Emergence of vegetative propagules of *Potamogeton nodosus*, *Potamogeton pectinatus*, *Vallisneria americana*, and *Hydrilla verticillata* based on accumulated degree-days

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Abstract

The purpose of this study was to develop equations that predict emergence from vegetative propagules for four species of aquatic plants. We established artificial propagule banks by growing monoecious and dioecious *Hydrilla verticillata* (L.f.) Royle, *Potamogeton pectinatus* L., *Potamogeton nodosus* Poiret in outdoor tanks in Davis, California. Dioecious *H. verticillata*, *P. pectinatus*, *P. nodosus* and *Vallisneria americana* L. were grown in similar tanks in Lewisville, Texas. Emergence of undisturbed propagules was monitored the following spring. In California, *P. pectinatus* tubers, *P. nodosus* winter buds, and axillary turions formed by monoecious *H. verticillata* began to sprout at about the same time in mid-February, while dioecious *H. verticillata* tubers did not begin to emerge until mid-August. The distinct separations of emergence times for propagules in the Texas experiment were similar to those observed in California, and *V. americana* showed the earliest emergence time. Using sediment temperature data from each location, we calculated degree-days using the single triangle method. We fit a single logistic equation relating cumulative emergence to accumulated degree-days for each species-propagule combination from the two locations. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: American pondweed; Sago pondweed; Hydrilla; Water celery; Sprouting; Tuber; Turion; Winter bud; Temperature

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1. Introduction

Many species of rooted aquatic plants persist because they produce underground vegetative propagules. In temperate populations, propagules typically survive winter and resume growth the following spring. In many circumstances, management of aquatic weeds can be achieved with existing technologies, however the ability to predict propagule sprouting would allow aquatic weed managers to implement more effective control strategies, perhaps leading to reduced herbicide usage and/or combinations of other control methods. Previous studies on propagule sprouting (Haller et al., 1976; van Wijk, 1983; van Wijk and Trompenaars, 1985; Madsen and Adams, 1988; Spencer and Ksander, 1992), using constant temperatures have indicated that propagule sprouting is in part regulated by temperature. However, such results are of limited value in predicting emergence in the field because temperatures fluctuate daily and seasonally.

Predictions of plant development in growth models have been successfully based on the accumulation of heat units or degree-days (Frank and Ries, 1990; Fidanza et al., 1996). Forcella and Banken (1996) developed an equation between green foxtail (*Setaria viridis* (L.) P. Beauv.) seedling height and degree-days with the aim of optimizing the timing of management operations. Degrandi-Hoffman et al. (1996) were able to define the duration of the blossoming period and fraction of open blossoms over time as a function of degree-days for five almond (*Prunus dulcis* (Mill) D.A. Webb) cultivars. Perry et al. (1997) were able to improve predictions of the timing of tomato harvest in the southeastern US using accumulated degree-days equations. Dunn et al. (1996) reported that the optimum time for taking cuttings of *Pistacia chinensis* Bunge could be predicted more accurately when a degree-day model was employed than when calendar days were used. McGiffen and Masiunas (1992) constructed exponential models relating growth of black and Eastern nightshade (*Solanum nigrum* L. and *S. ptycanthum* Dun.) to accumulated degree-days. Sanderson et al. (1994) related alfalfa (*Medicago sativa* L.) mean stage weight to accumulated degree-days using data from a number of sites, years, and cultivars. They reported that this relationship differed among locations, years, seasons, and cultivars, and concluded that degree-days would not be a broadly applicable predictor of mean stage weight. Nesmith and Hoogenboom (1994) related flowering time of five squash cultivars (*Cucurbita pepo* L.) grown at different locations and times in Georgia, to degree-days. They reported cultivar differences in the number of degree-days required for the formation of staminate and pistillate flowers. Hayhoe and Dwyer (1990) reported good correspondence between degree-days (based on soil temperature) and emergence of corn (*Zea mays* L.) seedlings and suggested that useful estimates of emergence could be made for a wide range of climates, soils, and tillage practices based on their empirical relationships. Arazi et al. (1993) reported that use of degree-days improved the ability to predict the timing of tuber appearance in potatoes grown in southern Israel.

The purpose of this study was to develop equations that relate emergence from vegetative propagules to accumulated degree-days for four species of aquatic plants. The species of *Potamogeton* and *Vallisneria* examined are native to North America and may be important components of aquatic plant communities. *Hydrilla verticillata* is an invasive introduced species that has frequently been associated with negative impacts on water use or native plant communities.

2. Materials and methods

2.1. Outdoor studies

We established artificial propagule banks in spring, 1994 by growing monoecious and dioecious *H. verticillata* (L.f.) Royle, *Potamogeton pectinatus* L., and *Potamogeton nodosus* Poiret in outdoor cultures at Davis, CA, USA (latitude 38°33′29.6″N, longitude 121°44′17.1″W). The dioecious *H. verticillata* tubers originally came from a culture maintained at the USDA Aquatic Weed Laboratory in Gainesville, Florida; the monoecious *H. verticillata* tubers were originally collected from the Potomac River, Virginia (Spencer et al., 1987), the *P. nodosus* winter buds were originally collected from the Richvale Irrigation District, California (Spencer et al., 1992); and the *P. pectinatus* tubers from the Solano Irrigation District, California (Spencer et al., 1992). During this experiment, axillary turions were formed by the monoecious *H. verticillata* plants. We noticed that they accumulated on top of the sediment. We followed their sprouting in the same manner as for the reproductive structures produced below ground, i.e., subterranean turions, hereafter referred to as tubers. Twenty-four 6 l containers were planted during the spring of 1994 with two propagules of one of the four aquatic plants for a total of six containers per species. The sediment used was modified UC mix as described in Spencer and Anderson (1986). The 24 containers were placed in 1437 l tanks filled with water from a well to a depth of 0.57 m. Water was replaced at weekly intervals. The aquatic plant propagules were allowed to sprout and grow undisturbed through an annual cycle, including production of the appropriate overwintering structure. In December 1994, all aboveground biomass, including stem bases were removed, leaving only the underground propagules. During the following spring, we monitored emergence of the new, undisturbed propagules at 2 to 3 day intervals. Upon emergence, the plant propagule was carefully removed from the container, counted and discarded. The final harvest occurred in November 1995. All containers were washed to remove sediment and remaining propagules counted and discarded. We also measured sediment temperatures at 30 min intervals with a data logger. These measurements began in spring 1994 and continued through termination of the experiment in November 1995. For the days when water temperature data were missing due to equipment problems, we estimated water temperature from regression equations relating water temperature to air temperature. Air temperature data were obtained from the Statewide IPM Project, University of California, Division of Agriculture and Natural Resources, for a station located in Davis, California.

An additional portion of the study was conducted at the Lewisville Aquatic Ecosystem Research Facility, in Lewisville, TX, USA (latitude 33°04′45″N, longitude 96°57′30″W) during spring 1994–1995, utilizing six 1845 l fiberglass tanks. Water levels for each tank were maintained at approximately 0.6 m depth using Lewisville Lake reservoir water. Sediment and water temperatures were monitored as described previously. For missing water temperature data equations relating water temperature to air temperature were used with air temperature data from the National Oceanic and Atmospheric Administration monthly summary for the Dallas-Ft. Worth Regional Airport. Twenty-four 6 l containers were planted during the spring of 1994 with two propagules of one of the four aquatic plant species for

Table 1
Equations used to calculate degree-days by the single triangle method[a]

Conditions	Equation	
If mxtemp>tup and mntemp>tup	1	Degree-days=tup−low
If mxtemp<low and mntemp<low	2	Degree-days=0
If mxtemp<tup and mntemp>low	3	Degree-days=(6(mxtemp+mntemp−(2low)))/12
If mxtemp<tup and mntemp<low	4	Degree-days=$((6(\text{mxtemp}-\text{low})^2)/(\text{mxtemp}-\text{mntemp}))/12$
If mxtemp>tup and mntemp>low	5	Degree-days=$((6(\text{mxtemp}+\text{mntemp}-(2\text{low})))/12)$ $-(((6(\text{mxtemp}-\text{tup})^2)/(\text{mxtemp}-\text{mntemp}))/12)$
If mxtemp>tup and mntemp<low	6	Degree-days=$(((6(\text{mxtemp}-\text{low})^2)/(\text{mxtemp}-\text{mntemp}))$ $-((6(\text{mxtemp}-\text{tup})^2)/(\text{mxtemp}-\text{mntemp})))/12$

[a] Mxtemp=maximum daily temperature; mntemp=minimum daily temperature; tup=upper threshold; low=lower threshold.

a total of six containers per species. The sediment used was modified UC mix (Spencer and Anderson, 1986). The aquatic plants employed in this part of the study were dioecious *H. verticillata* (L.f.) Royle, *P. nodosus* Poiret, *P. pectinatus* L., and *Vallisneria americana* L. With the exception of *V. americana*, the propagules were sent to Texas from California, so they were from the same sources. *V. americana* were from an outdoor culture maintained at the Lewisville Aquatic Ecosystem Research Facility for about 10 years, but originally from Wisconsin. One container of each aquatic plant species was placed into each of the six mesocosm tanks.

The aquatic plant propagules were allowed to sprout and grow undisturbed through an annual cycle, including production of the appropriate overwintering organ. In December 1994, all aboveground biomass, including stem bases were removed, leaving only the underground overwintering organs. These new, undisturbed overwintering organs were observed weekly for germination. Upon germinating, the plant propagule was carefully removed from the container, counted and discarded. The final harvest occurred in November 1995. All containers were washed to remove sediment and remaining propagules counted and discarded.

Using the sediment temperature data from each location, we calculated degree-days using the single triangle method using equations (Table 1) described by Zalom et al. (1983). In the case of monoecious *H. verticillata* axillary turions, we used water temperature instead of sediment temperature. We estimated the lower and upper thresholds for sprouting from published studies with *H. verticillata* (8–16°C monoecious, 12–21°C dioecious, Steward and Van, 1987), *P. pectinatus* (3–15°C, Madsen and Adams, 1988; Spencer and Ksander, 1992), and *P. nodosus* (10–20°C, Spencer and Ksander, 1992, Flint and Madsen, 1995). We used 7–20°C as the lower and upper thresholds for *V. americana* based on Korschgen and Green (1988) and unpublished data (J. D. Madsen).

When calculating accumulated degree-days, it is necessary to determine the starting point, i.e. the date to begin accumulating degree-days. An examination of the temperature data for 1994 and 1995 indicated that low temperatures occurred around the end of December to beginning of January. Since these temperatures were lower than the thresholds for *P. nodosus* and *H. verticillata*, we started accumulating degree-days from 1 January 1995. For *V. americana* and *P. pectinatus*, the thresholds were low enough that the starting point

could have been in early December 1994. Therefore for these species we used temperatures from 1 November 1994 forward to calculate accumulated degree-days.

2.2. Statistical treatment

Sprouting data collected in these experiments were binary (i.e., sprouted versus not sprouted). They were analyzed by linear logistic regression (SAS Institute Inc., 1989). Using the procedure in SAS, we fit the following equation for each species-propagule combination: Proportion sprouted$=\exp^{logit}/1+\exp^{logit}$, where logit$=$Intercept $+$(Coefficient$\times$Degree-day). We also used this procedure to test whether or not adding a term for location (i.e., latitude) to the model improved the equations predictive capabilities. In all cases the co-efficient for this term was not significant (Chi-square test, $p>0.1$) so it was not included in calculation of the final equation. The goodness-of-fit for each equation was evaluated using Hosmer and Lemeshow goodness-of-fit test. The equation's predictive ability was assessed using four indices of rank correlation, c, Somer's D (-1 to 1), Gamma (-1 to 1), and Kendall's Tau-a (-0.5 to 0.5) (SAS Institute Inc., 1989). These coefficients measure the degree of association between equation predictions and observed values. We used the PROBIT procedure in SAS to calculate the accumulated degree-days associated with 50% sprouting for each species.

3. Results

3.1. Sediment temperature

Sediment temperatures varied daily and seasonally. Daily temperature ranges were less in winter and spring and greater during the summer months. The daily variation for the California and Texas experimental sediments is illustrated in Fig. 1. Sediments warmed slightly earlier in the Texas experiment than in California experiment, reflecting latitudinal differences in climate.

3.2. Propagule emergence

There were clear differences in emergence among the five propagule types examined in the California experiment (Fig. 2). In California, *P. pectinatus* tubers, *P. nodosus* winter buds, and axillary turions formed by monoecious *H. verticillata* began to sprout at about the same time in mid-February 1995. Sprouting by monoecious *H. verticillata* axillary turions increased monotonically and continued through late May. Similarly, *P. nodosus* winter bud sprouting continued through mid-July. *P. pectinatus* tubers displayed a different pattern. *P. pectinatus* sprouting increased sharply through mid-April, leveled off slightly until late June and began to increase sharply again. *P. pectinatus* tubers continued to sprout until early September. Monoecious *H. verticillata* tubers did not begin to emerge until mid-March. The proportion of monoecious *H. verticillata* tubers sprouting was greater than 95% by the first of August. In the California experiment, dioecious *H. verticillata* tubers did not begin to
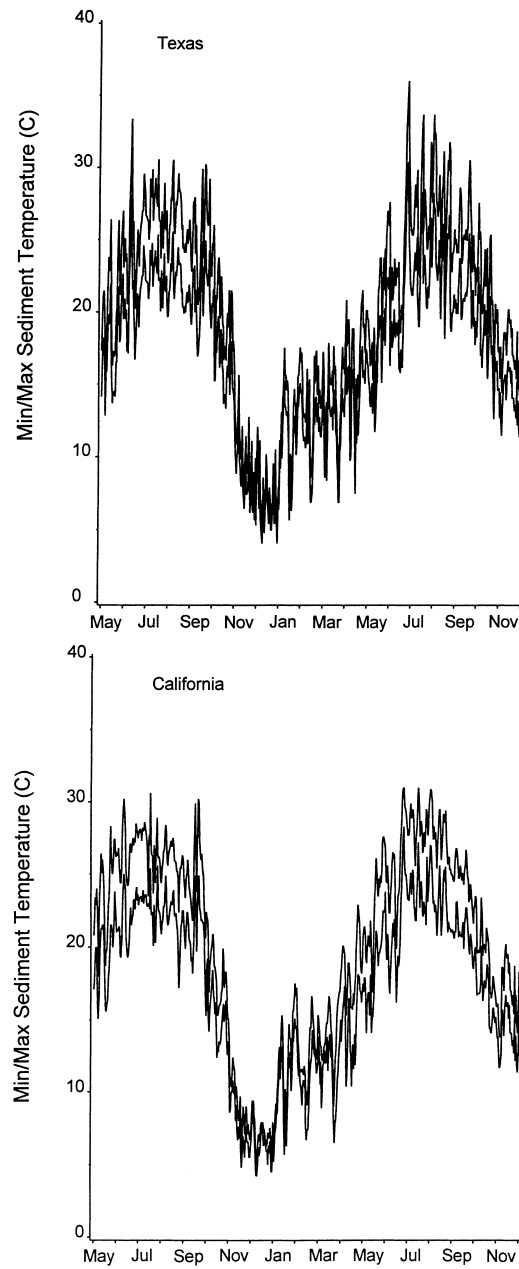
Fig. 1. Daily minimum and maximum sediment temperature (C) for tanks in Lewisville, Texas and Davis, California during 1994 and 1995.
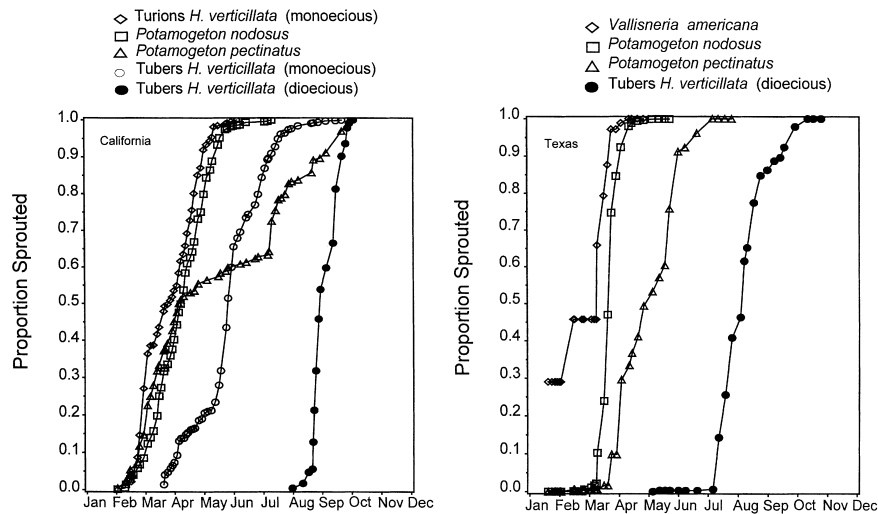
Fig. 2. Cumulative proportion sprouted vs time for species-propagule types grown in cultures at Davis, California and Lewisville, Texas. Cumulative proportion sprouted calculated by dividing the cumulative number that had emerged by a particular sample time by the total number that emerged during the course of the experiment, for each species-propagule type.

emerge until mid-August. Sprouting by dioecious *H. verticillata* tubers was maximal by October. The total number of vegetative structures that sprouted in both California and Texas are shown in Table 2.

The distinct separations of emergence times for propagules in the Texas experiment were similar to those observed in California (Fig. 2). *V. americana* tubers were the earliest to emerge in Texas. Nearly 20% had emerged by the first sampling date. Emergence continued through early April. Similar to California observations, both *P. nodosus* winter buds and *P. pectinatus* tubers began to emerge in mid-February. All of the *P. nodosus* winter buds had emerged by mid-April. Emergence of *P. pectinatus* tubers occurred at a slower rate and did

Table 2
Number of vegetative propagules that sprouted and did not sprout in plant cultures during 1995 at Davis, California and Lewisville, Texas[a]

Location	Species	Number sprouted	Number not sprouted	Percent sprouted
California	*P. nodosus* winter buds	622	0	100
	P. pectinatus tubers	204	1025	17
	H.verticillata tubers (M)	766	1769	30
	H. verticillata turions (M)	643	0	100
	H. verticillata tubers (D)	236	12	95
Texas	*P. nodosus* winter buds	1158	0	100
	P. pectinatus tubers	182	40	82
	V. americana tubers	179	0	100
	H. verticillata tubers (D)	328	77	81

[a] The letter 'D' indicates plants of the dioecious biotype and 'M' plants of the monoecious biotype.
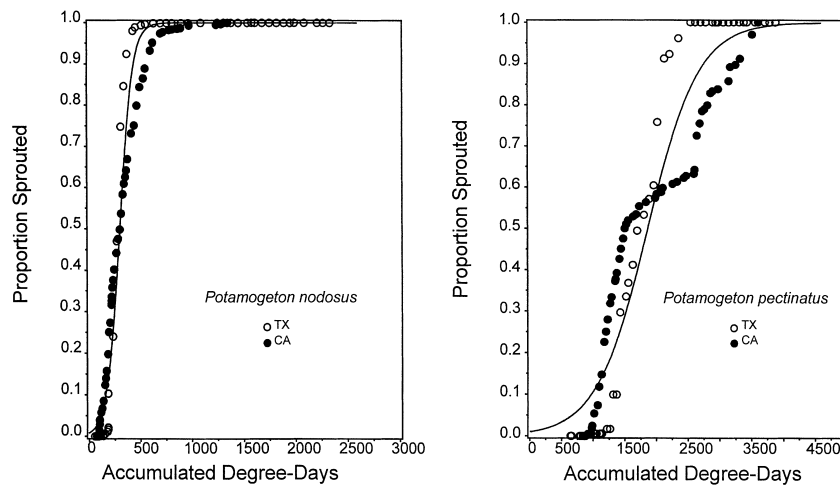
Fig. 3. Cumulative proportion sprouted as a function of accumulated degree-days for *Potamogeton nodosus* and *Potamogeton pectinatus* at Davis, California and Lewisville, Texas. The lines represent the logistic equations whose parameters are given in Table 3.

not achieve maximal values until early July. *P. pectinatus* emergence in Texas leveled off midway through the emergence period but it was less pronounced than that observed in the California experiment. Dioecious *H. verticillata* tubers were the last to emerge, beginning in early July and continuing through October.

3.3. Degree-days

The relationships between emergence from the sediment and accumulated degree-days are illustrated in Figs. 3–5. The predicted emergence based on fitting a logistic equation to these data are indicated by the solid lines on the graphs. In all cases the goodness-of-fit test and the correlation indices revealed that there was good agreement between the actual data and the equations predictions (Table 3). The parameters for the equations for individual species-propagule types are also listed in Table 3.

4. Discussion

While it has been recognized that temperature is an important determinant in aquatic plant growth and distribution (Barko et al., 1986; Pip, 1989), to our knowledge this is the first attempt to describe the emergence of aquatic plant propagules from the sediment as a function of degree-days. The equations developed for the species studied represent good fits to the data, and provide an underlying explanation for the temporally distinct patterns of emergence for four species (and two biotypes) of aquatic plants. It may also aid in development of growth models for submersed aquatic plants. This information will also be useful in deciding on the timing of management techniques. Ross and Lembi (1985)
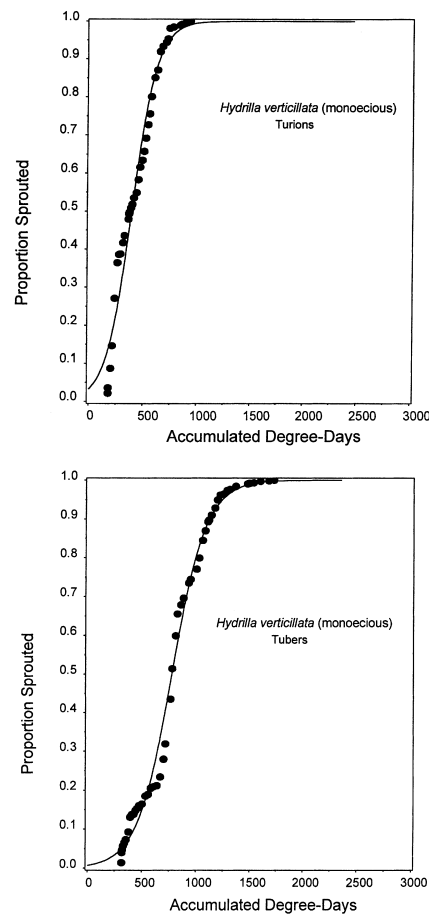
Fig. 4. Cumulative proportion sprouted as a function of accumulated degree-days for monoecious *H. verticillata* tubers, and axillary turions from monoecious *H. verticillata* at Davis, California. The lines represent the logistic equations whose parameters are given in Table 3.

indicate that it is important to identify susceptible growth stages for optimum control of perennial weeds (those that develop from vegetative reproductive structures). They state that in many perennial weeds, the carbohydrate reserves are depleted when the plant has attained one-fourth of its maximum height or is at the early flower bud stage. Accordingly, the plant is most susceptible to removal of the aboveground biomass at this time (Ross and Lembi, 1985). By monitoring sediment temperatures and applying the equations developed here, an aquatic plant manager would be able to estimate the window when the greatest proportion of the population would be most susceptible to management practices designed to remove aboveground biomass. This information may be also useful in other aspects of plant management. For example, management actions taken early in the season may have more effect on recruitment in populations of monoecious *H. verticillata* plants than on those of the dioecious strain. In situations where management is aimed at enhancing growth of
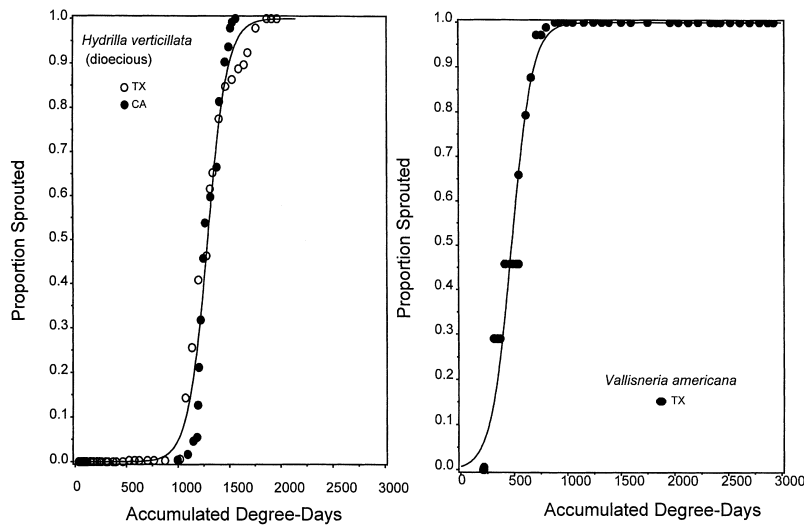
Fig. 5. Cumulative proportion sprouted as a function of accumulated degree-days for tubers from dioecious *H. verticillata*, at Davis, California and Lewisville, Texas and *Vallisneria americana* at Lewisville, Texas. The lines represent the logistic equations whose parameters are given in Table 3.

some species (such as wetlands managed for waterfowl production), this information could be used to identify periods when water level fluctuations should be avoided.

In the present study, a single equation was capable of describing emergence for a given species grown at two locations. This was due to the incorporation of both lower and upper thresholds for propagule sprouting into the calculation of degree-days. Sanderson et al. (1994) related alfalfa (*Medicago sativa* L.) mean stage weight to accumulated degree-days using data from a number of sites, years, and cultivars. They reported that the relationship differed among locations years, seasons, and cultivars and concluded that degree-days would not be a broadly applicable predictor of mean stage weight. However, Sanderson et al. (1994) did not use an upper threshold in their calculation of degree-days. Eliminating upper and lower thresholds may lead to estimates of degree-days which are either too low or too high (Zalom et al., 1983). Depending on temperature differences between locations, this defect may give the appearance of differences between locations, which in reality may be artifacts of the methods of calculation. Thresholds are important in arriving at accurate estimates of degree-days. In the present study we estimated upper and lower thresholds based on published data, but more precise estimates of these parameters for additional aquatic plant species would be useful.

There is good agreement between the emergence patterns and the geographic distribution of these species. For example, *P. nodosus*, *P. pectinatus*, and *V. americana*, which are common at northern latitudes (Pip, 1987; Korschgen and Green, 1988), emerged earlier in the season and had lower degree-day requirements to achieve 50% emergence than dioecious *H. verticillata*, which generally has a more southerly distribution in North American (Netherland, 1997). Interestingly, monoecious *H. verticillata* tubers and turions emerged earlier in the season than dioecious *H. verticillata*. In fact, monoecious *H. verticillata* propagules

Table 3

Analysis of Maximum Likelihood Estimates for logistic regression of propagule sprouting vs degree-days at Davis, California and Lewisville, Texas[a]

Species	Variable	DF	Parameter estimate	Standard error	Wald Chi-square	Pr> Chi-square	Degree-days to 50% sprouted[b]	Somers' D.	Gamma	Tau-a	c	Hosmer and Lemeshow goodness-of-fit test
P. nodosus	Intercept	1	−4.7625	0.0375	16162	0.0001						
	Coefficient	1	0.0160	0.000132	14548	0.0001	298	0.95	0.95	0.45	0.98	0.0001
V. americana	Intercept	1	−4.8461	0.1291	1409	0.0001						
	Coefficient	1	0.0109	0.000299	1325	0.0001	445	0.92	0.93	0.38	0.96	0.0001
P. pectinatus	Intercept	1	−4.6144	0.0603	5847	0.0001						
	Coefficient	1	0.00247	0.000032	5847	0.0001	1865	0.82	0.83	0.41	0.91	0.0001
H. verticillata	Intercept	1	−3.3995	0.0516	4332	0.0001						
Turion (monoecious)	Coefficient	1	0.00864	0.000117	5431	0.0001	393	0.70	0.71	0.33	0.85	0.0001
H. verticillata	Intercept	1	−4.9273	0.0475	10775	0.0001						
Tuber (monoecious)	Coefficient	1	0.00634	0.000059	11402	0.0001	777	0.83	0.84	0.42	0.92	0.0001
H. verticillata	Intercept	1	−13.3157	0.2649	2526	0.0001						
Tuber (dioecious)	Coefficient	1	0.0103	0.000203	2572	0.0001	1295	0.95	0.95	0.40	0.97	0.0001

[a] The fitted equation is: Proportion sprouted=exp(logit)/(1+(exp(logit))), where logit=Intercept +(Coefficient×Degree-day).

[b] Upper and lower thresholds are not the same for all species.

behaved more like those of *P. nodosus*, *P. pectinatus*, and *V. americana*, suggesting the possibility that monoecious *H. verticillata* may be better suited to invade aquatic plant communities in the northern U.S. (Spencer and Anderson, 1986; McFarland and Barko, 1987). (This characteristic seems more significant since McFarland and Barko (1999) have shown that both strains are equally tolerant of high temperatures in other physiological parameters.) Indeed, the northernmost population of *H. verticillata* known in North America (near Olympia, Washington) are plants of the monoecious biotype.

The results of this study also raise questions about the importance of tuber production as an overwintering strategy for dioecious *H. verticillata*. It appears that some habitats (at northern latitudes) may not provide sufficient degree-days to support extensive sprouting of dioecious *H. verticillata* tubers, raising the possibility that spring growth in these systems is from root crowns or evergreen shoots. In such systems, dioecious *H. verticillata* may propagate more from fragments in a manner similar to *Elodea* or *Egeria*.

The information reported here should also aid in understanding competitive relationships among aquatic plant species. For example, the outcome of competitive interactions may be influenced by the timing of emergence, which may offset other apparent advantages in the ability to capture resources (Firbank and Watkinson, 1985).

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