Hydrothermal and thermal time models for the invasive grass, *Arundo donax*

Anthony Graziani, Scott J. Steinmaus

Biological Sciences Department, California Polytechnic State University, 1 Grand Avenue, San Luis Obispo, CA 93407, USA

ABSTRACT

Controlled laboratory and field experiments were performed to determine the developmental response to temperature and moisture of *Arundo donax*, a riparian invasive grass and potential bioenergy crop. A logistic function was parameterized and used to predict thermal times to sprouting and the nine-leaf stage. Consistent estimates of the base temperature (T_b) and base water potential (ψ_b) below which development ceases were obtained from various statistical and mathematical analyses. Estimates of T_b and ψ_b were $12.7 \pm 1.7\,°C$ and -1.56 ± 0.43 MPa, respectively, for the median fraction of sprouting rhizomes. Median hydrothermal time to sprouting was 124.1 MPa °Cd under laboratory conditions and median thermal times, or degree-day (°Cd), to sprouting and nine-leaf stage was estimated to be 94 and 129 °Cd under field conditions, respectively. A degree-day is defined as one day (24 h) spent one degree above T_b. Results demonstrated that thermal time alone is sufficient to accurately predict time to sprouting under field conditions. Further, there may be a fixed moisture threshold of about 6% volumetric water content above which sprouting rate was constant. This threshold corresponded very closely to the -1.5 MPa for ψ_b that was estimated under laboratory conditions for the soil typically infested by *A. donax*. This information is crucial for assessing risk of invasive spread for *A. donax*.

1. Introduction

Predicting invasive potential is the first step to prevent plant invasions, which is the most cost-effective management strategy. Models predicting plant invasivity and locations most susceptible to invasion are powerful tools used to combat the spread of invasive plants (Rejmánek, 2000). At the same time these predictive models are useful in determining the best locations to grow an exotic species for desirable purposes such as biomass for alternative fuel production, soil stabilization, or water and soil remediation (Cosentino et al., 2006; Ovez et al., 2006). Climate often regulates plant distribution and abundance, and therefore, the probability of growth and invasive success (Woodward, 1987). If climate is not conducive to growth then other abiotic and biotic factors that might otherwise regulate development are inconsequential. Temperature and moisture availability are the two most important climate factors defining a species ecological niche. Models based on these two factors have been used to accurately predict such phenological events as seed germination, flowering, and emergence from vegetative structures following winter dormancy (Angus et al., 1981; Bradford, 1995; Holt and Orcutt, 1996; Satorre et al., 1996; Rosales-Robles et al., 2003).

One such model, the hydrothermal time model, combines the thermal time model, based on heat units or degree-days, and an analogous model, the hydrotime model (Gummerson, 1986; Bradford, 1995). These models are based on the idea that development is determined by the accumulation of units, or time spent, in excess of a base temperature, T_b, and base moisture, ψ_b (Gummerson, 1986; Alvarado and Bradford, 2002). The parameters, T_b and ψ_b, are the temperature and water potential below which development ceases and above which development increases, respectively. The number of units required to reach a particular stage of development is referred to as the hydrothermal time constant and can be used by biological modelers to predict when a species will be at a particular phenological stage in a region where temperature and moisture levels are known. Although this model has successfully been used to describe seed germination times across a range of suboptimal temperatures and water potentials (Gummerson, 1986; Finch-Savage and Phelps, 1993), other studies have found it unsatisfactory for certain species due to a significant interaction between temperature and moisture effects (Kebreab and Murdoch, 1999).

The parameters, T_b and ψ_b, are usually estimated from data collected under controlled laboratory conditions. However, field trials should be used to validate laboratory estimates to insure

biologically meaningful estimates by incorporating more of the complexity and natural variation inherent in the field (Angus et al., 1981). The parameter, T_b, is often estimated as the x-intercept of germination rate regressed on suboptimum temperatures. This linear method was found to be suitable to defining T_b for a range of annual crops (Angus et al., 1981) and perennial weeds dependent on vegetative sprouting (Holt and Orcutt, 1996). In comparing four conventional approaches used to determine T_b, Steinmaus et al. (2000) concluded that the reciprocal time to median germination approach to be the most robust in terms of linear response and minimal variation associated with the x-intercept. That study also considered two alternative methods, a repeated probit analysis and a series of mathematical approaches. All proved to be sufficient although the mathematical approaches tended to overestimate T_b by 2–3 °C compared to the other indices. The strength of these alternative methods is that extrapolation is not required to estimate T_b (Steinmaus et al., 2000).

Arundo donax L. (giant reed) is a highly aggressive non-native perennial C_3 grass that invades riparian habitats throughout California and southwestern states (Bell, 1997). Once established in California, it is capable of displacing native vegetation and altering the fire cycle and hydrology within natural riparian ecosystems and flood control channels (Bell, 1997; Dudley, 2000). This Indian subcontinent native is also being grown for its capacity to accumulate biomass quickly for the purpose of alternative fuel production (Lewandowski et al., 2003; Cosentino et al., 2006). Research has also shown *A. donax* to be a cost-effective candidate for phytoremediation of nitrate or heavy metal contaminated water and soil (Ovez et al., 2006; Tzanakakis et al., 2007). *Arundo donax* is believed to spread solely by clonal propagation primarily by rhizome fragmentation, as it is not known to produce viable seeds in North America (Bell, 1997; Dudley, 2000).

The objective of this study was to determine the critical suboptimal temperature and moisture requirements for sprouting and development of *A. donax* rhizomes. Secondly, these values were used to determine the hydrothermal and thermal time required for rhizome development under field conditions which are necessary parameters in models of climatic suitability of *A. donax* in invaded or cultivated locations. We hypothesized that *A. donax* rhizome development can be described using methods conventionally used to parameterize seed response to moisture and temperature, i.e. hydrothermal time, and thus would exhibit a graded response to suprathreshold temperature and moisture.

2. Materials and methods

2.1. Lab study

Arundo donax rhizomes were collected from multiple populations throughout San Luis Obispo County, CA, USA. Exhumed rhizomes with at least one existing tiller were stored at 4 °C no more than a week prior to the beginning of each trial conducted on the California Polytechnic State University, San Luis Obispo campus. Rhizomes were cleaned of soil debris and pruned of extraneous tillers and roots. The initial covariates recorded were mass, length, width, number of nodes, number of lateral and terminal buds. The effect of these covariates on time to sprouting was assessed using the proportional hazards procedure in SAS (Version 9.1, SAS Institute, Cary, NC, USA). The mean initial mass and length for rhizome segments were 158.5 ± 33.1 g and 12.4 ± 3.4 cm, respectively. Twelve trials were initiated between December 2004 and November 2006. Rhizomes were placed in isothermal incubators (Model 307C, Fisher Scientific International, Inc., Pittsburg, PA, USA; Model 125L, Conviron, Winnipeg, Manitoba, Canada) held at constant temperatures from 10 to 35 °C (± 0.5 °C)

with a 16 h light:8 h dark photoperiod. Each chamber contained three shelves, each with four moisture conditions. Polyethylene glycol (PEG 8000, Fisher Scientific, www.fishersci.com) and deionized water were used to simulate differing moisture conditions (0 to -1.40 MPa) based on the equation from Michel (1983) and verified separately to within ± 0.01 MPa of their target osmotic level by a vapor pressure osmometer (VAPRO 5520, Wescor, www.wescor.com). Rhizomes were placed in plastic containers filled with 380 ml of the various PEG solutions. Rhizomes were observed daily and time to sprouting, defined as 2 cm of exposed new growth, was recorded.

2.2. Field study

Rhizomes were collected and prepared as described for the lab trials. Six trials, each lasting about 3 months, were conducted on the California Polytechnic State University, San Luis Obispo campus research farm (35.3012N:120.6708W) beginning July 2004 and ending December 2006. The experimental design was a completely randomized block design replicated four times with three moisture conditions: field capacity, 50% field capacity, and 25% field capacity. Each replicate was established in a 89 cm diameter by 18 cm deep plastic basin, filled with a sandy-loam silt mix collected from Chorro and Pennington Creeks (35.3306N:120.7605W) where *A. donax* was invasive. Each replicate had 10 rhizomes planted 1–4 cm below the surface. An automated micro-sprinkler system was used to maintain the prescribed soil moisture levels. Time to sprouting (soil emergence) and the time to each tillering stage up to nine tillers were recorded for each rhizome two to three times per week. Volumetric water content was measured on these days with a water content sensor based on time-domain reflectometry (CS620, Campbell Scientific, Inc., Logan, UT, USA). Average volumetric water content across all field trials was 12.75 ± 2.64, 10.07 ± 1.64, and 7.32 ± 1.83 for the high, medium, and low treatments, respectively. Temperature was recorded on a micrologger using nickel–constantine thermocouples at 10 and 5 cm below and 5 cm above the soil surface (CR23X, Campbell Scientific, Inc., Logan, UT, USA).

2.3. Data analysis

To determine the base temperature, T_b, and base moisture, ψ_b, statistical and mathematical approaches were used as described in Steinmaus et al. (2000). These methods have been tested and utilized to develop seed germination models but few studies have used them to parameterize rhizome sprouting models. The statistical approach involved calculating the reciprocal time to median sprouting (RTMS) for each temperature and moisture combination. The number of days that had elapsed when 50% of the viable rhizomes had emerged was considered the median value. Typically, there is less variation in developmental time associated with the median fraction of a population than with any other fraction (Dahal et al., 1990; Steinmaus et al., 2000). These median values were plotted against suboptimal temperature or water potential and T_b or ψ_b was determined by solving for the x-intercept from the best-fit linear regression equation. The standard error of the x-intercept, S.E.$_{x\text{-int}}$, was determined extracting values from the variance–covariance matrix for the estimated slope, b, and estimated y-intercept, a, and was computed as

$$\text{S.E.}_{x\text{-int}} = \sqrt{\frac{V_{aa}}{b^2} - \frac{2aV_{ab}}{b^3} + \frac{a^2 V_{bb}}{b^4}} \qquad (1)$$

where V_{aa} is the variance associated with the y-intercept estimate, V_{bb} is the variance associated with the slope estimate, and V_{ab} is their covariance (Steinmaus et al., 2000). To test the hypothesis

that T_b did not vary with water potential, lines were fitted and T_b was calculated separately for data from 0 and -0.20 MPa treatments (Garcia-Huidobro et al., 1982; Covell et al., 1986; Kebreab and Murdoch, 1999). Similarly, ψ_b and S.E.$_{x\text{-int}}$ were estimated separately for the 28, 20, and 18 °C treatments.

Secondly, a repeated probit analysis was used to estimate T_b using laboratory data from the 0 MPa condition, as this was assumed optimal and least prone to error for estimating the parameter. Cumulative percentage of sprouting rhizomes at each temperature level was transformed to a normal equivalent deviate (NED) and these values were pooled and regressed against a function of thermal time as

$$\text{NED}(g) = a + b[\ln(T - T_b)t_g] \tag{2}$$

where a and b are the intercept and slope coefficients, respectively, T is the actual temperature (°C), and t_g is the time in days to sprouting for percentage, g. Base temperature, T_b, was estimated by varying T_b in Eq. (2) until the best fit was obtained by minimizing the mean square residual term for the regression of Eq. (2) (Steinmaus et al., 2000).

The mathematical approach involved three formulae based on least standard deviation in degree-days (Eq. (3)), least coefficient of variation in degree-days (Eq. (4)), and a regression coefficient (Eq. (5)). They were used to estimate $\psi_b(50)$ for each trial, i, by

$$\psi_b = \frac{\sum_{i=1}^{n} \psi_i t_i \sum_{i=1}^{n} t_i - n \sum_{i=1}^{n} t_i^2 \psi_i}{\left(\sum_{i=1}^{n} t_2\right)^2 - n \sum_{i=1}^{n} t_i^2} \tag{3}$$

$$\psi_b = \frac{\sum_{i=1}^{n} \psi_i t_i^2 \sum_{i=1}^{n} \psi_i t_i - \sum_{i=1}^{n} t_i \sum_{i=1}^{n} \psi_i^2 t_i^2}{\sum_{i=1}^{n} t_i^2 \sum_{i=1}^{n} \psi_i t_i - \sum_{i=1}^{n} t_i \sum_{i=1}^{n} \psi_i t_i^2} \tag{4}$$

$$\psi_b = \frac{\sum_{i=1}^{n} \psi_i \sum_{i=1}^{n} t_i \psi_i - n \sum_{i=1}^{n} t_i \psi_i^2}{\sum_{i=1}^{n} t_i \sum_{i=1}^{n} \psi_i - n \sum_{i=1}^{n} t_i \psi_i} \tag{5}$$

where t_i was the median time to sprouting, ψ_i is water potential experienced for rhizomes in the 28 °C treatment, and n equals the number of lab trials. To estimate T_b, the temperature experienced for rhizomes in the 0 MPa treatment was substituted for ψ_i (Steinmaus et al., 2000). Estimates of T_b were also made from the field study where the mean of median times to emergence of viable rhizomes for each moisture level was used as t_i in Eqs. (3)–(5). The mean temperature, T_i, between the start of the trial and the average day of emergence was calculated using daily minimum and maximum temperatures. Data from the high moisture treatment were used because sprouting times were highly variable in the drier treatments.

The strength of this mathematical approach is its simplicity but unfortunately it does not consider the daily variation in temperature inherent in a field study because only the average temperature is used. In order to account for this daily temperature cycling, thermal time (DD) to median sprouting for each trial was calculated using the single sine numerical integration method available on the University of California Integrated Pest Management Project website (Zalom et al., 1983; www.ipm.ucdavis.edu). Daily maximum and minimum temperatures from National Climatic Data Center (NCDC) station #7851 at the Cal Poly campus were used to compute DD. To estimate base temperature, the lower threshold of the integrator was varied and degree-days were calculated for each rhizome from each trial. The lower threshold that simultaneously minimized the coefficient of variation and variance for cumulative degree-day for all the field trials was deemed the best estimate of T_b by this method.

The T_b and $\psi_b(50)$ estimates from the lab data averaged across all methods were used to determine the hydrothermal time, θ_{HT}, required for 50% of the population to sprout estimated as

$$\theta_{HT} = (T - T_b)(\psi - \psi_b(g))t_g \tag{6}$$

where T is the observed temperature, T_b is the base temperature, ψ is the observed water potential, ψ_b is the base water potential, and t_g is the time to germination for population fraction, g (Gummerson, 1986). A base moisture value for each population fraction, $\psi_b(g)$, was estimated so that all population fractions would have a constant hydrothermal time to sprouting in order to satisfy Eq. (6). Population fractions were converted to NED using the NORMSINV function in Microsoft® EXCEL (2003). These values were fitted to a straight line in order to assess the normality of the distribution of base moisture potentials (Bradford, 2002). A best-fit cumulative distribution function for percent of population sprouting, $S(g)$, was

$$S(g) = \frac{a}{1 + (\theta_{TT}/b)^c} \tag{7}$$

where a is the fitted maximum cumulative sprouting percentage, b estimates the thermal time of the most rapid rate of sprouting approximating the median sprouting time, c is a fitting parameter to accommodate a non-symmetrical inflection caused by long sprouting times for the last fractions of the population, and θ_{TT} is thermal time (°Cd) to sprouting for each rhizome. Eq. (7) was also used to describe the thermal time to the nine-leaf stage of development in the field.

3. Results

The covariate, initial number of nodes, was found to have a significant ($p < 0.01$) hazards ratio (1.096) for all pooled rhizomes. Therefore, each additional node on a rhizome increased the likelihood of sprouting by 9.6%. Initial number of nodes were randomly distributed among the rhizomes in all treatments and trials, therefore, the variation associated with this covariate became unaccounted experimental error. Even though the other covariates were correlated with initial node number, they were found not significant at the 5% level. In the lab, rhizome segments sprouted at all temperatures tested, 10–35 °C, although the percentage of segments sprouting decreased at lower temperatures, 8.3 and 16.7% at 10 and 13 °C, respectively. Sprouting rates increased with temperature from 10 to 28 °C above which they began to decline suggesting an optimal temperature of around 28 °C. The T_b estimates were no more than 2 °C different among the approaches (Table 1). The RTMS produced estimates ($\pm$S.E.$_{x\text{-int}}$) of 12.1 ± 2.2 and 14.3 ± 1.0 °C for 0 and -0.20 MPa, respectively (Fig. 1A). The convergence of the RTMS regressions on temperature (Fig. 1A) and $\overline{\text{S.E.}}_{x\text{-int}}$ (Table 1) indicated that T_b did not vary significantly with water potential. In the mathematical approach, Eqs. (3)–(5) estimated T_b to be 12.8, 11.6, and 12.1 °C, respectively, with a mean value of 12.2 °C (Table 1). The repeated NED analysis (Eq. (2)) resulted in a T_b estimate of 13.3 °C, although the linear fit was poor, $r^2 = 0.07$, due to the small sample size for each temperature and moisture combination.

The RTMS method generated $\psi_b(50)$ estimates ($\pm$S.E.$_{x\text{-int}}$) of -1.63 ± 0.29, -2.24 ± 0.79, and -1.22 ± 0.24 MPa at 28, 20, and 18 °C, respectively (Fig. 1B). The mathematical approach produced $\psi_b(50)$ estimates of -1.31, -1.59, and -1.39 MPa, respectively, with a mean value of -1.43 MPa (Table 1). The mathematical approach using field data estimated T_b to be 2–3 °C lower than those estimates from the lab study (Table 1). The iterative approach (DD) using the single sine degree-day numerical integrator estimated T_b to be 12.7 °C, similar to what was determined in the lab.

The base moisture potentials for each population fraction, $\psi_b(g)$, that resulted in a constant hydrothermal time for all

Method	Laboratory				Field
	T_b		ψ_b		T_b
	Treatment (MPa)	Estimate (°C)	Treatment (°C)	Estimate (MPa)	Estimate (°C)
RTMS	0	12.1	28	−1.63	
	−0.20	14.3	20	−2.24	
			18	−1.22	
M1		12.8		−1.31	10.5
M2		11.6		−1.59	10.3
M3		12.1		−1.39	10.4
NED/DD		13.1			12.7
Mean		12.7		−1.56	11.0
$\overline{\text{S.E.}}_{x\text{-int}}$		1.7		0.43	

fractions were approximately normally distributed based on a line fitted to NED versus $\psi_b(g)$ (Fig. 2). Hydrothermal time to median sprouting in the lab, calculated with Eq. (6) using the mean estimates of 12.7 °C and −1.56 MPa for T_b and $\psi_b(50)$, respectively (Table 1), was computed to be 124.1 MPa °Cd. Thermal times to

sprouting for rhizomes in the 0 MPa lab treatment had a computed median value of 70 °Cd (Table 2). Thermal times for these rhizomes in the lab were compared to rhizomes in the high moisture treatments in the field trials, which had a computed median time to sprouting of 90 °Cd (Fig. 3A and Table 2). Thermal time to sprouting had similar median time requirements among the field trials compared across moisture treatments estimated as 90, 92, and 99 °Cd for the high, medium, and low treatments, respectively (Fig. 3 and Table 2). About 40 additional degree-days following sprouting were required under field conditions to attain the nine-leaf stage for a total 129 °Cd from initiation (Fig. 4 and Table 2).

4. Discussion

Rate of sprouting for *A. donax* rhizomes increased in response to an increase in suboptimal temperature and moisture levels. Growth rate increased linearly from T_b to the optimal temperature with the greatest rate at 28 °C and 0 MPa. This agrees with an upper threshold estimate of 30 °C in Spencer and Ksander (2006). The mean T_b estimate from lab data of 12.7 °C was high but within the range of 8–14 °C estimated by Spencer and Ksander (2006). One rhizome segment sprouted after 68 days at 10 °C. This may suggest
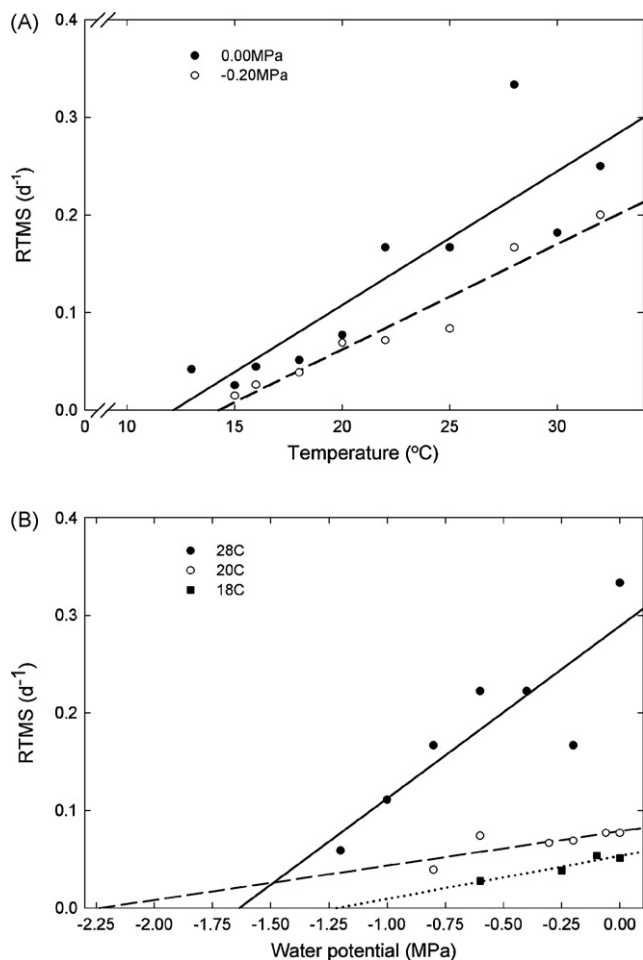

Fig. 1. Reciprocal time to median sprouting (RTMS, d^{-1}) for *A. donax* regressed on temperature (°C) for 0 and −0.20 MPa with coefficients of determination of 0.77 and 0.94, respectively (A). The RTMS regressed on water potential for 28, 20, and 18 °C with coefficients of determination of 0.75, 0.60, and 0.90, respectively (B).
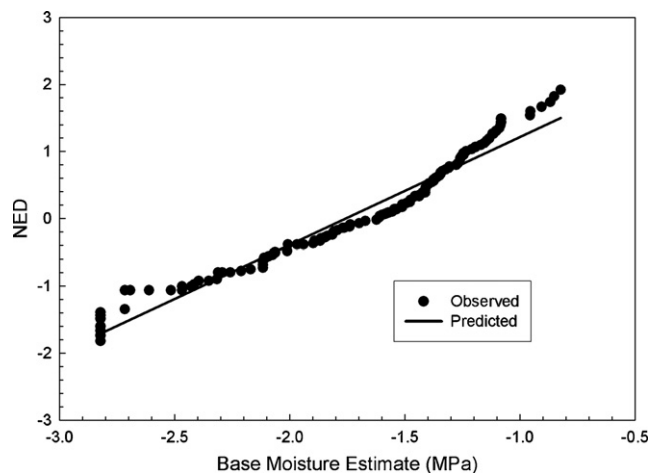

Fig. 2. Base moisture (ψ_b, MPa) estimate for each fraction of the population (normal equivalent deviate, NED). The NEDs are in units of standard deviation and are defined by the standard normal cumulative density function where an NED of zero is the median population fraction. The line (predicted) represents the fitted linear regression equation, NED = 2.82 + 1.61 ψ_b (r^2 = 0.98).

Stage	Data source	Estimate				r^2	Figure(s)
		A	B	C	$\theta(50)$[a]		
Sprouting	Lab						
	0 MPa	158.6 ± 17.8	96.4 ± 9.2	−2.4 ± 0.2	69.8	0.98	Fig. 3
	Field High	104.3 ± 6.8	91.4 ± 3.6	−4.2 ± 0.6	89.5	0.71	Figs. 3–4
	Medium	94.7 ± 4.6	89.6 ± 2.4	−5.1 ± 0.7	91.7	0.70	Fig. 3
	Low	114.7 ± 15.5	107.2 ± 10.2	−3.4 ± 0.7	99.3	0.67	Fig. 3
9-Leaf	High	98.3 ± 5.6	128.6 ± 4.0	−5.2 ± 0.8	129.4	0.73	Fig. 4

Parameter estimates (±S.E.) for the cumulative logistic function $S(g)$ from Eq. (7) for predicting median thermal time requirements of *A. donax* rhizome development to sprouting and the nine-leaf stage (9-leaf) using data from lab trials, from the high (0 MPa) treatment, and field trials at specified moisture levels. Median thermal times, $\theta(50)$, were computed from each fitted function. Parameters were used to generate prediction curves depicted in Figs. 3–4.

[a] degree-days (°Cd).

12.7 °C to be a slight overestimate and the true value to be more in line with the field trial estimates of between 10.3 and 12.7 °C. The data at 10 °C were not considered in the analyses due to this low success and the proximity of this temperature to the presumed actual T_b. Even small fluctuations in temperature above and below the actual T_b for *A. donax* will tend to underestimate that T_b.

The assumption that ψ_b was independent of temperature and T_b was independent of moisture appears reasonable. Unlike the dependencies found by Kebreab and Murdoch (1999) with *Orobanche* seeds, the RTMS estimates of $\psi_b(50)$ in the present study at different temperatures were not significantly different

from each other based on a paired *t*-test at the 5% significance level using $\overline{S.E.}_{x\text{-int}}$ as an error term. The same was true for T_b at different moisture levels.

No prior study was found which assessed the effects of soil–water potential on the development of *A. donax*. Our estimates of base moisture potential for each population fraction, $\psi_b(g)$, were approximately normally distributed around the median value as might be expected for seeds (Bradford, 2002). The $\psi_b(50)$ estimate of −1.56 MPa found here was within the estimates from seed germination studies using crop species which ranged from −1.10 to −1.96 MPa (Gummerson, 1986; Finch-Savage and Phelps, 1993; Kebreab and Murdoch, 1999). In the field trials, 5–6% volumetric water, which is about −1.5 MPa based on moisture release curves for the sandy loam used here (Brady, 1974), seems to be the critical moisture level below which development ceases. Rhizomes kept at this 5–6% moisture level in the dry treatment were unable to sprout whereas those in the moderate moisture treatments with volumetric water content ranging from 7 to 10% had 86% of the rhizomes sprouting. Therefore, 5–6% volumetric water content may be a biologically reasonable estimate of a base threshold in sandy-loam soil typical of the stream banks infested by *A. donax*. Interestingly, contrary to a similar study involving the vegetatively reproducing *Cyperus esculentus* L. and expectations based on the hydrothermal time model, higher moisture levels in the field did not result in a significant decrease in thermal time to sprouting (Wilen et al., 1996). This suggests that *A. donax* rhizomes may be
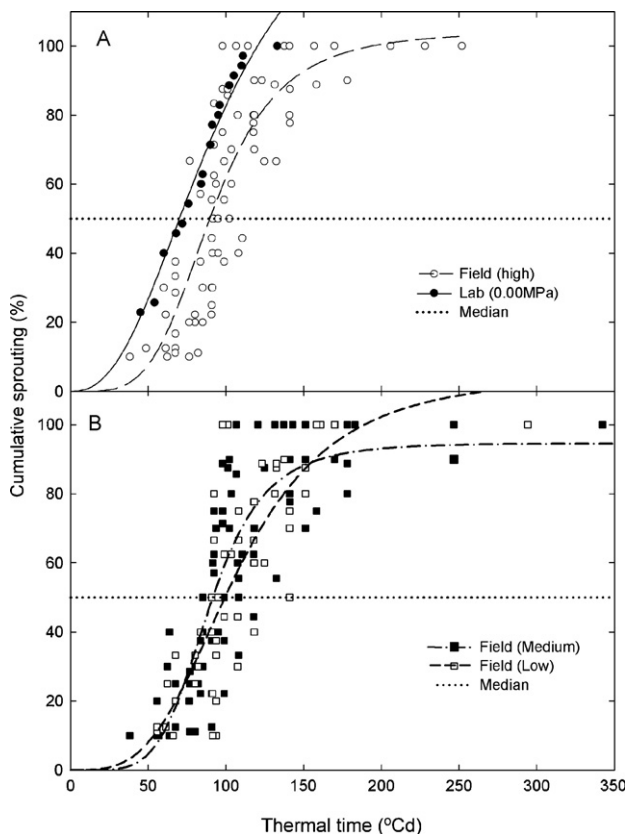

Fig. 3. Thermal time (°Cd) to cumulative sprouting (%) for *A. donax* rhizomes under optimal moisture levels in the lab at 0 MPa and in the high moisture treatment in the field (A). Thermal (DD) time requirements for cumulative sprouting at the medium and low moisture levels from data pooled across all field studies (B). Prediction lines for thermal time were generated using Eq. (7) fitted to observed thermal times with parameter estimates in Table 2. A degree-day (°Cd) is defined as one day (24 h) spent one degree above T_b.

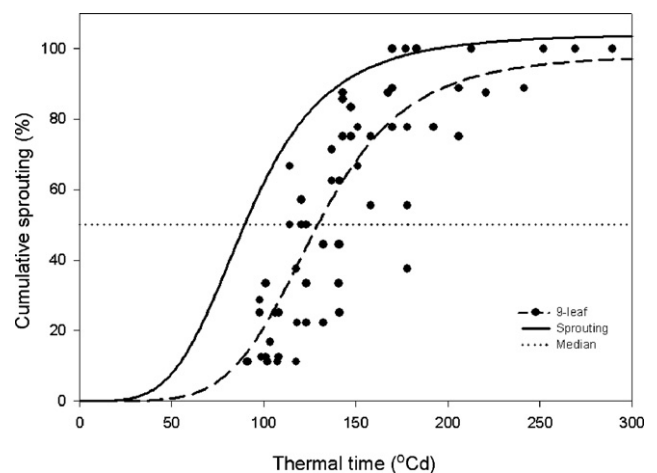**Fig. 4.** Thermal time requirements (DD, °Cd) for cumulative nine-leaf stage for *A. donax* from the field trials. The predicted thermal time for sprouting under high moisture conditions in the field shown for reference. Prediction lines for DD times were generated using Eq. (7) fitted to observed thermal times with parameter estimates in Table 2.

buffered because of their larger size relative to *C. esculentus* tubers against minor fluctuations in soil–water potential above or below ψ_b as might occur at the expanding edge of an invasion under field conditions. Therefore, incorporating a hydrotime component into a model to describe time to sprouting may be unnecessary for predictions at the ecosystem level. The consistency between our field trials provides evidence for thermal time to be a good predictor of emergence when soil moisture exceeds 6% volumetric water content regardless of the timing of the trial. Based on a lower threshold of 12.7 °C sprouting began after around 35 °Cd with about 50% of the rhizomes sprouted by about 90 °Cd with adequate moisture. The difference between the 90 °Cd in the field and 70 °Cd in the lab represents a difference of 4–8 actual days during the typical spring sprouting period in riparian ecosystems. The difference may be an artifact of the fluctuating conditions and other suboptimal factors experienced in the field.

A constant water potential (volumetric water content) could not be maintained in initial attempts for the lab studies where a prescribed amount of water was added to a known volume of soil. The use of PEG to simulate a high-resolution moisture gradient in the lab appeared to be an effective method to assess moisture response. Although PEG 8000 has been successfully used in seed germination studies to induce controlled drought stress (Bradford, 1995; Cheng and Bradford, 1999; Kebreab and Murdoch, 1999), few studies were found involving rhizomes (Harradine, 1982). Time to sprouting increased linearly as water potential decreased revealing a tightly coupled moisture regulatory effect in the lab. Previous studies involving relatively small seeds or plant tissues compared to the rhizomes used in the present study have reported deleterious effects on plant growth as a result of PEG (Verslues et al., 1998). This may be due to the relatively high surface area to volume ratio that seeds have compared to larger rhizomes. PEG may have some detrimental effect on rhizome performance and viability when rhizomes were exposed for extended periods of time. The low temperature trials required up to 2 months for any sprouting to occur. This extended time partially submerged in PEG solution may affect sprouting independent of any temperature effect. While rhizomes in pure water exhibited green healthy looking leaves weeks after sprouting, those in PEG solutions were stunted and chlorotic.

Only one prior study was found in which *A. donax* emergence was described as a function of degree-days (Spencer and Ksander, 2006). Accumulated degree-days to new shoot emergence were calculated for each of six rhizomes using 7 °C as the lower threshold making direct comparisons to the present study difficult. However, using the dates from their initial field trial and the nearest recorded minimum and maximum air temperature we calculated the number of degree-days required to first sprouting using our estimated T_b of 12.7 °C to be 32 °Cd. This is comparable to the 35 °Cd we calculated from our field data which corresponds to within one actual day.

All estimates for T_b and $\psi_b(50)$ and therefore thermal and hydrothermal times were calculated using the median sprout because this population fraction often has the lowest variation in development time (Dahal et al., 1990; Steinmaus et al., 2000). Seed germination studies have found that ψ_b varies normally within a population (Bradford, 2002). We found evidence for a normally distributed ψ_b as a function of population fraction for the rhizomes of *A. donax*. Therefore, using only $\psi_b(50)$ could lead to errors depending on the fraction of the population being considered. Phenotypic variation in germination times for seeds in a common environment may be attributed primarily to genetic variation. However, genetic variation is not likely explanation for the variation in sprouting time for *A. donax*. Clonal propagation is the only known form of reproduction within its non-native range

(Bell, 1997) and, consequently, very little genetic variation exists among *A. donax* populations in California (Ahmad et al., 2008). The variation associated with $\psi_b(g)$ would appear to be attributed to some inherent variation among rhizome fragments due to factors associated with viability and, perhaps, sprouting potential analogous to seed dormancy. Indeed, Decruyenaere and Holt (2001) found time of year of collection to be an important determinate of sprouting and establishment potential for *A. donax* as it is correlated with resource allocation between above and below ground storage organs. The effects of rhizome size on sprouting time or, perhaps, the age of the rhizome may have also contributed to the variation observed in $\psi_b(g)$, which caused the sigmoid-shaped sprouting progression observed in real time.

Calculated T_b, ψ_b, thermal and hydrothermal time are important parameters used in climate matching models such as CLIMEX (Sutherst et al., 1999). These models predict the potential range and success of a species by matching its thermal and moisture requirements for growth to the temperature and moisture levels at a location. This is important when prioritizing the potential threat of invasive plant species or the growth potential of a desired species at a location.

The objective of this study was to determine biologically meaningful estimates of the effects of temperature and moisture on the development of *A. donax*. Ultimately, these climatic parameters will be necessary in developing predictive models to assist with invasive or desirable plant management decisions.

References

Ahmad, R., Liow, P., Spencer, D.F., Jasieniuk, M., 2008. Molecular evidence for a single genetic clone on invasive *Arundo donax* in the United States. Aquat. Bot. 88, 113–120.

Alvarado, V., Bradford, K.J., 2002. A hydrothermal time model explains the cardinal temperatures for seed germination. Plant Cell Environ. 25, 1061–1069.

Angus, J.F., Cunningham, R.B., Moncur, M.W., Mackenzie, D.H., 1981. Phasic development in field crops. I. Thermal response in the seedling phase. Field Crop Res. 3, 365–378.

Bell, G.P., 1997. Ecology and management of *Arundo donax*, and approaches to riparian habitat restoration in southern California. In: Brock, J.H., Wade, M., Pysêk, P., Green, D. (Eds.), Plant Invasions: Studies from North America and Europe. Backhuys Publishers, Leiden, The Netherlands, pp. 103–113.

Bradford, K.J., 1995. Water relations in seed germination. In: Kigel, J., Galili, G. (Eds.), Seed Development and Germination. Marcel Dekker, New York, pp. 351–396.

Bradford, K.J., 2002. Applications of hydrothermal time to quantifying and modeling seed germination and dormancy. Weed Sci. 50, 248–260.

Brady, N.C., 1974. The Nature and Properties of Soils, 8th edition. Macmillan Publishing Co., Inc., New York, p. 86.

Cheng, Z., Bradford, K.J., 1999. Hydrothermal time analysis of tomato seed germination response to priming treatments. J. Exp. Bot. 50, 89–99.

Cosentino, S.L., Copani, V., D'Agosta, G.M., Sanzone, E., Mantineo, M., 2006. First results on evaluation of *Arundo donax* L. clones collected in Southern Italy. Ind. Crop Prod. 23, 212–222.

Covell, S., Ellis, R.H., Roberts, E.H., Summerfield, R.J., 1986. The influence of temperature on seed germination rate in grain legumes. J. Exp. Bot. 37, 705–715.

Dahal, P., Bradford, K.J., Jones, R.A., 1990. Effects of priming and endosperm integrity on seed germination rates of tomato genotypes. J. Exp. Bot. 41, 1431–1439.

Decruyenaere, J.G., Holt, J.S., 2001. Seasonality of clonal propagation in giant reed. Weed Sci. 49, 760–767.

Dudley, T.L., 2000. *Arundo donax* L. In: Bossard, C.C., Randall, J.M., Hoshovsky, M.C. (Eds.), Invasive Plants of California's Wildlands. University of California Press, Berkeley, CA, pp. 53–58.

Finch-Savage, W.E., Phelps, K., 1993. Onion (*Allium cepa* L.) seedling emergence patterns can be explained by the influence of soil temperature and water potential on seed germination. J. Exp. Bot. 44, 407–414.

Garcia-Huidobro, J., Monteith, J.L., Squire, G.R., 1982. Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. & H.). J. Exp. Bot. 33, 288–296.

Gummerson, R.J., 1986. The effect of constant temperature and osmotic potentials on the germination of sugar beet. J. Exp. Bot. 37, 729–741.

Harradine, A.R., 1982. Effect of salinity on germination and growth of *Pennisetum macrourum* in southern Tasmania. J. Appl. Ecol. 19, 273–282.

Holt, J.S., Orcutt, D.R., 1996. Temperature thresholds for bud sprouting in perennial weeds and seed germination in cotton. Weed Sci. 44, 523–533.

Kebreab, E., Murdoch, A.J., 1999. Modelling the effects of water stress and temperature on germination rate of *Orobanche aegyptiaca* seeds. J. Exp. Bot. 50, 655–664.

Lewandowski, I., Scurlock, J.M.O., Lindvall, E., Christou, M., 2003. The development and current status of perennial rhizomatous grasses as energy crops in the US and Europe. Biomass Bioenerg. 25, 335–361.

Michel, B.E., 1983. Evaluation of water potential of solutions of polyethylene glycol 8000 both in the absence and presence of other solutes. Plant Physiol. 72, 66–70.

Ovez, E., Ozgen, S., Yuksel, M., 2006. Biological denitrification in drinking water using *Glycyrrhiza glabra* and *Arundo donax* as the carbon source. Process Biochem. 41, 1539–1544.

Rejmánek, M., 2000. Invasive plants: approaches and predictions. Austral. Ecol. 25, 497–506.

Rosales-Robles, E., Chandler, J.M., Wu, H., Senseman, S.A., Salinas-Garcia, J., 2003. A model to predict the influence of temperature on rhizome johnsongrass (*Sorghum halepense*) development. Weed Sci. 51, 356–362.

Satorre, E.H., Rizzo, F.A., Arias, S.P., 1996. The effect of temperature on sprouting and early establishment of *Cynodon dactylon*. Weed Res. 36, 431–440.

Spencer, D.F., Ksander, G.G., 2006. Estimating *Arundo donax* ramet recruitment using degree-day based equations. Aquat. Bot. 85, 282–288.

Steinmaus, S.J., Prather, T.S., Holt, J.S., 2000. Estimation of base temperatures for nine weed species. J. Exp. Bot. 51, 275–286.

Sutherst, R.W., Maywald, G.F., Yonow, T., Stevens, P.M., 1999. CLIMEX. Predicting the effects of climate on plants and animals.In: User Guide. CSIRO Publishing, Melbourne, Australia.

Tzanakakis, V.E., Paranychianakis, N.V., Angelakis, A.N., 2007. Performance of slow rate systems for treatment of domestic wastewater. Water Sci. Technol. 55, 139–147.

Verslues, P.E., Ober, E.S., Sharp, R.E., 1998. Root growth and oxygen relations at low water potentials. Impact of oxygen availability in polyethylene glycol solutions. Plant Physiol. 116, 1403–1412.

Wilen, C.A., Holt, J.S., McCloskey, W.B., 1996. Effects of soil moisture on observed and predicted yellow nutsedge (*Cyperus esculentus* L.) emergence. Weed Sci. 44, 890–896.

Woodward, F.I., 1987. Climate and Plant Distributions. Cambridge University Press, Cambridge.

Zalom, F.G., Goodell, P.B., Wilson, L.T., Barnett, W.W., Bentley, W.J., 1983. Degree-Days: The Calculation and Use of Heat Units in Pest Management. University of California, Division of Agriculture and Natural Resources Leaflet 21373.