

Variation in *Hydrilla verticillata* (L.f.) Royle Propagule Weight

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ABSTRACT

Weight distributions for hydrilla (*Hydrilla verticillata* (L. f.) Royle) vegetative propagules (axillary or subterranean turions) were skewed in eleven of thirteen sample populations. Seven of the thirteen sample populations exhibited tendencies toward bimodal distributions. The coefficient of variation ranged from 24 to 148%. Subterranean turion weights exhibited more variability than published values for subterranean turion lengths. Subterranean turions from dioecious plants weighed more than those from monoecious plants when grown under similar conditions. Axillary turions weighed less than subterranean turions. The data support the notion that, although they are anatomically similar, axillary and subterranean turions represent alternate reproductive mechanisms.

Key words: hydrilla, turions, reproductive strategy, weight distribution

INTRODUCTION

Hydrilla (*Hydrilla verticillata* (L. f.) Royle) is a serious aquatic weed in the United States. *Hydrilla* can reproduce through seed formation, shoot fragmentation, or the production of axillary and subterranean turions (Pieterse 1981; Swarbrick *et al.* 1982). Although monoecious plants capable of producing seeds have recently been reported in the United States (Steward *et al.* 1984; Langeland and Smith 1984; Rybicki *et al.* 1985), the production of axillary and subterranean turions appears to be the most important means of perennation and regrowth following periods of adverse conditions (Sutton and Portier 1985; Haller *et al.* 1976; Miller *et al.* 1976). Axillary turions (also referred to as turions and green turions) are short thickened growths covered with scale leaves which form at the axils of leaves. Anatomically similar structures are formed underground at the ends of positively geotropic shoots and are commonly referred to as subterranean turions, brown turions, or tubers (Pieterse 1981).

Numerous studies with terrestrial plants have shown that seed size affects some aspects of plant fitness including emergence, growth, and dispersal ability (Dolan 1984; Marshall 1986; Peters 1985; Stanton 1984; Wulff 1986). Recent studies indicate that seed size may be more variable than previously believed (Thompson 1984), suggesting that data on variation in propagule size may be useful to understanding the dynamics of plant populations (Schaal 1980). A better understanding of aquatic plant population

dynamics might allow the timely application of management practices, so that differences in plant susceptibility related to age or developmental state could be exploited (Hodgson 1966). Many submersed aquatic plants rely more heavily on the production of vegetative structures for perennation than upon the production of seeds (Sculthorpe 1967; Hutchinson 1975). Recent experimental results indicate that tuber fresh weight is a good predictor of successful emergence from the substrate, growth, and competitive ability for sago pondweed (*Potamogeton pectinatus* L.) (Spencer 1986). There are, however, relatively few studies that have examined the size distributions of vegetative propagules produced by submersed aquatic macrophytes. Sutton and Portier (1985) and Haller *et al.* (1976) provide data on the lengths of subterranean turions collected from natural populations of hydrilla in Florida lakes. Yeo (1965) has also reported on the lengths of chains (groups) of sago pondweed tubers collected from a Montana irrigation canal. Because of the apparent importance of propagule weight in plant growth and survivability, and the relative lack of quantitative information about propagule weight for submersed aquatic plants, the purposes of this study were 1) to quantify the variation in vegetative propagule fresh weights; 2) to describe the distributions of propagule fresh weights; and 3) to compare these data for propagules from monoecious and dioecious plants from natural populations, and from plants grown in outdoor cultures at the USDA Aquatic Weed Control Research Laboratory in Davis, CA. Such data are necessary prerequisites for understanding the population dynamics of this important aquatic weed.

MATERIALS AND METHODS

Hydrilla subterranean turions were collected (from random, 15 cm diameter cores) from the following natural populations: Wysteria canal, Imperial Irrigation District, CA, March, 1984; Dog Lake, Redding, CA, October, 1985; Belle Haven Marina, VA, October, 1985. Axillary turions were also collected from the Belle Haven Marina by harvesting the standing crop in six 0.25 m² quadrats and removing the axillary turions by hand. Subterranean turions and axillary turions were transported to the lab in sealed plastic bags; washed with tap water; patted dry with paper towels; and weighed to the nearest mg.

Individual apical segments of hydrilla originally collected from several places in the United States (Lake Wheeler, NC; Aquatic Gardens, MD; Dyke Marsh, VA; Ft. Lauderdale, FL) were planted in separate rectangular plastic tubs (67 by 42 by 15 cm) filled with soil (Rieff fine sandy loam) (1 tub per hydrilla provenance). Each tub was placed

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in a separate 1000 l concrete vault. The vaults were outdoors and located at the USDA Aquatic Weed Control Research Laboratory, Davis, CA. After 8 months (May, 1985 to January, 1986), the plants were harvested and the axillary and subterranean turions separated. Individual fresh weights of axillary and subterranean turions for each provenance were determined as above.

Hydrilla from the Belle Haven Marina site is monoecious. Plants from the Imperial Irrigation District have been characterized by Verkleij *et al.* (1983) on the basis of morphological and isoenzymic criteria. These are dioecious female plants, apparently identical to those found in Florida. Extracts of subterranean turions from Dog Lake, CA, have been characterized by their protein and isoenzymic patterns after native electrophoresis (Ryan, unpublished). The protein pattern and the isoenzymes of glutamate-oxaloacetate transaminase and phosphoglucomutase are identical to those from subterranean turions from the Imperial Irrigation District, CA. Extracts of the subterranean turions of the monoecious plants from Lake Wheeler, NC have been compared to those from Dyke Marsh, VA (near Washington, D. C.): preliminary evidence indicates that the two strains differ in a number of isoenzymes (Ryan unpublished). The plants from Lake Wheeler may represent a third North American strain.

The size distributions for axillary turions and subterranean turions were analyzed using the UNIVARIATE procedure within the Statistical Analysis System (SAS Institute, 1985). This procedure provides a number of statistics useful in describing a variable's distribution. For a detailed discussion of these statistics and their interpretation the reader is referred to Sokal and Rohlf (1969). Knowledge of whether or not a variable is normally distributed may provide insight into the factors which influence that variable. For example, many biological phenomena are normally distributed, so that a non-normal distribution implies that some factor, such as selection, may be affecting that variable (Sokal and Rohlf 1969).

RESULTS AND DISCUSSION

The characteristics for hydrilla propagule fresh weights indicate that subterranean and axillary turion weights vary considerably (Table 1). Mean fresh weight for axillary turions from monoecious plants ranged from 36 to 77 mg. The coefficient of variation (CV) for the four samples ranged from 66 to 105%. The distributions for monoecious axillary turion fresh weights were significantly skewed to the right as indicated by G_1 and the relative positions of the mean, median, and mode. Turion weights from the AQG and BH sources were significantly leptokurtic, indicating that more weights were present near the mean and toward the tail of the distribution with fewer at the intermediate region. None of the sample populations of monoecious axillary turion weights were normally distributed. Subterranean turions from monoecious plants were heavier than axillary turions; the mean fresh weight of subterranean turions ranged from 117 to 202 mg. The CVs for monoecious subterranean turions were somewhat smaller varying from 24 to 44%. Monoecious subterranean turion weights for three of the four samples were not normally distributed and in all cases except one significantly skewed to the left. One of the four samples displayed a significant tendency toward a bimodal distribution.

Only a few dioecious axillary turions were produced (Table 1). The mean fresh weight for dioecious subterranean turions ranged from 160 to 386 mg. Mean subterranean turion weight was greater for subterranean turions produced by plants grown in outdoor cultures than for those from the two natural populations. The CVs for dioecious subterranean turion weights ranged from 28 to 51%. Tuber weights in three of the four samples were not normally distributed. Dioecious subterranean turion weights were significantly skewed to either the right or left and exhibited a tendency to being leptokurtic.

The distributions of hydrilla propagule fresh weights did not follow a normal distribution in eleven of the thirteen sample populations examined. Similar results have been observed for the distribution of sago pondweed tuber

TABLE 1. DISTRIBUTION CHARACTERISTICS FOR FRESH WEIGHTS (mg) OF AXILLARY TURIONS (AT) AND SUBTERRANEAN TURIONS (ST) OF HYDRILLA COLLECTED FROM NATURAL POPULATIONS AND OUTDOOR CULTURES AT DAVIS, CA.

PROPAGULE TYPE	STRAIN	SOURCE	F/L	N	MEAN	MODE	MEDIAN	CV	G_1	G_2	P NORMAL ¹
AT	D	FL	L	10	112	6	61	148	7.3	2.6	< 0.01
AT	M	AQG	L	561	41	21	25	105	2.3	7.1	< 0.01
AT	M	DYK	L	496	72	38	49	77	1.0	-0.1	< 0.01
AT	M	NC	L	288	77	52	58	77	1.0	-0.04	< 0.01
AT	M	BH	F	1256	36	19	30	66	3.1	1.5	< 0.01
ST	D	FL	L	173	376	421	402	36	-0.4	-0.5	< 0.01
ST	D	IMP	L	288	386	270	380	28	0.4	1.5	> 0.15
ST	D	RED	F	342	305	273	273	51	0.9	0.9	< 0.01
ST	D	IMP	F	110	160	95	149	51	0.7	-0.04	< 0.01
ST	M	BH	F	175	117	58	112	44	0.1	-0.8	> 0.15
ST	M	AQG	L	1349	179	192	182	30	-0.1	-0.4	< 0.01
ST	M	DYK	L	1754	191	221	199	35	-0.4	-0.2	< 0.01
ST	M	NC	L	288	202	232	212	24	-0.7	-0.01	< 0.01

¹F/L = field (F) or outdoor culture (L); G_1 = skewness; G_2 = kurtosis; P NORMAL = the probability of the sample coming from a normally distributed population based on Kolmogorov's D statistic. Strain designations are D = dioecious and M = monoecious. Sources are as follows: FL = Ft Lauderdale, FL; AQG = Aquatic Gardens, MD; DYK = Dyke Marsh, VA; NC = Lake Wheeler, NC; BH = Belle Haven Marina, VA; RED = Redding, CA; IMP = Wysteria Canal, Imperial Irrigation District, CA.

weights (Spencer 1986). Hydrilla axillary turion size distributions were skewed to the left, while subterranean turion size distributions were skewed either to the right or left. The asymmetrical distributions of hydrilla propagule weights imply that there may be selection for or against the production of propagules with weights falling in one tail of the distribution or the other. Although the effects of propagule weight on the survivability of the subsequent plant are not known for hydrilla, Haller *et al.* (1976) have reported that subterranean turions between 7 and 14 mm long had a higher percentage germination than those outside this range. It has recently been demonstrated that tuber fresh weight is directly related to the likelihood of emerging from the substrate and subsequent growth of sago pondweed (Spencer 1986). Experiments designed to evaluate the relationship between propagule weight and growth for monoecious and dioecious hydrilla are currently underway at the USDA Aquatic Weed Control Research Lab.

Hydrilla axillary and subterranean turions are less variable in weight than sago pondweed tubers collected from a California irrigation system (CV = 88%) or grown in greenhouse culture (CV = 110%) (Spencer 1986). It thus appears that a generalized growth model for submersed aquatic plants must allow for interspecific and intraspecific differences in propagule weight distributions. The CVs for hydrilla vegetative propagules are near the low end of the range of CVs reported for seed weights (15 to 250%) in Thompson (1984). Hydrilla subterranean turion weights are more variable than the subterranean turion lengths reported by Haller *et al.* (1976) or Sutton and Portier (1985). CVs calculated from the data in Table 1 of Haller *et al.* (1976) and Table 6 of Sutton and Portier (1985) ranged from 17 to 19%, and are less than the CVs for subterranean turion weight.

Axillary and subterranean turions are believed to be produced as a means of surviving adverse environmental conditions (Pieterse 1981). There appear to be size differences between subterranean turions and axillary turions and between monoecious and dioecious strains for plants grown under similar conditions (the outdoor cultures). The mean subterranean and axillary turion weights for each hydrilla provenance were calculated and used as the response variable in a two-way analysis of variance (ANOVA) following a split plot design (Kirk 1968) to evaluate the effects of strain (monoecious, dioecious) and propagule type (subterranean turion, axillary turion). The ANOVA indicated that the statistical interaction between strain and propagule type was significant ($P < 0.01$). We therefore calculated t-statistics using the CONTRAST and ESTIMATE options within GLM (SAS Institute Inc. 1985) to compare mean weight for axillary and subterranean turions within and between strains (i.e. monoecious subterranean turions vs. monoecious axillary turions; monoecious subterranean turions vs. dioecious subterranean turions; etc.). The SAS estimates of the standard errors for the between strain comparisons were calculated with the appropriate degrees of freedom calculated from Satterthwaite's approximation (Satterthwaite 1946). The results indicate that axillary turions are smaller than subterranean turions for dioecious ($t = -27.18$; $P < 0.01$) and monoe-

cious plants ($t = -22.71$; $P < 0.01$). Similarly subterranean turions for dioecious plants are significantly larger than those for monoecious plants ($t = 14.22$; $P < 0.01$) and so are axillary turions ($t = 3.57$; $P < 0.05$). Anderson (1985) reported similar findings for different provenances of monoecious and dioecious hydrilla grown under conditions similar to those used in this study. Anderson (1985) reported that monoecious subterranean turions were on average only 34% of the weight of dioecious subterranean turions (186 ± 43 vs. 548 ± 18 mg fresh weight; mean \pm SD), and that the mean monoecious axillary turion was 36% of the weight of the mean dioecious axillary turion (43 ± 8 vs. 118 ± 26). These results suggest that while anatomically similar (Pieterse 1981; Yeo *et al.* 1984) hydrilla axillary and subterranean turions represent different reproductive strategies. It thus appears that the smaller axillary turions provide a dispersal mechanism and the larger subterranean turions a means to insure continued survival in the currently occupied habitat. Axillary turions are produced above ground and are thus liable to dispersal by water movements. They are therefore more likely to colonize areas not already inhabited by hydrilla, and have likely been subjected to selective pressures for greater dispersal ability (i.e. small size). Subterranean turions on the other hand are produced below the sediment surface and barring disturbances are not likely to move from place to place. The selective pressures on subterranean turion production would therefore favor the production of larger subterranean turions, since larger propagule size is an advantage when immature plants must compete with members of the same species (Schaffer and Gadgil 1980).

The results of this study and those of Anderson (1985) further suggest that dioecious and monoecious plants differ in the manner by which photosynthate is allocated to turion production, supporting previous suggestions that the two strains possess different survival strategies (Verkleij *et al.* 1983; Spencer and Anderson 1986).

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