig. 3. Seasonal biomass for leaves, rhizomes and roots of *Typha orientalis* in the Murrumbidgee Irrigation Areas, Griffith, Australia. Vertical bars represent standard errors of the mean. (From Mitchell & Chick, unpubl.).

In the south temperate lake, Swartvlei, biomass of the submerged *P. pectinatus* is present over a full annual cycle, although growth of individual plants and hence structure of the community is highly seasonal (Fig. 4). New shoots, which arise from perennial stolons, emerge each spring and reach maturity in autumn but, persist through winter and senesce the following spring. Branching and the

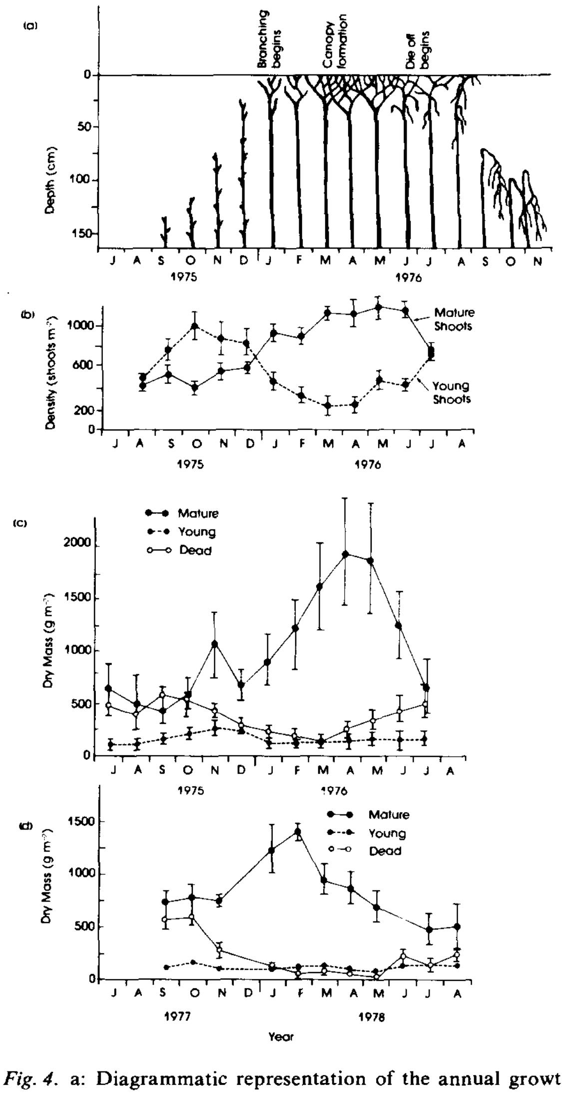

Fig. 4. a: Diagrammatic representation of the annual growth cycle of *Potamogeton pectinatus* in Swartvlei, South Africa. b: Changes in shoot density of *Potamogeton pectinatus*. c: Changes in mean mass of individual live shoots. d: Production rate curve for *Potamogeton pectinatus*. Vertical bars in b and c represent two standard errors. (From Howard-Williams, 1978).

formation of a canopy reduce light penetration and from mid-summer through winter there is a progressive loss of the lower leaves. When total production of dry matter was calculated this resulted in a production/maximum biomass (*P/B*)ratio of 1.2:1. In contrast, *P. crispus* on the Pongolo Floodplain shows distinct seasonal changes in biomass (Fig. 1), with the population only being present for 6–8 months of the year, but it may have a *P/B* ratio as high as 2.8:1 (Rogers, 1984). In this case, individual plants have a life span of only 4–5 months, but since germination is staggered over a period of 3–4 months, the population is replaced at least once in any season. The adaptive significance of this is that it permits the population to exploit most or all of the 8 month autumn-spring favourable period for plant growth. These examples emphasize the importance of understanding the characteristics of both individual plants and populations in order to assess both the response of species to environmental change and in interpreting the periodicity of biomass changes.

The seasonal cycle of vegetative growth for *Typha* spp., growing near Griffith (Fig. 3), is also characteristic of most emergent aquatic macrophytes in the Northern Hemisphere (McNaughton, 1966; Fiala, 1978) and in the tropics. Howard-Williams (1973) has shown that in Lake Chilwa (15° S), where temperatures are uniformly high (monthly means range from 18.7 °C in July to 27.2 °C in December), regrowth of *Typha domingensis* from cut stands varied seasonally in relation to solar radiation, water depth and phenology of the plant (Table 2). The pattern of regrowth from cut stands was presumed to reflect the pattern of actual growth in undamaged leaves. Growth was most rapid in the summer from December to March reaching a peak in the latter month when solar radiation was highest. Growth declined in autumn but increased somewhat from July to August due to the flowering of the plants. Growth was least in November when the second year old flowering shoots died and the plants collapsed due to a combination of low water levels and maximum biomass. Howard-Williams (1973) noted that below-ground biomass was approximately equal to above-ground biomass, although at the period of minimum-shoot biomass, the former constituted 67% of the total. However, these observations were based on limited sampling and may be contrasted with the data of Mitchell & Chick (unpubl.) (Fig. 3) and Fiala (1978), which demonstrate a clear seasonal increase in rhizome biomass during autumn, prior to the adverse winter growth conditions. In this case, the rhizomes clearly function as perennating organs for the plant.

The periodicity of change in production and biomass in the established phase of a plant's life cycle

Table 2. Annual growth pattern of *Typha* in Lake Chilwa as demonstrated by regrowth of plants in cut stands (from Howard-Williams, 1973).

Date	Regrowth (g m^{-1} day^{-1})	Solar radiation* (J cm^{-2} d^{-1})	Water depth (cm)	Phenology
Oct. '71	3.6 (0.93)	2473	71	End of flowering
Nov.	1.6 (0.57)	2355	65	2nd year shoots die
Dec.	6.6 (0.88)	2264	74	New growth
Jan. '72	6.6 (0.60)	2355	70	New growth
Feb.	4.9 (0.63)	2387	85	
Mar.	7.1 (1.58)	2447	90	
Apr.	4.2 (0.55)	2069	100	
May	2.4 (0.26)	1899	80	
Jun.	2.5 (0.26)	1743	N.D.	
Jul.	4.0 (0.73)	1743	70	Inflorescences develop
Aug.	3.0 (0.74)	1964	67	Flowering

*Solar radiation figures are monthly means for 1968 to 1971.
Standard error of the mean in parenthesis.

N.D. = no determination.

therefore shows as much variation as the reproductive cycle. Different species and plant parts respond on different time scales, independently of habitat and latitude, and these responses can have specific implications for the periodicity of response of the population as a whole.

Response of aquatic macrophyte communities to fluctuations in water level and flow rate

Considering that wetlands are predominantly shallow habitats and that evaporation in the Southern Hemisphere generally exceeds precipitation, it is surprising that so few studies have assessed the effects of water level and flow rate fluctuations on aquatic plant communities (Howard-Williams & Ganf, 1981; Brock & Lane, 1983; Dohmeier, 1984). We consider this complex topic separately as it is of vital importance to the survival of most macrophyte species and is the primary determinant of community composition in space and time.

Fluctuations in water level and flow rate are often seasonal in origin but their intensity, duration and periodicity can vary markedly both within and between seasons. Thus the duration, periodicity and predictability of periods favourable for plant growth may vary both seasonally and aseasonally. It is very difficult to categorize habitats on this basis as their variability is continuous over a wide spectrum of fluctuations but, the major effects of changes in water level and flow rate on plants and plant communities can be more easily grouped into five categories:

(i) Saturation of the rooting medium with the subsequent stress of anoxia (Grace & Wetzel, 1981a).
(ii) The stress imposed by desiccation during dry periods (Mitchell, 1978; Rogers & Breen, 1980; Brock, 1983).
(iii) Changes in salinity associated with evaporation and precipitation cycles (Brock, 1983).
(iv) The effects of changes in light climate induced by changes in depth and suspended particle load (Rogers & Breen, 1980; Dohmeier, 1984).
(v) The physical damage (disturbance) caused by the mechanical action of floods and water turbulence (Mitchell, 1978; Neiff, 1979).

Each of these effects may occur seasonally or aseasonally and the major determinant is the precipitation cycle which has both seasonal and longer term periodicities.

Anoxia

The responses of emergent macrophytes to anoxia may be exemplified by reference to *Typha* spp. This plant frequently occurs in situations where its rhizomes are growing in anaerobic sediments. The rhizomes survive because oxygen is made available to them *via* the aerenchyma which connects them to the photosynthetic portions of the plant projecting above the water surface. Indeed, Sale & Wetzel (1983) have demonstrated that if this supply is blocked by cutting the stems below the surface of the water, oxygen levels in the rhizome decline rapidly from about 15% to zero within 8 hours.

The slow rate of oxygen diffusion may thus limit the depth to which *Typha* spp. can grow and thus its competitive ability in communities. For example, Howard-Williams (1973) demonstrated that the growth of *Typha domingensis* from Lake Chilwa declined if subjected to depths greater than 1.5 m for prolonged periods. However, competitive ability between different *Typha* species may differ in different water depths. Grace & Wetzel (1981a) showed that the competitive ability of *T. latifolia* was reduced in deeper water because of the greater cost of producing the relatively broad leaves which characterize this species, although otherwise, it was able to outcompete *T. domingensis* (characterized by narrow leaves) for light. *Typha domingensis* was therefore only able to compete successfully with *T. latifolia* at depths greater than 80 cm at this site. Since oxygen concentrations in the sediment change markedly, in both space and time, down the depth gradient in wetlands, adaptations to survive anoxia of the root zone play an important rôle in determining species distribution and succession. It can be expected that species adapted to regular seasonal anoxia will occur near mean water level, while others only able to tolerate occasional flooding or drying out on a longer time scale, will occur further up or down the depth gradient respectively.

Desiccation

There is very little information on the response of aquatic plants to desiccation. In general, responses seem rather to be of avoidance by production of resistant propagules than of tolerance of water stress by established plants. Thus, both *Typha* spp. (Grace & Wetzel, 1981b) and *P. crispus* (Hunt & Lutz, 1959; Rogers, 1984) respond to decreases in water level and periodic drying out by increasing seed production. Although avoidance of dry periods is usually achieved by sexual reproduction, some species (e.g. *Ruppia* spp.) also produce turions which are capable of surviving 'several years' of desiccation (Brock, 1983). Indeed, the extreme variability of the frequency and duration of droughts and associated fluctuations of water level seems to select for species with multiple regenerative adaptations (Grime, 1979) which allows them to respond to both seasonal and aseasonal changes in environment as described for *P. crispus* above.

Salinity

There is again a marked paucity of information on the responses of plants to fluctuations in salinity of inland waters of the Southern Hemisphere, the most detailed work being from Australia (Brock, 1982a, b, 1983; Brock & Lane, 1982). Changes in salinity are often associated with changes in cycles of evaporation and precipitation and so plants in these habitats generally have life histories similar to those of temporary waters. Annuals tend to show typical monocarpic reproductive patterns of rapid development, early maturity and the production of large numbers of small propagules. Perennials, however, exhibit polycarpic reproductive patterns with slow development, late maturation and the production of a small number of large propagules (Brock, 1983). Some halophytic species, however, do show special adaptations to changes in salinity. Brock (1982a) has shown that while an increase in salinity acts as a signal for germination of the annual *Ruppia tuberosa*, Davis & Tomlinson, a decrease in salinity illicits the same response from seeds of the perennial *Ruppia megacarpa* Mason. Germination is not, therefore, in response to any predictable seasonal factor, but rather to salinity, the major stress of the environment, which can change seasonally or aseasonally.

The light climate

The light climate is probably the most important factor determining the distribution of submerged macrophytes in space and time and has been extensively covered by Spence (1982). Here we only consider an aspect of particular importance to semiarid areas; the reduction in light penetration caused by high silt loads. Highly turbid flood waters on the Pongolo River Floodplain during summer, for example, prevent submerged plant growth. Thus *P. crispus* exhibits winter growth (Fig. 1), even though optimal temperature conditions for photosynthesis (c. 30 °C; Ikusima, 1965) occur during summer (Rogers & Breen, 1980).

Resuspension of bottom sediments can also reduce light penetration in shallow systems and adaptations such as floating leaves and avoidance as a dormant stage are typical of plants in habitats where this occurs regularly. In other systems where occasional or aseasonal droughts cause an unusual marked reduction in water levels it can have important effects on the plant community. In Rolfe's Pan, a permanent endorheic lake on the highveld of South Africa, resuspension of bottom sediments during the 1982/83 drought resulted in death of a diverse submerged macrophyte community and a change to a phytoplankton dominated system (Dohmeier, 1984).

Flood disturbance

The variable flooding régime of a major river such as the Paraná in Argentina (Bonetto, 1975) provides a good example of the effect of fluctuations in water level and flow rate on aquatic macrophyte communities. In this case, the occurrence of the floods is seasonal but the variation in their extent is markedly different from year to year, so that effects on aquatic communities differ to such an extent that they can almost be regarded as aseasonal.

Neiff (1979) carried out a study of the effects of the floods on aquatic vegetation of the Middle Paraná River between 1970 and 1977 and distinguished between annual or 'ordinary' floods with a flow of 25 000 m s^{-1} and 'extraordinary' or 'exceptionally extraordinary' floods with a flow of 40 000 m s^{-1} and above, the latter generally occurring every 5–10 yrs. Extraordinary floods occurred in 1973 and 1977. During ordinary floods, the rise in water level is usually gradual but nevertheless causes temporary changes to the morphology of the system, with lagoons being enlarged so as to coalesce with one another and the main river. The inflows of flood water also affect the chemical and physical characteristics of the water. All these effects are variable and depend upon the magnitude of the floods (Bonetto, 1975).

The aquatic vegetation of the system is adapted to these regular seasonal flood events and when the changes are gradual there is little marked change in plant zonation. However, during more rapid changes, rooted emergent species such as *Paspalum repens* Berguis, *Panicum elephantipes* Nees and *Polygonum punctatum* Ell may be dislodged and carried away as floating debris. Depending on the intensity of the flood and the velocity of flow, these are either eliminated or moved to a more favourable area. Rooted submerged plants may undergo a temporary reduction in density and cover as a consequence of a decrease in the transparency of the water caused by the high turbidity of the flood water. However, this change is accompanied by a tendency for increased species diversity. Floating islands of aquatic vegetation can be moved in large quantities from the tributary rivers into the main Paraná River during flood seasons, the extent of this phenomenon again depending on the extent of the flood. When the flood subsides and the rooted vegetation begins to regrow, species with a capacity for rapid colonization, such as *Eichhornia crassipes* and *Salvinia herzogii* De La Sota will dominate the more lentic systems, as these are progressively isolated from the flow.

Extraordinary flood disturbance has a devastating effect on the vegetation and Neiff (1979) distinguished four stages of effect:

(i) a critical period when flood waters inundate the valley and reduce both extent and species diversity of aquatic vegetation;
(ii) a compensation period when the macrophytes begin to recover following a fall in water level;
(iii) a normal water level period when the various water bodies are once more isolated from the main stream and the vegetation is potentially different in each;
(iv) a low water period when the hydrophyte cover is reduced and helophytes colonize the exposed mud.

Although these changes in communities take place in response to the effect of seasonal floods, their effects may be perceived for a number of years. Similarly, the rate of successional changes such as those described above, may be affected by variable seasonal factors such as temperature, even though the change itself will often take place over several seasons. For example, the replacement of *Pistia stratiotes* L. by *Eichhornia crassipes* in a lentic water body associated with the Paraná River took 17 months to occur (Neiff & Poi de Neiff, 1979).

The pattern of water level changes in Lake Kariba in its first few years provides an interesting example of how man-made dams can alter the way in which water level fluctuations determine community composition (Mitchell, 1970). The disturbance caused by changes in water level and of flow rate in the Zambezi River prior to impoundment by the dam provided an environment for aquatic plants similar to that of the Paraná River. The shifting substratum, characteristic of so-called sand-bank rivers, and the mechanically damaging effect of the annual flood waters, was a major disturbance to all but the most hardy perennial emergent macrophytes. Inter-flood periods were characterized by receding water levels in backwaters and isolated river pools. These were seasonally colonized by a complex of floating plants such as *Pistia stratiotes* and annual submerged species such as *Potamogeton* spp. and *Lagarosiphon* spp., with typically ruderal life histories which permitted rapid growth and colonization between floods.

The formation of Lake Kariba had three major effects on the conditions for aquatic plant growth; all of an aseasonal nature. First, the effect of river flood was largely removed. Second, the extent of fluctuations in water level was markedly diminished and standing water bodies of varying degrees of calmness were permanently available. Third, the flooding of land, vegetation and animals provided a source of plant nutrients which gradually declined over the first few years. The first macrophytes to take advantage of these more favourable growing conditions were *Ceratophyllum demersum* L. and *Salvinia molesta*. Both are free-floating species capable of forming populations that would have been unaffected by the extensive changes in water depth and area consequent on the flooding of the lake bed. The propagules of the original flora were submerged at such a depth as to be virtually eliminated. As the lake began to mature and shorelines began to stabilize, a permanent lake flora started to develop and species able to accommodate to regular fluctuations in water level began to colonize zones of the shoreline. Thus *Lagarosiphon verticillifolius* Oberm. formed large beds in the deeper water and *Panicum repens* L. was particularly successful in colonizing the exposed shorelines. *Salvinia* continued to move up and down with the water level and provided a substratum for emergent swamp species such as *Scripus cubensis*, Poeppig & Kwith ex Kunth, *Typha domingensis* and *Phragmites mauritianus* to form floating sudd islands. These swamp species were, however, not able to adapt to the extent of the lake level fluctuations and died when stranded on the shore by a receding lake level. In more sheltered situations, however, some aquatic plants (e.g. *Potamogeton schweinfurthii* A. Benn) left by receding water levels adopted different growth forms and were able to survive several months until resubmerged. These responses occurred whenever the lake level fell regardless of the season, though increased insolation in the summer increased desiccation and decreased survival.

Responses to nutrient supply

Plants which derive their nutrient supply entirely or largely through their roots from the substratum in which they are growing do not normally respond rapidly to changes in nutrient supply. In most of these situations plant nutrients are not limiting growth. The growth of emergent plants, such as *Typha* spp., in swamps is, therefore, generally a reflection of seasonal temperature fluctuations rather than of nutrient supply. Where *Typha* populations experience reduced nutrient supply, the plants compensate by directing more of their resources to root growth (Grace & Wetzel, 1981b). The capacity of such plants to cycle resources such as nutrients between different parts of the plant and to take up and lose nutrients to the surrounding environment has led to them being called nutrient pumps (Klopatek, 1978). This phenomenon occurs in response to seasonal changes and can be described by referring to the work of Davis & Van Der Valk (1983), with *Typha glauca* Godr. in pothole marshes on the prairies of Iowa. These workers showed that the plant shoots accumulate nitrogen, phosphorus, potassium, calcium and sodium in spring. After peak biomass is achieved in mid-summer, both phosphorus and nitrogen are translocated within the plant, principally to the rhizome, but also to the inflorescences. Most of the nutrients remaining in the shoots that die at the end of the growing season are probably leached into the interstitial water during decomposition. However, the nitrogen and phosphorus in the rhizomes are stored over winter and are translocated into the shoots again in the following spring, together with nutrients absorbed by the plant from external sources. Potassium is also translocated within the plant but appears to leak into the environment without being stored in the rhizome. Sodium and calcium are not translocated from the shoot during the summer; the former is leached into the environment during decomposition, the latter is retained. This example demonstrates that when studying seasonality of nutrient supply it is important to recognize both internal translocation of nutrients and changes of supply in the external environment.

Floating species and some submerged species (Denny, 1972) obtain nutrients from the water in which they are growing. In this regard they are similar to phytoplankton, and rather like phytoplankton they can respond rapidly to changes in nutrient supply. Extensive growth of *Eichhornia crassipes* and *Salvinia molesta* in all continents of the Southern Hemisphere occurs in nutrient-rich waters where temperatures are sufficiently high for rapid rates of growth. In tropical regions this growth persists year round as shown for *S. molesta* in the Sepik River, Papua New Guinea (Mitchell *et al.*, 1980), whereas in temperate regions this is seasonal and only occurs in the summer. In Lake Kariba, a single large input of nutrients from decay of terrestrial vegetation when the lake filled, caused explosive growth of *S. molesta* but as this supply was flushed from the system during successive summers, growth declined to such an extent that the species was no longer a problem (Mitchell, 1970). The periodicity of nutrient supply can therefore have important implications for management of aquatic plants in different habitats.

Conclusion

This examination of seasonal and aseasonal phenomena in aquatic plants clearly exposes the complexities of plant-environment interactions which are superficially marked by the broad rhythm of seasonal changes in higher latitudes. Thus the questions set out in the introduction cannot be answered in simple terms. Seasonality versus aseasonality cannot be considered only in terms of whether or not habitats at low latitudes experience a lack of marked seasonal change without grossly oversimplifying the variety of periodicities with which environmental factors affect plants, or denying the complexity of plant responses to fluxes in environmental conditions. It has to be recognized that some components of the environment (e.g. water level fluctuations) change with periodicities which may be longer or shorter or with less predictability of occurrence, than those of direct seasonal origin (e.g. photoperiod) and that they also act as selective forces on the plant genotype.

Plants are adapted to and thus respond to, environmental factors such as stresses, disturbances or signals of forthcoming conditions and may do so with seasonal or aseasonal periodicities regardless of latitude. Thus, a change from asexual to sexual reproduction in floating plants can occur aseasonally in response to density changes in the tropics but in temperate habitats the same response may be to seasonal changes in temperature. Another example is that the seasonality of *P. crispus* flowering is reduced in north temperate lakes where water level changes are small but increased in hot sub-tropical habitats where low water levels are more frequent.

These examples demonstrate that differences in seasonal behaviour between aquatic plants in the two hemispheres are less related to global than to local factors and this appears to be generally true for other supposed differences in seasonal behaviour of aquatic macrophytes between the two hemispheres. However, the interactions between plant and environment within the rhythm of the seasons is so complex and incompletely understood that even this general statement has to be made with caution. Further studies of these interactions are clearly required. In the Southern Hemisphere these should concentrate on assessing the effects of biotic factors such as grazing, disease and, most importantly, water level fluctuation and its subsequent effect on habitat conditions. It is only by means of investigations such as these that unifying principles of the patterns of plant responses to regular and irregular changes in the environment can be elucidated to the benefit of our understanding of these complex phenomena.

Acknowledgements

We would like to thank Carol Sam, Margaret Marshall and Margie Walker for assistance with manuscript preparation.

References

Ashton, P. J., 1982. The autecology of *Azolla filiculoides* Lamarck with special reference to its occurrence in the Hendrik Verwoerd Dam Catchment Area. Ph.D. Thesis, Rhodes Univ., Grahamstown, South Africa, 312 pp.

Bonetto, A. A., 1975. Hydrologic regime of the Paraná River and its influence on ecosystems. In A. Hasler (ed.), Coupling of land and water systems. Springer-Verlag N.Y.: 175–197.

Brock, M. A., 1982a. Biology of the salinity tolerant genus *Ruppia* L. in salt lakes in South Australia. I. Morphological variation within and between species and ecophysiology. Aquat. Bot. 13: 219–248.

Brock, M. A., 1982b. Biology of the salinity tolerant genus *Ruppia* L. in salt lakes in South Australia. II. Population ecology and reproductive biology. Aquat. Bot. 13: 249–268.

Brock, M. A., 1983. Reproductive allocation in annual and perennial species of the submerged aquatic halophyte *Ruppia*. J. Ecol. 71: 811–828.

Brock, M. A. & J. A. K. Lane, 1983. The aquatic macrophyte flora of saline wetlands in Western Australia in relation to salinity and performance. Hydrobiologia 105: 63–76.

Calow, P. & C. R. Townsend, 1981. Energy, Ecology and Evolution. In C. R. Townsend & P. Calow (eds), Physiological Ecology: An Evolutionary Approach to Resource Use. Blackwell Sci. Publ., Oxford: 3–19.

Campbell, R. B. & B. Gardiner, 1979. A comment on possible relationships between rainfall, crop yields and the sunspot cycle. J. Aust. Inst. Agric. Sci. 45: 50–51.

Davis, C. B. & A. G. Van Der Valk, 1983. Uptake and release of nutrients by living and decomposing *Typha glauca* Godr. tissues at Eagle Lake, Iowa. Aquat. Bot. 16: 75–89.

Denny, P., 1972. Sites of nutrient absorption in aquatic macrophytes. J. Ecol. 60: 819–826.

Dohmeier, R. A., 1984. The standing crop and production of the benthic plants and phytoplankton at Rolfes Pan. Honours Thesis, Dept Botany, Univ. Witwatersrand, Johannesburg, South Africa, 34 pp.

Fiala, K., 1978. Seasonal development of helophyte polycormones and relationship between underground and aboveground organs. In D. Dykyjova & J. Kvet (eds), Pond Littoral Ecosystems. Springer-Verlag, Berlin: 174–181.

Finlayson, C. M., J. Roberts, A. J. Chick & P. J. M. Sale, 1983. The biology of Australian Weeds. II *Typha domingensis* Pers. and *Typha orientalis* Presl. J. Aust. Inst. Agric. Sci. 49: 3–10.

Grace, J. B. & R. G. Wetzel, 1981a. Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. Am. Nat. 118: 463–474.

Grace, J. B. & R. G. Wetzel, 1981b. Phenotypic and genotypic components of growth and reproduction in *Typha latifolia:* experimental studies in marshes of differing successional maturity. Ecology 62: 789–801.

Grime, J. P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111: 1169–1184.

Grime, J. P., 1979. Plant Strategies and Vegetation Processes. J. Wiley & Sons, Chichester, 222 pp.

Haller, W. T., J. L. Miller & L. A. Garrod, 1976. Seasonal production and germination of *Hydrilla* vegetative propagules. J. Aquat. Pl. Mngmt 14: 26–29.

Hillman, W. S., 1961. The Lemnaceae, or duckweeds. A review of the descriptive and experimental literature. Bot. Rev. 27: 221–287.

Hopkins, C. S., J. G. Gosselink & R. T. Parrondo, 1980. Production of coastal Louisiana marsh plants calculated from phenometric techniques. Ecology 61: 1091–1098.

Howard-Williams, C., 1973. Vegetation and Environment in the marginal areas of a tropical African lake L. Chilwa, Malawi. Ph.D. Thesis, Univ. London, 312 pp.

Howard-Williams, C., 1978. Growth and production of aquatic macrophytes in a south temperate saline lake. Verh. int. Ver. Limnol. 20: 1153-1158.

Howard-Williams, C. & G. G. Ganf, 1981. Shallow Waters. In J.-J. Symoens, M. J. Burgis & J. J. Gaudet (eds), The Ecology and Utilization of African Inland Waters. UNEP Reports and Proceedings Series 1, 191 pp.

Hunt, G. S. & R. W. Lutz, 1959. Seed production in curly leaved pondweed. J. Wildl. Mngmt. 23: 405-408.

Hutchinson, G. E., 1975. A Treatise on Limnology, Vol. III, J. Wiley & Sons, N.Y., 660 pp.

Ikusima, I., 1965. Ecological studies on the productivity of aquatic plant communities. I. Measurement of photosynthetic activity. Bot. Mag., Tokyo 78: 202 211.

Kadono, Y., 1984. Comparative ecology of Japanese *Potamogeton:* An extensive survey with special reference to growth form and life cycle. Jap. J. Ecol. 34: 161-172.

King, J. W., 1973. Solar radiation changes and the Weather. Nature 245: 443 446.

Klopatek, J. M., 1978. Nutrient dynamics of freshwater riverine marshes and the role of emergent macrophytes. In R. E. Good, D. F. Whigham & R. L. Simpson (eds), Freshwater Wetlands: Ecological Processes and Management Potential. Academic Press, N.Y.: 195 216.

Lewis, H., 1962. Catastrophic selection as a factor in speciation. Evolution 16: 257 271.

MacArthur, R. H. & E. O. Wilson, (1967). The Theory of Island Biogeography. Princeton Univ. Press, Princeton, N.J., 203 pp.

McNaughton, S. J., 1966. Ecotype function in the *Typha* community-type. Ecol. Monogr. 66: 297-325.

McNaughton, S. J., 1975. r- and K selection in *Typha*. Am. Nat. 109: 251 261.

Menges, E. S. & D. M. Waller, 1983. Plant strategies in relation to elevation and light in floodplain herbs. Am. Nat. 122: 454 473.

Mitchell, D. S., 1970. Autecological Studies of *Salvinia auriculata* Aubl. PhD. Thesis, Univ. London, 669 pp.

Mitchell, D. S., 1978. Freshwater plants. In M. J. A. Werger & A. C. Van Bruggen (eds), Biogeography and Ecology of southern Africa. W. Junk, The Hague: 1113-1138.

Mitchell, D. S., T. Petr & A. B. Viner, 1980. The water-fern *Salvinia molesta* in the Sepik River, Papua New Guinea. Envir. Conserv. 7: 115-122.

Mitchell, D. S. & P. A. Thomas, 1972. Ecology of water weeds in the neotropics. Technical Papers in Hydrology 12. Unesco, Paris, 50 pp.

Mitchell, D. S. & N. M. Tur, 1975. The rate of growth of *Salvinia molesta (S. auriculata* Auct.) in laboratory and natural conditions. J. appl. Ecol. 12: 213 225.

Muenchner, W. C. L., 1936. Storage and germination of seeds of aquatic plants. Cornell Univ. Agric. Exp. Sta. Bull. No. 652.

Neiff, J. J. , 1979. Fluctuaciones de la vegetacion acuatica en ambientes del valle de inundacion del Paraná Medio. Physis 38: 41 53.

Neiff, J. J. & A.Poi de Neiff, 1979. Estudios sucesionales en los camalotales Chaquenos y se fauna asociada. I. Etapa seral *Pistia stratiotes Eichhornia crassipes*. Physis 37: 29-39.

Nichols, N., 1981. Sunspot cycles and Australian rainfall. Search 12: 83-85.

Rice, H. S., 1963. Seasons. In W. D. Halsey & L. Shores (eds), Collier's Encyclopedia, 20: 557-559.

Rogers, K. H., 1982. Death of the Bullrush (*Typha latifolia* L.) in the Rietspruit. Unpubl. Rep. Dept Botany, Univ. Witwatersrand, Johannesburg, South Africa, 12 pp.

Rogers, K. H., 1984. The Role of *Potamogeton crispus* L. in the Pongolo River Floodplain Ecosystem. Ph.D. Thesis, Univ. Natal, Pietermaritzburg, South Africa, 299 pp.

Rogers, K. H. & C. M. Breen, 1980. Growth and reproduction of *Potamogeton crispus* in a South African lake. J. Ecol. 68: 561 571.

Sale, P. J. M. & R. G. Wetzel, 1983. Growth and metabolism of *Typha* species in relation to cutting treatments. Aquat. Bot. 15: 321-334.

Sastroutomo, S. S., 1980. Environmental control of turion formation in curly leaf pondweed, *Potamogeton crispus* L., Physiol. Plant. 49: 261-264.

Sculthorpe, L. D., 1967. The Biology of Aquatic Vascular Plants. Edward Arnold, Lond., 610 pp.

Spence, D. H. N., 1982. The zonation of plants in freshwater lakes. Adv. Ecol. Res. 12: 37-126.

Solbrig, O. T., 1981. Energy, information and plant evolution. In C. R. Townsend & P. Calow (eds), Physiological Ecology: An Evolutionary Approach to Resource Use. Blackwell Sci. Publ., Oxford: 274-299.

Stearns, S. C., 1976. Life-history tactics: A review of ideas. Quat. Rev. biol. 51: 3-47.

Stebbins, G. L., 1974. Flowering Plants. Evolution above the species level. Edward Arnold, London, 399 pp.

Stuckey, R. L., 1979. Distributional history of *Potomogeton crispus* (curly pondweed) in North America. Bartonia 46: 22-42.

Stuckey, R. L., J. R. Wehrmeister & R. J. Bartolotta, 1978. Submersed aquatic vascular plants in ice-covered ponds of central Ohio. Rhodora 80: 575 580.

Teltscherova, L. & S. Hejný, 1973. The germination of some *Potamogeton* species from south Bohemian fishponds. Folia Geobot. Phytotax. 8: 231-239.

Troup, A. J., 1965. The 'southern oscillation'. Quat. J. Roy. Meteorol. Soc. 91: 490-506.

Tyson, P. D. & T. G. J. Dyer, 1978. The predicted above-normal rainfall of the seventies and likelihood of droughts in the eighties in South Africa. S. A. J. Sci. 74: 372-377.

Vines, R. G., 1977. Possible relationships between rainfall, crop yields and the sunspot cycle. J. Aust. Inst. Agric. Sci. 43: 3 13.

Waisel, Y., 1971. Seasonal activity and reproductive behaviour of some submerged hydrophytes in Israel. Hydrobiologia 12: 219-227.

Weber, J. A. & L. D. Nooden, 1976. Environmental and hormonal control of turion formation in *Myriophyllum verticillatum*. Amer. J. Bot. 63: 936-944.

Whittaker, R. H. & D. Goodman, 1979. Classifying species according to their demographic strategy. I. Population fluctuations and environmental heterogeneity. Am. Nat. 113: 185 200.

Wood, C. A. & R. R. Lovett, 1974. Rainfall, drought and the solar cycle. Nature 251: 594-596.