Toward predicting reproductive success in submersed freshwater angiosperms

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ABSTRACT

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Reproduction is central to changes in distribution and abundance patterns of submersed freshwater macrophytes. In this paper we seek to identify potential 'bottlenecks' limiting sexual or vegetative reproduction or its predictability for these plants. To this end we consider the regulation of seed production, seed fate, vegetative propagule production, and vegetative propagule fate in turn, both in general terms and for the perennial *Vallisneria americana* Michx. in particular.

Plant biomass appears to be an important determinant of the incidence of flowering for greenhouse-grown *Vallisneria americana*: 88% of 425 plants either failed to flower if below a threshold dry weight of 0.75 g, or flowered if above it. The number of flowers (in females) or inflorescences (in males), however, was only moderately well correlated with *Vallisneria* biomass, and the flowering 'threshold rule' weakened considerably in the field. Closer examination of the dependence of seed output on plant biomass and pollination intensity, and of the importance of seed or fruit abortion is needed for submersed species.

Our ignorance of seed fate is exemplified by the paucity of quantitative studies on dispersal distances and seed deposition patterns, on seed banks, and on features of seed microenvironments pertinent to germination, although the sensitivity of seed dormancy and germination to a variety of environmental conditions has been tested in the laboratory for many species. Further, losses of seeds and seedlings as a result of unfavorable environments, sediment disturbance, flotation, pathogens, and herbivores are generally not well characterized. Overall, the principal limiting step for sexual reproduction may in some cases be lack of floral induction, and in others, ineffective pollination, but dispersal away from the local population, failure of seeds to germinate, and the challenges of seedling establishment cannot be ruled out.

Plant size is well correlated with vegetative propagule production for both greenhouse and field *Vallisneria* populations. As with seed germination, the germination of vegetative propagules has been relatively well studied in the laboratory, but important regulators of germination and establishment in the field warrant further study.

We suggest that more investigations at two interfaces of physiological ecology and demography may be particularly fruitful. Regarding propagule production, experimental focus on allocation patterns which 'translate' accumulated resources into seeds or vegetative propagules should prove rewarding. Regarding propagule fate, post-dispersal mortality of seeds and vegetative propagules may be rooted in physiological tolerance limits, but could also be attributable to pathogen or herbivore attack.

INTRODUCTION

Reproductive success is an integrative measure of plant response to environmental conditions. Further, reproduction is the sine qua non for the maintenance of any dynamic population, and indeed, "all populations are in a continuous state of flux" (Begon et al., 1986). Thus, reproduction underlies both the heterogeneity of macrophyte distribution, from small patches within habitats to broad geographic patterns, and variations in abundance from sparse populations to weedy infestations. How can we best enhance our comprehension of macrophyte reproduction to improve prediction of temporal changes in distribution and abundance for dominant macrophyte populations? To address this focal question for submersed freshwater species, we briefly consider reproductive modes and functions, outline stages of sexual and vegetative reproduction, then proceed with a more detailed treatment of each stage.

Reproduction is unitary neither in mode nor in function. Arber (1920), Sculthorpe (1967), and Hutchinson (1975) each discuss a broad array of specific forms of sexual and asexual reproduction in freshwater angiosperms, from hydrophilous self-pollinating species and anemophilous outcrossing species, to producers of rhizomes, viable leafy stem fragments, perennating buds, or turions. For our purposes in this paper, we initially reduce this diversity of reproductive modes into sexual vs. vegetative (Fig. 1). Whether sexual or vegetative, reproduction may function as a mechanism for multiplication of individuals, for perennation, for resistance to unfavorable environmental conditions, and for dispersal. Further, sexual reproduction effects the creation of novel genotypes, while vegetative reproduction preserves success-
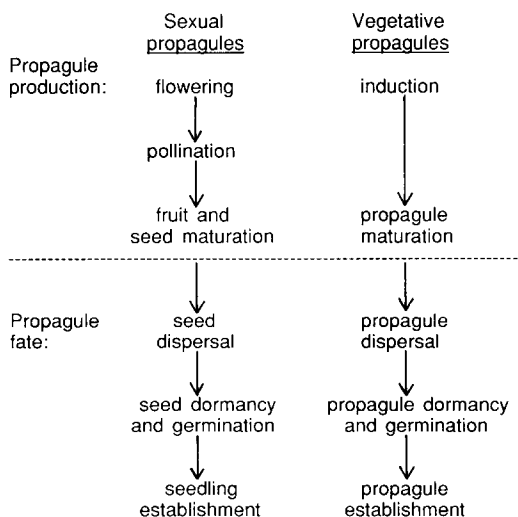

Fig. 1. Stages in the production and fate of sexual and vegetative propagules.

ful genotypes. Functional variations within each basic reproductive mode, for example differences in dispersability between positively and negatively buoyant (i.e. less or more dense than water, respectively) seeds, or between rhizomes and leafy stem fragments, may have profound ecological consequences. Our goal here, however, is not to match the detail of earlier, more encyclopedic treatments (Sculthorpe, 1967; Hutchinson, 1975), rather to probe the current understanding of the environmental regulation of reproduction in natural populations.

We also partition reproduction, in actuality a nearly continuous process, into discrete steps involving first the production, then the fate, of seeds or vegetative propagules (Fig. 1). It is certain that each stage is vital, whether for sexual or vegetative reproduction, as each is simply part of a life cycle. It is possible that, for a given species, each stage may exhibit unique environmental requirements and sensitivities. It is likely that our quantitative grasp, either in terms of physiological ecology (e.g. 'what are the requirements for breaking dormancy in seeds of species X?') or demography (e.g. 'for what number of seeds of species X will dormancy be broken?') varies greatly among stages. In this paper we address environmental influences on each stage in turn, both for sexual reproduction and for vegetative reproduction, all within the framework of predicting reproductive success. We assume such influences are hormonally mediated, but we do not explicitly consider hormones here.

The central biological importance of reproduction has spurred myriad studies of plant structure, systematics, evolution, physiology, and ecology in freshwater, marine, and terrestrial habitats. Although reproductive biology surely holds many similarities for different plants in contrasting habitats, we offer here a selective treatment, biased by our own experience with the submersed freshwater angiosperms *Najas flexilis* (Willd.) Rostk. & Schmidt and especially *Vallisneria americana* Michx. A second bias lies in our interest in linking physiological ecology, which often emphasizes patterns of resource gain, with demography, which is more likely to address the numbers and fates of propagules produced. In our effort to forge this link, we relate components of reproduction to plant biomass, which we use as an index of resources acquired. One might argue that our typically simultaneous measurement of reproduction and biomass cannot by itself lead to true predictions. We agree, but also contend that published data quantifying the dependence of macrophyte gas exchange and growth on environmental conditions create the potential for predicting biomass. If reasonable predictions of biomass can be derived for a specified range of environmental conditions, and a quantitative relationship between reproduction and biomass can be clearly established, then a measure of predictability for reproduction can be attained for those conditions. This is our rationale for focusing on biomass, the environmental regulation of which is beyond the scope of this paper.

We cite published works, provide original data, and in some cases simply outline our ignorance, to highlight three types of relationships: (i) those which

are potential 'bottlenecks' on the route to successful reproduction in nature;
(ii) those which may reveal important differences between laboratory and
field environments; (iii) those which offer striking contrasts between terres-
trial and submersed plant reproduction. After brief species descriptions, we
will discuss each stage (Fig. 1) in turn, first for sexual reproduction, then for
vegetative reproduction.

SPECIES DESCRIPTIONS

Najas flexilis (hereafter referred to as *Najas*) is a monoecious annual, which
in Chenango Lake (Broome County, central NY) germinates in late spring to
form a leafy, often highly branched plant. Inconspicuous, apparently axillary
flowers develop during the summer, and underwater pollination is effected
passively, at least in related species, when the elongated stigmas receive the
precociously germinated, hence filamentous, pollen (Sculthorpe, 1967). Fruits
are borne singly, and remain attached to the stems until after the fragmenta-
tion of parent plants, which occurs in late August and September in Chenango
Lake. Negatively buoyant seed-bearing stem fragments readily become lodged
in the sediment, thereby limiting dispersal for at least some seeds.

Vallisneria americana (hereafter referred to as *Vallisneria*) is a dioecious
perennial which begins its annual growth cycle in the northeastern and north-
central United States as a winter bud buried at a depth of about 3 to about 15
cm in the sediment (mean depth ± standard deviation (SD) was $7(\pm 4)$ cm
for 144 plants randomly sampled from soft sediments of Chenango Lake in
June 1978). In late spring, an initial rosette of ribbon-like leaves develops at
the top of a short stem grown from the winter bud to the sediment–water
interface, and soon forms a stolon and a fibrous root system. The stolon, aris-
ing from the axil of a rosette leaf, creeps at or just below the sediment surface
for about 10 to about 30 cm ($\bar{x}(\pm SD) = 19(\pm 6)$ cm for 201 stolons of Chen-
ango Lake plants), where a new rosette becomes established. Stolons and ro-
settes continue to develop in this fashion throughout the growing season, re-
sulting in plants averaging 7.1 interconnected rosettes for a *Vallisneria*
population in Chenango Lake (Titus and Stephens, 1983), but as many as
24.5 interconnected rosettes in our experimental plants grown in Otsego Lake
(Otsego County, NY).

One or more rosettes of an intact plant may begin to flower by mid-July.
We have grown female plants with as many as 10 flowers, and males with 21
inflorescences. The highly reduced male flowers are released in batches from
basal spadices to float on the water surface, where they may encounter female
flowers borne singly on long peduncles (Wylie, 1917; C.D.K. Cook, 1982).
Although flowering may continue for over 3 months, most fruits appear to
mature between late August and mid-September in Chenango Lake. The neg-
atively buoyant seeds may be released from disintegrating positively buoyant

fruits either before (Kaul, 1978) or after the fruits become detached from their peduncles, increasing the potential for seed dispersal over a range of distances. We can at present offer little insight into the fate of these seeds because, despite the excavation of well over 1000 *Vallisneria* plants in the field, we have observed few naturally established seedlings.

Toward the close of the growing season, new stolons grow down into the sediment and form compact, carbohydrate-rich (Titus and Adams, 1979) winter buds. Chenango Lake plants produced an average of 10.8 winter buds in 1978 (Titus and Stephens, 1983), a number far exceeded by the 42.5 buds per plant we observed for experimental Otsego Lake plants. According to Wilder (1974), rosette- or bud-producing stolons may develop in every third leaf axil, so the number of leaves present may be an important regulator of the number of buds. The production of winter buds is followed by the disintegration of the parent rosettes with their stolons and root systems, leaving only buds as perennating organs. Thus *Vallisneria* falls into Hutchinson's (1975) 'asexual annual' category.

SEED PRODUCTION

Figure 1 masks the multipartite nature of seed production, which is itself comprised of many steps: floral induction, floral initiation, morphogenesis and anthesis; pollen transport to receptive stigmas; pollen tube germination and growth; fertilization; embryogenesis and fruit maturation. We surmise that two principal bottlenecks are floral induction and pollen transport, which thus command our attention here. We make the simplifying assumption that the other steps, once initiated, tend to proceed inexorably to their conclusion under typical field conditions. It remains possible, however, that self-incompatibility (Barrett, 1988) or seed and fruit abortion (Stephenson, 1981; Lee, 1988) are important limiters of seed set, but little of these processes has been reported for submersed macrophytes.

Flowering

Qualitative and quantitative questions arise. What conditions are required for any flowering to occur? If flowering occurs, what governs the number of flowers a plant produces? To predict the extent of flowering in a field population, one must consider both plant and environmental characteristics: in order to flower, a plant must (a) attain the necessary stature; (b) acquire the necessary carbon and mineral resources; (c) be exposed to appropriate environmental conditions.

One prerequisite for flowering and pollination in most submersed angiosperms is growth to the water surface, as few species exhibit underwater pollination (Arber, 1920; Sculthorpe, 1967). The need to produce an aerial flow-

ering axis on a buoyant stem in entomophilous and anemophilous species poses a challenge unique to the aquatic realm. This challenge may preclude flowering for plants that are of small stature or that reside in deep water, and may favor vegetative reproduction (Sculthorpe, 1967), although not necessarily for the apparently cleistogamous *Lobelia dortmanna* L. (Farmer and Spence, 1987) and certainly not for the hydrophilous *Najas*. For *Vallisneria*, only the female flowers on their slender peduncles need to grow to the surface, but in Chenango Lake, *Vallisneria* rarely flowers at depths greater than 2 m despite its occurrence to 5 m (Titus, 1983). Simply reaching the surface, however, may be necessary but not sufficient – surely many plants of aerially flowering species reach the surface without flowering, and *Vallisneria* often occurs in shallow water without flowering.

Plant size is likely to be positively correlated with the quantity of resources acquired. Terrestrial studies (Werner, 1975; Gross, 1981) have demonstrated that, at least in several nominal biennials, the probability of summer flowering rises directly with increasing plant size above a critical rosette diameter measured near the close of the preceding growing season. Similarly, Farmer and Spence (1987) reported that larger *Lobelia dortmanna* plants are more likely to flower than smaller plants. We have determined in the greenhouse that the incidence of flowering in *Vallisneria* can show a strong relationship with plant biomass (Fig. 2), in this case measured at the time of a destructive harvest when we also noted reproductive state.

The percentage of plants flowering rose linearly from 7% for plants less than 0.5 g dry weight to 100% for all 148 plants above 2.0 g. Of 425 plants, 88% followed a 0.75 g threshold rule, i.e. plants less than 0.75 g failed to flower, and those greater than 0.75 g did flower. Thus a threshold weight for flowering can be defined with moderate precision for these plants, and Fig. 2 readily yields an estimate for population-level flowering if the size structure of the population is known.
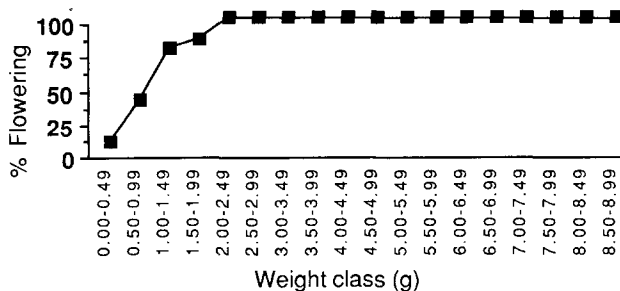

Fig. 2. Percent flowering for greenhouse-grown *Vallisneria* plants grouped in 0.5 g dry weight classes. Plants rooted at 0.7 m water depth were grown for 6 or 7 weeks on various sediments and exposed to different levels of pH and dissolved inorganic carbon availability (Titus et al., 1990; J.E. Titus, unpublished data, 1987).

Biomass, however, appeared to be a far stronger correlate of the occurrence of flowering in controlled greenhouse experiments than for a natural population (plants rooted at 1.3–2.2 m water depth randomly sampled on 1 September 1978 in Chenango Lake; Titus and Stephens, 1983 and unpublished). Only four of 21 plants followed a 0.75 g 'threshold rule', and only three of 15 plants greater than 2.0 g flowered in the field population. With predictability at issue, this greenhouse/field contrast is disconcerting, although perhaps not surprising, and well worth further study. A size threshold may still be a useful concept for field plants, but the threshold could change with altered mineral nutrient availability or increase with increasing depth.

Few pertinent reports on the environmental conditions required for floral induction in submersed freshwater angiosperms have appeared since Sculthorpe (1967) noted that there was little evidence to support or refute his suggestions regarding the importance of daylength and/or temperature. In one illuminating study, Dawson's (1980) experimental alterations of photoperiod did not substantially change initial flowering date for *Ranunculus penicillatus* (Dum.) Bab. var. *calcareus* (Butcher) Cook, thus weakening the case for photoperiodic control in this surface-flowering species. Szmeja (1987) noted a high degree of synchrony in the initiation of the annual reproductive cycle for *Lobelia dortmanna*, with peduncle elongation beginning at a similar water temperature ($19 \pm 1.5°C$) for 5 consecutive years. Flowering in this species, however, continued for many months in Scotland (Farmer and Spence, 1987). This prolonged flowering season and that for *Vallisneria* suggest that daylength and temperature requirements, if they are at all important, interact with other factors to determine when flowers will appear.

Two hypotheses offer differing views of the regulation of flower number. One is that flower number is determined by the quantity of available plant resources, which may often be well correlated with biomass. Weiner (1988) and Waller (1988) both tentatively subscribe to the importance of the relation between reproductive output, of which flower number is a component, and biomass, but also note the sparse literature examining this relation. A second is that morphogenetic constraints (Watson and Casper, 1984) may limit flower production in that a plant may have a limited number of meristems able to develop into flowers or inflorescences. This was apparently true for *Potamogeton richardsonii* (H. Benn.) Rydb. – clipping shoot tips led to more profuse branching and flowering (Sheldon, 1986). These may not be strictly competing hypotheses, as resource availability and morphogenetic constraints may interact to regulate flower number. For example, flower buds in *Vallisneria* may develop only in every third leaf axil (Wilder, 1974), but the number of leaves is essentially indeterminate as new rosettes are continuously formed. We have determined that flower production in greenhouse-grown *Vallisneria* is positively correlated with plant biomass (Fig. 3). The
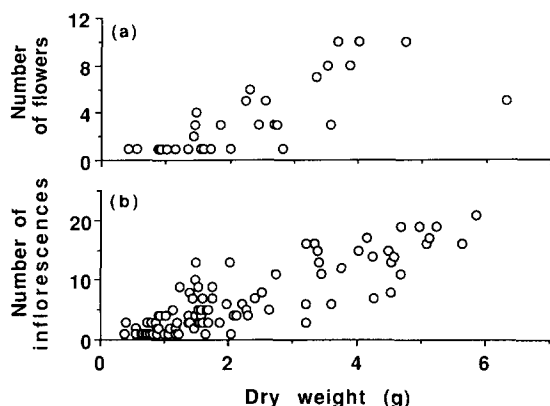
Fig. 3. Number of (female) flowers and (male) inflorescences in relation to dry mass for green-house-grown (see Fig. 2 caption) *Vallisneria* plants. Coefficients of determination (r^2) from linear regression are: (a) 0.56; (b) 0.74.

ratio of female flower number to plant biomass ($\bar{x} = 1.47$ flowers g^{-1} dry weight; $n = 33$) is significantly lower (t test; $P < 0.001$) than the ratio of male inflorescence number to biomass ($\bar{x} = 2.87$ inflorescences g^{-1} dry weight; $n = 94$). The coefficients of variation for these ratios are high (50% and 54%, respectively), however, demonstrating limits to predictability even in a relatively uniform greenhouse environment.

Pollination and fruit maturation

The number of flowers produced by a plant is not always a good predictor of seed set (Willson and Price, 1977). Given a specified number of flowers, it is conceivable that low pollination intensity could limit seed set as studied for *Potamogeton pectinatus* L. (Kautsky, 1987; You-Hao and Cook, 1989), although pollen limitation needs further documentation (Zimmerman, 1988). Several reviews have recently appeared (Philbrick and Anderson, 1987; C.D.K. Cook, 1988; Cox, 1988; Les, 1988), laying important groundwork for future advances in our understanding of macrophyte pollination. There is as yet for submersed species no experimentally determined answer to the question of whether pollen transport limits seed set, a question which has been primarily directed towards terrestrial plants. The issue of predictability hinges on the answer – if seed set is not limited by pollination, then attention can be focused elsewhere. If it is, more quantitative studies of pollination will be necessary.

The degree of pollen limitation may differ for submersed species differing in pollination mechanisms. Entomophilous and anemophilous (C.D.K. Cook, 1988) species may behave similarly to their terrestrial counterparts – for which seed set is apparently more often resource limited than pollen limited (Lee, 1988) – although the presentation of pollen near the water surface may re-

duce pollen transport in anemophiles. Hydrophilous species, for which water serves as a pollen transport medium, have no terrestrial angiosperm counterparts. They are themselves quite diverse in pollen transport mechanisms (Cox, 1988), which may be highly stochastic (Les, 1988). On the other hand, pollination efficiency may be relatively predictable and high in self-pollinating species for which the pollen needs only to travel a short distance (Philbrick and Anderson, 1987; Les, 1988).

We have few quantitative data on pollination or seed set in *Najas* or *Vallisneria*. The strictly underwater hydrophily of the monoecious *Najas* might seem a simpler and more predictable affair, particularly if plants are self-compatible, and pollination can be effected over a few millimeters within a plant. For *Vallisneria*, variables such as population density, sex ratio in the population, the degree of flowering synchrony between male and female plants, and the vagaries of wind and water currents could all be important influences on the efficiency of surface pollination. In addition, efficiency could vary in that the free-floating male flowers of *Vallisneria* form aggregations of various sizes and configurations. Cox and Knox (1988) have demonstrated that potentially analogous aggregations of pollen of the intertidal macrophyte *Amphibolis antarctica* (Labill.) Sonder & Aschers. act as 'search vehicles', whose likelihood of encountering stigmas increases with size.

The number of pollinated flowers on a plant may not be a good predictor of seed set, but the literature on self-incompatibility (Barrett, 1988), fruit and seed abortion, or other predispersal losses of fruits and seeds (Stephenson, 1981; Fenner, 1985; Lee, 1988) is limited for submersed freshwater macrophytes.

We conclude that the challenge of predicting seed set for submersed macrophytes has not yet been met, but that relationships between flowering and plant biomass provide a useful starting point.

SEED FATE

Dispersal

The dispersal of seeds and vagile vegetative propagules may be the most capricious of reproductive stages, but our lack of knowledge limits firm statements in this regard (C.D.K. Cook, 1987). Dispersal curves (Fenner, 1985) or other quantifications of seed deposition patterns do not appear to be available for any submersed freshwater species, yet are essential to the prediction of reproductive success at the local population level. Given that the relative importance of wind and water dispersal are essentially reversed for submersed macrophytes in comparison with terrestrial plants (C.D.K. Cook, 1987), fruit and seed buoyancy may be key determinants of dispersal dis-

tances (see Sculthorpe, 1967), although in many cases animals may be important vectors (Agami and Waisel, 1986; C.D.K. Cook, 1987).

Sculthorpe (1967, p. 329) maintains that submersed species "generally have no great powers of flotation", yet the difference between the negatively buoyant seed-bearing stem fragments of the annual *Najas* and the positively buoyant fruits of the perennial *Vallisneria* could have considerable ecological and evolutionary significance. We have observed *Najas* as an important component of littoral zones which consistently have bare patches of sediment. We speculate that these habitats are not simply aquatic counterparts to the early successional terrestrial habitats with abundant annuals and biennials, because open space underwater may be less ephemeral, i.e. the spatial distribution of 'safe sites' (Harper, 1977) for *Najas* seeds may tend to be temporally stable. If such sites are common, this could result in selection for limited dispersibility, resulting more in the maintenance of existing populations in favorable sites, than in longer distance dispersal to sites no more likely to have abundant safe sites. Appropriate terrestrial analogies might include wind-dispersed plants on remote islands (Carlquist, 1965) or in deserts (Ellner and Shmida, 1981), for which longer distance dispersal offers few advantages.

Vallisneria, occurring in many of the same habitats as *Najas*, may maintain populations in favorable sites through vegetative reproduction. Effective dispersal of buoyant fruits on the water surface or of seeds in or on waterfowl would suggest that the consequences of sexual reproduction in *Vallisneria* might lie primarily in the colonization of new sites, as also proposed by Bartley and Spence (1987; see also van Wijk, 1989), rather than in the maintenance of existing populations as we suggest for *Najas*. Further, the effective dispersal of the *Vallisneria* seed crop away from the parent site, if it occurs, could account for the low numbers of seedlings observed. Unfortunately, quantitative dispersal or seed deposition data are not yet available to support these propositions. Whatever seed dispersal patterns may exist for *Vallisneria*, however, it will be difficult to generalize to other vegetatively reproducing perennials: while *Potamogeton pectinatus* seeds are also readily dispersed (van Wijk, 1983), those of *Lobelia dortmanna* (Farmer and Spence, 1987) and other species (Sculthorpe, 1967) sink quickly upon their release from the parent plant.

Dormancy and germination

The long history of studies on freshwater macrophyte seed dormancy and germination has seen experimental seed exposure to variations in light intensity and quality, temperature regime during and subsequent to dormancy, oxygen tension and redox potential, drying, and seed coat thinning by physical, chemical, or biological means (Hutchinson, 1975; van Vierssen, 1982; Agami and Waisel, 1984; Farmer and Spence, 1987; Frankland et al., 1987).

Seed dormancy and germination requirements are clearly multifaceted, just as in terrestrial plants, but the underwater realm may be simpler than the terrestrial in key respects. The seasonal progression of temperature may be more predictable underwater, and both diurnal temperature fluctuations which may trigger germination on land or in shallow water (Fenner, 1985; Frankland et al., 1987) and water stress are unlikely to be important at depths at which most submersed species become established. Further, the ratio of radiant energy at red vs. far-red wavelengths is less likely to be a reliable indication of light environments underwater than it is on land (Spence, 1981; Spence et al., 1987), although underwater spectral quality may regulate *Nitella* oospore germination (Stross, 1979).

Seeds buried only a few millimeters apart in the sediment may experience radically different regimes of light intensity (e.g. Farmer and Spence, 1987) and redox potential (Chen and Barko, 1988). Should a sizable 'bank' of buried, viable seeds exist – little studied for submersed communities (Keddy and Reznicek, 1982; Haag, 1983; C.D.K. Cook, 1987; but see Rogers and Breen, 1980; van Wijk, 1989) – the quantification of depth distribution and microenvironments for such seeds in various lakes would be a valuable contribution.

A further confounding factor in the prediction of field germination percentages is that different investigators have documented different germination responses for the same species (e.g. Muenscher, 1936 vs. Farmer and Spence, 1987 for *Lobelia dortmanna*). It is usually not clear whether such germination differences can be attributed to differences in the genetic composition of different seed batches, in seed morphology (Agami and Waisel, 1988), in developmental stage at the time of seed collection, in handling and storage procedures, or in experimental conditions. One complex experimental variable is sediment type, which we have found may markedly influence seedling emergence from the sediment. We sowed seeds with the same overlying water but on different sediments in the greenhouse. Seedlings emerged to a much lesser extent from circumneutral, organic pond and acidic bog sediment than from alkaline, silty lake sediment for *Najas* and to the same extent but after a substantial delay for *Vallisneria* (Table 1). Perhaps redox potential, unmonitored in this experiment, could account for the differences, but another largely unexplored possibility is organic inhibitors of germination or seedling growth (El-Ghazal and Riemer, 1986).

All told, there appears to be a forbidding array of factors and factor interactions to consider. Fortunately, it is likely that not all play a limiting role for any given field population. For example, germination in *Najas flexilis* is reportedly indifferent to redox potential (Wetzel and McGregor, 1968), as it is in *Vallisneria* (A. Chernjavski and J.E. Titus, unpublished data, 1986). Further, in some cases we may be able to assume that chilling requirements are met each winter, particularly in north temperate lakes, but this does not ne-

TABLE 1

Mean percent seedling emergence (±SD) from *Najas* and *Vallisneria* seeds sown at about 1 to about 2 mm deep in sediment from an alkaline lake (Otsego), a circumneutral pond (Pickerel), and an acidic bog (Otselic), based on ten replicates of 25 seeds each. The significance of the t value is given (NS, $P>0.05$; **$P<0.01$) for each treatment pair with the same water source

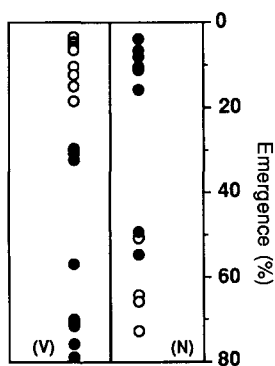| Sediment source	Water source	*Najas* emergence (%)		*Vallisneria* emergence (%)		
		9 days	>30 days	9 days	16 days	>30 days
Otsego	Pickerel	39±18**	49±15**	48± 9**	76±12**	79±12 NS
Pickerel	Pickerel	3± 5	11± 9	2± 2	35±17	76±17
Otsego	Otselic	34±10**	55± 8**	28±13**	64±17**	70± 1 NS
Otselic	Otselic	6± 6	16±11	7± 5	29±17	71±13

Fig. 4. Percent seedling emergence from *Najas* (N) and *Vallisneria* (V) seeds sown on various sediments beneath different natural waters in field (open symbols) and greenhouse (closed symbols) environments.

gate the value of chilling requirement studies to guide the design and interpretation of experiments on seeds collected in summer or autumn.

It does seem prudent, before elaborate models are constructed, to measure seed germination in situ (Rogers and Breen, 1980; Agami and Waisel, 1984; Szmeja, 1987), both for undisturbed and hand-sown seed populations. This would determine whether seed germination does, or at least can, occur naturally, and whether the poor correspondence we have observed between greenhouse and field germination results for *Najas* and *Vallisneria* is a general problem. We determined seedling emergence percentages for a variety of different treatments (key variables were sediment source and water chemistry), generally unpaired between greenhouse and field, and always obtained a lower percentage emergence for *Vallisneria* seedlings in the field than in the greenhouse, but generally found the opposite to be true for *Najas* (Fig. 4). No single hypothesis can easily account for the observed differences.

Alternative fates of seeds in the sediment, rarely followed in situ for freshwater macrophytes (Cook, 1987), include germination, losses to herbivores,

pathogens, or erosive wave action, succumbing to an unfavorable carbon balance during prolonged dormancy, or continuing dormancy, whether innate, enforced, or induced (Harper, 1977).

Seedling establishment

The submersed macrophyte literature is replete with references to the dominance of vegetative reproduction, but only a few authors (Rogers and Breen, 1980; Szmeja, 1987) offer quantitative data on seedling abundance. One reason for an apparent seedling scarcity may simply be that small seedlings are inconspicuous. Further, they may mature rapidly under favorable conditions, as we determined by transplanting 24 *Vallisneria* seedlings into Otsego Lake. The 16 seedlings which survived physical disturbance (by nesting fish?) grew to the substantial mean size of 1.9 g dry mass with 6.3 rosettes each in less than 4 months from seed. Actual seedling scarcity, undoubtedly quite common, may be due to small seed banks or to inappropriate conditions for germination or seedling establishment. The latter has rarely been investigated carefully, but has not generally been considered as an explanation for the dominance of vegetative reproduction in many species. Although it cannot be a universal explanation in view of successful establishment by annuals such as *Najas* and perennials such as *Lobelia dortmanna* (Szmeja, 1987), it cannot yet be dismissed.

Seedling establishment may pose several potential hazards, largely unexamined to date, as follows.

(1) The seedling microenvironment may not provide adequate levels of oxygen to meet the nighttime respiratory demands of small seedlings with limited capacity for lacunar oxygen storage.

(2) Physical instability of the substrate, at least partially countered by the early development of anchoring hairs in many young seedlings (Arber, 1920; Kaul, 1978), may lead to seedling loss by sediment bioturbation and erosion (Keddy and Constabel, 1986) or seedling flotation (C.D.K. Cook, 1987; J.E. Titus, personal observation, 1987).

(3) Carbon or mineral nutrient balance may be impaired in the presence of more mature clonally produced neighbors (Waller, 1988) or simply in the low light regimes within the sediment or at the bottom of the water column – Farmer and Spence (1987) reported that the light requirements for seedling establishment are greater than those for seed germination in *Lobelia dortmanna*, so that seedlings may appear briefly in zones without adequate light.

(4) Seedlings may be particularly susceptible to pathogens or herbivores.

The problems of limited oxygen supply, flotation, and low light regimes in the absence of a vegetation canopy are either likely to be more characteristic of an aquatic environment or unique to it. We conclude that, despite significant research on seed dormancy and germination, our overall understanding of physiological and demographic aspects of dispersal, seed banks, seed ger-

mination, and the potential challenges to seedling establishment severely limits our ability to predict sexual reproductive success in field conditions. We must agree that "the fate of seeds after sinking has very rarely been studied" (Cook, 1987).

VEGETATIVE PROPAGULE PRODUCTION

Bartley and Spence (1987) recently categorized several types of vegetative propagules and characterized their roles in perennation, dispersal, and propagation. They further addressed environmental induction of vegetative propagule formation (see also Spence et al., 1987), which several authors have shown to be sensitive to water temperature, photoperiod, spectral quality, and/ or quantum flux density (Klaine and Ward, 1984; Chambers et al., 1985; Spencer and Anderson, 1987). Environmental requirements for induction may be broadly similar for vegetative propagules and flowers, but data are at present too sparse to allow meaningful comparisons for freshwater taxa. Two contrasts are evident for *Vallisneria*.

(1) The size threshold for winter bud formation, if it exists, appears to be substantially less than that for flowering. Sixteen of 25 plants less than 0.1 g dry mass produced at least one winter bud in a 13 week greenhouse experiment, whereas the smallest flowering plant observed to date has been 0.38 g. Perhaps winter bud production in the asexual annual *Vallisneria* is the perennating counterpart to seed production in the sexual annual *Najas*, which we have observed to produce seed in plants below 0.003 g dry mass. Certainly *Vallisneria* allocates far more biomass to winter bud production than to sexual reproduction (Titus and Stephens, 1983).

(2) *Vallisneria* apparently must reach the surface to set seed, but not to produce winter buds. On the other hand, *Potamogeton crispus* L. must grow to within 1.5 m of the surface before stem turions are formed (Chambers et al., 1985).

Three hypotheses regarding the regulation of vegetative propagule number can be offered. As with flower number, the availability of internal plant resources or the availability of meristems capable of differentiating into propagules may limit vegetative reproduction. Further, particular environmental conditions may be required for propagule induction. Chambers et al. (1985) presented evidence that phytochrome response to red:far ratios could influence the number of turions produced on a *P. crispus* shoot. The same authors demonstrated that total photon flux density could also influence turion production quantitatively, perhaps by altering the pool of available plant resources. We have determined that the number of winter buds produced by *Vallisneria* is well correlated with biomass (Fig. 5). The agreement among slopes (3.25–3.60 buds g^{-1} dry mass) for plants grown from winter buds in a variety of greenhouse and field contexts (Table 2) is striking. There appears
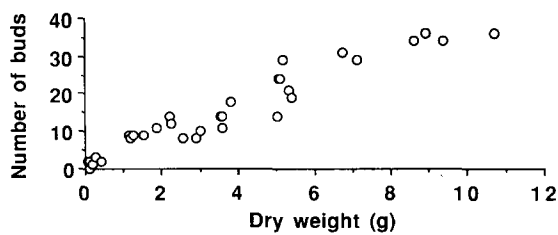
Fig. 5. Number of winter buds produced in relation to dry mass for *Vallisneria* plants grown from winter buds for 13 weeks in the greenhouse. Plants were rooted at 0.7 m water depth in sediment from Otsego Lake, NY and exposed to pH levels from 5.0 to 7.5 (Hoover, 1984). Coefficient of determination from linear regression is 0.92.

TABLE 2

Summary of linear regression statistics for the relation between the number of winter buds produced and biomass of *Vallisneria* plants grown in various field and greenhouse environments[1]

Site	n	Slope (buds g^{-1} dry wt.)	r^2	Remarks
Chenango Lake	21	3.26***	0.84	Randomly sampled plants
Chenango Lake	21	3.25***	0.88	Competition experiment
Selected New York lakes	60	3.39***	0.88	Grown from transplanted rosettes
Greenhouse	32	3.60***	0.92	Grown from rosettes
Greenhouse	28	14.92***	0.78	Grown from seed

***$P < 0.01$.
[1]For further details on Chenango Lake plants, see Titus and Stephens (1983), and for others see Hoover (1984).

to be considerable promise for predicting bud production given plant biomass, thus translating from physiological to demographic terms. In contrast, the relatively high slope (14.92) for greenhouse plants grown from seed indicates that these smaller plants from seed placed a higher 'priority' on producing winter buds. The allocation of biomass to buds, however, was similar for both groups of plants in that slopes from linear regressions of bud fresh mass vs. plant dry-mass (1.87 for plants from seeds and 2.04 for plants from winter buds) did not differ significantly.

The possibility of limitation by the number of available meristems as a morphogenetic constraint exists. Just as plant architecture varies, so does the potential for vegetative and sexual reproduction to 'compete' for meristems. The rate of ramet production is slowed during floral induction in *Eichhornia crassipes* (Mart.) Solms (Watson and Casper, 1984), but in *Lobelia dortmanna*, vegetative reproduction requires that flowering occurs first (e.g. Farmer and Spence, 1987). In a third pattern, stolons and flower buds are

apparently initiated simultaneously in *Vallisneria* (J.E. Titus, personal observation, 1989; Wilder, 1974), precluding direct competition between vegetative and sexual reproduction for meristems. Any competition might more likely develop between rosette and winter bud production, but even this seems unlikely given the usual switch from rosette to bud development toward the close of the growing season. To determine if ample meristems are available to support winter bud development, we estimated the potential number of winter buds for each plant by counting every third leaf on each rosette (see Section "Species descriptions"), summing these figures for all rosettes in a plant, and subtracting the existing number of stolons giving rise to rosettes rather than winter buds. Finally we subtracted the actual number of winter buds, and plotted the resulting differences between potential and actual bud production as a histogram (Fig. 6). Forty-two percent of these 64 sampled field plants were within two buds of their potential, implicating available meristems as a constraint on winter bud output. As before, however, the indeterminacy of steady rosette production through the growing season may weaken the case for meristem limitation. We have observed a great range of sizes in turions of *Potamogeton crispus* (also see Chambers et al., 1985) and *Utricularia vulgaris* L., as well as in winter buds of *Vallisneria*, 700 of which showed nearly an order of magnitude variation in fresh mass (Fig. 7). Spencer (1987)
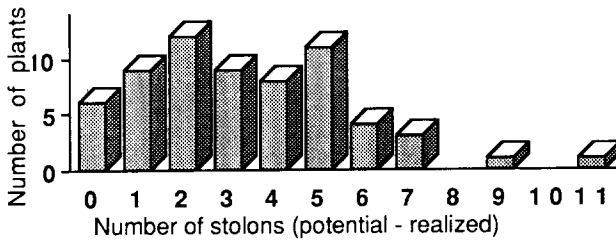

Fig. 6. Histogram of the number of potential, but undeveloped, bud-bearing stolons for *Vallisneria* plants randomly sampled in Chenango Lake, NY (see text).
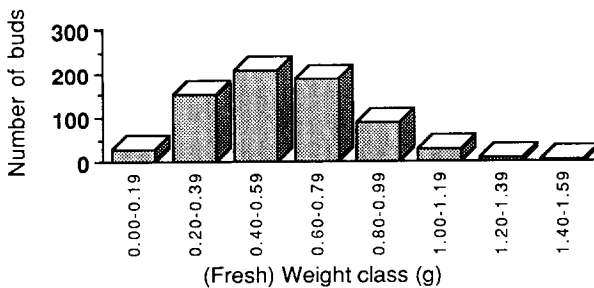

Fig. 7. Histogram of winter bud fresh weight for 700 *Vallisneria* buds collected in Chenango Lake, NY.

similarly observed considerable size variation in *P. pectinatus* tubers. Perhaps this great variation in propagule size is a counterpart to seed or fruit abortion during sexual reproduction, except that parent plants may limit the commitment of resources to propagule development without sacrificing propagules. In any case, because the size of an individual vegetative propagule may have implications for its fate (see below and Spencer and Rejmanek, 1989), it is clearly desirable to predict not only the number of propagules formed, but also their size distribution.

VEGETATIVE PROPAGULE FATE

Dispersal

Our ignorance of vegetative propagule dispersal is no less than it is for seed dispersal. Anecdotes relate waterfowl transport of submerged macrophyte stem fragments (see Hutchinson, 1975, pp. 244–245), but it is likely that the most readily transported vegetative propagules rely on buoyancy for dispersal from parent plants. Buoyancy for vegetative propagules may be positive (Kunii, 1984) or negative (Waisel, 1971; Agami et al., 1986), although negatively buoyant turions may be attached to floating stem fragments (Weber and Noodén, 1974). Water dispersal, whether resulting from positive buoyancy of propagules or swift currents alone, probably results in considerable mortality for propagules not transported to safe sites. It is likely to provide an important means of establishing new populations, but plays an uncertain role in the maintenance of existing populations.

Vegetative reproduction by rhizomes, stolons, and their associated tubers or turions typically limits dispersal to within a few tens of centimeters of the parent plant. Even this limited dispersal, however, may be advantageous in providing a potential means to 'forage' for favorable microenvironments (R.E. Cook, 1985; Hutchings and Bradbury, 1986). In contrast, submersed perennials without rhizomes or stolons may be unable to escape sites in which they have themselves depleted mineral nutrients (see Chen and Barko, 1988). A possible disadvantage of vegetative reproduction within the sediment is that propagules may commonly encounter anaerobic microenvironments, in which case the propagules may rely on parent plants for an oxygen supply from above the sediment, at least until metabolic rates decline in the autumn with decreasing sediment temperature or with the onset of dormancy. The variations we have observed in the color of *Vallisneria* winter buds, from pure ivory (no deposits) to rusty (presumably iron deposits) to black-tinged (sulfide deposits?) suggest that bud-bearing stolons disperse into varied sediment microenvironments, and/or parent plants may vary in their ability to supply oxygen to developing buds.

The quantitative determination and prediction of dispersal patterns for

tubers or turions produced in the sediment is likely to be more straightforward than that for buoyant turions or stem fragments. As yet, however, little evidence is available to characterize relationships between dispersal distance for propagules borne on rhizomes or stolons and its potentially important determinants – parent size, sediment texture, sediment redox potential, sediment nutritive quality, or patchiness in any of these sediment traits. The resulting propagule distributions, which can themselves be quite patchy (Haller et al., 1976), may in turn subsequently influence growth.

Clearly much remains to be learned regarding dispersal of vegetative propagules from the parent population by animal or water vectors and within the local population owing to patterns of rhizomatous or stoloniferous growth.

Dormancy and germination

Bartley and Spence's (1987) recent review summoned evidence for the occurrence of innate dormancy and enforced dormancy (quiescence) in macrophyte vegetative propagules, and tended "to support the view that turions have come in their physiology and ecology to resemble seeds remarkably closely". Indeed, the effects of light, water temperature, freezing and desiccation on vegetative propagule germination ("stem elongation leading to a resumption of vegetative growth" – Bartley and Spence, 1987) have all been examined, just as they have for seeds. Less obvious is a focus on redox potential or its correlates (but see Haller et al., 1976; Miller et al., 1976), but that may be less germane to germination than to subsequent establishment. Germination, at least after chilling, may often occur in response to rising spring sediment temperatures, or to light–temperature (see e.g. Kadono, 1988) interactions, perhaps especially for vegetative propagules incompletely buried in the sediment. If so, predicting germination could be a relatively simple matter, but would nevertheless require field data on the distribution of vegetative propagules within the sediment, and the seasonal (typically springtime) progression of temperature and light intensity in appropriate microenvironments. Such field data are scarce, but exist for the depth distribution of *Vallisneria* winter buds in sediment (see species description above; Rybicki and Carter, 1986) and of *Potamogeton pectinatus* (Spencer, 1987).

Alternative fates to dispersal from or germination within the parent site include prolonged dormancy and mortality. Little is known about secondary dormancy in vegetative propagules. We have observed that *Vallisneria* winter buds, often borne in pairs or even triplets, differ considerably in germination responses. The planting of 20 double buds at 23°C in the greenhouse led to the germination of 19 rosettes, all from the first-formed bud. Rosettes developed from the second-formed bud only if the connection to the first rosette was severed, or if leaves of the first rosette were clipped. This relationship, reminiscent of apical dominance, suggests that a viable winter bud 'bank' may
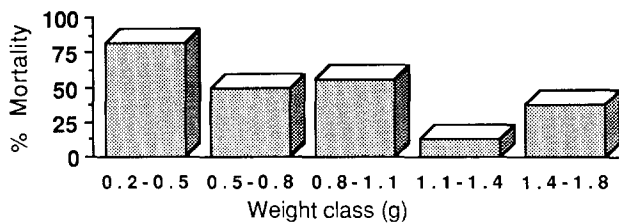
Fig. 8. Percent mortality for *Vallisneria* winter buds differing in fresh weight and buried approximately 5 cm in sediment, maintained from autumn to late spring in Chenango Lake, NY.

exist even during the growing season (as also implied for *P. crispus* turions, see Rogers and Breen 1980). The more important bud bank, at least for *Vallisneria*, is that which overwinters. Although an individual plant may produce 10 or more winter buds in the field (Titus and Stephens, 1983), most apparently succumb before producing a rosette the following spring. We have seen evidence of herbivory on winter buds, and fungi have destroyed entire bud collections in the laboratory, but the relative importance of herbivores, pathogens, low redox potential, or inadequate energy stores as agents of bud mortality in the field is unknown. We do know that mortality tends to be higher for small than for large *Vallisneria* buds (Fig. 8). Overall, however, it appears that few studies have followed the fate of vegetative propagules in the field through the dormancy and germination stages.

Establishment

Upon germination, a vegetative propagule may face essentially the same challenges as a young seedling: (i) oxygen limitation; (ii) unfavorable carbon or mineral nutrient budgets, perhaps especially for propagules buried relatively deep in the sediment; (iii) flotation or physical disturbance, as we have observed for *Vallisneria* rosettes dislodged from loosely consolidated Chenango Lake sediment; (iv) pathogens or herbivores. More deeply planted vegetative propagules are less likely to survive in *Vallisneria* (Rybicki and Carter, 1986), and exhibit lower subsequent growth rates in *Potamogeton pectinatus* (Spencer, 1987). However, the specific effects of depth in the sediment, which could include greater exposure to most of the above challenges, may vary for different sediment types. Herbivory on germinated vegetative propagules of submersed freshwater macrophytes has seldom been examined experimentally, but clear evidence of vertebrate herbivory on young transplanted *Vallisneria* rosettes has been observed (Carter and Rybicki, 1985; N. Krmenec and J.E. Titus, unpublished data, 1986). Data on the effects of sediment type and herbivores are probably too few to yield effective predictions of vegetative propagule mortality.

The ability of a vegetative propagule to meet environmental challenges may

depend not only on the severity of its environment and on its depth in the sediment, but also on its resource capital. A propagule more richly endowed with non-structural carbohydrates or key mineral nutrients might more likely support the establishment of a root system, or vertical growth through a relatively thick sediment layer and up toward the higher light environment of surface waters. Fragments of *Myriophyllum spicatum* L. with higher non-structural carbohydrate content have a greater chance of survival (Kimbel, 1982), and larger *P. pectinatus* tubers (presumably with more stored carbohydrates) support higher growth rates than smaller tubers (Spencer, 1987). Similarly, larger *Vallisneria* rosettes are produced from larger winter buds (Hoover, 1984). Thus, size and perhaps more specifically, non-structural carbohydrate storage, could be a useful predictor of survival and early growth rates for germinated vegetative propagules. If vegetative propagule size is pivotal for submersed macrophyte establishment, severe restrictions may be placed on seedling establishment, as seeds are typically much smaller than vegetative propagules. Perhaps the number of safe sites in any given macrophyte community is greatest for large vegetative propagules, and least for seeds in species with both sexual and vegetative reproduction.

SEXUAL VS. VEGETATIVE REPRODUCTION

Submersed freshwater macrophytes span the range from obligately sexually reproducing annuals to populations which apparently persist by vegetative reproduction alone (Sculthorpe, 1967; C.D.K. Cook, 1987). Many populations are intermediate, and capable of both sexual and vegetative reproduction, but the conventional view is that the prevalent reproductive mode in submersed freshwater habitats is vegetative. This view, supported more by qualitative than quantitative field observations, has occasioned several explanatory hypotheses. Arber (1920, p. 226) essentially held that (intraplant) competition with vigorous vegetative growth could act "as a deterrent to sexual reproduction". Sculthorpe (1967, p. 333) suggested that vegetative reproduction would be advantageous in "evading the hazards of aerial flowers". Bartley and Spence (1987) considered that freedom from water shortage may eliminate the need for seed production. Along similar lines, Les (1988) noted that vegetative reproduction may effectively preserve genotypes adaptive in the relatively uniform submersed plant habitat, and further that outcrossing in dioecious clonal species can prove difficult. While most of these arguments seem reasonable, they do not explain the apparent prevalence of vegetative reproduction in *Vallisneria*, a dioecious clonal species which we have observed to produce abundant viable seed highly germinable in the laboratory and moderately so in the field (Fig. 4). We can only suggest that a further obstacle to sexual reproduction within local populations exists: seed dispersal away from the parent population, seed burial to unfavorable depths, and the rigors of seedling establishment are all candidates.

The apparent prevalence of vegetative reproduction in many submersed species may significantly simplify the task of predicting season to season reproductive success for field populations. The production of vegetative propagules seems principally to be a question of determining plant resource allocation patterns, not a simple matter, but seed production may often be less predictable, given the uncertainties of flowering (Fig. 3), and the difficulty of predicting seed output from the abundance of flowers (Kautsky, 1987). At least for *Vallisneria*, a better correlation appears to exist between vegetative propagule production and plant size in the greenhouse and the field (Fig. 5; Table 2). We further surmise that, in general, the larger size of vegetative propagules may tend to buffer them against the rigors of establishment, and thus establishment from such propagules may be not only more likely, but more predictable than that from seeds inasmuch as the spatial and temporal distributions of safe sites for seedlings may be capricious.

CONCLUSIONS

An important goal of this paper has been to identify steps which may be bottlenecks limiting sexual or vegetative reproduction or its predictability in submersed freshwater macrophytes, both in general terms and for *Vallisneria americana* in particular. This effort has in some cases been hampered by ignorance – some relationships may seem more predictable as we come to understand them better, while others may inherently comprise strongly stochastic elements. Furthermore, even identifying bottlenecks in each of several different stages does not clarify which stage is most likely to limit reproduction or its predictability overall. We can nevertheless report pertinent points of the production and fate of seeds and vegetative propagules.

Plant biomass can be viewed as an important determinant of the incidence of flowering, at least in *Vallisneria* (Fig. 2): 88% of 425 greenhouse-grown plants either failed to flower if below a threshold dry weight of 0.75 g, or flowered if above it. The number of flowers or inflorescences per plant was only moderately well correlated with *Vallisneria* biomass (Fig. 3), however, and the flowering threshold rule weakened considerably in the field. Further, the extent of flowering may be a poor indicator of seed set as in *Potamogeton pectinatus* (Kautsky, 1987). The roles of pollination and seed or fruit abortion as limiters of seed output are poorly known for submersed plants.

Our ignorance of seed fate is exemplified by the paucity of quantitative studies on dispersal distances and seed deposition patterns, on seed banks, and on features of seed microenvironments pertinent to germination, although the sensitivity of seed dormancy and germination to a variety of environmental conditions has been tested in many species. Further, losses of seeds and seedlings to oxygen deficiency, negative carbon budgets, sediment disturbance, flotation, pathogens, and herbivores are generally not well char-

acterized. Overall, we suggest that the principal limiting step for sexual repro-
duction can surely in some cases be floral induction, and in others ineffective
pollination, but neither dispersal away from the local population, failure of
seeds to germinate, nor the challenges of seedling establishment can be ruled
out.

Plant size is a promising predictor of vegetative propagule production in
Vallisneria (Fig. 5; Table 2), both for greenhouse and field populations. Evi-
dence for morphogenetic constraints on propagule production (Fig. 6) is in-
conclusive. The size of the propagules formed may be quite variable (Fig. 7),
which has implications for survival (Fig. 8) and subsequent establishment.
Like seed germination, the germination of vegetative propagules has been rel-
atively well studied, but important regulators of germination and establish-
ment in the field warrant further study. Overall, no stage of vegetative repro-
duction stands out to us as a likely limiting step, although it is clear that most
Vallisneria winter buds do not survive to establish new plants.

We summarize in more general terms by suggesting that more investigation
at two interfaces of physiological ecology and demography may be particu-
larly fruitful. Regarding propagule production, experimental focus on the po-
tentially complex allocation patterns which translate accumulated resources
into seeds or vegetative propagules should prove rewarding. To what extent
can we rely simply on plant size as a predictor of propagule production? Re-
garding propagule fate, post-dispersal mortality of seeds and vegetative pro-
pagules may be rooted in physiological tolerance limits. To what extent can
we attribute decreases in propagule population sizes, whether during dor-
mancy or during early stages of establishment, to physiological challenges en-
countered in propagule microenvironments, and to what extent to herbivory
or pathogen attack?

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