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Turion Ecology of Hydrilla

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ABSTRACT

A literature survey was conducted to compile the numerous papers on the ecology of subterranean and axillary turions produced by the exotic macrophyte hydrilla (*Hydrilla verticillata* (L.f.) Royle). The monoecious and dioecious biotypes of hydrilla exhibit distinct differences in seasonal turion production, turion production in response to photoperiod, quantity and size of turions produced, and geographic distribution. Although a high level of variability exists within and between aquatic systems, several million subterranean turions per hectare have been reported. These propagules have been noted to remain quiescent in undisturbed sediment for up to 4 years and they represent the key target in breaking the life-cycle of hydrilla. The detached turions allow hydrilla to survive abiotic, biotic, and anthropogenic induced stress. Although turions sprout optimally at temperatures between 15 and 35 C, factors such as light, CO_2, oxygen, and various plant hormones and herbicides have been shown to either promote or inhibit sprouting. Improving control strategies for hydrilla requires a better understanding of factors that influence turion quiescence, sprouting, and longevity.

Key words: *Hydrilla verticillata*, subterranean turion, tuber, axillary turion, vegetative propagule.

INTRODUCTION

Despite extensive control efforts during the past 25 years, the exotic macrophyte hydrilla remains the dominant submersed weed problem in the southeastern United States (US), and it continues to spread northward. Perennation and spread of hydrilla by the asexual production of copious numbers of subterranean and axillary turions has received considerable research attention because they represent the key target in breaking the life-cycle of hydrilla. These detached turions serve as a persistent meristem bank (analogous to a seed bank) that allows for reinfestation several years following applications of control techniques (Steward 1969, Haller et al. 1976, Langeland 1993). Improving current control strategies for hydrilla requires a better understanding of factors that influence propagule formation, quiescence, sprouting, and longevity.

Background Information on Hydrilla

Cook and Lüönd (1982) provided a taxonomic revision of the single species genus providing information on the ecology, floral biology, anatomy, chromosomes, genetics, and variation. The native range of hydrilla is uncertain, but they suggest most evidence points to an origin in the warmer regions of Asia, although the possibility of an origin in central Africa was also suggested. A wide geographically disjointed distribution is reported, with hydrilla populations found on all continents except Antarctica (Cook and Lüönd 1982, Pieterse 1981).

Both monoecious (staminate and pistillate flowers on the same plant) and dioecious (staminate and pistillate flowers on separate plants) biotypes have been described (Cook and Lüönd 1982), and both are present in the US. Cook and Lüönd (1982) report that on a worldwide basis, the monoecious strain dominates in climatically tropical regions, whereas the dioecious strains are largely temperate. However, the current distribution and estimates of potential distribution for both monoecious and dioecious biotypes in North America are contrary to this observation. The dioecious strain (female plants only), was first reported in the US in south Florida in the late 1950's, while the monoecious strain was first reported in the Potomac River in the mid 1980s (Steward et al. 1984). A current distribution map is presented in Figure 1. These biotypes show several differences in terms of vegetative growth habit and asexual propagule production.

To conform to the majority of published literature, and to facilitate reading of this manuscript, the subterranean turion will be referred to as a tuber. From a botanical standpoint, true tubers do not have leaf scales or leaves (Sculthorpe 1967), and they are generally characterized by the swelling of a slender rhizome containing several buds (with undeveloped internodes) from which new growth arises. This is in contrast to the single apical meristem contained within the tip of a subterranean turion. Axillary turions will be referred to simply as turions throughout the remainder of the text.

Morphology of Hydrilla Tubers and Turions

Morphological descriptions of tubers and turions have been reported by Yeo et al. (1984) using light and electron microscopy supported by photographs, and by Mitra (1955) using light microscopy and line drawings. Turions form in the axils of leaves or branches while tubers form at the terminal nodes of typically underground stems (rhizomes that can penetrate up to 20 cm deep) that exhibit positive geotropism. Turions and tubers are similar anatomically as both propagules form when overlapping leaf scales and leaves surround a dormant plant meristem. Turions appear as simple green compressed shoots approximately 3 to 12 mm in length (Lakshmanan 1951, Mitra 1964). Tubers are generally 4 to 15 mm long and can vary in color from off-white to near black. The basal two-thirds of the tuber are swollen and filled with starch (Miller et al. 1976). The terminal one-third of the structure contains the apical meristem which bends at a 90

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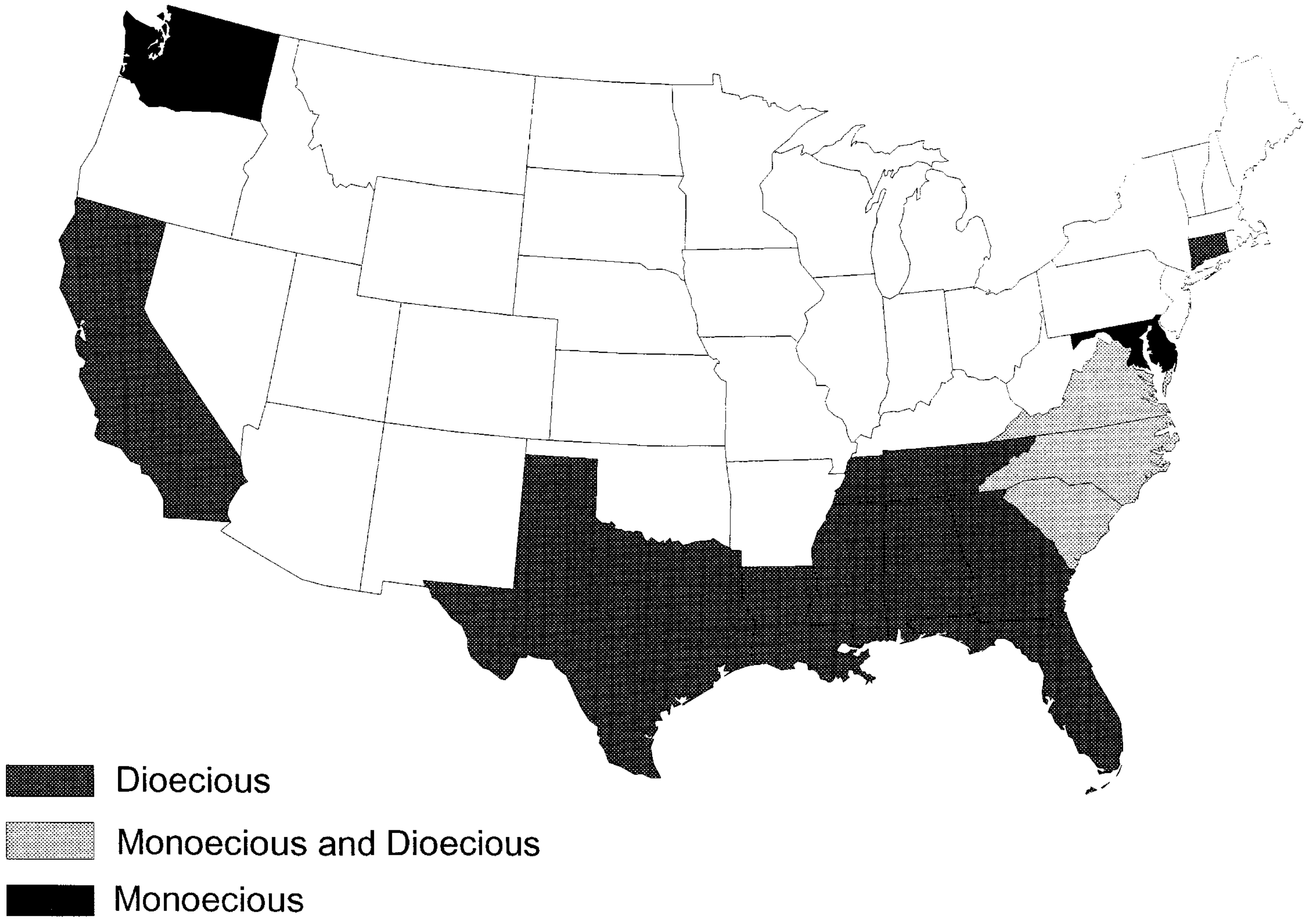

Figure 1. Current distribution of dioecious and monoecious hydrilla in the continental United States.

degree angle (Yeo et al. 1984). Spencer et al. (1987) reported that mean weights of propagules collected throughout the US ranged from 160 to 376 mg and 179 to 202 mg for dioecious and monoecious tubers respectively and from 36 to 77 mg for monoecious turions.

Although both types of propagules become detached from the parent plant, detachment is caused by different mechanisms. Turions develop an abscission zone and fall to the substrate in late autumn, whereas, tubers become free from the parent plant when the attached rhizome decomposes (Yeo et al. 1984). The time required for a subterranean turion to become detached from the rhizome (parent plant) is largely unknown, but is likely enhanced by increased temperatures.

The detached tuber has been described as tough and fleshy, likely due to the fact that the leaf scales are several cells thick and that a thick cuticle covers the external cell walls of the epidermis (Yeo et. al 1984, Pieterse 1981). While the cuticle is usually described as highly reduced in elodeid species such as hydrilla (Sculthorpe 1967), no research has been conducted on the effects of the substantial cuticularization of the subterranean turion in relation to longevity, pest resistance, quiescence, and sprouting.

Tuber and Turion Initiation and Formation

Many aquatic plants produce specialized propagules in order to survive conditions that are unfavorable for growth and to ensure vegetative reproduction (Sculthorpe 1967). Mitra (1955, 1956, 1960, and 1964) noticed the increasing presence and problems caused by hydrilla in the freshwaters of India, and published a series of papers describing the autecology of hydrilla and the likely contribution of tubers and turions to its spread and continued dominance. In India, Mitra (1955) noted that hydrilla produced both tubers and turions beginning in November and continuing through March.

In the US, Haller et al. (1976) reported that dioecious hydrilla formed tubers from October through April in Florida, whereas Harlan et al. (1985) reported that monoecious hydrilla formed tubers from June through October in North Carolina. Subsequent work has shown that initiation of tubers and turions in dioecious hydrilla is primarily a response to short days with a critical daylength of less than 13 hr; however, increasing temperatures from 10 to 33 C can markedly increase tuber production under short days (Van et al. 1978). McFarland and Barko (1990) also reported that dioecious tuber formation was greatest under short days, but could be stimulated during long days (14 hr) at lower temperatures (20 C).

The classic phytochrome-mediated and photoreversible system is involved in the initiation of tuber and turion production in dioecious hydrilla with red light (660 nm) stimulation and far-red (750 nm) repression (Klaine and Ward 1984). The dependence of dioecious tuber formation on photoperiod and the phytochrome system, has led to suggestions that night-interruption by a brief exposure to low-level light (such as that around boat marinas) could prevent tuber formation (Klaine and Ward 1984, Spencer and Anderson 1986).

Studies comparing the differential photoperiodic response between monoecious and dioecious hydrilla have produced some contrasting results. Spencer and Anderson (1986) reported the monoecious biotype grown from a tuber produced new tubers 28 to 56 days following a 10-12 hr photoperiod at 24 ± 0.3 C, but no tubers were produced during a 14 to 16 hr photoperiod. The dioecious biotype did not produce tubers at any photoperiod tested. The lack of tuber production by dioecious hydrilla reported by Spencer and Anderson (1986) at the shorter photoperiods, is in direct contrast to several other studies (Van et. al. 1978, Sutton et al. 1980, Klaine and Ward 1984). However, Spencer and Anderson (1986) suggested that the use of shoot apices instead of tubers left open the possibility that the source plants used in other studies had already been induced to form tubers. Subsequent work by Van (1989) in which tubers were used as the source tissue showed that the monoecious biotype produced new tubers after 28 d exposure to a 10 hr photoperiod and after 56 d exposure to a 16 hr photoperiod. Dioecious hydrilla formed tubers after a 56 d exposure to a 10 h photoperiod, whereas no tubers were formed during the 16 hr photoperiod. Furthermore, both the monoecious and dioecious biotypes increased tuber production severalfold when temperatures averaged 29 C compared to 21 C (Van 1989).

Although differences in study protocols likely influence eventual production of tubers, data from the studies conducted to date agree that monoecious and dioecious hydrilla respond to photoperiod in a differential manner. Monoecious hydrilla is capable of forming turions and tubers under much longer photoperiods (up to 16 hr d). These comparative studies showed that monoecious hydrilla is more prolific in the formation of tubers and turions (2 to 7 fold greater) than dioecious hydrilla under similar experimental conditions (Spencer et al. 1987, Steward and Van 1987, Van 1989, Sutton et al. 1992). Sutton et al. (1992) used a single tuber for starting material and showed that monoecious hydrilla produced large numbers of propagules in both winter and summer in south Florida, whereas dioecious hydrilla showed a distinct seasonality with tubers produced only during the fall and winter. It is unlikely that significant tuber production from monoecious hydrilla occurs in the late fall and winter in the northern climates as the monoecious hydrilla dies back in the winter and exhibits an annual growth habit (Harlan et al. 1986).

Despite monoecious tuber production being more than 50% greater than that of dioecious hydrilla, the average weight of individual dioecious tubers was 32% greater than monoecious tubers (Sutton et al. 1992). McFarland and Barko (1987) and Spencer et al. (1987) also reported that on average, monoecious tubers were significantly smaller than dioecious tubers, leading these authors to speculate that under field conditions the smaller monoecious tubers may not contain adequate starch reserves to survive as long as dioecious tubers.

Although overlap of monoecious and dioecious hydrilla in the same body of water has been reported in North Carolina and Virginia (Ryan et al. 1995), for the most part, the genetically distinct biotypes (Verkleij et al. 1983, Ryan et al. 1991) continue to remain geographically separated. The initial geographic separation is likely due to different anthropogenic introductions, however, it has been related to the life history of the biotypes, and to potential vegetative reproductive success at varying latitudes. Spencer and Anderson (1986) used a 9 C temperature cutoff and a 13 hr photoperiod for tuber production by dioecious hydrilla, and suggested that the monoecious strain may be better able to colonize more northerly areas due to its ability to form greater number of tubers in a shorter period of time. Van (1989) also noted the ability of monoecious hydrilla to form tubers under long summer days and temperatures which favor active growth. It was suggested monoecious tuber development in the summer would assure survival in the northern parts of the United States (Van 1989).

A recent report of a persistent population of dioecious hydrilla in Connecticut (Les et al. 1997), contradicts earlier speculation concerning the potential northward expansion of dioecious hydrilla in the US. Furthermore, the authors state that dioecious hydrilla is overwintering in this area due to the production of numerous tubers.

To date, studies addressing the competitive interactions and ability of the two biotypes to produce vegetative propagules under differing environmental conditions have not been adequately addressed. However, difficulties in distinguishing between monoecious and dioecious tubers without the use of isoenzymic analyses is a significant impediment. Areas of overlap in lakes of North and South Carolina may provide insight into the competitive success between these biotypes at different latitudes.

Information on production of turions is quite limited compared to that of tubers. Spencer et al. (1994) noted that once the plant is initiated under a short photoperiod (11 h), carbon and nitrogen are directed from shoots and roots into newly formed tubers and turions; however, approximately 15 times more carbon and nitrogen were allocated to tuber production than to turion formation in rooted plants.

Miller et al. (1993) report that in dioecious hydrilla, turion production begins under short days in September, decreases during cold months of the winter, increases again in late spring and essentially ceases during June through August. Free-floating plants produced three times more turions than rooted plants and increased plant density resulted in decreased turion formation.

Thullen (1990) reported that dioecious turion production from floating plant fragments was influenced by daily temperature ranges, the source of the plants, the length of time the plants were in the study, and aeration. Pieterse et al. (1984) have suggested that turion formation is stimulated by low levels of nitrogen and phosphorous in the water. Free floating plants would be much more subject to this stress as compared to rooted plants which receive the majority of these nutrients from the sediments. However, Thullen (1990) concluded that turion production was not stimulated solely by low levels of nitrogen and phosphorous, but required an adequate daily temperature range (17 to 27 C) and photoperiod.

It is interesting to note that while the production of tubers is generally much greater than turion production in the US, Pieterse (1981) states that in Europe only axillary turions are formed by dioecious hydrilla. Similarly, Nakamura and Kadono (1993) report that in Japan, the dioecious biotype produces only turions, whereas the monoecious biotype produces tubers. To date, no hypotheses have been proposed to explain these discrepancies in tuber and turion production.

It has been hypothesized that larger plant propagules increase the competitive abilities of a plant (Grace 1985). Spencer and Rejmanek (1989) evaluated the competitive abilities of tubers versus turions of monoecious hydrilla and concluded that the smaller turions produce plants that are weaker competitors. Spencer et al. (1987) have suggested that turions and tubers represent different survival strategies, with turions better suited for dispersal and possible occupation of non-vegetated areas where they are likely to face little competition. In contrast, tubers are not mobile and may need the extra storage reserves as they are more likely to face intraspecific competitive pressures. In support of this, Bowes et al. (1979) noted that larger dioecious tubers showed increased survival rates compared to smaller tubers when deprived of light for up to 4 months.

The monoecious and dioecious biotypes of hydrilla differ in many aspects of asexual reproduction and vegetative growth habit. Therefore management plans will likely require modification as these biotypes spread and begin to overlap in the continental US.

Quantification and Tuber Distribution

Spencer and Ksander (1993) have speculated that clonal species such as hydrilla would be expected to produce a clumped distribution of tubers versus a random or uniform distribution. Field sampling has supported this assertion. Haller et al. (1976) noted that following extensive sampling during a draw-down, core samples taken in the same location produced a high level of variability (0 to 12 tubers per 10 cm core). Due to the non-random distribution and seasonal and site differences, numbers reported from field sampling are often quite variable and substantial replicate sampling is required to achieve meaningful values. The length of time a site has been infested with hydrilla or recent management practices may also affect tuber values within a given sample site. However, the history of hydrilla and recent management practices are generally not provided in reports. Sampling techniques usually involve sediment coring devices such as one described by Sutton (1982).

Values of dioecious tuber densities reported from field sampling are presented in Table 1. The production of millions of propagules per hectare following 2.5 years of hydrilla infestation led Haller and Sutton (1975) to suggest that control methods would be extremely difficult and competition from native aquatic plant species almost impossible. Bowes et al. (1979) noted large variations in tuber numbers between lakes in north and south Florida, and between time of season sampled. Sutton and Portier (1985) reported on the density of tubers of dioecious hydrilla in five south Florida lakes and showed significant differences between lakes and yearly differences within lakes, but no distinct seasonal fluctuations were noted. Subsequent work by Sutton (1996) at one of these sites has shown that differences in the number of hydrilla propagules collected occurred due to collection date, location, and site within the location sampled (interactions were noted between these three variables).

Harlan et al. (1985) reported that field densities for monoecious tubers on three North Carolina lakes ranged from 200 to 1228/m^2 with no seasonal trends noted. These authors also noted that generally 93 to 100% of monoecious tubers were located in the top 12 cm of hydrosoil. Turion densities were quite low compared to tuber densities and ranged from 0 to 42/m^2. Information on field densities of monoecious tubers is scarce compared to reports for dioecious hydrilla.

Miller et al. 1976 suggested that tuber production increased with increasing water depths (up to 3 m); however, subsequent research suggests that the shallow water sites (< 1.0 m deep) had been dominated with emergent vegetation prior to sampling.[2] Mitra (1964) has reported that tuber density decreased with increasing water depth. MacFarland and Barko (1995) reported that monoecious tuber density and percent germination was greatest at approximately 1 m water depths (compared to 0.5, 1.5, and 2.0 m depths) in samples

TABLE 1. SELECTED REPORTS OF DIOECIOUS HYDRILLA TUBER DENSITIES FROM FIELD AND MESOCOSM STUDIES.

Tuber densities (m^{-2})	Citation
Field	
257[1]	Haller and Sutton (1975)
300-600	Miller et al. (1976)
20-510	Bowes et al. (1979)
36-207 (882[2])	Sutton and Portier (1985)
62-900[1]	Steward (1980)
200-1228 (Monoecious)	Harlan et al. (1985)
Mesocosm	
3542-6046[3]	Sutton et al. (1992)
700-2200	Joyce et al. (1992)
869-4200	Steward (1984)
2099-9053	Steward and Van (1987)

[1] Studies conducted in experimental ponds.
[2] Highest value reported from 1800 samples.
[3] Includes some values for monoecious tubers.

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[2] Haller, W. T., and J. V. Shireman. 1984. Monitoring study for Lake Ocklawaha management plan. Final Report, US Army Corps of Engineers, Jacksonville, FL. 329 pp.

taken from the tidally influenced Potomac River. However, to date, the role that water depth plays in either significantly reducing or increasing tuber production and/or sprouting and quiescence is largely unknown.

Difficulties in obtaining uniform core samples from different types of sediments and the high spatial variability of tubers often results in a rather substantial standard error associated with tuber sampling. Sutton and Portier (1985) reported that statistically valid results were obtained through the collection of 25 core samples (10 cm diameter) for each of 5 sample locations and 18 sample times. Spencer (1993) has evaluated several data sets and reported that when tuber density is low (<200 m^2) between 25 and 200 samples (10 cm diameter) are required to estimate tuber number to within 20% of the mean value, whereas, between 8 and 25 samples are required to estimate to within 20% of the mean value when tuber density is high (200-1000 m^2). Increasing the core diameter can decrease the number of samples required, but will increase the processing time per sample and the level of effort required to collect the sample.

To overcome problems with variability in the field, mesocosm studies (i.e. outdoor tank or pool) have been conducted to determine potential for tuber production. Sutton et al. (1980) reported on the intraspecific competition of hydrilla and found that the initial number of shoot tips planted significantly increased the number of tubers produced, whereas biomass remained the same regardless of the initial number of stems planted. Values for tuber production in mesocosm studies are also presented in Table 1. Few studies have reported on turion production in field or mesocosm conditions, but Miller et al. (1993) reported turion production for mats of detached dioecious hydrilla as high as 861 turions/kg fresh wt./month.

Discrepancies between tuber values reported in the field and mesocosms have not been discussed in the literature. However, this difference appears to be somewhat anomalous, as vegetative biomass values are often quite similar between the field and mesocosms. Potential reasons for this discrepancy in tuber values may include the following; 1) higher stem densities per unit area (more loci for tuber formation) in mesocosm chambers (Sutton et al. 1980) 2) optimal growth conditions (limited competition and herbivory, and adequate nutrients) in mesocosms, 3) shallow and uniform depth of the mesocosms, and 4) different rates of tuber death and/or sprouting in the mesocosms. Sutton and Portier (1985) suggest that in the field, tuber density may reach a steady state condition in which formation of new propagules equals those sprouting (and those dying and decaying) with the maximum number for a body of water dependent on sediment type, nutrients in the sediment, water quality, and other unknown factors. In contrast, mesocosm studies are set up to determine maximal tuber production within a short time period and studies are likely terminated before a steady state can be reached.

Bruner and Batterson (1984) concluded that tuber formation was independent of soil type (sand, marl, and potting mix) and was an intrinsic property of the plant, however, these authors suggested that soil fertility influences tuber production. In contrast, Sutton (1985) reported that although vegetative biomass was directly related to increased fertilization, tuber production in a sand medium was independent of three levels of fertilizer following a 16-week study. It should be noted that both tuber and biomass production were reduced 8-10 fold in an unamended muck-sand soil versus the fertilized sand. Steward (1984) compared sediment fertility and texture and concluded that increased fertility had a greater influence on vegetative biomass than on dioecious tuber production by hydrilla during a 70 week study. McFarland and Barko (1990) also report that while vegetative growth was reduced on sand- versus nutrient-amended sediment, dioecious tuber formation was unaffected by sediment type. In addition, Sutton and Portier (1995) noted that while sediments from four different Florida lakes supported different levels of shoot biomass, tuber numbers were not directly dependent on sediment type, but were indirectly affected by the amount of shoot biomass the sediment would support.

Spencer et al. (1992) reported that sediment type and organic amendment affected both tuber mass and number in monoecious hydrilla. Addition of a straw or peat organic amendment (5 to 20%) to any of the six substrates tested (sand, loam, 2 clays, silt-loam, and sand-clay-loam), resulted in significantly increased tuber production. The authors speculate that addition of organic matter increased sediment nitrogen, leading to increased vegetative growth and tuber production.

Field sampling for hydrilla propagules remains notoriously difficult due to the distribution of tubers and difficulties associated with blindly sampling sediment. However, long-term management plans for hydrilla control must include tuber sampling in order to determine at what point a propagule bank no longer presents a viable threat of reinfestation.

Response to Abiotic, Biotic, and Anthropogenic Induced Stress

The formation of subterranean propagules not only ensures vegetative reproduction, but often allows the plant to survive biotic, abiotic, and anthropogenic induced stress. Basiouny et al (1978b) reported that dioecious hydrilla tubers could survive and sprout following drying of up to 64 h at 30 C and 40% humidity. In contrast, turions only survived for up to 8 hr. The authors make no mention of it, but the thickened cuticle of the tuber likely enhances its ability to survive desiccation.

Dioecious tubers incubated in complete darkness over a 4 month period showed that increased survival and shoot length were directly related to initial tuber size, with larger tubers showing increased survival rates (Bowes et al. 1979). These authors suggested that a sprouting tuber must reach a quantum flux density of at least 12-20 $\mu E/m^2/sec$ within 0.5 to 0.75 m above the hydrosoil or it cannot survive.

Carter et al. (1987) examined the effect of salinity on sprouting of monoecious hydrilla tubers and concluded that salinities of 0-3 parts per thousand (ppt) had little affect on sprouting, while salinities of 5-9 ppt resulted in only 4 to 20% sprouting and none sprouted at salinities greater than 9 ppt. The ability to withstand varying periods of high salinity may be quite significant in tidally influenced estuarine areas.

Although there are no reports on effects of salinity on sprouting of dioecious tubers, Steward and Van (1987) compared salinity tolerance of monoecious and dioecious hydrilla grown for 2 weeks from sprouted tubers and reported no differences in growth up to 11 ppt, whereas, growth was severely retarded above 13 ppt.

Phenolic acid content of tubers and axillary turions of both hydrilla biotypes was investigated by Spencer and Ksander (1994), with values ranging from 6 to 20 μM/g dw. The phenolic acid content may be quite important as plant phenols may serve as defenses against attack by microorganisms and herbivores. Berhardt and Duniway (1986) noted a high incidence of propagule decay in drained irrigation canals and showed that three fungal isolates (*Fusarium sp., Papulaspora sp.* and *Geotrichium sp.*) were able to colonize apparently healthy hydrilla tubers, reduce sprouting and increase decay rates in a subsequent laboratory study. The susceptibility of tubers to pathogenic attack has received little attention, but the fact that the tuber normally resides in an anaerobic environment, reduces the potential for aerobic pathogens to play a significant role outside of drawdown situations. Little, if any research has been conducted on seasonal tuber mortality and the role it plays in the stability of the propagule bank.

Godfrey and Anderson (1994) showed that insect feeding by *Bagous affinis* larvae can significantly reduce dioecious hydrilla tuber sprouting and suggested that *B. affinis* should be released in the field (during drawdown or dry season) with an egg to tuber ratio of 2:1 or greater. However, in areas of high tuber densities this would require that several million insects be released per hectare.

Sutton (1986) has evaluated the effects of several potential allelopathic compounds on tubers and showed that sprouting could be greatly reduced by many of these compounds. He concluded that with the exception of salicylic acid, the usefulness of these compounds in the management of hydrilla was limited due to the large amounts required. Sutton and Portier (1991) reported that two species of *Eleocharis* applied as dried, ground material at rates of 5 to 10 g/Kg of hydrosoil, reduced shoot dry weight and tuber production by greater than 80%. The authors attributed these significant reductions to phytotoxic allelochemicals released by the *Eleocharis.* The submersed arrowhead *Sagittaria subulata* grown in conjunction with hydrilla was reported to reduce tuber production by 59% (Sutton 1990). However, it was not reported whether the primary factor responsible was allelopathy or competition.

Spencer and Ksander (1995) noted that the microbial metabolite, acetic acid, applied to sediments at rates of 17 to 696 mmol/liter completely inhibited tuber sprouting at exposure times as short as one day. While these rates are likely prohibitive from a management perspective, it does point out that very little is known about the effects of pH on tuber survival and sprouting. However, based on the wide variety of sediments in which hydrilla can grow, a fairly broad range of pH tolerance is suspected. Steward and Center (1979) evaluated the feasibility of using the fumigant metham (sodium methyldithiocar-bamate) for control of hydrilla regrowth from tubers and concluded that subsoil injection at rates of 75 to 373 liters/ha of metham on moist soil followed by leaching was the most effective treatment.

Steward (1980) evaluated 25 herbicides and found that the preemergence herbicides fenac [(2,3,6-trichlorophenyl) acetic acid] and dichlobenil (2,6-dichlorobenzonitrile) were the only compounds registered for use at that time that retarded sprouting or growth of shoots from tubers in laboratory studies. Subsequent pond studies showed that fenac at 1 to 2 mg/L inhibited hydrilla regrowth for 13 to 18 months, whereas, dichlobenil treatments (0.7 to 1.2 mg/L) resulted in regrowth comparable to controls in 6 to 8 months. Propagules collected from dichlobenil treated ponds readily sprouted and grew while those collected from fenac treated ponds did not sprout and subsequently decomposed. Interestingly, no differences were noted between pretreatment and 13 month posttreatment tuber densities, suggesting a low rate of sprouting/death of tubers occurred a full year following treatment. Neither fenac or dichlobenil currently have a Federal Aquatic Use Registration.

Use of the sulfonyl urea herbicide, bensulfuron methyl (methyl 2-[[[[[(4,6-dimethoxy-2-pyrimidinyl)amino]carbonyl]amino]sulfonyl]methyl]benzoate) has been reported to significantly reduce or prevent tuber formation in both monoecious and dioecious hydrilla up to 6 months after treatment at rates of 50 to 200 μg/L for 28 exposure days (Van and Vandiver 1992, 1994). The authors suggested that proper timing of bensulfuron methyl (BSM) application would be critical to stopping vegetative reproduction due to differential seasonal tuber production by the monoecious and dioecious biotypes. Langeland and LaRoche (1992) reported that BSM at rates of 25 to 200 μg/L applied in either June or November completely inhibited dioecious tuber production during the following winter season. Haller et al. (1992) showed that BSM treatments as low as 5 μg/L could prevent tuber formation depending on the time of application and number of treatments. Anderson (1988) has suggested a growth regulator mechanism for prevention of tuber formation, as vegetative biomass is often not greatly affected by the lower treatment rates of BSM. Langeland (1993) reported on several lake treatments with BSM and concluded that even though there were large reductions in tuber numbers, high tuber densities (up to 300 m^2) remained in two of the lakes and tubers were not eliminated in any of the lakes up to 2 years after application. It was suggested that elimination of hydrilla tubers would be a long-term process that would likely require several years of annual sequential applications. Despite its excellent ability to inhibit hydrilla tuber production (and potential sprouting), BSM is not currently being considered for aquatic registration.

MacDonald et al. (1993) showed that the currently registered herbicide fluridone (1-methyl-3-phenyl-5-[3-(trifluoromethyl) phenyl]-4(1H)-pyridinone) applied at rates of 5 to 50 μg/L could also greatly inhibit tuber formation, and suggested the mode of action was due to decreased abscisic acid (ABA) formation. However, these studies also showed that at rates of 0.05 to 0.5 μg/L fluridone, young (but not mature) plants were stimulated to increase tuber formation, suggesting a growth regulator response. Miller et al. (1993) reported that fluridone and BSM reduced dioecious turion production at rates of 2.5, 5, and 10 μg/L.

Steward (1969) conducted laboratory evaluations on the effects of such currently registered contact herbicides as endothall (7-oxabicyclo[2.2.1] heptane-2,3-dicarboxylic acid) and diquat (6,7-dihydrodipyrido [1,2-α:2',1'-c]pyrazinediium ion) on sprouting of hydrilla tubers and found these herbicides exhibited little phytotoxicity to quiescent propagules. It is highly unlikely that most herbicides ever come in contact with the tubers following a submersed application. However, due to its longer persistence, tendency to accumulate in the sediment, and activity at comparatively low concentrations, fluridone has the potential to impact tuber sprouting, or show phytotoxicity to newly sprouted tubers. Although contact herbicides do not reach the tubers, the resultant rapid removal of biomass has been reported to significantly stimulate *in situ* sprouting of tubers (Van and Haller 1979, Joyce et al. 1992).

Growth regulating compounds have been shown to have stimulatory and inhibitory effects on both tuber initiation and germination. Klaine and Ward (1984) reported that application of exogenous ABA greatly stimulated turion production, whereas addition of GA and ethylene (applied as ethephon) reduced turion production by 80%. Klaine (1986) showed that the compound thidiazuron (an ethylene stimulator) at a concentration of 10^{-6} M completely inhibited both tuber and axillary turion formation over a 227 day test period in dioecious hydrilla. MacDonald et al. (1993) suggested that inhibition of ABA production by the herbicide fluridone also reduces formation of tubers.

Steward (1969) reported that germination and growth of tubers was enhanced by gibberellic acid (GA), while that of axillary turions was enhanced by indole acetic acid (IAA) and 2,4-D. Sastroutomo (1980) reported that GA at 10^{-5} M broke dormancy of non-cold treated axillary turions, but was toxic to their development after germination. Tuber sprouting was also enhanced by ethephon, GA, and thiourea (Basiouny et al. 1978a).

Numerous chemical and non-chemical evaluations, have led to strategies that inhibit tuber production, however, the presence of large numbers of underground propagules that are resistant to treatment continues to complicate hydrilla management.

Environmental Factors and Tuber and Turion Germination

Mitra (1956) provided the first accounts on the sprouting and autecology of hydrilla tubers and turions in India. She noted that tubers greatly outnumber turions and could be found in the sediment up to 18 cm deep. Germinating tubers are characterized by long internodes and pale rudimentary leaves until they reach the soil surface, and it generally takes about 12-14 days for the formation of a fully developed plant. Observations in plexiglass chambers (kept in the dark) suggest that once a tuber has sprouted it can remain viable in the anaerobic sediment for several months prior to emergence into the water column (M.D. Netherland personal observation).

Haller et al. (1976) reported that dioecious tubers and turions removed from the substrate showed optimum sprouting at 15 to 35 C, with low rates of sprouting (< 10%) noted below 15 and above 35 C. Steward and Van (1984) reported 35 to 68% germination rates for monoecious tubers exposed to 15 C, whereas, sprouting rates for dioecious hydrilla were only 3% at this temperature. Miller et al. (1976) showed light (12 μE/m²/sec) to have a stimulatory effect on the rate of dioecious tuber sprouting; however, light quality had no effect on sprouting percentage. Although light stimulated sprouting, a high percentage of tubers (63-68%) also sprouted under dark conditions during the 14 day incubation period. The role that light plays in stimulating *in situ* sprouting remains intriguing, as it seems highly unlikely that light could penetrate more than a few mm of sediment. Miller et al. (1976) also reported that a 100% CO_2 environment inhibited sprouting, whereas a nitrogen sparged medium (anaerobic conditions) had no effect on sprouting.

Kojima and Izawa (1989) reported that optimum conditions for tuber sprouting included soil moisture between 40 and 60%, temperature between 20 and 25 C, and <4 cm of overlying sediment. The authors reported that short periods of low temperature easily broke dormancy. Basiouny et al. (1978a) also reported that maintaining winter-collected dioecious tubers at 5 C enhanced sprouting, whereas, summer collected tubers required no cold treatment. It should be noted that the authors were not able to distinguish between tubers that were formed within that season and those carried over from previous seasons and it is possible that some of the tubers used for the winter germination studies were not fully mature. Carter et al. (1987) showed that monoecious tubers collected in the fall and chilled for 42 days at 7 C resulted in 92% germination, whereas propagules that were not chilled failed to germinate. In contrast, Harlan et al. (1985) showed a high percentage of germination of monoecious tubers stored at 26 C and germinated in the laboratory. Sastroutomo (1980) reported that axillary turions of hydrilla germinated best when exposed to a cold treatment of 2 C for 33 days and when stimulated by red and far-red irradiation. While the evidence is fairly substantial that monoecious tubers require a chilling period to stimulate sprouting, the evidence for a chilling requirement for dioecious tubers is not as well supported.

Van and Steward (1990) reported that, *in situ*, monoecious tubers survived in the undisturbed sediment for a period of over 4 years in a study conducted in south Florida. It was suggested that the persistence of monoecious tubers was regulated by an environmentally-imposed enforced quiescence which prevented a rapid depletion of the tuber population through excessive germination *in situ*. Unfortunately, this is the only published study with the direct objective of dealing with tuber persistence and viability. Moreover, the longevity of monoecious tubers in more temperate areas of the United States where cold stratification is more likely has not been addressed. Harlan et al. (1985) reported that in three North Carolina lakes monoecious tubers began to sprout in late March when water temperatures reached 11 to 13 C and continued through August. These authors noted it was peculiar that tuber sprouting stopped in the field in late August even though temperatures remained optimal. Subsequent laboratory studies suggested no seasonality existed (chilling was not required) as sprouting rates were 85 to 100%. Although no studies have dealt specifically with tuber persistence in dioecious populations, Langeland (1993) has reported persistence of large numbers of tubers (300/m²) for up to 2 years following treatment with the herbicide BSM. Sutton (1996) reported that following measurement of tuber densities as high as 887/m^2 in the North New River Canal, Florida, five years of contact herbicide treatment and the introduction of grass carp removed vegetative growth and resulted in depletion of the tuber bank within 3 to 4 years.

Van and Steward (1990) also investigated longevity of monoecious turions and reported that turions either germinated or died after 1 year. Differences in germination between tubers and turions was attributed to differences in environmental conditions and more extreme fluctuations near the sediment surface (where the turions are located) favoring breaking of quiescence and increased sprouting *in situ*. Spencer et al. (1987) and Van and Steward (1990) suggest that the smaller size of the turions limits the amount of storage reserve for long-term survival.

Determination of factors that either inhibit or promote tuber germination are important in developing new strategies for long-term control of hydrilla.

FUTURE RESEARCH

While it is obvious that a great deal of research has been conducted on hydrilla propagules, the data are sometimes conflicting and several questions remain. In order to determine the best management alternatives available, research on factors affecting sprouting of hydrilla tubers *in situ*, or in systems which better simulate *in situ* conditions deserves attention.

To date, the vast majority of research on tuber sprouting has been conducted on tubers that have been removed from the sediment, thereby disturbing the propagules and exposing them to environmental factors (light, oxygen, reduced CO_2) that they do not experience in flooded hydrosoils. Sprouting of these propagules is often greater than 90% within a two week period, which strongly suggests an environmentally-imposed quiescence, as opposed to an innate dormancy. Furthermore, laboratory tests are often conducted for 1 to 2 weeks and conclusions that are drawn may be misleading. For example, addition of exogenous growth regulators, or light may stimulate the rate of sprouting, but not necessarily the overall sprouting rate. In addition, application of exogenous growth regulators (especially ethylene) is known to have different effects in an aerobic versus an anaerobic environment. The effect of exogenous hormone application on tuber sprouting in an anaerobic environment is currently unknown.

While suitable temperatures (13-35 C) are an absolute requirement for sprouting, it would not appear that temperatures in this range necessarily trigger *in situ* sprouting. In a study of 5 South Florida lakes, Sutton and Portier (1985) found no seasonal trend apparent for the sprouting of dioecious tubers or turions even though water temperatures were never below 15 C.

One phenomenon that has been observed by several authors (Mitra 1964, Haller et al. 1976, Van and Haller 1979, Joyce et. al. 1992, Langeland 1993) is that dioecious tuber sprouting remains quite limited under a vegetative canopy, whereas, rapid removal of the canopy by mechanical or chemical means greatly stimulates sprouting. Many hypotheses have been proposed to explain this phenomenon, but none have been tested. Chemical and physical changes in the rooting medium such as changes in CO_2, increased oxygenation, increased light penetration, and temperature changes have all been proposed.

Based on the previous scenarios that have been suggested to stimulate tuber sprouting, the vertical position of the tuber within the substrate may play a significant role in its potential for sprouting and survival. Data from natural plant populations of *Potamogeton* spp. and *Vallisneria americana* suggests non-uniformity in vertical distribution of propagules (Rybicki and Carter 1986, Spencer 1987, and Spencer and Ksander 1990). However, Rybicki and Carter (1986) showed that the majority of *Vallisneria* tubers were found at distinct depth intervals that differed based on sediment type. Harlan et al. (1985) record that monoecious hydrilla tubers in most samples collected in three North Carolina lakes were most dominant at depth intervals of 0 to 8 cm, however, up to 50% of the propagules could be found from 8 to 12 cm deep.

Depth distribution of hydrilla tubers may be particularly important in regards to the potential of light and oxygen to stimulate sprouting. Whereas previous studies have evaluated the effect of planting depth on propagule survival, no studies have evaluated if *in situ* sprouting is related to vertical position in the sediment. Moreover, sediment type may play a significant role in the sprouting of hydrilla tubers. Van and Haller (1979) demonstrated higher rates of sprouting following herbicide treatments of hydrilla growing in builders sand or gravel versus clay or organic soils. It was suggested that changes in gaseous constituents may have played a key role.

The longevity of dioecious tubers is currently unknown and would provide valuable information for plant managers. Evidence from field sampling following fluridone treatments suggests a decrease in tuber populations over time; however, tubers can at least remain up to three years posttreatment (Alison Fox, personal communication).

Although much research has been conducted on hydrilla tubers, our knowledge of the factors affecting their *in situ* longevity, quiescence, and sprouting remains inadequate.

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