The Decline of Submerged Vascular Plants in Upper Chesapeake Bay: Summary of Results Concerning Possible Causes

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This paper provides a summary and synthesis of research conducted to investigate possible causes of the decline in abundance of submerged aquatic vegetation (SAV) in upper Chesapeake Bay beginning in the late 1960s. Three factors were emphasized in this study; runoff of agricultural herbicides; erosional inputs of fine-grain sediments; nutrient enrichment and associated algal growth. Widespread use of herbicides in the estuarine watershed occurred contemporaneous with the SAV loss; however, extensive sampling of estuarine water and sediments during 1980-81 revealed that typical bay concentrations of herbicides (primarily atrazine) rarely exceeded 2 ppb. On two occasions relatively high values (20-45 ppb) were observed for brief (2-4 h) periods in a small cove following runoff events. Short (2-6 h) and long (4-6 wk) term experiments indicated that ephemeral phytotoxic effects would be expected in response to these highest herbicide concentrations followed by rapid recovery. However, normal concentrations ($<$ 5 ppb) had little measurable effect on plants. Historical increases in turbidity have been documented for some bay tributaries since the 1940s. During our study light (PAR) attenuation by suspended fine-grain sediments contributed more to total turbidity in bay shallows ($<$ 1.5 m) than did phytoplankton chlorophyll *a*. Diel cycles of PAR available in SAV beds indicated that plant photosynthesis was light-limited for much of the day, and PAR often fell below the compensation level (I_c) needed for minimal plant growth. Although some SAV species exhibited considerable ability to adapt to reduced light by such mechanisms as increased pigmentation and stem elongation, increased turbidity has probably reduced overall depth distribution of SAV markedly. Effects of the continual increase in nutrient enrichment of the bay (documented since 1930) were tested by experimentally fertilizing pond mesocosms at levels common to the upper estuary. Moderate to high nutrient loadings resulted in significant increases in growth of epiphytic and planktonic algae and decreases in SAV production, as well as premature seasonal senescence of fertilized plant populations. Direct measurements demonstrated the inhibitory effect of epiphytic growth on SAV photosynthesis, due largely to light attenuation. The results of these various experiments were synthesized into an ecosystem simulation model which demonstrated the relative potential contributions of the 3 factors to SAV declines, where nutrients $>$ sediments $>$ herbicides. Other factors and mechanisms are also discussed along with possible resource managements options.

INTRODUCTION

It is widely recognized that submerged vascular plants play an important role in the ecology of littoral regions of lakes, estuaries and oceans.[1,2,3] While a number of studies have noted the ability of these plant communities to attenuate variability of nutrient, sediment and production cycles,[4,5,6] several such communities have themselves undergone extreme fluctuations in distribution and abundance. For example, in the mid 1930s a widespread die-off of the seagrass, *Zostera marina,* was well documented throughout the North Atlantic coastal regions.[7] The cause of this occurrence has never been unequivocally established, although recent suggestions have pointed to subtle climatic shifts.[8] Other reports of regional declines in abundance of submerged aquatic vegetation (SAV) have indicated the possible influence of human activities.[9,10]

Few of the reported SAV declines have occurred in estuarine environments, and most have involved one or two plant species. However, in one of the world's largest estuaries, Chesapeake Bay, a major loss of SAV has continued since the mid 1960s to the present.[11,12,13] More than ten species have experienced significant decreases in abundance, including *Potamogeton perfoliatus, P. pectinatus, Valisneria americana, Zannichellia palustris, Ruppia maritima* as well as the marine species *Z. marina.*[12] In the upper estuary this decline in native species was preceded by an invasion of the exotic, *Myriophyllum spicatum* (Figure 1a) which eventually also died-back.[11] Studies of seed and pollen distribution in sediment cores from the upper bay have demonstrated that his dimunition in plant abundance is unprecedented (Figure 1a) for at least the last century.[13] In general, it appears that the recent decline occurred first and with greatest intensity in the brackish waters of the estuary, with *Z. marina* communities in the lower bay being affected less and somewhat later.[13]

Numerous mechanisms have been cited as possible causes of this occurrence.[12] The concept that natural entrained population cycles or global climatic events might be responsible seems unlikely in view of the range of biological and physiological characteristics for the numerous species involved. In addition, there is no parallel trend in plant abundance apparent in nearby coastal regions.[13] Other factors, including animal foraging and grazing and major storm events, are probably of occasional and local importance, but these are part of the normal milieu to which SAV are exposed and hence are insufficient to explain this abnormal decline. The absence of correlations between distribution of SAV and industrial pollutants renders such anthropogenic wastes an unlikely cause; however, more general changes in water quality associated with diffuse sources (e.g., runoff) do represent a potential explanation.[12] In an extensive review concerning SAV in Chesapeake Bay and elsewhere,[12] it was suggested that three categories of environmental changes deserved further attention: (1) increased fine-grain sediments from land erosion; (2) increased algal growth from nutrient enrichment of estuarine waters; and (3) aqueous concentrations of herbicides arising from agricultural runoff.

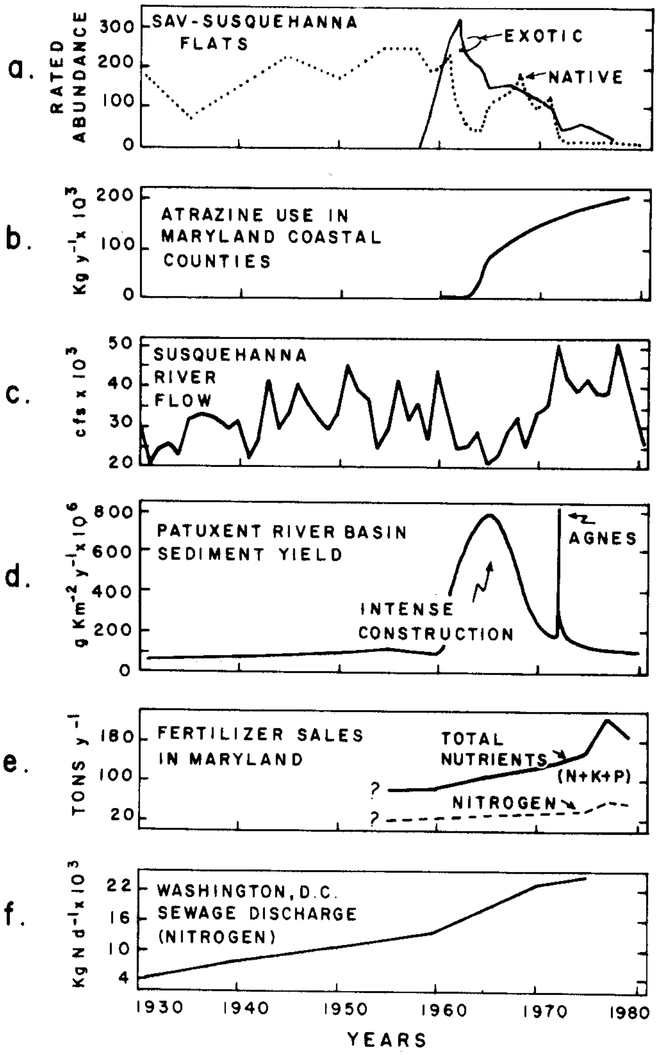

Figure 1. Summary of long-term trends (1930-1980) in selected variables for Chesapeake Bay and its tributaries: (a) submerged aquatic vegetation abundance in the upper bay (1958-1976),[11] prior to 1958;[14] (b) use of atrazine in coastal plain counties draining into the bay;[12] (c) Susquehanna River flow;[69] (d) idealized sediment yield for Patuxent River basin;[28,29] (e) fertilizer sales in Maryland;[35] (f) nitrogen in sewage discharge from Washington, D.C. into Potomac River estuary.[35,69]

This paper summarizes the results from recent studies examining possible causes of the SAV decline in upper Chesapeake Bay. Specifically, we report the salient findings of investigations concerning: estuarine distributions, degradation, sorption, and SAV phytotoxicity of selected herbicides; light availability and vertical attenuance by suspended material, distribution of this suspended matter, and photosynthetic responses of SAV to different light regimes; effects of nutrient enrichment on algal growth, and responses of SAV growth and production to elevated levels of planktonic and epiphytic algal biomass. We also synthesize these results toward reconstructing a plausible scenario vis a vis this loss of submerged vascular plants, and we provide comments on resource management options and the future of SAV in upper Chesapeake Bay.

APPROACH TO PROBLEM

In 1978 we initiated a three-year study to investigate various aspects of the ecology of SAV communities in Chesapeake Bay. While intensive research was conducted at several locations along the estuarine salinity gradient, our work focussed on communities located in the low salinity (5-15°/oo) region. The research was designed to address three general questions: (1) factors potentially responsible for the observed decline in SAV distribution and abundance; (2) SAV community interactions and characteristics; and (3) resource management options.

This research program was organized in a hierarchical fashion to deal with the complexity of the ecosystems studied in addressing these questions. Depicted in Figure 2 is the manner in which (c) specific research approaches were integrated into (b) broad research objectives which were, in turn, related to (a) research questions.[15,16] General objectives of this research program involved: the development of mechanistic relationships among ecological factors through controlled experimentation; the interpretation of these results in terms of actual conditions in nature; and the establishment of a framework to extend specific results into a general con-

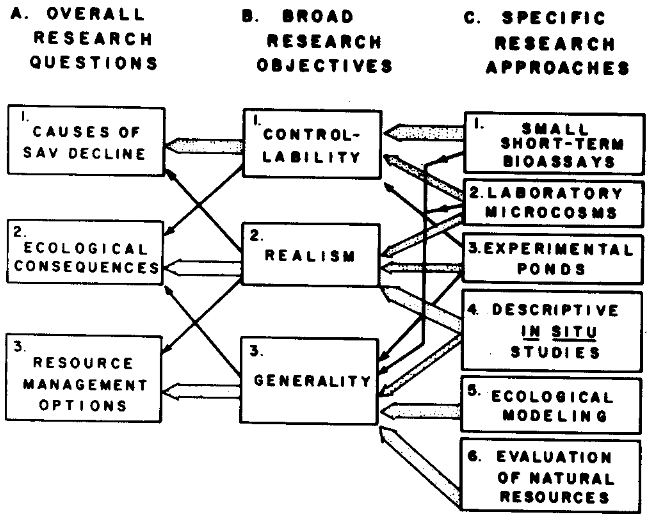

Figure 2. Schematic flow chart illustrating the relationships between specific research approaches, broad research objectives and overall research questions. Three thicknesses of arrows suggest levels of influence for these items.

text. The specific research approaches employed ranged from short-term laboratory experiments to seasonal measurements in the estuary and experimental ponds, with ecological modeling at all levels for analysis, interpretation and generalization. In the following sections we review the results of our field, laboratory and modeling studies to evaluate the possible roles of herbicides, suspendable sediments and nutrients in the SAV decline in the bay.

HERBICIDE INPUTS, FATE AND PHYTOTOXICITY

For the last two decades the most widely used herbicide in the Chesapeake Bay watershed (and particularly in the surrounding coastal plain) has been atrazine.[12,17] Since its introduction to the region in the early 1960s, its use, which is particularly important for corn crops, has grown steadily to the present (Figure 1b). Atrazine was thus selected as the primary compound for intensive investigation. Our research also considered the distribution and phytotoxicity of a second important compound, linuron, which is used for weed control in soybean crops.

Herbicide Distribution and Degradation

In general, about 0.2-2.0 percent of atrazine applied to agricultural fields is transported into adjacent waters in runoff, and resulting concentrations in the estuary depend on dilution, dispersion, adsorption and degradation.[17,21,27] In the open waters of Chesapeake Bay observed concentrations of atrazine and linuron have rarely exceeded 1 ppb.[18,19,20] In major tributaries such as the Choptank and Rappahanock Rivers, concentrations of 5 ppb may occur following a major spring runoff event. Such events can generate transient (2-6 h) concentrations up to about 40 ppb in secondary tributaries and small coves.[20,21,22]

Our data indicate that atrazine and linuron degrade rapidly in estuarine conditions with half-lives of 1-6 wk.[17,23] In addition, these herbicides exhibit strong tendency for sorption to particles and colloids,[20,24] and degradation of particle-bound atrazine appears to be even more rapid.[25] As a result of dilution and degradation, concentrations of atrazine on suspended and deposited sediments in the estuary were seldom greater than 5 μg/kg suggesting little accumulation potential,[20] and moreover, once bound to particles atrazine becomes virtually unavailable for plant uptake.[25]

Herbicide Uptake and Phytotoxicity

Using ^{14}C-ring labelled atrazine Jones et al.[25] found that uptake by *P. perfoliatus* was rapid, reaching equilibrium within 1 h. The observations that atrazine concentrations were low in sediments,[20] combined with the relatively slow translocation of the herbicide measured within plant vascular tissues[25] suggest the primary mode of uptake is foliar. A strong correlation was observed between atrazine uptake and short-term depression of photosynthesis. After a sequence of washes in atrazine-free water, a portion of the incorporated atrazine was released and photosynthesis returned to control levels within 4-8 h.[25]

In addition to short-term (2 h) experiments relating photosynthetic depression to atrazine exposure, microcosms containing estuarine water and sediments with *P. perfoliatus* or *M. spicatum* were used to test longer duration (4-6 weeks) effects of atrazine and linuron on plant growth and production. At concentrations less than 100 ppb of either herbicide, both plants exhibited a significant trend of photosynthetic recovery within 1-2 weeks after initial exposure despite the continued presence of herbicides in microcosm waters.[25] Using a linear dose-response model for apparent photosynthesis (or net biomass accumulation) versus the logarithm of initial herbicide concentration, significant ($r^2 \geq 0.93$) relationships were observed for all combinations of herbicides and plants (Figure 3). Values of $I_{1.0}$ and I_{50} (concentrations resulting in 1 percent and 50 percent inhibition of photosynthesis) ranged from about 2-4 ppb and 70-120 ppb, respectively, for the 4 combinations of herbicides and plant species tested.[25]

At 5-10 ppb (the upper limit of herbicide concentrations typically occurring in most of the estuarine shallows) a 10-20 percent loss of photosynthesis would be expected. However, the ephemeral nature of such elevated herbicide levels and the tendency toward rapid photosynthetic recovery in these plants would render such effects short in duyration. Overall, atrazine phytotoxicity has been tested for seven species in Chesapeake Bay in various experiments, and some differences in sensitivity were apparent.[25,26,27] For example, the exotic species, *M. spicatum,* exhibited greater tolerance than most native plants, and the seagrass, *Z. marina,* appeared

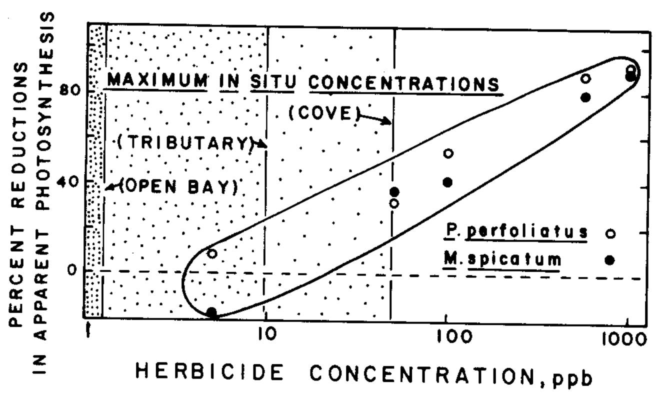

Figure 3. Reduction in apparent photosynthesis (%) for two species of submerged aquatic vegetation resulting from treatment with the herbicide atrazine at 5 initial concentrations. Three degrees of shading represent (from heavy to light) maximum *in situ* atrazine concentrations observed in: open Chesapeake Bay waters; main bay tributaries; and a small cove within one tributary.[17,25]

also to be less sensitive, while the freshwater member of the Hydrocharitaceae, *V. americana,* was among the least tolerant species tested.

Some concern about the possible phytotoxicity of atrazine metabolites formed during degradation was allayed in recent experiments, again using ^{14}C-labelled compounds (provided by Cipa-Geigy Corporation, Greensboro, NC), where I_{50} values were found to be at least ten times greater than for the parent compound.[25] Thus, while conditions certainly occur sporadically in the estuary where herbicide stress could induce some loss in SAV production, the possibility that herbicides led to the SAV decline seems remote.

SUSPENDABLE SEDIMENTS AND SAV LIGHT RESPONSES

Substantial changes in both sediment yield to and turbidity in Chesapeake Bay and some tributaries have occurred over the last several decades (Figure 1d). In one major tributary (Patuxent River), there have been periods of increasing and decreasing sediment yields, punctuated by occasional major input events during the last 50 years.[14,28,29,30] Overall, it seems that turbidity in this tributary is higher now than 30 years ago[33] even though inputs of fine-grain sediments have recently decreased,[29] indicating there is not a simple relationship between these factors.

Light Attenuation due to Suspended Sediments

Laboratory and field experiments were conducted to assess the relative contributions of suspended sediments and chlorophyll-*a* to diffuse, down-welling light attenuation. Diffuse attenuation of phytosynthetically active radiation, PAR (400-700 nm), due to different concentrations of suspended materials was measured in stirred, opaque-sided, cylindrical chanbers (60 cm dia, 120 cm ht) by observing PAR at 10 cm vertical intervals. Known amounts of dried, sieved (62 μ) sediment or algal culture suspensions were added to the chambers to develop relations between attentuation coefficient (k) and suspended concentrations. The slope of k versus algal biomass (in terms of dry wt.) was found to be about twice that for k versus inorganic suspended sediments due to the high absorbance of algal pigments at PAR wavelengths.[31] However, the relative ranges of these two materials typical of shallow estuarine environments suggest that suspended solids are a far greater component to total turbidity. Concentrations of suspended sediments (seston) often increase from 20-100 mg/ℓ within 1-2 h due to moderate (5-10 m/s) summer winds,[25,31] while chlorophyll-*a* concentrations typically range from 5-15 μg/ℓ over a tidal cycle (Figure 4) and are not markedly influenced by wind events. These common excursions in seston and chlorophyll-*a* would result in about 50 percent and 8 percent reductions in PAR at 50 cm depth, respectively.

To assess *in-situ* light conditions, measurements of seston, chlorophyll-*a,* attentuation coefficient, water depth and PAR were made over tidal cycles in littoral areas with and without SAV communities.[25,31] Data from a typical cycle (Figure 4) indicate that both chlorophyll-*a* and suspended particulate concentrations were lower within SAV communities than in non-vegetated littoral areas, and the differences were greatest at low slack tide, probably due to settling of particulates in the quiescent waters of the bed. It is evident here that PAR attenuation followed seston consistently at both sites, while not so for chlorophyll-*a*. Consistent with laboratory data, most ($>95\%$) light attenuation could be attributed to suspended solids other than chlorophyll-*a.* Sediments may also be important in light attenuation when they settle from the water column onto SAV leaves. For example, Staver et al.[31] found 80-90 percent of total epiphytic material (attached to leaves) to be inorganic sediments as opposed to algae or other organic materials in a Chesapeake Bay SAV community. However, there is a continuous cycle of deposition and resuspension of these loosely attached sediments, and the integrated, long-term effect of these processes on photosynthesis is not known.

Light Response of SAV

In laboratory chambers the responses of *P. perfoliatus* and *M. spicatum* photosynthesis to light intensity followed a basic rectangular hyperbolic form. Values of I_K (intersection of initial slope and P_{max}) ranged from 200-300 $\mu Em^{-2}s^{-1}$ and were similar to values reported for other SAV species.[31] A second important parameter of the photosynthesis-irradiance (P-I) relationship is light compensation point (I_c), which is the PAR intensity at which net production (in excess of respiration) approaches zero. Values of I_c at about 50 $\mu Em^{-2}s^{-1}$ were reported for apical 10 cm growing tips of *P. perfoliatus.*[25] However, I_c values for whole plants (including non-photosynthetic root-rhizome tissue) would be substan-

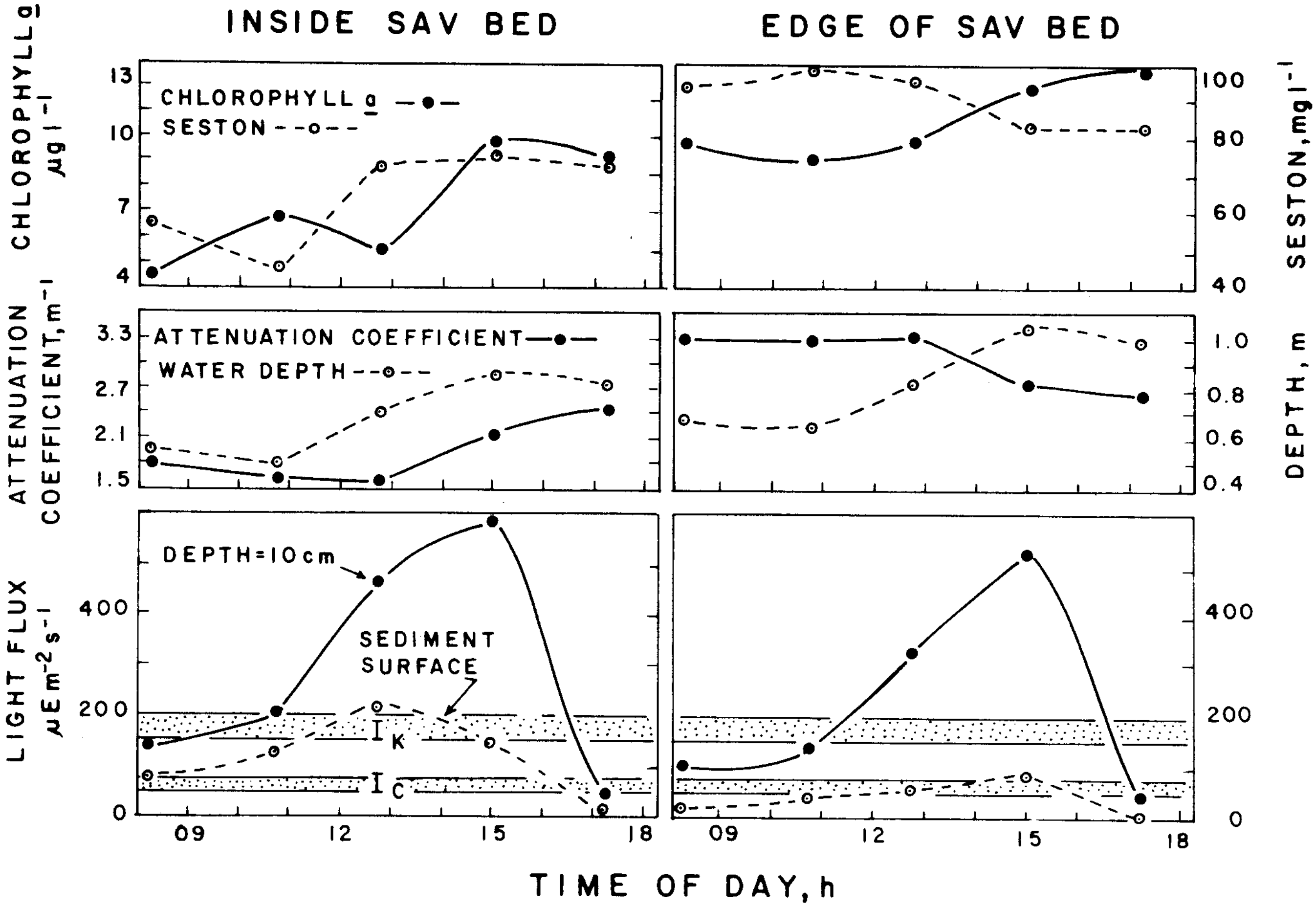

Figure 4. Time-course observations for planktonic chlorophyll *a*, total seston, water depth, light attenuation coefficient and light available at 10 cm depth and at the bottom of a 1.0 m (mean depth) water column for a bed of submerged plants (*P. perfoliatus*) and for an adjacent unvegetated area on 22 September 1980. Shaded regions represent typical ranges for I_K (intersection of initial slope and maximum photosynthesis in a photosynthesis-irradiance function) and I_c (compensation light level for 10 cm apical growing tips of plants).[31,32]

tially higher, probably in the range of 75-150 $\mu Em^{-2}s^{-1}$. Given the ambient turbidity levels generally observed in the bay ($k > 2/m$) in addition to light reduction associated with epiphytic materials, it would appear that SAV are generally exposed to light regimes approaching I_c. Unless these plants can adjust to such light stress, net growth would not be possible.

In fact, Goldsborough[32] found that at least one species *(P. perfoliatus)* has considerable ability to adapt to reduced light conditions via morphological changes (such as stem elongation and increased leaf area: weight ratio) and biochemical changes (such as increased chlorophyll-*a* per leaf area) which influence P-I relationships. However, under extreme shading (~75 $\mu Em^{-2}s^{-1}$) the capacity of adaptive mechanisms was exceeded, resulting in reductions in new shoots, number of flowering plants, and root storage nodules (which appear to be overwintering organs).[1]

Overall Effects of Suspendable Sediments on SAV

In the Patuxent Estuary, which formerly contained extensive SAV communities, chlorophyll-*a* concentrations increased from about 10 to 40 μg/ℓ and secchi disc depths decreased from about 0.8 m to 0.35 m (or $k = 1.8 - 4.0/m$, assuming $k = 1.4/\text{secchi}$) for spring-summer during the 1960s decade.[33] Partitioning these attenuation coefficient values between chlorophyll-*a* and other particulate and dissolved materials[34] shows about 7 percent of total attenuation could be attributed to the algal pigment in the early 1960s, while about 14 percent could be so partitioned for the 1970 data. While the relative importance of phytoplankton attenuation increased over this period, it appears that most light attenuation was still associated with inorganic particulates and other non-chlorophyllous organics.

In any case, the observed increase in turbidity would cause a significant reduction in the depth distribution of SAV. For example, if we take summertime irradiance at the water surface to be 1200 $\mu Em^{-2}s^{-1}$ (a typical value at noon on a sunny Aug-Sep day) and I_c to be 100 $\mu Em^{-2}s^{-1}$, the depth to which sufficient light penetrates to support SAV growth would be reduced from 1.4 m to 0.6 m for the aforementioned scenario in the Patuxent between 1960 and 1970. Similar turbidities were observed[25] throughout littoral zones in upper

Chesapeake Bay, suggesting that the depth distribution of SAV has been restricted due to reduced PAR availability.

NUTRIENT ENRICHMENT AND ALGAL-SAV RELATIONS

Watershed inputs of nitrogen (N) and phosphorus (P) to Chesapeake Bay have increased several-fold in the last two decades (figures 1e, f), and aqueous concentrations of inorganic nutrients have likewise increased appreciably in many areas of the estuary.[33,35] Correspondingly, phytoplankton populations (as measured by chlorophyll-*a*) have also expanded during this period.[33,35] Since it appears that submerged vascular plants can obtain their N and P requirements from sediment pore waters[36,37] which are rich in nutrients, it is expected that nutrient additions to overlying waters would increase SAV growth to a limited extent only. In fact, there are a number of mechanisms where fertilization may lead to decreases in SAV production and abundance. Nutrient enrichment tends to promote algal growth, either phytoplanktonic[38] or epiphytic[10] which in turn can inhibit SAV photosynthesis via reductions in light and molecular transport across SAV epidermis.[39,40] In addition, it has been postulated that increased phytoplankton populations can stimulate growth of animal fouling communities on SAV leaves and other firm, stable substrates[25,41] leading to similar photosynthetic stress for the plants. In this section we consider this question terms of correlations from field observations and results of nutrient enrichment studies in experimental ponds.

Algal Responses to Nutrient Enrichment

The effects of nutrient enrichment on algal and SAV growth were investigated in eight experimental ponds (area = 350 m^2; depth = 1.2 m) treated in duplicate with three nutrient levels (plus controls) at eight to ten day intervals for a ten-week period during the summer of 1981. Initial nutrient concentrations after dosing were 120, 60 and 30 μM inorganic nitrogen (50% NH_4^+; 50% NO_3^-), with N:P (atomic) ratios of 10:1. Nutrient loading rates at medium dosage were equivalent to runoff from a typical watershed (26% agriculture, 11% residential) draining into a small Chesapeake Bay tributary.[42]

Phytoplankton biomass (as chlorophyll-*a*) generally increased with treatment levels (significantly greater at low and high doses), particularly at the highest nutrient amendments (Figure 5). A sequence of phytoplankton bloom events were evident in high dose ponds, where chlorophyll-*a* increased by one to two orders of magnitude on several occasions within a one to two-day period. This response was similar to those previously reported for nutrient enrichment studies.[43,44] Epiphytic algal biomass was significantly higher than controls in all treated ponds (Figure 5). Levels of epiphytic material in nutrient treated ponds were similar to those observed in the estuary on scenescent plants while control levels were comparable to those occurring early in the SAV growing season.[32,45] Again, this pattern of increased epiphytic algal growth is consistent with results from nutrient enrichment experiments elsewhere.[10,46,47]

Effects of Algal Growth on SAV

Correlations between PAR attenuation in the water and phytoplankton chlorophyll-*a* were obtained from measurements in the experimental ponds using only those data where the estimated weight of algal cells comprised a major fraction ($>$ 10%) of total seston weight.[25] The slope of this relationship (0.0146 $m^2 mg^{-1}$; $r^2 = 0.95$) is quite consistent with observations from deep coastal waters[48] and slightly greater than those derived from laboratory cultures.[31,49] We also obtained a strong relationship between PAR attenuance through a plane (estimated by scraping epiphytes from leaves of known area into a petri dish and measuring PAR attenuation)[50] and epiphytic biomass ($r^2 = 0.87$). The slope of this relation was 0.36 percent $(mg/cm^2)^{-1}$, which again is comparable to previous reports.[10,50,51] Direct measurements of SAV photosynthesis (using both ^{14}C uptake and oxygen evolution methods) over a range of epiphytic colonization levels (0-5 gdw epiphyte/gdw SAV) yielded significant correlations with about 50 percent reduction in photosynthesis at 4 gdw/gdw.[25] After eight weeks of nutrient treatment, SAV biomass in medium and high fertilization systems had decreased significantly compared to controls (Figure 5). While the contribution of the water column to total attenuation (from water surface to plant leaves) was generally small compared to that associated with epiphytic material, without such light reduction due to turbidity, epiphytic growth would have been insufficient to reduce light below compensation levels (I_c). Similar observations on the relative roles of phytoplankton and epiflora have been reported for Danish lakes.[51]

Nutrient Enrichment and SAV Decline

While nutrient fertilization has been occurring in Chesapeake Bay over the last century or more, the upper bay outbreak of *M. spicatum* in the early 1960s (just preceding the general SAV decline) may have marked the onset of critical nutrient enrichment levels. It appears that this species has competitive advantage over other SAV under conditions of elevated nutrient inputs.[52] During the last several years numerous investigators have postulated that eutrophication was responsible for observed losses of SAV in freshwater systems including: Loch Leven, Scotland;[38] Lake Erie, Ohio;[53] Whitewater Lake, Ontario; [54] and Norfolk Broads, England.[10] Others have suggested that nutrient enrichment may be one of several factors contributing to diminution of seagrasses in such coastal ecosystems as the Dutch Waddenzee,[9] the French Mediterranean[55] and Western Australia estuaries.[56] In all cases, these declines have occurred progressively over decade-long periods, consistent with observations in Chesapeake Bay.[13]

In our experimental pond studies, SAV biomass reductions in high dose ponds amounted to a foreshortening

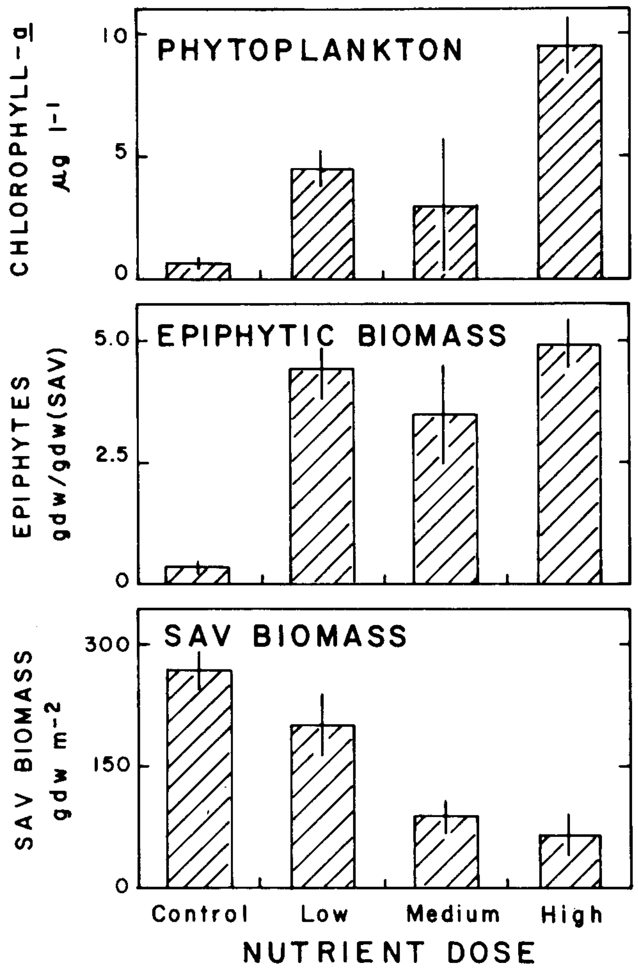

Figure 5. Summary of phytoplankton stocks (as chlorophyll *a*), weight of epiphytic material, and submerged aquatic vegetation biomass in August 1981, for experimental ponds treated with 4 levels of nutrient enrichment after 8 weeks. Given are means ± 1 standard error.[25]

of the normal growing season; however, some effects on vegetative reproduction were also apparent. For example, shoot production from budding was markedly reduced in experimental ponds the spring following a summer of high nutrient treatment, and after a second year of identical treatment vegetative root nodules were also significantly reduced.[25] To interpret these results in the context of long-term declines in abundance, it may be necessary to relate premature seasonal scenescence to decreased reproductive success in a more quantitative fashion.

SYNTHESIS OF FINDINGS AND IMPLICATIONS

Ecosystem Modeling as a Tool for Synthesis

The research discussed in this paper has identified and described a wide range of detailed interactions between submerged vascular plants and their environment. We used a variety of numerical simulation models for these SAV ecosystems to place the complex interactions into a unified ecological framework. One of these models was designed to address questions relating to management of SAV resources in the estuary, including both the role of these plants in secondary production and the environmental factors influencing plant growth.[57] Generally, this model consisted of 14 simultaneous, non-linear differential equations, with time as the independent variable. Each equation described the temporal behavior of a state variable, with each term in a given equation representing a connection between that variable and another internal or external variable. The model was calibrated with data collected from field and laboratory measurements and was used to interpolate between discrete observations in time and space and to both hindcast and forecast consequences of changing external factors (e.g., temperature, nutrient loading and flushing rate).

Digital computer simulations were performed (using finite difference numerical methods) to consider the effects of herbicide, sediment and nutrient inputs to the estuary individually and combined (Figure 6). Under simulated conditions based on maximum observed herbicide concentrations in a shallow embayment, annual mean SAV biomass (B) and total net production (NP) decreased by about 2 percent and 4 respectively (Figure 6a), with greatest effects during May-June runoff events. A doubling of sediment loading to the SAV bed and surrounding waters resulted in 13 percent and 22 percent reductions in B and NP, and the effects were most pronounced in the late summer and fall periods when heavy winds stimulated sediment resuspension (Figure 6b). A two-fold nutrient enrichment resulted in marked reductions in B and NP (29% and 48%), with strongest depressions occurring in June (Figure 6c). Apparently, relatively high nutrient and light levels in spring promoted rapid growth of epiphytic algae which was retarded subsequently in summer due to nutrient depletion. These simulation results are similar to findings from pond fertilization experiments.[25] Combining these three stresses in a single simulation resulted in an average of 35 percent and 56 percent losses of biomass and production, and the net effect of the three factors thus appeared to be somewhat antagonistic (Figure 6d).

It is interesting to note that under combined stresses the growing season (period of continuous biomass accumulation) was reduced from about four and a half months to less than two months. In addition, plant biomass at the end of the simulated year was considerably lower than initial levels under combined factors. While this might suggest an affect on reproductive success of this population, multi-year simulations produced recurring patterns similar to that shown in Figure 6. However, this is not surprising because reproductive biology, per se, was not an explicit function in the model.

Gradual Reductions in Abundance versus Population Demise

Most of the species occurring in upper Chesapeake Bay undergo clear annual cycles of above-ground structure,

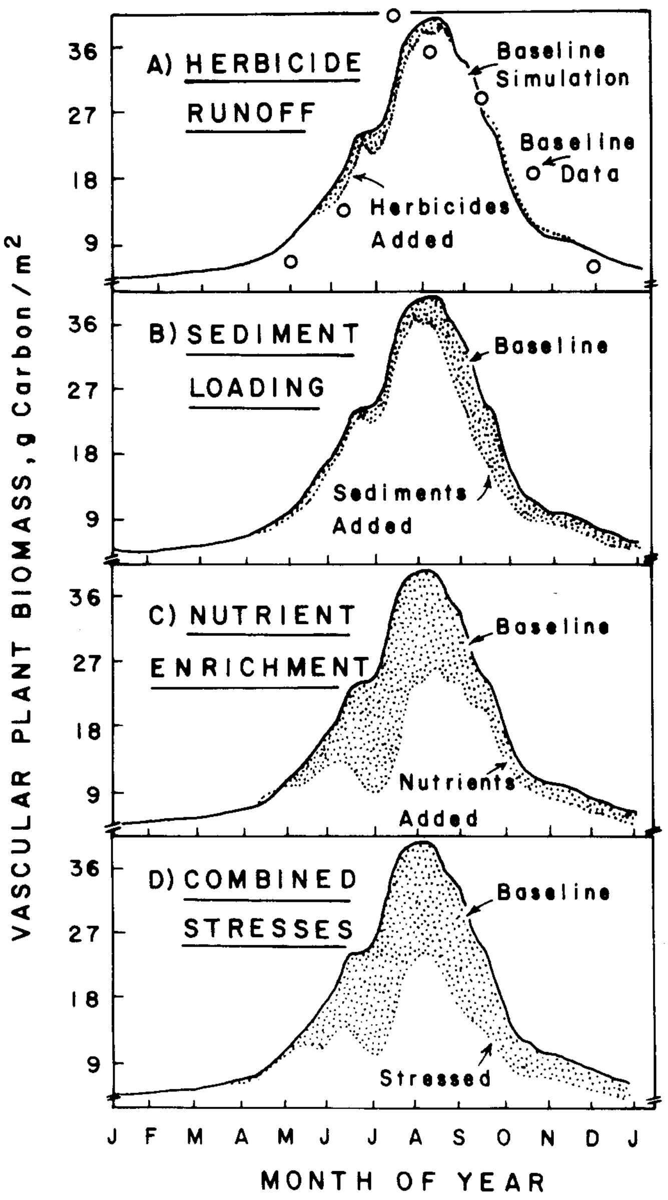

Figure 6. Results of numerical simulations of submerged vascular plant biomass over an annual cycle under conditions of maximum herbicide runoff, doubled sediment loading, doubled nutrient enrichment, and a combination of these three stresses. In all cases the upper line (shown for comparative purposes) represents the baseline conditions which are compared to means of field observations in the upper panel.[57]

and new growth in spring may be generated either from seeds or from underground storage organs. The model simulations indicated that under environmental stress, net growth available for allocation to sexual or vegetative reproduction is reduced. Experimental observations have demonstrated that extreme light stress, related either to turbidity or epiphytic growth, results in significant decreases in both flowering and production of underground storage nodules.[25,32] We hypothesize that the observed gradual reductions in abundance of stressed plants in model and field experiments would eventually result in a local demise of these populations due to reproductive failure. This final outcome would require a repetitive sequence of annual stressed growth conditions, incrementally undermining reproductive vitality.

In general, SAV communities exhibit considerable ability to modify their local environment and thereby reduce stresses; however, this "buffering capacity" can be exceeded and lead to premature seasonal die-back. Two examples involve nutrients and suspended particulates. While SAV communities are capable of rapid uptake of nutrients from overlying water,[4] nutrient enrichment beyond the assimilative capacity can promote epiphytic algal growth to the detriment of vascular plant production.[10,25] Secondly, the well established ability of seagrasses and other SAV to trap and bind suspended particulate matter[5,58] is limited in silty estuarine environments,[25] and associated turbid waters tend to reduce light availability and plant production. It appears that while moderate levels of these stresses result in little if any reductions in plant production and distribution, extreme levels can overwhelm the ability of such plant communities to ameliorate these factors.

Reconstructing the SAV Decline

Historical trends in data for SAV distribution and abundance, sediment and nutrient loading and herbicide use (Figure 1) coupled with experimental results and model simulations reported here allow development of a plausible, although not conclusive, scenario concerning the observed decline of SAV in Chesapeake Bay.

Accelerated soil erosion and sediment loading associated with extensive land development in the late 1950s apparently led to elevated turbidity in several regions of the estuary.[28,29,30,35] Nutrient loading also increased from point sources associated with population centers and from regional diffuse sources associated with intensifying agriculture. In the Patuxent River estuary, marked declines in SAV populations[59] coincided with increased turbidity and nutrient concentrations. In the Potomac River, invasion by *M. spicatum* followed by proliferation of blue-green algal mats, correlated with expanding sewage discharges and incipient declines in native SAV.[60] The establishment of *M. spicatum* in brackish portions of Chesapeake Bay preceded a general SAV decline,[11] which may have been a response to euthrophication.[52] In the late 1960s, it appears that strict erosion control practices reduced sediment runoff inputs and associated turbidities in some regions; however, nutrient inputs continued to rise. The general use of herbicides for agricultural weed control in the watershed in the mid-1960s may have contributed slightly to deteriorate SAV growth conditions, and the greater tolerance of *M. spicatum* to herbicides is consistent with the observed brief proliferation of this species. Possibly further compounding these stressed conditions was the drought of the 1960s (Figure 1) which led to increased salinities[61] and probably salinity stress for various freshwater species.[62] In the summer of 1972, a 200-year storm event resulted in rates of sediment deposition up to 25 cm[63] in some locations, virtually burying local plant communities. While this storm occurred well after the initial evidence of SAV decline, its effects are apparent in plant abundance data (Figure 1a). There is also evidence for considerable damage to SAV populations from intense grazing and foraging episodes by waterfowl and fish.[64,65]

While it is impossible to definitely demonstrate what caused the SAV decline, data from controlled experiments, as well as recent field observations and historical records all suggest that nutrient enrichment and increased turbidity probably played major roles. Herbicide runoff may represent an ephemerally and locally important stress, but our data indicate its contribution to this general die-back has been minimal. Major meteorological events and direct grazing certainly have contributed to the rigors of SAV existence and may have accelerated the recent decline, but historical records indicate these factors probably also played a secondary role.

Management of SAV Resources

The potential for improving environmental conditions for propagation and growth of submerged vascular plants in the estuary can be considered in terms of the relative importance and controllability of key factors. Herbicide losses from croplands to adjacent watercourses can be reduced by such measures as alternative weed control techniques and "buffer stripping" at the margins of fields; however, the socio-economic costs of such strategies would be considerable.[66] Research results presented here indicate herbicides exert a minor influence on SAV, so that the wisdom of such measures may be questionable.

Three major sources of suspendable sediments to the estuary are runoff, shoreline erosion and resuspension of bottom sediments.[67] Both shore erosion, which is important in the middle bay and eastern shore tributaries,[67,68] and resuspension, which dominates in most estuarine shallows,[25] are largely uncontrollable. Existing soil conservation practices have been reasonably effective in reducing sediment runoff[29,30] and probably represents a realistic management option, given the apparent contribution of suspendable sediments to the SAV decline.

Although nutrient inputs to Chesapeake Bay from sewage effluents represent less than 20 percent of the total for nitrogen,[69] in some areas such as the Potomac and Patuxent Rivers, they are a major source which can be controlled, albeit at considerable cost. Diffuse sources, dominated by agricultural runoff, represent the largest nutrient input to the estuary, and efforts to develop effective controls are crucial. The substantial experimental and correlative data available strongly suggest that nutrient enrichment has resulted in losses of submerged vascular plants in a variety of aquatic systems, including Chesapeake Bay. This, coupled with other documented consequences of excessive fertilization (e.g., noxious algal blooms and anoxic bottom waters) point to a considerable need to focus on nutrient waste management.

The role of SAV communities in maintaining water quality and promoting secondary production has been well established in general and in Chesapeake Bay in particular. For example, it has been estimated that about 50 percent of the current sewage derived nutrient inputs to the bay could have been assimilated by healthy SAV communities which existed in 1960.[70] Kahn[71] has calculated that previous SAV populations supported a fishing resource valued in excess of a million USA dollars per year. Nevertheless, estuaries are characteristically stressed environments, and such natural stresses combined with anthropogenic factors tend to make estuarine littoral regions only marginally compatible with SAV physiological requirements. If a decision were made to attempt a reversal of this SAV decline, it appears that several steps would be required. First, nutrient inputs should be reduced and efforts should be made to continue and improve soil erosion control practices. Second, a better understanding of propagation and reproduction mechanisms and capabilities of these plants is needed. Finally, a substantial program (possibly involving direct transplating) might be required to accelerate restoration of these SAV communities.

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