

1994

Decline and restoration of *Vallisneria americana* in the Upper Mississippi River

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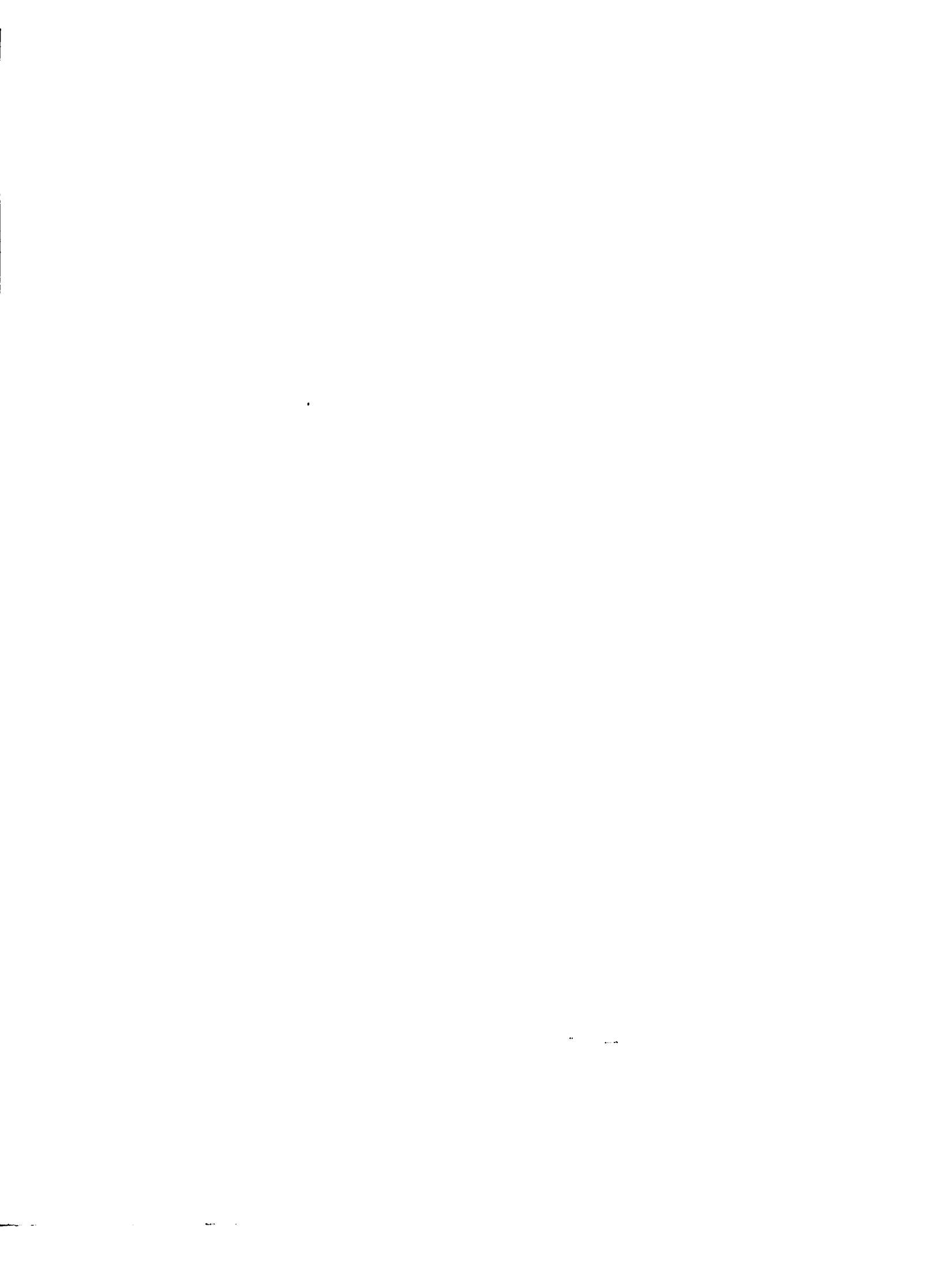
**Decline and restoration of *Vallisneria americana* in the upper
Mississippi River**

Kimber, Anne, Ph.D.

Iowa State University, 1994

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**Decline and restoration of *Vallisneria americana* in the
Upper Mississippi River**

by

Anne Kimber

**A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of the
Requirements for the Degree of
DOCTOR OF PHILOSOPHY**

Department: Botany
Interdepartmental Major: Ecology and Evolutionary Biology

Approved:

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In Charge of Major Work

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For the Interdepartmental Major

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For the Major Department ✓

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For the Graduate College

**Iowa State University
Ames, Iowa**

1994

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GENERAL INTRODUCTION

The Upper Mississippi River and its watershed have been extensively altered by European settlement since 1824 (GREAT, 1980, Fremling and Claflin, 1984). The most significant alteration has been the creation of a 9-foot navigation channel and construction of 29 locks and dams in the 1930s, which resulted in the River becoming a series of interconnected reservoirs with water elevations and flows controlled by the U.S. Army Corps of Engineers. Marshes and floodplain forests bordering the river were inundated as the locks and dams were completed, creating shallow backwater lakes.

Submersed aquatic vegetation has since grown abundantly in many of these pools, stabilizing sediments and providing food and habitat for invertebrates, fish and waterfowl (Sparks, 1984). Since the 1940's one of the backwater lakes in particular, Lake Onalaska (Pool 7, River mile 702.5 to 714.3) had supported abundant populations of wild celery, or *Vallisneria americana* (Korschgen, unpublished data). The abundance of *V. americana*, however, has declined since 1988.

Vallisneria americana Michx. (Hydrocharitaceae) is a dioecious submersed plant that grows from basal rosettes, producing long, flexible, strap leaves (Wilder, 1974, Lowden, 1982). Plants reproduce vegetatively by stolons and buds during the summer and, towards the end of summer, produce tubers. These tubers are largely storage organs that provide a high-energy source for growth in the following spring. *Vallisneria* flowers in the Upper Mississippi River (Korschgen, pers. comm.), providing a classic example of hydrophilous pollination, in which free-floating male flowers fall into female flowers (Wylie, 1917, Cox and Knox, 1989). Seed set commonly occurs in *Vallisneria* in the Upper Mississippi River, but seedlings are rarely observed (Korschgen, pers. comm.). Rather, populations persist by means of overwintering tubers. Although tubers are favored, all parts of the *Vallisneria* plant are eaten by waterfowl (McAtee, 1917), especially by canvasback ducks (*Aythya valisineria*). As habitats deteriorated in the eastern U.S. in the 1960's and 1970's, canvasbacks increasingly migrated to *Vallisneria* beds on the Upper Mississippi River, to the extent that during fall migration, 75% of canvasbacks from the eastern flyways fed on tubers and benthic invertebrates on the

Upper Mississippi River, and especially on Pool 7, Lake Onalaska (Korschgen and Green, 1988).

In spite of grazing pressure from waterfowl, populations of *Vallisneria* appeared stable (Korschgen, unpublished data) until a precipitous decline following a drought in the summer of 1988. During the drought, flow rates at Lock and Dam 7 fell to 6,500 cubic ft/s (U.S. Army Corps of Engineers) compared with a typical flow rate of 26,000 cfs. Water quality measurements in Pool 5 (Weaver Bottoms) showed that water temperatures reached record highs, hydraulic residence times in the backwaters increased, light penetration decreased as blooms of cyanobacteria developed, and dissolved oxygen concentrations dropped (Sullivan, 1991). In years following the drought, light penetration has been low due to increased algal blooms and suspended sediment concentrations (Sullivan, 1991, Owens, 1993) and *Vallisneria* has not reestablished itself in areas where it formerly grew.

Vallisneria has been a common component of the submersed aquatic plant communities of eastern North America. Its decline in the Upper Mississippi River is perhaps the most recent in a series of declines that have taken place this century including those in the Chesapeake Bay (Chamberlain, 1948, Bayley et al., 1978, Davis and Brinson, 1980) and Potomac River (Haramis and Carter, 1983, Carter et al., 1985), the Detroit River (Hunt, 1963, Schloesser and Manny, 1989), the Illinois River (Mills et al., 1966, Sparks, 1984), and Lake Mendota (Lind and Cottam, 1969). The causes of decline have been most commonly linked to light limitation from increasing epiphytic and filamentous algal blooms resulting from increasing nutrient input and from increased suspended sediment from watershed erosion (Phillips et al., 1978, Davis, 1985, Carter and Rybicki, 1985).

Submersed aquatic plants like *Vallisneria* are inherently shade-tolerant (Sand-Jensen, 1989), having low light compensation points. Numerous studies have examined relationships between light penetration and the lower depth limits of both freshwater and marine submersed plants; the maximal depth at which plants can grow has been reported to be from 5% to 16% of ambient surface light (Spence, 1975, Sheldon and Boylen,

1977, Carter and Rybicki, 1986, Bulthuis, 1983b). Reproduction may require greater light, however.

The optimum temperature for photosynthesis in *Vallisneria* has been reported to be 32.5 C, at saturating light levels (Titus and Adams, 1979). However, the effects of high temperatures on photosynthesis at low light levels have not been described for this species. For seagrasses, high summer water temperatures result in decreased net photosynthesis (Bulthuis, 1983a, Wetzel and Penhale, 1983, Marsh et al., 1986) and may have contributed to seagrass declines.

Following the loss of *Vallisneria* turbidity has been high in backwaters (Sullivan, 1991, Owens, 1993), possibly due to wind and navigation-generated resuspension of unconsolidated sediment. There has been continuing interest in restoring *Vallisneria* to the Upper Mississippi River, since in addition to providing food for waterfowl, it stabilizes sediments and provides habitat for invertebrates and fish. For successful restoration, the minimum light conditions required for establishment, growth and especially, tuber production by local *Vallisneria* ecotypes need to be known both for adult plants and for seedlings, since it is possible that revegetation could occur from the seed bank if a suitable seed bank is present, as well as from planted tubers. While requirements for submersed aquatic seed germination have been investigated (Muenscher, 1936, Choudhuri, 1966, van Wijk, 1989), and there have been studies of the species composition of submersed seed banks (Haag, 1983, Kautsky, 1989, Rogers and Breen, 1980), the light requirements for seed germination and for seedlings to grow and produce seeds and/or tubers are generally unknown.

Explanation of the Dissertation Format

The dissertation consists of two papers written for submission to journals, describing studies designed to determine the minimum seasonal light requirements for *Vallisneria* to grow and produce tubers. The first paper, will be submitted to the journal *Ecology*. Anne Kimber will be first author; and A.G. van der Valk will be coauthor. This study consists of a field transplant study, a pond study and a series of laboratory measurements of photosynthesis and respiration.

In the field study, *Vallisneria* was grown in Lake Onalaska at two locations and 0.5, 1.0 and 1.5 m depths. At each location ambient terrestrial and underwater light levels were monitored continuously by Owens (1993). Growth and tuber production were examined at the end of the summer.

In the pond study *Vallisneria* was grown from tubers in a pond experiment in which four shade treatments were established using neutral density screens. Within each shade treatment, plants were grown on either lake sediment or lake sediment diluted 1:4 (v:v) with sand. The two sediment treatments were established to test the significance of light versus sediment type on growth, and to provide another estimate of the minimum light levels necessary for tuber production. At light levels lower than the minimum light level, sediment effects were expected to be non-significant. Light and temperature response curves were developed from measurements of net photosynthesis, to determine the effects of increased temperature on photosynthesis. Growth and tuber production of *Vallisneria* in the eight treatments was measured biweekly during the growing season. The minimum seasonal light requirements for survival and for tuber production were estimated, and compared with results from the field transplant experiment. Leaf and tuber nutrient concentrations were compared among the eight treatments to determine the significance of light availability versus sediment type on nutrient uptake. The effects of increasing temperature on respiration, compensation points and net photosynthesis were measured. Whole plant compensation points were estimated using aboveground:belowground biomass ratios and instantaneous compensation points measured at 20, 25 and 30C; these estimates of minimum light requirements were compared with those from growth and tuber production data.

The second paper has been written for submission to the Canadian Journal of Botany. Anne Kimber will be the principal author of this paper; C.E. Korschgen and A.G. van der Valk will be coauthors. This paper describes the submersed plant seed bank study from Lake Onalaska. The species composition and seedling density from 103 sites are described and compared with depth, sediment characteristics and location within the lake. The germination and survivorship of seedlings as a function of light are

described, and the light requirements for tuber production are estimated. Figures 1 and 2 of this paper were reprinted from a PCB contaminants study by Pavlou et al., (1982). Figure 8 was provided by Carl Korschgen, based on unpublished data. All other figures and tables were prepared by Anne Kimber.

The General Summary briefly describes conclusions from each paper. References cited in the General Introduction and General Summary are listed following the General Summary.

PAPER 1
SEASONAL LIGHT REQUIREMENTS
FOR
VALLISNERIA AMERICANA
FROM THE UPPER MISSISSIPPI RIVER

ABSTRACT

Declines in *Vallisneria americana* populations were observed in Pools 5 through 14 of the Upper Mississippi River after a drought in 1988. The combination of high water temperatures and low light levels may have increased respiration rates and decreased net photosynthesis during formation of overwintering tubers. Field transplants and pond experiments were carried out to determine the minimum light requirements, and the sensitivity of light requirements to temperature change, for *Vallisneria americana* in the Upper Mississippi River.

Seasonal minimum light requirements based on plant growth responses at three water depths in Lake Onalaska were estimated to be 9% of surface light. This estimate was confirmed by growing plants from locally collected tubers in lake sediment and sand-amended low fertility lake sediment under four shade regimes (2%, 5%, 9% and 25% of ambient surface light) in outdoor ponds. It was assumed that sediment - light interactions would be significant only at light levels not limiting to growth. Growth and tuber production were measured over the season, and light and temperature response curves were developed from photosynthesis and respiration measurements.

Sediment fertility effects on growth were significant ($\alpha = 0.05$) in the 9 and 25% shade treatments in late summer. Nitrogen and iron may both have been limiting. Tissue nitrogen concentrations were similar in all treatments, but biomass was lower in plants grown in sand sediment at 9 and 25% light treatments. Phosphorus concentrations were similar in leaves grown in 9 and 25% light, and were higher in leaves grown in 2 and 5% light. Iron concentrations were affected by sediment type and light availability and increased in more fertile sediment and in higher light. All tissue nutrient concentrations were above minimum critical concentrations estimated from previous studies, and were within the range of nutrient concentrations previously reported for *Vallisneria*. Tuber nitrogen and phosphorus concentrations were similar among treatments, indicating that in spite of leaf nutrient differences, tubers of similar quality were produced in all treatments.

Instantaneous light compensation points ranged from 8 to 24 $\mu\text{mole photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$

$\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and were affected only by temperature. Net photosynthesis decreased as temperature increased from 20 to 30 C at light levels of $100 \mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ or less. Conversely, at light levels greater than $200 \mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ increasing temperature increased net photosynthesis. These results supported the hypothesis that high water temperatures decreased rather than stimulated *Vallisneria* growth at low light levels. Later in the season, higher water temperatures caused a greater decrease in net photosynthesis at low light levels, indicating that plants may be particularly susceptible to declines in net photosynthesis during the period of tuber formation and the presumed increase in below-ground respiration during tuber formation.

INTRODUCTION

Vallisneria americana, a submersed macrophyte that grows clonally from basal rosettes, has been a common constituent of the submersed aquatic plant community found in rivers and lakes throughout central and eastern North America (Pip, 1979, Carter and Rybicki, 1985, Rybicki and Carter, 1986, Korschgen and Green, 1989). In recent decades *Vallisneria* beds have declined in the Yahara Lakes (Lind and Cottam, 1969) the Detroit River (Hunt, 1963, Schloesser and Manny, 1990), the Chesapeake Bay and Potomac River (Bayley et al., 1978, Haramis and Carter, 1983, Carter et al., 1985), the Illinois River (Mills et al., 1966) and in the Upper Mississippi River (Serie et al., 1983). Declines have been associated with increased nutrient and sediment loads from surrounding watersheds (Carter and Rybicki, 1985, Schloesser and Manny, 1989) and competition from other submersed macrophyte species, especially *Myriophyllum spicatum* (Titus and Adams, 1979).

Although plant growth and distribution is affected by interaction of numerous abiotic and biotic factors, the main cause of these declines has generally been attributed to decreased light availability from increased physical or biogenic turbidity (e.g. Hunt, 1963, Phillips et al., 1978). Increased physical turbidity from sediment decreases light availability for submersed plants, especially rosette forms; increased nutrients in the water column are thought to favor the development of filamentous and epiphytic algae that also shade macrophytes and may ultimately out-compete them for light (Phillips et al., 1978, Twilley et al., 1985). These conditions would be exacerbated for basal-rosette species such as *Vallisneria* that do not concentrate their photosynthetic biomass at the water surface (Titus and Adams, 1979). Although high temperatures stimulate growth in high light levels in greenhouse studies (Madsen and Adams, 1989, Barko and Smart, 1982), high water temperatures have been implicated in declines of seagrasses (Bulthuis, 1987b) and declines in net photosynthesis with increasing temperature have been recorded for seagrasses (Bulthuis, 1983a, b, Wetzel and Penhale, 1983, Marsh et al., 1986).

The recent decline of *Vallisneria* in shallow backwaters of the Upper Mississippi River (from Pool 5 to Pool 19) occurred after a drought in 1988 during which record low

flows, long hydraulic residence times, high water temperatures (27-29 C), high turbidity, low dissolved oxygen and low light availability were recorded in backwaters (U.S. Army Corps of Engineers, 1988, NOAA, 1988, Wisconsin Department of Natural Resources unpublished data, Sullivan, 1991). Few observations of plant beds were recorded during the summer of 1988. However, poor light penetration caused by algal blooms, both planktonic and filamentous, may have been exacerbated by long hydraulic residence times (Sullivan, 1991). In years following the drought, *Vallisneria* has not reestablished itself in areas where it formerly grew and light penetration has been low due to increased algal blooms and resuspended sediments (Sullivan 1991, Owens, 1993).

Vallisneria produces overwintering tubers that enable it to persist from year to year. The tubers are a desirable high-energy food source for waterfowl (Martin and Uhler, 1939, Korschgen and Green, 1988). There has been continuing interest in restoring *Vallisneria* to this system and especially to Lake Onalaska, Pool 7, in part because in recent years up to 75% of the global canvasback (*Aythya valisineria*) population has fed on *Vallisneria* tubers and on fingernail clams in Pool 7 during fall migration (Korschgen et al., 1987).

For successful restoration, the minimum light conditions required for growth and tuber production by local *Vallisneria* ecotypes need to be known. These studies were designed to provide estimates of the seasonal light requirements for *Vallisneria* to produce tubers, and to describe how these light requirements may change due to interactions with other environmental variables, specifically temperature and sediment type. In the field study (Lake Onalaska), plant growth response to ambient light levels was measured using plants in buckets suspended at three depths and at two locations in the lake, where surface and underwater light was measured continuously (Owens, 1993). Using plant growth data coupled with continuous light measurements at each depth, a seasonal light requirement for tuber production could be estimated. The second study (pond study) was designed to examine the relative importance of light availability versus sediment fertility on tuber production, to examine the effects of temperature on respiration and net photosynthesis, and to estimate whole-plant light compensation points based on

instantaneous light compensation points and respiration measurements. Sediment-light interactions were expected to become significant only for plants growing in light exceeding the minimum requirement for tuber production; below these levels, sediment-light interactions were expected to be negligible. If sediment effects were significant only at light levels greater than those estimated to be the minimum required for tuber production, then light availability rather than sediment type would be the primary factor limiting plant growth and tuber production. Temperature increases were expected to increase leaf respiration and instantaneous light compensation points, and decrease net photosynthesis in low light. The effects of higher water temperatures on respiration and compensation points were expected to be more pronounced later in the growing season, as leaf tissue aged and as plants had greater respiratory costs associated with tuber formation.

METHODS

Lake Onalaska Study

In June, 1990, plants were collected from Lake Onalaska. Two plants were planted into each 2-liter bucket filled with local garden top soil. The buckets were suspended from booms in a randomized block design of three replicates each at 0.5, 1.0 and 1.5 m depths. The booms were constructed of reinforced PVC strapped to wood and were oriented North-South at two sites. Site 6H was an exposed site in the northern portion of the lake, and site 8D was a more sheltered site in the southern end (Figure 1). Plants were suspended from booms, rather than transplanted to depths within the lake, to ensure that water depth would remain constant with fluctuating water levels. Booms were deployed on June 27.

The numbers of *Vallisneria* ramets and numbers and lengths of leaves were measured biweekly. Plants were harvested and tuber biomass measured at the end of September (growing season of 94 days). At each of these sites, Owens (1993 and unpublished data) measured the photosynthetic photon flux density at 0.5 m depth continuously. The light data have been recalculated here using extinction coefficients provided by Owens, to determine the percentage of surface light reaching the top of a bucket at each depth.

Pond Study

The pond study was done in two concrete basins (16 m by 31 m) at the U.S. National Biological Survey Fisheries Research Laboratory, located on an island between the Black and Mississippi Rivers near La Crosse, Wisconsin. Each pond ranged in depth from 0.9 m to 1.2 m. Two small submersible aquarium pumps in each pond circulated and aerated water, and the water turnover rate was once every 2.4 days. The source of water was groundwater (average pH 7.7) pumped from a well (depth 23 m) in the Black River alluvial aquifer.

Vallisneria tubers from Pool 4 of the Upper Mississippi River, Lake Pepin, were harvested two weeks before planting. Single tubers (1 to 1.5 g fresh weight) were planted April 26 into 5-quart plastic buckets containing 1 liter of either lake sediment, or

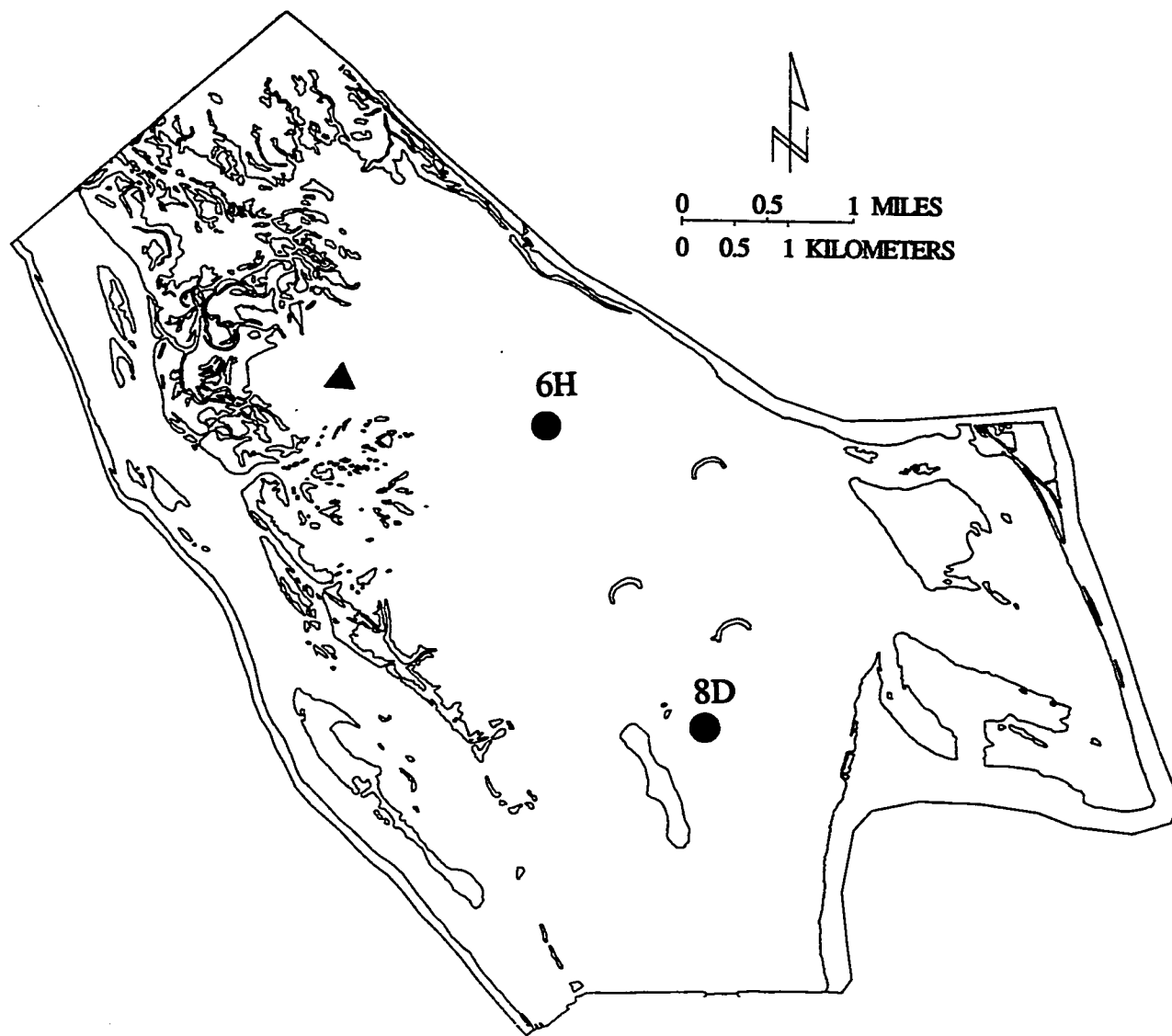


Figure 1. Sampling sites within Lake Onalaska. Circles indicate transplant sites; triangle indicates sediment collection site for pond experiment

sand-amended lake sediment. Lake sediment was collected from Pool 7, Lake Onalaska, Wisconsin from a former *Vallisneria* bed (Figure 1). The sand-amended sediment treatment was created by adding four parts washed builder's sand to one part sediment. Three samples of each sediment treatment were collected for particle size and nutrient analysis.

The experimental design was a split-plot, with two levels of sediment type within each of four levels of light. To create the light levels, black plastic shade screen was stapled to frames to reduce light levels by 65%, 78% and 93%. A fourth treatment had no shade cloth. In the ponds five buckets of each sediment type were placed in each of 48 shade cells (24 cells in each pond), that were arranged in rows (randomized blocks) of four shade treatments each. Each cell was isolated from the next by black plastic side walls that extended down to approximately 20 cm from the bottom of the ponds, to allow water flow among cells and to decrease water temperature differences among light treatments. The tops of the cells were covered with the removable shade cloth frames.

In each pond two LiCor underwater quantum sensors (LiCor Corporation, Lincoln, Nebraska) were installed on PVC pipe brackets at a depth of 35 cm in open areas of the pond between shade cell blocks. Two terrestrial LiCor quantum sensors were used to measure surface photosynthetic photon flux density (PPFD). Sensors were connected to a LiCor datalogger and integrated measurements of terrestrial and underwater PPFD were recorded hourly. Extinction coefficients (k 's) were calculated as averages from 11:00 AM to 2:00 PM central standard time, using Beer's law, data for terrestrial PPFD (I_0) reduced by a factor of 6% for surface reflectance (Wetzel and Likens, 1991), underwater PPFD (I_x) and the depth of the sensor (x). The amount of light reaching the top of a bucket was calculated using corrected terrestrial PPFD, a mean water depth (z) to the bucket of 1.00 m and the average of the extinction coefficients, thus only the contribution from direct overhead PPFD was included in these measurements. Hourly measurements were summed to obtain PPFD received daily for open cells. To determine the amount of PPFD reaching buckets for cells in a shade treatment, the corrected terrestrial PPFD was reduced by the percent of light passing

through the shade cloth, and the PPFD was then calculated as for the open cells described above. At the beginning of the experiment, the data logger malfunctioned and data collection was sporadic (period from May 13 to May 20, May 27 to May 29, May 31 to June 9). To compensate for missing data, terrestrial pyrheliometer data collected by the Wisconsin Department of Natural Resources (Sullivan, 1992, unpublished data), at a station in La Crosse were used. A linear regression ($r^2 = 0.97$) was used to fit these data to PPFD data from the local pond sensors for the period with no gaps. The regression equation was used to estimate missing values of PPFD. Hourly measurements of PPFD were summed over the growing season and divided by the total amount of light received by terrestrial sensors to obtain a seasonal estimate of the total photosynthetically active radiation (PAR) and the percentage of terrestrial light reaching a bucket. The PPFD reaching leaf midpoints or tops of leaves was estimated using average leaf lengths and extinction coefficients calculated above. Water temperature was measured in each pond using three thermocouples connected to a datalogger.

Plants were harvested every two weeks over the growing season with 8 harvests in total. On June 17, July 15 and August 15 one bucket of each sediment type was harvested from odd-numbered rows (6 replicates of each treatment); on June 30, July 27 and August 29, buckets from even-numbered rows were harvested (6 replicates). On September 23 and October 13 one bucket of each sediment type from each cell was collected (12 replicates). At harvest the number of ramets, number of leaves, length of each leaf, number of tubers, and fresh weight of leaves, roots, stolons and tubers (defined here as single growing points) were measured for each bucket. Samples were dried to constant weight at 65C.

Data from each harvest were analyzed statistically using an analysis of variance (ANOVA) that combined a randomized block design analysis for light and a split plot analysis for sediment and light sediment interactions (Table 1). Analyses were performed using SAS (Statistical Analysis Software, SAS Institute, 1987). Within the randomized block ANOVA for light, contrasts were used to determine significant differences between shade treatments. Tuber production rates as a function of light availability were

Table 1. Example of analysis of variance for split plot design testing significance of light, sediment and light sediment interactions on harvest biomass data (data from 15 August)

Dependent variable: total dry weight

Source	DF	Sum of Squares	F value	P > F
Model	51	35.60	3.56	0.0001
Error	42	8.24		
Corrected Total	93	43.84		

R-Square	C.V.	mean biomass (g)
0.81	65.30	0.68

Source	DF	Sum of Squares (Type I)	F value	P > F
Block	11	2.64	1.22	0.3018
Light	3	13.45	22.85	0.0001
Block*Light	33	6.66	1.03	0.4597
Sediment	1	5.27	26.89	0.0001
Light*Sediment	3	7.56	12.84	0.0001

Test of hypothesis using the Block*Light term as an error term¹

Source	DF	Sum of Squares	F value	P > F
Light	3	13.38	22.44	0.0001

¹ F values were initially calculated by SAS using the pooled error term. However, because of the split-plot design, this error applies only to sediment and light*sediment interactions. The F-value for the effect of light was calculated using the block*light sum of squares which is the error term for the randomized block design (Cochran and Cox, 1957).

estimated by linear regression of the change in tuber biomass over time for each shade treatment.

Sediment Analyses

Three sediment samples of each sediment type collected at the beginning of the experiment were analyzed. Particle size was determined using the hydrometer method (Patrick, 1958). Total carbon, nitrogen and inorganic carbon were determined on air-dried samples using a Leco carbon nitrogen analyzer (Wong and Kemp, 1977). The density of sediments was also determined on air-dried soil to enable estimates of total nutrients available per volume of sediment. Soluble phosphorus was extracted using NaHCO_3 (ratio 1:20) (Olson and Sommers, 1982). Extractable iron was extracted with diethylenetriaminepentaacetic acid (DTPA) (Olson and Ellis, 1982). Phosphorus and iron concentrations were measured using inductively coupled plasma emission spectroscopy.

Plant Analyses

Plants were divided into above ground and below ground samples. From sample dates August 15 and August 30 pairs of samples from each light-sediment combination were pooled into three samples. Pairs of the 12 replicates of the 23 September samples were pooled into 6 samples. Nutrient analyses were carried out at the Army Corps of Engineers Waterways Experiment Station, Vicksburg, MS. Samples that had been dried at 65 C were ground in a Cyclone Sample Mill (UDY Corp., Ft. Collins, CO) to pass a 40 mesh screen, and digested using a mixture of H_2O_2 and H_2SO_4 (Allen et al., 1974). Total nitrogen and total phosphorus were analyzed colorimetrically using a Lachat system; iron was analyzed by atomic absorption. The accuracy of analyses was estimated by including National Bureau of Standards reference samples with each sample set run. The average recovery of nutrients in these samples was: nitrogen (98.9 %); phosphorus (87.9 %); iron (78.7).

Statistical Analyses

In some cases samples from highly shaded treatments had to be pooled further to ensure that enough material could be digested; this resulted in unequal sample sizes from two to six replicates. Initially, dry weights and plant nutrient data were analyzed

statistically using the ANOVA described above for harvest data. Based on the overall significance ($\alpha = 0.05$) of sediment, light and sediment-light interactions from the split-plot analysis, an unweighted means analysis was done using least squares means. To determine the effects of light treatment on nutrient concentrations, means were compared between light treatments for each sediment type. To determine the effects of sediment type on nutrient concentration, means were compared for each sediment type within a light treatment.

Photosynthesis and Respiration

Measurements of photosynthesis were made on leaves collected 30 June, 27 July and 15 August. Plants were transported to Ames, Iowa in pond water in 1-liter containers kept in coolers. Plants were kept refrigerated (10 C) up to 36 hours before use. Photosynthesis and respiration rates were measured as oxygen production or consumption using 0.5 cm leaf segments in rapidly stirred solution in closed chambers. Oxygen was measured with oxygen electrodes (Rank Brothers, U.K.) connected to strip chart recorders. Six chambers were connected in parallel. For statistical analysis each chamber was considered a block, and leaves from the 8 light*sediment treatment combinations were assigned to each chamber randomly to control for chamber variation. To control for changes in photosynthetic characteristics in storage, one replicate from each of the eight treatments was measured in turn. Leaf segments were bathed in 10mM HEPES buffer, pH 7.8. Sodium bicarbonate (25 mM final concentration) was added to each chamber to ensure adequate carbon supply and to minimize photorespiration. A range of bicarbonate concentrations was tested; 25 mM was the optimum concentration for photosynthesis over the temperature ranges measured for these plants.

Leaves were rinsed gently to remove epiphytes and segments 5 cm long were cut 8 cm above the base of the fourth youngest leaf of each plant.

The age of leaves used for photosynthesis measurements was estimated from harvest data using the equation:

$$\text{age} = (\text{days since emergence}) * \{1 - (\text{leaves} - 4) / (\text{leaves})\}$$

where "leaves" were the number of leaves present on the sampling day.

The fresh weight of each segment was determined. Leaf segments were cut into 0.5 cm segments to minimize the effects of lacunae on gas storage and release.

Leaf segments were acclimated in chambers for 10 minutes at each temperature before dark respiration and photosynthetic rate were measured. Dark respiration was measured at the beginning and end of each run. Light was provided by halogen lamps shaded with neutral density filters (cheese cloth); light levels were established at 10, 30, 60, 100, 200, 500 and 800 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ PPFD; these were calibrated for each chamber with a LiCor quantum sensor. Chamber temperature was maintained by a refrigerating/heating water bath, at temperatures ranging from 20 to 30 C (within 0.5 C).

In general, measurements on a leaf segment were made sequentially at 20C, then at 25C, and then at 30C, to minimize the effects of high temperature membrane degradation on subsequent measurements (a complete run at each temperature lasted approximately 45 minutes). To address the question of leaf aging during measurement, and to control for this effect, temperatures (20, 25 and 30 C) were randomized during measurements made on 27 July. Because of the variations in protocol, measurements of respiration and calculations of instantaneous light compensation point as functions of temperature on each date were considered separate experiments. To determine changes in photosynthetic rate over the season, only data for photosynthetic rates for June 30 and August 15 were considered. Compensation points were calculated by linear interpolation. If the compensation point was between 0 and the lowest experimental light level (10 $\mu\text{mole} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), the compensation point was interpolated between these points. If the compensation point exceeded 10 $\mu\text{mole} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, the nearest light level for which respiration occurred, and the next higher light level for which photosynthesis occurred were used as endpoints.

The contributions of light, sediment and temperature treatment effects on respiration and compensation point were determined by three-way split-plot ANOVA (Table 2). Previous ANOVAs for harvest data had shown that the shade blocks did not contribute a significant source of variation to the analysis. For the analyses of photosynthesis data, the block was the oxygen electrode chamber. The effects of shade

Table 2. Example of analysis of variance for photosynthesis data, testing significance of light level for growth, sediment and experimental temperature on compensation point (data from 27 July)

Source	DF	Sum of Squares	F value	P > F
Model	47	4782.85	2.02	0.0091
Error	46	2314.08		
Corrected Total	93	7096.93		
	R-Square	C. V.	Compensation point mean	
	0.67	47.93	14.80	
Source	DF	Sum of Squares	F value	P > F
Chamber ¹	5	68.08	0.27	0.9269
Light	3	125.45	0.83	0.4836
Chamber*Light	13	1256.94	1.92	0.0524
Sediment	1	222.01	4.41	0.0412
Light*Sediment	3	511.93	3.39	0.0257
Chamber*Light*Sediment	6	1302.54	4.32	0.0016
Temperature	2	974.42	9.68	0.0003
Light*Temperature	6	137.21	0.45	0.8380
Sediment*Temperature	2	8.12	0.08	0.9226
Light*Sediment*Temperature	6	176.15	0.58	0.7415
Test of hypotheses using Chamber*Light as an error term ¹				
Light	3	125.45	0.43	0.7333
Test of hypotheses using Chamber*Light*Sediment as an error term				
Sediment	1	222.01	1.02	0.3509
Light*Sediment	3	511.93	0.79	0.5440

¹ The oxygen electrode chamber is used as the block term

² F-values were initially calculated by SAS using the pooled error term. Due to the split-plot design, this error applies only to temperature and its interactions with light and sediment. The F-value for the effect of light was calculated using the chamber*light sum of squares, which is the error term for the randomized block design; effects of sediment and interactions between light and sediment were calculated using Chamber*Light*Sediment as the error (Cochran and Cox, 1957).

and sediment treatments on photosynthetic rates above the compensation point were determined by individual split-plot ANOVAs at each light level (same analysis as shown in Table 1 but with oxygen chamber as the block). T-tests ($\alpha = 0.05$) were used to test the significance of differences between shade treatments.

To compare plant light requirements estimated from growth measurements, whole plant light compensation points were estimated from instantaneous light compensation points, and aboveground:belowground biomass ratios. Belowground respiration rates were assumed to be equal to leaf respiration rates. A photoperiod of 12 hours was used, based on LiCor logger data. Because roots, stolons and tubers likely have lower respiration rates than actively metabolizing leaf tissue, the estimates of whole plant compensation points represent a maximum estimate of light required.

RESULTS

Plant Growth in Lake Onalaska

At both transplant sites the number of ramets produced increased at 0.5 m depth, and declined at 1.0 m and 1.5 m depth (Figure 2).

Tubers were produced at 0.5 m at both sites; but tubers were fewer and smaller at site 6H (Table 3). At 0.5 m, the average percent of surface light transmission reaching the top of a bucket was 8.72 at site 6H, and 8.69 at site 8D; at 1.0 m average light transmission was 0.90% and 0.97% at sites 6H and 8D respectively; at 1.5 m transmission was 0.10% and 0.12%. One tuber was found in one replicate at 1.0 m at site 8D, otherwise no tubers were produced at 1.0 or 1.5 m depth at either site.

Plant Growth in Ponds

1. Light

Tubers sprouted on May 13, 17 days after planting, and were grown until October 12 (152 days). The terrestrial sensors received 5,546 moles/m² of photosynthetically active photons over this period, compared with 1,386 moles/m² (25% surface light) received in the open cell control treatment, 478 moles/m² (9% surface light) received in the 63 % shade treatment, 298 moles/m² (5% surface light) received in the 80 % shade treatment, and 95 moles/m² (2% surface light) received in the 92% shade treatment (Figure 3). (Light treatments are referred to hereafter by the percentage of light received during the growing season). Surface and filamentous algae became abundant in the ponds in mid-August and decreased light availability to all treatments; this was reflected in the decreasing slopes of the cumulative light curves. Assuming a twelve-hour day, (the average photoperiod during the course of the experiment), the mean instantaneous PPFD over the season was 210 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in the 25% treatment; 72 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in the 9% treatment; 45 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in the 5% treatment and 14 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in the 2% treatment. Pond water temperatures ranged from 13 C (30 September) to 23 C (24 August) and were similar to those reported for Pool 8 (Wisconsin DNR Long Term Resource Monitoring Program, 1992).

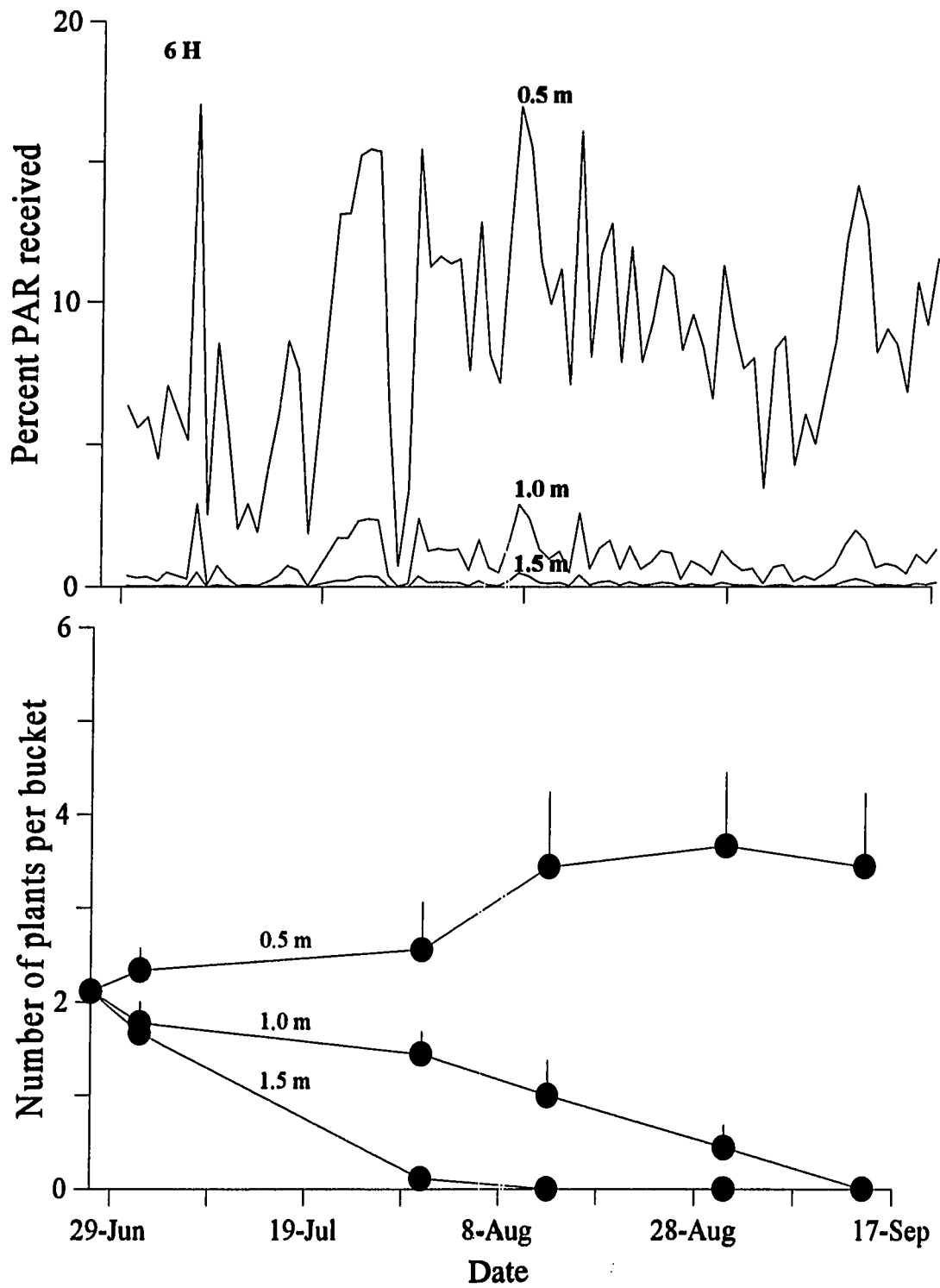


Figure 2. Percentages of PPFD and plant density at 0.5, 1.0 and 1.5 m depths at site 6H in Lake Onalaska. Results from Site 8D were similar. Vertical bars represent one standard error

Table 3. Tuber production by plants grown at 0.5, 1.0 or 1.5 m depths in Lake Onalaska

	N	% ambient light Mean (S.E.) ¹	number of tubers Mean (S.E.)	tuber biomass (g) Mean (S.E.)	T-test $\alpha = 0.05$
Site 6 H					
0.5 m	8	8.72 (3.85)	4.75 (0.65)	0.26 (0.04)	A ²
1.0 m	9	0.90 (0.71)	0	0	
1.5 m	9	0.10 (0.12)	0	0	
Site 8 D					
0.5 m	8	8.69 (4.64)	7.75 (1.03)	0.67 (0.13)	B
1.0 m	9	0.97 (0.86)	0	0	
1.5 m	9	0.12 (0.15)	0	0	

¹ Data collected by J. Owens, summarized in Owens, 1993.

² T-test for numbers of tubers and tuber biomass. Means with the same letter are not significantly different.

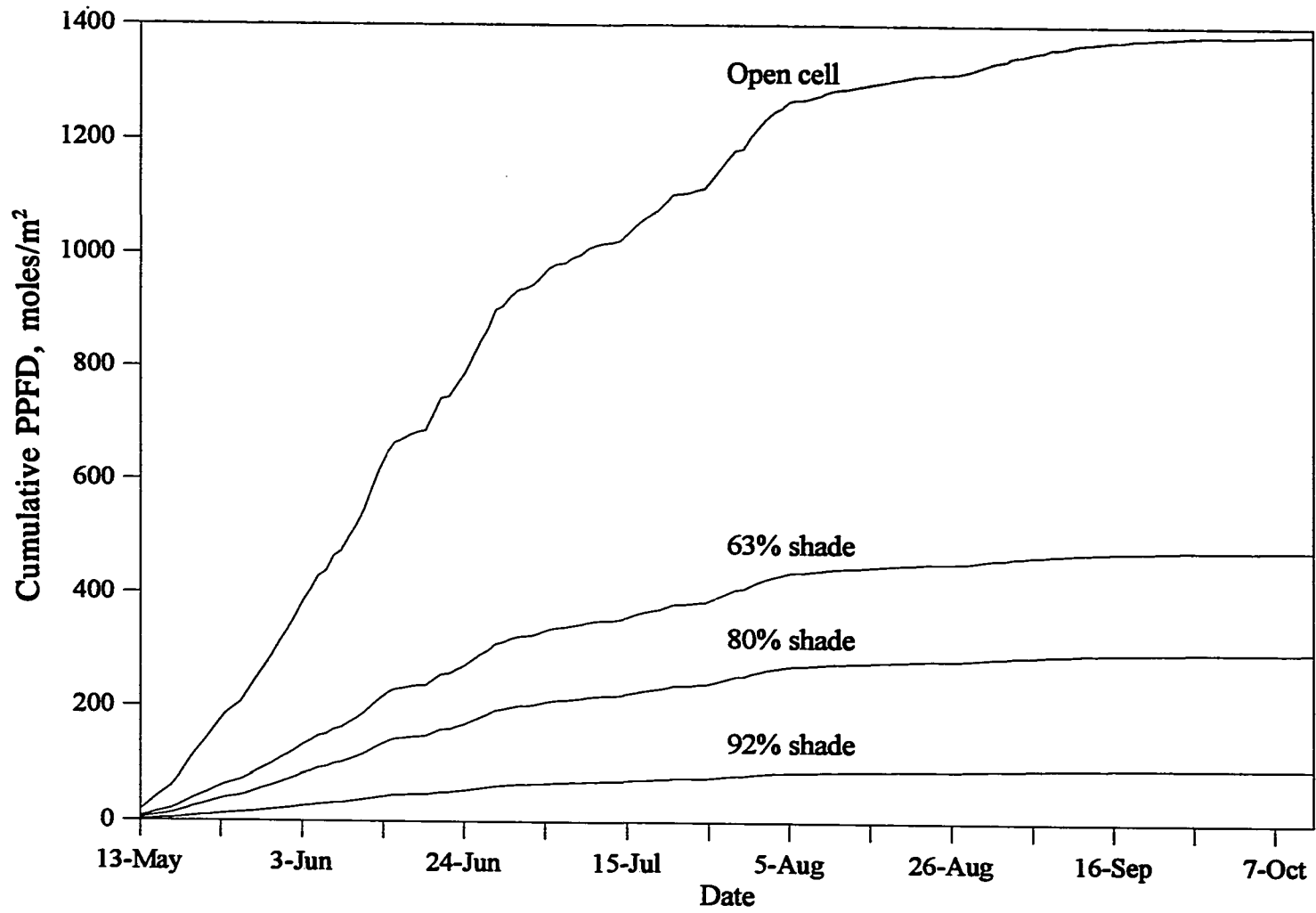


Figure 3. Cumulative PPFD received by each shade treatment during the growing season in the pond study

2. Growth

The numbers of leaves increased with increasing light only, except for the 23 September harvest when both sediment and light*sediment interactions affected the number of leaves and leaf senescence (Figure 4). Leaves in lower light treatments were older (Figure 5) and increased in age consistently over the season while leaves from the 25% treatment were younger, and their mean age was more nearly constant. The mean leaf age of plants grown in sand was significantly higher ($\alpha = 0.05$) than that of plants grown in lake sediment.

Leaves were longer in lower light (Figure 6), and after August 15 were also longer in plants grown in lake sediment ($\alpha = 0.02$). The onset of leaf senescence varied with sediment treatment and shade treatment; leaf dry weight declined sooner in plants grown in sand and high light (Figure 7, 25 S treatment). In contrast, leaves in the 2% and 5% light treatments had greater biomass than leaves in the 9 and 25% light treatments at the end of the season.

Patterns of biomass increase (Figure 7) were affected primarily by light most of the season. The effects of sediment on total biomass became significant on 15 August, ($\alpha = 0.005$) whereas light level significantly affected total biomass on 17 June ($\alpha = 0.05$). Biomass allocation to leaves or developing tubers varied with light; plants grown in 2% light had a greater proportion of biomass in leaves rather than tubers; the proportion of total biomass allocated to tubers increased with increasing light.

Root mass, including the initial tuber, decreased during the study (Figure 7) , from a mean dry weight of 0.127 g at the first harvest, but was never significantly different among treatments.

The date of tuber initiation depended on light availability alone; plants in the two highest light treatments (25 and 9%) had initiated tubers by 30 June (Table 4) whereas tubers in the 2% light treatment were not present until 27 July. While the timing of tuber production depended solely on light availability, the subsequent total weight and number of tubers were influenced by both light and sediment (Table 4 and Figure 8). Individual tuber biomass stabilized slightly above 0.1 g (Table 4) by August 15 in lake sediment in

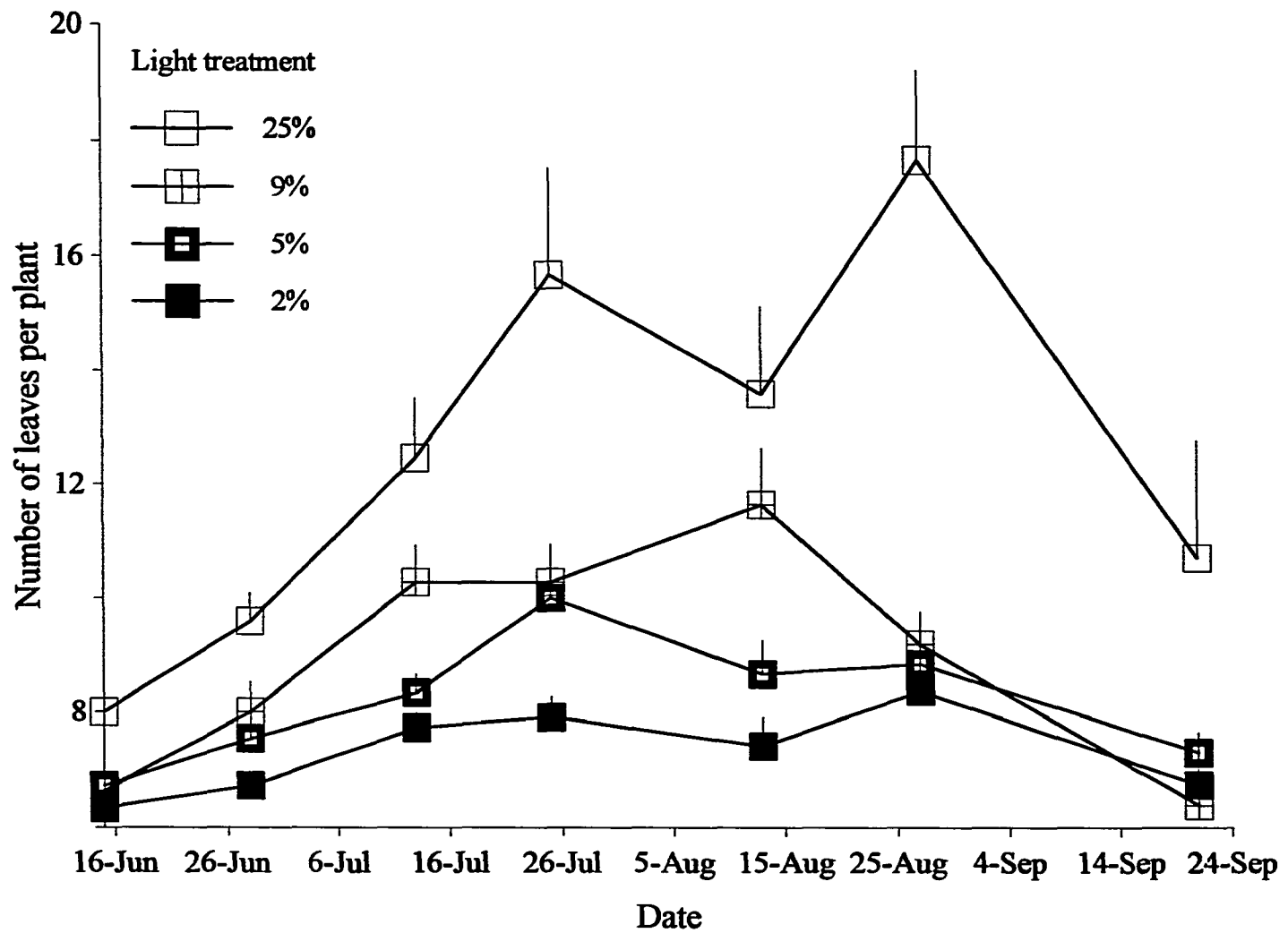


Figure 4. The effect of light on the numbers of leaves. Vertical bars represent one standard error.

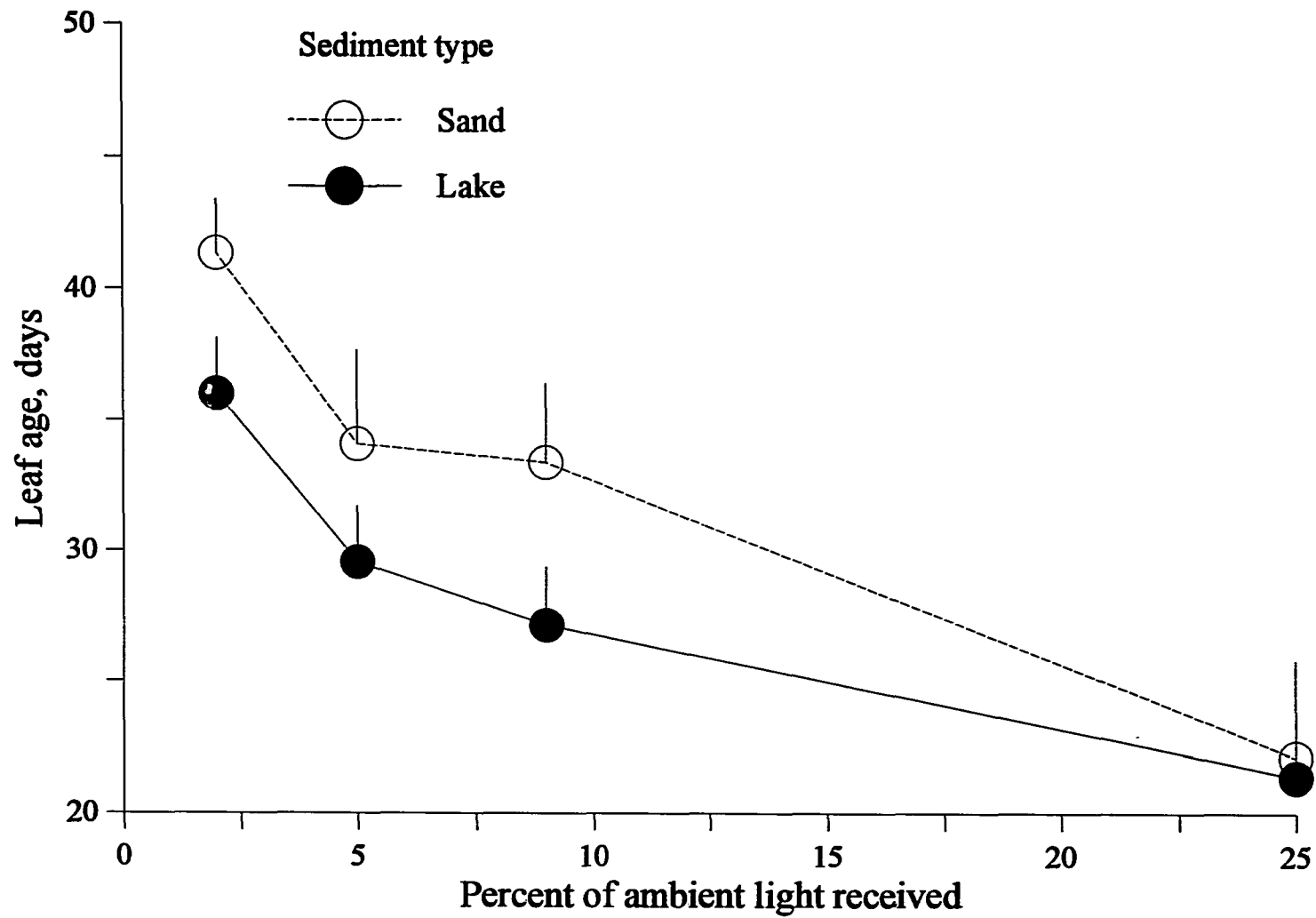


Figure 5. The effect of light and sediment on leaf age measured on July 27. Vertical bars represent one standard error.

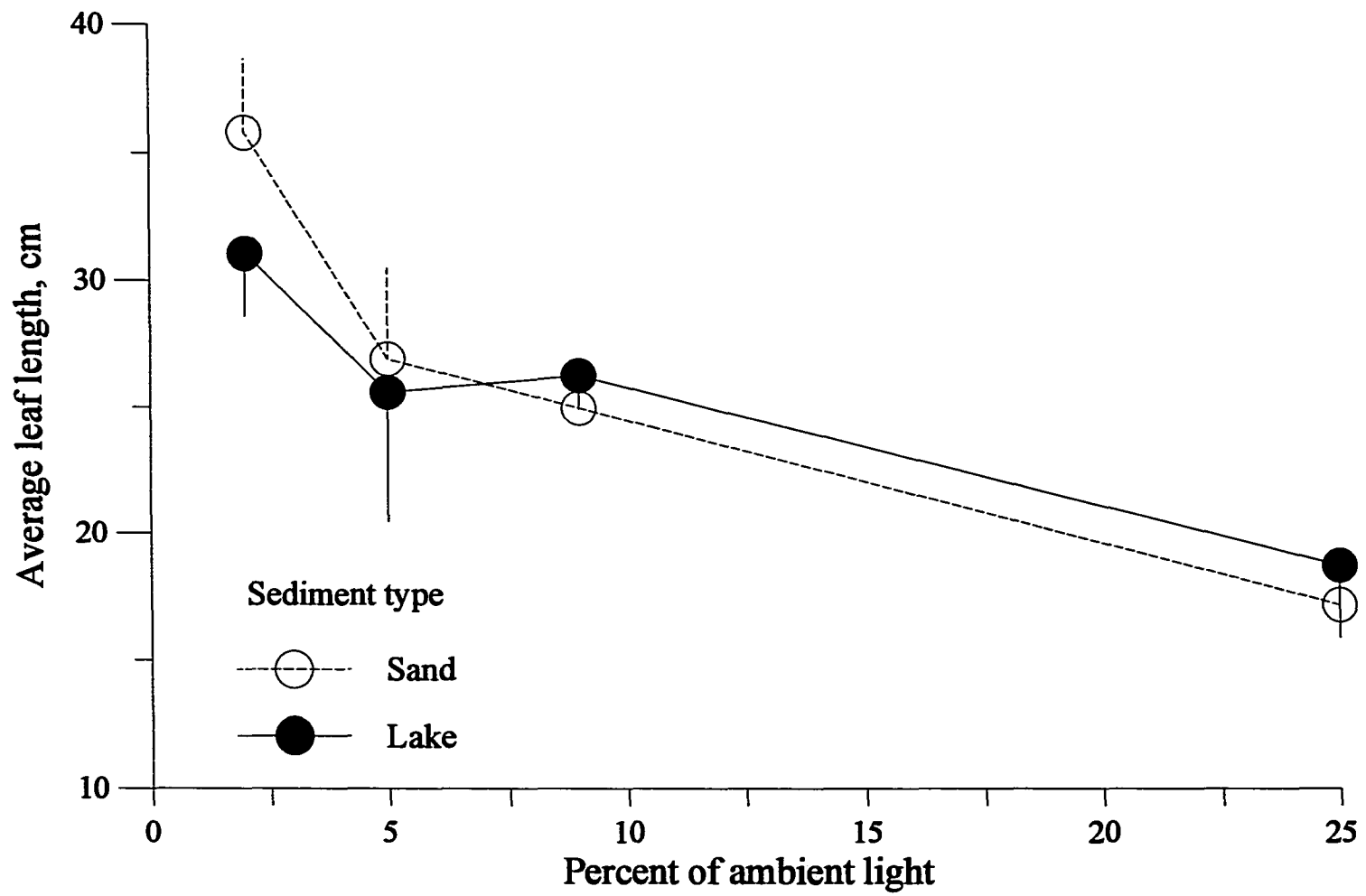


Figure 6. The effects of light on leaf length. Vertical bars represent one standard error

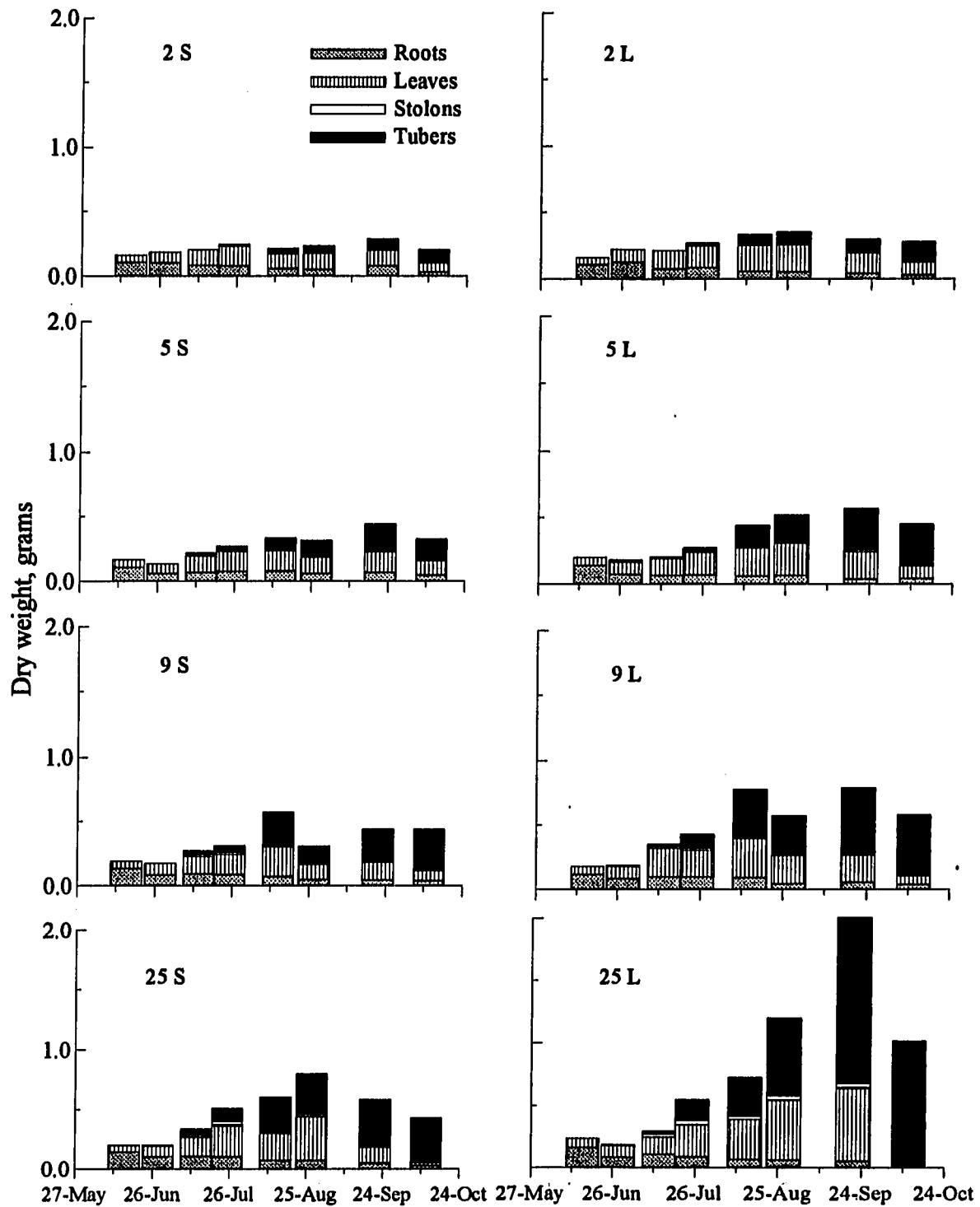


Figure 7. Mean biomass of plants grown in 2, 5, 9 or 25 % light in sand (S) or lake (L) sediment

Table 4. Effects of light and sediment treatments on individual tuber biomass (g); S = sand sediment; L = lake sediment

Treatment	30 June ¹	15 July		27 July		15 August		29 August		23 September		13 October	
		Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr
2 %													
S	0	0		0.012	0.001	0.036	0.003	0.032	0.006	0.044	0.006	0.046	0.006
L	0	0		0.016	0.003	0.046	0.006	0.043	0.007	0.044	0.005	0.061	0.005
5 %													
S	0	0.020	0.007	0.034	0.007	0.061	0.008	0.088	0.019	0.089	0.006	0.074	0.006
L	0	0.008	0.002	0.031	0.018	0.082	0.010	0.112	0.012	0.092	0.010	0.094	0.008
9 %													
S	0	0.037	0.008	0.047	0.012	0.096	0.010	0.064	0.017	0.117	0.011	0.089	0.006
L	0.009	0.030	0.007	0.082	0.020	0.100	0.011	0.126	0.018	0.132	0.006	0.103	0.010
25 %													
S	0.009	0.071	0.020	0.068	0.013	0.103	0.011	0.077	0.012	0.113	0.008	0.090	0.008
L	0	0.033	0.007	0.079	0.009	0.085	0.013	0.106	0.010	0.121	0.012	0.111	0.011

¹ On 30 June one tuber was produced in each of the treatments indicated

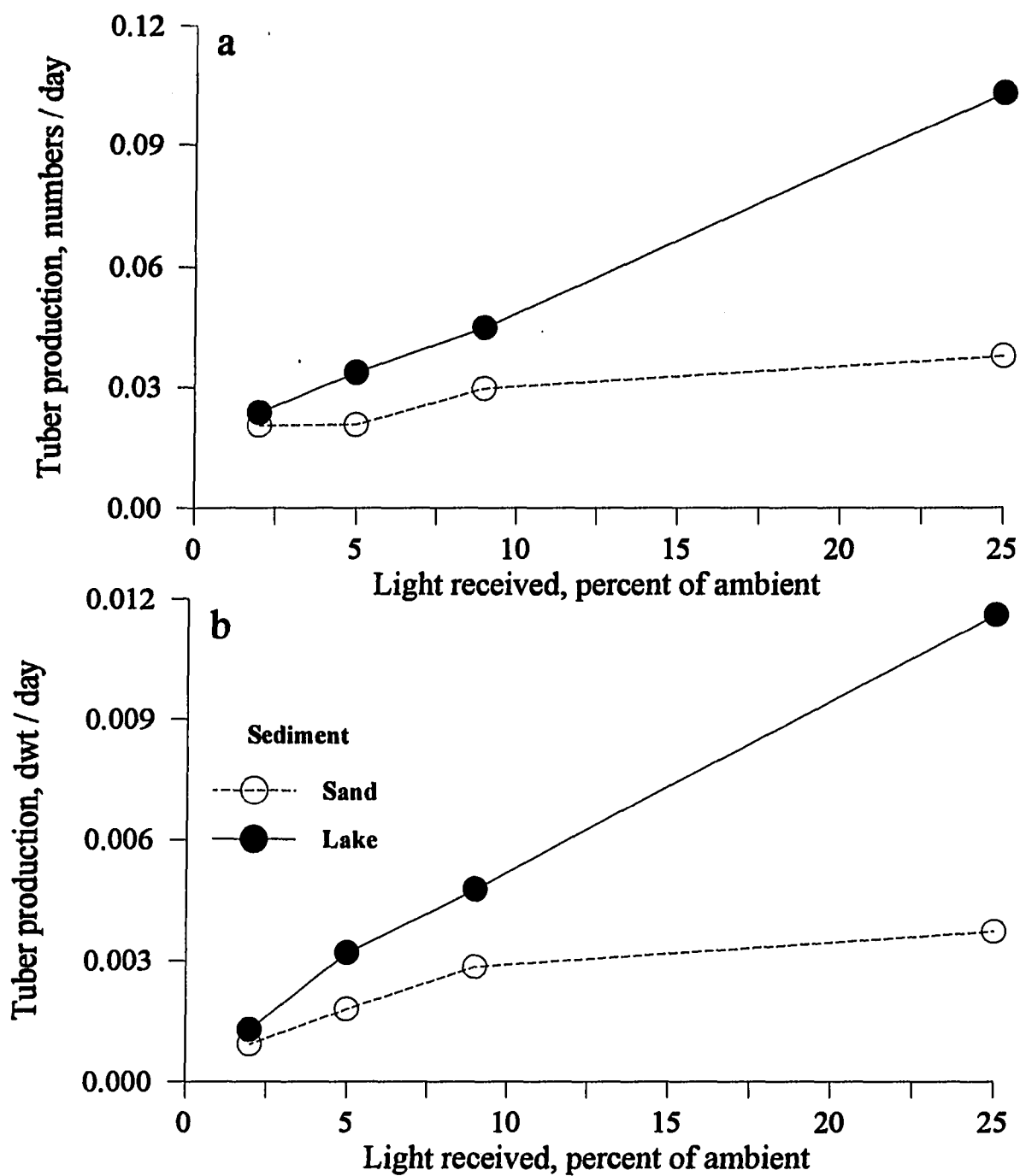


Figure 8. The effects of shade and sediment treatments on the rates of tuber production (a. numbers of tubers; b. tuber biomass)

9% or 25% light. With the exception of plants in the 5% light-lake sediment harvest of August 29, plants grown in 2% and 5% light treatments never achieved this per-tuber mass.

The cumulative amount of light necessary for plants to produce viable overwintering tubers was estimated by determining the total amount of PPFD received by the date on which (1) individual tuber weights stabilized, (2) total tuber dry weight exceeded that measured in the beginning of the study and (3) total tuber dry weight exceeded 0.20 g (estimated to be the mean tuber weight from tubers measured in Pool 9 by Donnermeyer, 1982). By August 15 (94 days after emergence) plants in the 9 and 25% light treatments had produced tubers that met these criteria (Table 4). The total amount of PAR received by the 9% treatment was 447 moles/m², corresponding to an average instantaneous flux of 110 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Table 5). Plants in the 5% light, lake sediment treatment had made replacement tubers by August 29, corresponding to an instantaneous flux of 61 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$.

3. Nutrients

The lake sediment (Table 6) was a sandy loam (69 % sand) while the sand-amended sediment was 91% sand. Although lake sediment was diluted 1: 4 (v:v) with sand, the dilution of most nutrient properties appeared more closely related to the decrease in clay content. Total nitrogen and soluble phosphorus concentrations in sand-amended sediment were about 40% of those in lake sediment.

Nitrogen concentrations were similar in leaves and tubers of all treatments. (mean concentration for leaves = 30.7 mg/g). Tuber nitrogen concentrations (mean = 19.5 mg/g) were consistently lower than those of leaves. The phosphorus concentrations in leaves and to a lesser degree tubers, decreased with increasing light, while sediment effects were not significant (Table 7). Tuber phosphorus concentrations were higher than those in leaves for all but the 2% light and the 5% light - sand-amended combination, and were highest in 2% light for plants grown in sand. For plants grown in lake sediment, significant differences in tuber phosphorus concentrations occurred only between the 2% and 25% treatments.

Table 5. Comparison of shade treatments, total PPFD and instantaneous PPFD received, and experimental light levels. Assumes 12 hour daylength.

a. Estimated light received by 15 August (94 days after germination) and tuber production in 15 August harvest

Light level	PPFD received 15 August ($\mu\text{moles}/\text{m}^2$)	Instantaneous PPFD ($\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	Total Tuber ¹ Dry weight (g)
25 % light	1,295	319	0.294 A ²
9 % light	447	110	0.308 A
5 % light	278	68	0.125 B
2 % light	89	22	0.054 C

b. Calculation of PPFD received after 94 days based on experimental light levels established for photosynthesis measurements

Experimental levels for photosynthesis PPFD ($\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$)	Daily PPFD ($\mu\text{moles}/\text{m}^2$)	PPFD received in 94 days ($\mu\text{moles}/\text{m}^2$)
10	0.43	40
30	1.29	121
60	2.59	244
100	4.32	406
200	8.64	812
500	21.60	2,030
800	34.56	3,249

¹ Pooled dry weights from sand and lake sediment treatments

² Contrasts: $\alpha = 0.05$. Means with the same letter are not significantly different.

Table 6. Sediment characteristics

Characteristics	Sand-amended		Lake		Ratio Sand:Lake
	Mean	Std. Dev.	Mean	Std. Dev.	
% Sand	91.43	1.06	68.77	1.61	1.33
% Silt	6.00	0.78	23.57	1.03	0.25
% Clay	2.57	0.29	7.60	0.51	0.34
Density (g/ml)	1.70	0.05	1.39	0.02	1.23
pH	7.67	0.09	7.07	0.54	1.08
% organic matter	0.63	0.02	1.00	0.09	0.63
% Total Nitrogen	0.02	0.01	0.06	0.01	0.41
% Total Carbon	0.36	0.01	0.58	0.05	0.63
Extractable P (mg/g)	0.02	0.00	0.05	0.01	0.41
Extractable Fe (mg/g)	0.04	0.01	0.17	0.02	0.23

Table 7. Leaf and tuber phosphorus concentrations (mg/g); S = sand sediment, L = lake sediment

Treatment	Leaf Concentration		T-tests ² light	Tuber Concentration		T-tests light
	LSM ¹	SEM		LSM	SEM	
2% light						
S	4.15	0.199	A	3.30	0.129	A
L	4.49	0.181	A	3.23	0.129	A
5% light						
S	2.89	0.222	B	2.64	0.129	B
L	2.70	0.181	B	2.94	0.091	A
9% light						
S	2.08	0.199	C	2.72	0.100	B
L	1.91	0.199	C	2.87	0.091	AB
25% light						
S	1.89	0.199	C	2.73	0.091	B
L	1.70	0.181	C	2.66	0.091	B

¹ LSM = least square mean. SEM = standard error of the mean

² Letters represent results of T-tests on unweighted means for difference between light treatments. The letter denotes differences between light treatments for the same sediment treatment; there were no significant differences between sediment treatments within any light level. Means with the same letter are not significantly different at $\alpha = 0.05$.

Iron concentrations (Table 8) were affected by both light and sediment treatments; iron concentrations were consistently lower in sand-amended treatments for both leaves and tubers regardless of light. Leaf iron concentrations increased with increasing light availability in both sediment types, while tuber iron concentrations were similar for all light treatments, and were significantly higher in lake sediment for all but those grown in 2% light.

4. Photosynthesis and Respiration

a. Temperature Effects

The 27 July experiment was considered the most conservative since it was controlled for tissue degradation by randomizing water temperatures. For this reason it was used as the best estimate of dark respiration rates, compensation points and temperature effects on photosynthesis above the compensation point.

Dark respiration rates increased with increasing water temperature from 20 to 30C (Table 9). Respiration rates were significantly higher in plants grown in lake sediment, and higher in plants grown in high light ($\alpha = 0.05$). Light compensation points also increased with increasing temperature (Figure 9) and were affected by temperature only; light and sediment had no significant effect. From 20 to 30 C the mean instantaneous light compensation point for all light and sediment treatments increased from 10.6 to 18.4 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$.

Increasing temperature from 20 to 30 C affected rates of net photosynthesis; the magnitude and increase or decrease depended upon the experimental light level at which photosynthesis was measured. At 60 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ higher water temperatures significantly decreased net rates of photosynthesis and the highest rates of photosynthesis occurred at 20 C (Figure 10). Conversely, at 800 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, net photosynthesis rate was significantly higher at 30 C (Figure 11). Net photosynthesis at light levels greater than 200 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ increased with increasing temperature. At light levels above the compensation point, net photosynthesis was significantly lower on a fresh weight basis in plants grown in sand-amended treatments.

Table 8. Leaf and tuber iron concentrations (mg/g); S = sand sediment, L = lake sediment

Treatment	Leaf		T-tests ²		Tuber		T-tests	
	Concentration LSM ¹	SEM	light	sed	Concentration LSM	SEM	light	sed
2% light								
S	0.914	0.212	A	A	0.443	0.229	A	A
L	1.505	0.193	A	B	0.897	0.229	A	A
5% light								
S	1.375	0.237	A	A	0.400	0.162	A	A
L	2.041	0.193	B	A	1.787	0.177	B	B
9% light								
S	1.338	0.212	A	A	0.476	0.162	A	A
L	2.343	0.193	B	B	1.348	0.162	A	B
25% light								
S	2.058	0.212	B	A	0.402	0.162	A	A
L	2.331	0.193	B	A	1.017	0.162	A	B

¹ LSM = least square mean; SEM = standard error of the mean

² Letters represent results of T-tests on unweighted means for difference between light or sediment treatments. The first letter denotes differences between light treatments for the same sediment treatment; the second letter denotes differences between sediment treatments for the same light treatment. Means with the same letter are not significantly different at $\alpha = 0.05$.

Table 9. Comparison of leaf dark respiration rates measured on 27 July

Light level ¹	Respiration rate, $\mu\text{moles}\cdot\text{g fwt}^{-1}\cdot\text{h}^{-1}$		
	N	Mean	Std Error
2%	24	10.35	1.09
5%	23	10.91	0.92
9%	24	10.06	0.76
25%	23	16.97	1.87
Sediment type ²			
Sand	46	9.32	0.55
Lake	48	14.63	1.08
Temperature ³			
20	31	9.89	0.88
25	32	12.83	1.24
30	31	13.35	1.24

¹ Light effects were significant at $\alpha = 0.002$

² Sediment effects were significant at $\alpha = 0.05$

³ Temperature effects were significant at $\alpha = 0.004$

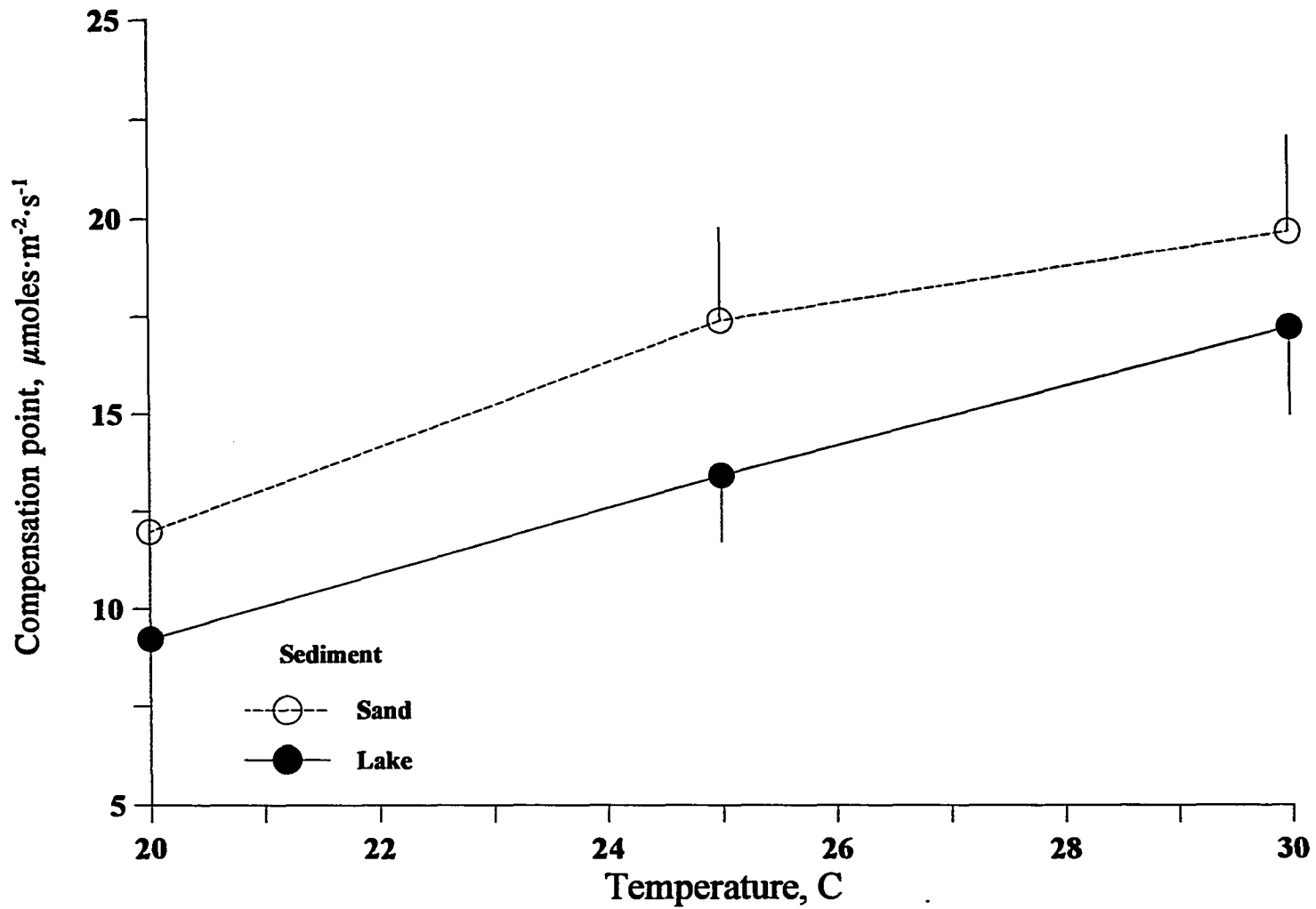


Figure 9. Leaf compensation points measured on July 27 harvest. Means of four light treatments. Vertical bars indicate standard errors. ANOVA: temperature $\alpha = 0.0006$; sediment $\alpha = 0.4238$; light $\alpha = 0.6730$

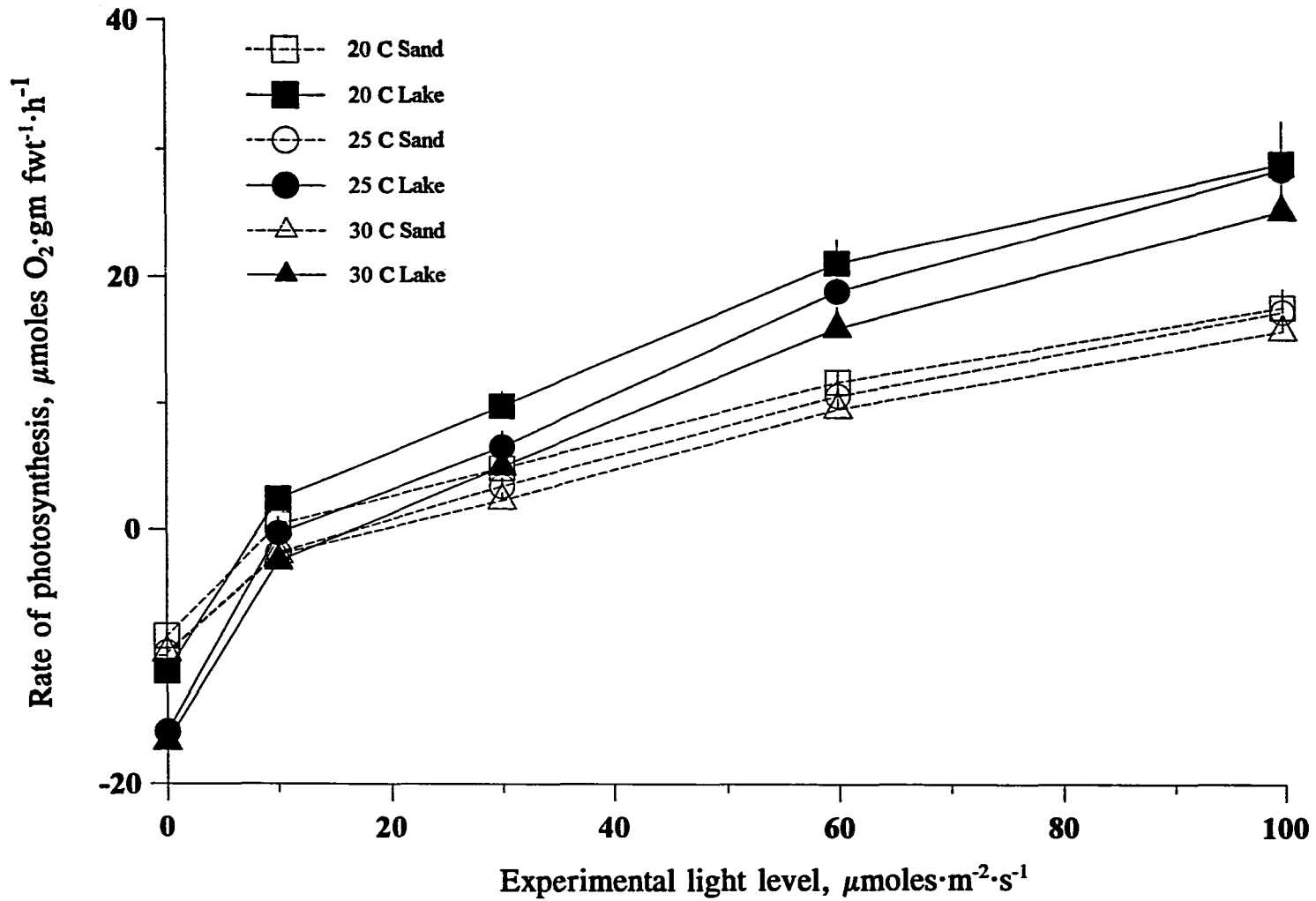


Figure 10. Temperature effects on photosynthesis in low light, measured on 27 July harvest. Means of four light treatments. Vertical bars indicate standard errors. Temperature $\alpha = 0.05$ for light levels less than 100 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$; at 100 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ temperature effects were not significant

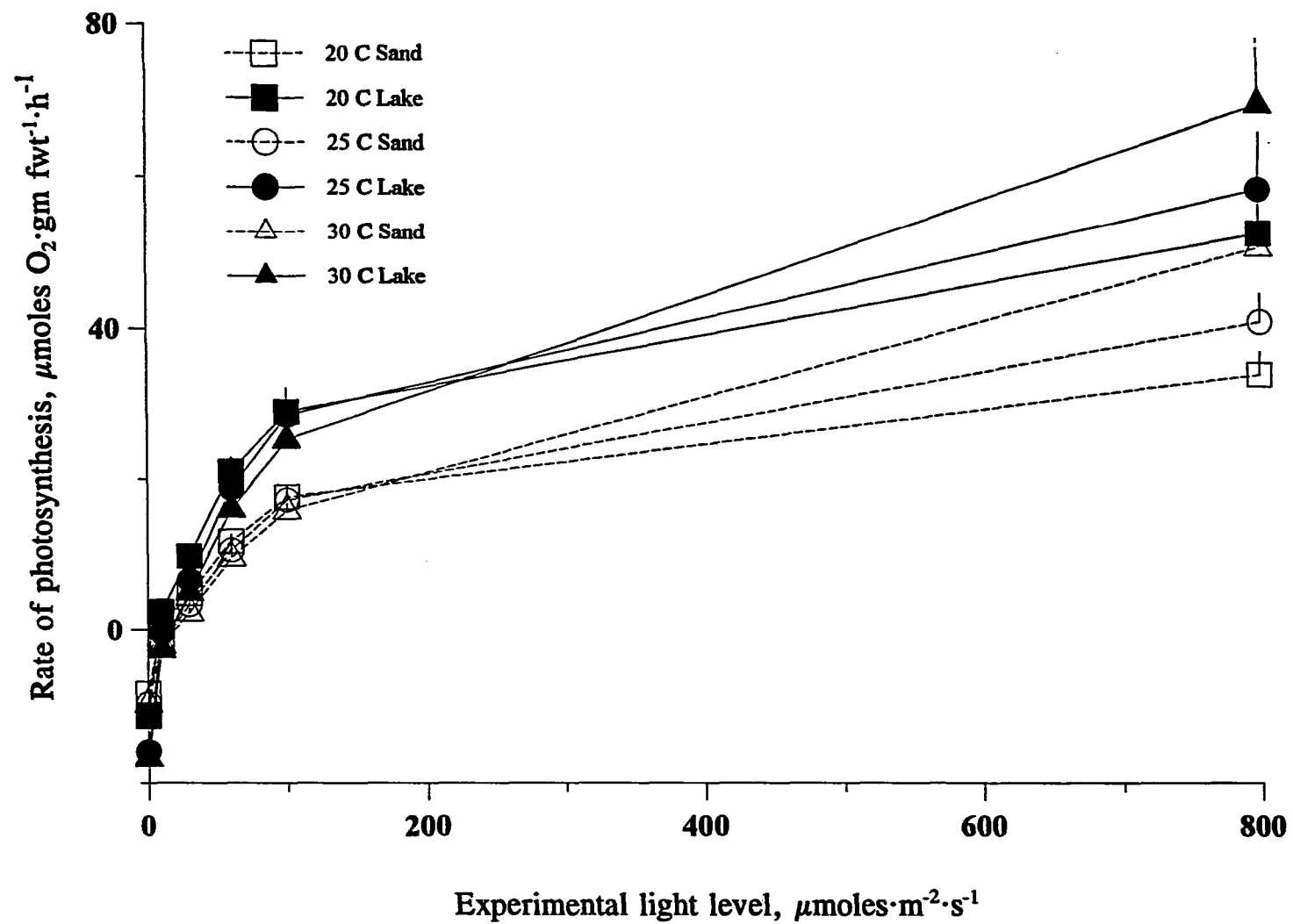


Figure 11. Temperature effects on photosynthesis at high light, measured on 27 July harvest. Means of four light treatments. Vertical bars indicate standard errors. Temperature $\alpha = 0.0005$ at $800 \mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$

b. Seasonal Effects

Mean rates of net photosynthesis averaged over all light treatments were similar on June 30 and August 15, with rates saturating at light levels of approximately 500 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Maximum rates at 800 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ occurred at 30 C. However, the sensitivity of photosynthetic rate to increased temperature was greater on August 15 than on 30 June (Figure 12). On 30 June photosynthesis significantly decreased at 10 and 30 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ as temperatures were increased from 20 to 30 C. On 15 August, photosynthesis declined significantly at light levels from 10 to 100 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, and the increase in photosynthesis at 800 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ was not significant, in comparison with 30 June. Respiration rates did not vary significantly with temperature on 30 June, while temperature increases significantly increased respiration on 15 August (Table 10). Instantaneous compensation points, which increased with temperature on both dates, were greater at 30 C on 15 August.

c. Whole plant Compensation Points

Whole plant compensation points (Table 11) were unaffected by shade level or sediment type, and represent conservative estimates of the minimum amount of light necessary for plant survival, not including tuber production. Based on these estimates, plants in the 2% light treatment received less (14 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) than the lowest minimum light requirement at 20 C, (39 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$). Plants in 5% light (45 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) would have received slightly above the minimum estimates for temperatures between 20 and 25 C (39-57 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), plants in the 9% (72 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) would have been limited only at 30C or above, and 25% (210 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) treatments would never have been light limited.

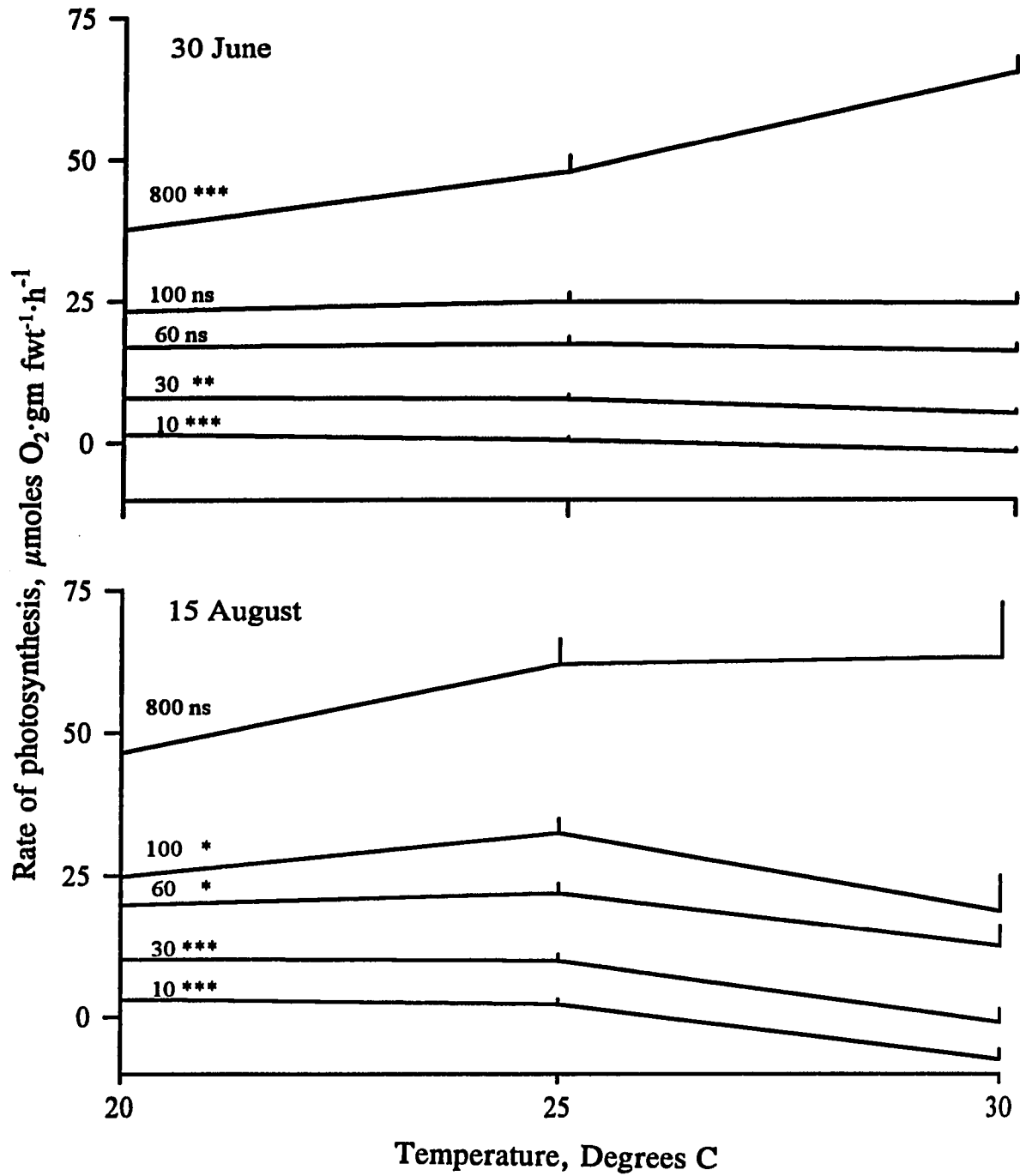


Figure 12. Comparison of sensitivity of photosynthesis to temperature increase between 30 June and 15 August. Stars indicate α of temperature effect from ANOVA: 0.05 = *; 0.005 = **; 0.0001 = ***; vertical bars indicate standard errors

Table 10. Comparison of temperature effects on leaf dark respiration and compensation point for June 30 and August 15 measurements.

		June 30		August 15		
Respiration rate ($\mu\text{moles O}_2 \cdot \text{gmfw}^{-1} \cdot \text{h}^{-1}$)						
Temperature (C)	N	Mean	Std Err	N	Mean	Std Err
20	30	16.18	3.40	9	14.81	3.61
25	31	21.10	3.60	40	17.09	1.62
30	32	17.32	1.80	10	20.72	4.32
α for temperature		0.4870		0.0024		
Compensation point ($\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ of light)						
Temperature (C)	N	Mean	Std Err	N	Mean	Std Err
20	30	8.72	0.33	9	7.78	0.35
25	31	10.59	0.65	40	10.73	0.81
30	32	15.62	1.48	10	23.20	2.71
α for temperature		0.0001		0.0008		

Table 11. Estimates of whole plant compensation point for plants harvested 27 July

Temperature ¹ C	Whole compensation point ($\mu\text{moles}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)		
	N	Mean	Standard Error
20	31	39.46	5.17
25	32	56.93	5.55
30	31	68.58	6.33

¹ Temperature effects were significant at $\alpha = 0.001$. Shade level and sediment effects were not significant.

DISCUSSION

The results of the Lake Onalaska field experiment indicate that plants required at least 8.7% of surface light for tubers to be produced in 94 days. In addition, both numbers and biomass of tubers were affected by site characteristics, with greater production at the more sheltered site. Only one tuber was produced at 1.0 m, and typically plants did not grow at 1.0 m or 1.5 m, where light levels were on average less than 1.0 %. The mean depth of Lake Onalaska is 1.43 m (Korschgen et al., 1987); revegetation may be restricted to the shallow margins of the lake.

Plants from all light and sediment combinations produced tubers in the pond study, but in both the 2% treatments and the 5% sand amendment treatment plants failed to make viable replacement tubers (mean mass less than 0.10g). For the 94 day period corresponding to the Lake Onalaska experiment, data from the pond experiment confirmed the results of the Lake Onalaska experiment. Plants growing in at least 9% light, an average daily instantaneous rate of $110 \mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ for 94 days, produced replacement weight overwintering tubers. However, plants from the 5%, lake sediment treatment also made replacement tubers by August 30 (109 days), corresponding to an instantaneous rate of $61 \mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, or 286 moles over the this period. Thus, plants in lower light environments could produce overwintering tubers at lower light levels if the season was sufficiently long, and, based on the estimates of whole plant compensation points, if the season was sufficiently cool.

Vallisneria plants growing from tubers in the Upper Mississippi River generally emerge in late May (assume day 144), begin producing tubers by mid-August, and senesce in early September (day 244) (Donnermeyer, 1982). For a 100 day growing season, the minimum instantaneous PPF_D necessary at the mean sediment surface (1.43m) for tuber production would be $103 \mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, based on an overall requirement of 447 moles received.

In our study, plants required 5% of surface light for survival, and 9% of surface light for tuber production. Other estimates of the light requirements for plant growth vary widely: Sand-Jensen and Madsen (1991) estimated that 7% of surface light, or 505

moles/m²/yr was needed for rooted aquatic plants to grow; Carter and Rybicki (1990) estimated an average of 100 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ was necessary at the sediment-water interface for submersed macrophytes to survive in the tidal Potomac River. Agami and Waisel (1980) estimated that for *Najas marina*, an average midday irradiance of at least 250 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ would be necessary for seed production. Goldsborough and Kemp (1988) estimated that 11% of surface irradiance was required for *Potamogeton perfoliatus* growth, whereas Chambers and Kalff (1985) estimated that the light level that determined the lower depth limit of plant colonization could be as much as 21% of surface light.

Plants grown under low light have a lower capacity for nutrient uptake, due to lower root: shoot ratios (Mooney and Winner, 1991) and inherently lower uptake capabilities. The greatest effect of light intensity on nutrient uptake occurs when light is the limiting factor for growth. In contrast, nutrient uptake by plants that are nutrient limited appears to be insensitive to light intensity since carbohydrate supply for root metabolism is not limiting (Chapin, 1991). Thus, nutrient limitations for growth should become evident where light is not the limiting factor for growth. In this study, sediment fertility significantly affected dry weights of leaves and tubers at light levels of 9% and above, indicating that below 9%, light availability rather than sediment fertility was limiting.

Previous studies on plant nutrient uptake as a function of light availability have shown that nitrogen (Dale and Causton, 1992) and phosphorus concentrations (van Wijk, 1989) increase in shaded leaf tissues. In this study phosphorus concentrations were significantly higher in the 2 and 5% light treatments, while the 9 and 25% treatment concentrations were similar. However, leaf nitrogen concentrations were similar in all light treatments. Similar results have been reported by Murray et al. (1992), in which *Zostera* biomass increased though tissue nitrogen concentrations did not change with nitrogen fertilization. The similarity of leaf phosphorus concentrations at light levels of 9% and above indicate that at those levels nutrient uptake was not a response to low light availability. Iron concentrations in plants differed between sediment treatments at all light levels. Low iron concentrations in the sand-amended treatments may have contributed to lower respiration and maximum net photosynthesis due to lower

cytochrome abundance and thus lower rates of electron transport in chloroplasts and mitochondria.

Minimum nutrient concentrations for *Vallisneria* were estimated by Gerloff and Krombholz (1966) and Gerloff (1975) to be 1.3% of dry weight for nitrogen and 0.3% for phosphorus. In this study, nitrogen concentrations in leaves and tubers were higher than minimum critical levels reported by Gerloff and Krombholz, were higher than those reported for *Vallisneria* collected in September from Lake Mendota (Gerloff and Krombholz, 1966, 1.98% dwt) and lower than *Vallisneria* collected from the Pamlico River: (4.3% dwt, Zamuda, 1976). Phosphorus concentrations were higher than the critical concentration for leaf tissue reported by Gerloff and Krombholz (1966, 0.13% dwt), and were higher than values reported for *Vallisneria* collected in September by Linn et al. (1975) of 0.16 % dwt. Zamuda reported higher values (0.60 %) for *Vallisneria* from the Pamlico River. The increase in phosphorus concentration in low light may be similar to the finding by van Wijk (1989) that luxury phosphorus uptake occurs at low light levels. The lack of variation in phosphorus concentration due to sediment type is in contrast to studies by Murray et al., (1992), Overath et al., (1991) and Chambers et al. (1989) where higher sediment nutrient concentrations were related to higher tissue nutrient concentration.

No critical iron concentrations have been published for *Vallisneria*; for *Elodea*, Gerloff (1975) reported a critical value of 60 ppm, a low value compared with the minimum iron concentration found in this study of 400 ppm.

Plants in this study grown at levels of less than 9% of ambient light were light limited for tuber production, and plants grown at higher light levels produced overwintering tubers in spite of nutrient limitations. Tuber quality (concentrations of nitrogen, phosphorus and potassium) was similar regardless of light treatment, in spite of differing leaf nutrient concentrations for phosphorus and potassium.

Where sediment significantly affected growth and rates of photosynthesis at high light levels, there was typically no interaction between sediment type and light treatment, thus plants grown in sand sediment were inherently different from those grown in lake

sediment, and plants from each sediment type were similarly affected by light availability. Since plants from both sediment types in high light produced tubers by 94 days, light availability, not sediment type, was the primary limiting factor in growth.

A survey of *Vallisneria* distribution indicates that it typically grows in substrates that are 67 % sand/gravel (Pip, 1979); these substrates would be typical of areas with flowing water, and higher light availability due to decreased suspension of fine sediments, and imply that *Vallisneria* may be distributed in nature based on light availability rather than sediment nutrient availability. In contrast, the distribution of *Myriophyllum*, a species that concentrates photosynthetic biomass at the water surface, is more likely to be limited by sediment nutrient availability (Chambers, 1987).

It appears that at light levels of $100 \mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ or less, temperature increases of 5C, especially those in late summer, would decrease rather than increase net photosynthesis. At $30 \mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ net photosynthesis is estimated to decrease by 25% for a 5C temperature increase. In addition, whole-plant dark respiration is estimated to increase by 17%. Late summer declines in plant growth and net photosynthesis with increasing summer temperature have been described for seagrasses by Wetzel and Penhale (1983), Bulthuis (1983b) and Marsh et al. (1986). For *Vallisneria*, temperature increases would be expected to increase net photosynthesis only at light levels greater than $200 \mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. While a temperature optimum of 32.5 C for light-saturated photosynthesis by *Vallisneria* has been reported by Titus and Adams (1979), the temperature optimum for shaded plants would be lower, and dependent on the light available for photosynthesis (Bulthuis, 1983a). At low light levels, gross photosynthesis is dependent on electron transport, and would not be expected to increase as a function of temperature. Net photosynthesis in low light thus is reduced at high temperatures due to increases in respiratory enzyme activity (Perez and Romero, 1992, Taiz and Zeigler, 1991).

Plant respiration was affected by shade treatments and sediment type as well as by increasing temperature. Plants in shaded treatments and those grown in sand had lower respiration rates. Lower respiration rates may have indicated lower contributions of

growth respiration in slower-growing plants (Hutchinson, 1975) Some species of *Potamogeton* adapt to low light levels by increasing photosynthetic efficiency (Spence and Chrystal, 1970a, b, Hutchinson, 1975), however in this study net rates of photosynthesis were similar at low light levels regardless of the shade conditions under which plants were grown; while plants adapted morphologically, they did not adapt photosynthetically to the shade treatments imposed. Similar morphological responses have been reported for *Vallisneria* (Barko et al., 1982) and for seagrasses (Dennison and Alberte, 1982).

In this study, the temperature increases that significantly affected net photosynthesis were relatively small (25 to 30 C), as were the changes in temperature reported for backwaters of the Upper Mississippi River. Sullivan (1991) reported a maximum daily average temperature of 29 C for July 1988 in Weaver Bottoms, Pool 5, compared with maxima of 26 and 27 in July 1987 and July 1989 respectively. For Lawrence Lake, a Pool 8 backwater site, the Wisconsin DNR Long Term Resource Monitoring Program (unpublished data) reported surface and bottom temperatures of 30.5 and 28.5 on 17 August, 1988. In contrast, the surface water temperature on 17 August, 1992 was 22 C. Thus it appears that moderate increases in water temperature can significantly increase respiration and decrease net photosynthesis in the ecotypes of *Vallisneria* from the Upper Mississippi River (UMR). Temperature increases associated with low flows in the UMR and the probable algal blooms that would occur in late summer, could have significantly decreased the amount of carbon fixed and stored in overwintering tubers and precipitated the decline in *Vallisneria* following the 1988 drought.

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PAPER 2
THE DISTRIBUTION OF *VALLISNERIA AMERICANA* SEEDS AND SEEDLING
LIGHT REQUIREMENTS IN THE UPPER MISSISSIPPI RIVER

ABSTRACT

Vallisneria americana declined in backwaters of the Upper Mississippi River, U.S.A., after a drought in 1988. It has not reestablished itself in most pools and light availability has been low. To determine whether viable seeds of *V. americana* occurred in the seed bank of Lake Onalaska, the upper 5 cm of sediment was collected from 103 sites in May, 1990. These sediment samples were kept in pots at a depth of 1.0 m in an outdoor pond for 12 weeks. *Vallisneria americana* seeds germinated from sites throughout the lake and some seedlings produced tubers by the end of the study. Seeds of twelve other species of aquatic plants also germinated. The sensitivity of seed germination to light availability was examined by incubating fresh and stored seeds under shade cloth and determining germination percentages of each. Germination was insensitive to light. To determine the light requirements for seedling survival and tuber production, sediment from Lake Onalaska was incubated in ponds under neutral density shade screens reducing light to 2%, 5%, 9% and 25% of full sun. Seeds germinated under all shade treatments but survival was significantly higher in the 9% and 25% light treatments, and tuber production was restricted to these light levels.

INTRODUCTION

Studies of submersed aquatic plant populations have generally concluded that these populations appear to be maintained by clonal reproduction and growth from overwintering tubers, with little recruitment from seed banks (Sculthorpe, 1967, Rogers and Breen, 1980, Haag, 1983, Kautsky, 1990). Although flowering and seed set commonly occur in *Vallisneria americana* populations, seedlings appear to be rare in nature in temperate zones (Virginia Carter, pers. comm.; Titus and Hoover, 1991). Nevertheless, seed banks may be important for the reestablishment of submersed vegetation that has been eradicated by overgrazing, disease, or adverse environmental conditions. This could be analogous to the role of the seed bank in prairie wetlands for reestablishing extirpated emergent species during a drawdown (van der Valk and Davis, 1978). The success of revegetation from the seed bank would depend on the abundance and viability of seeds of different species, and on their physiological growth requirements.

Unlike the positive- or neutral-buoyant seeds and fruits of emergent aquatic vegetation, *Vallisneria* seeds and fruits are negatively buoyant, sinking to the sediment surface (McAtee, 1917, Kaul, 1978, Wilder, 1974, Davis, 1985). This implies that seed densities should be greatest in areas where adult plant densities are highest. Fruits may also be dispersed by water currents when plants are uprooted; by water fowl (Korschgen and Green, 1988), since diving water fowl will consume fruits (McAtee, 1917, Sculthorpe, 1967); and possibly by fish, as shown for *Najas* (Agami et al, 1988), since the crude protein content of fruits is high (Donnermeyer, 1982). Seeds may secondarily be dispersed as bed-load transport in rivers, but the extent to which this occurs is unknown.

Although some physiological information is available about seed germination requirements and seedling growth of aquatic plants under laboratory conditions, i.e. Muenscher, (1936), Spencer, (1987), van Wijck, (1989), recruitment, growth and spread are not well understood and published studies give differing results. For example, Muenscher (1936) reported that seeds of *Vallisneria americana*, *Najas flexilis*,

Potamogeton spp, *Heteranthera dubia* and *Sagittaria* died if dried. However, Choudhuri (1966) reported that seeds of *Vallisneria spiralis*, which appears to behave as an annual in monsoonal wetlands, germinated after drying.

Populations of *Vallisneria* declined in Pools 5-19 of the Upper Mississippi River after the summer of 1988, during which record low flows and high water temperatures were recorded (U.S. Army Corps of Engineers unpublished data, Sullivan, 1991). This native plant species, especially its overwintering tubers, has been highly valued in the backwater wildlife refuges along the Upper Mississippi River that were staging grounds for as much as 75% of the global canvasback duck population (Korschgen et al., 1987). Its loss has raised a number of questions related to the potential rate of recolonization of backwater habitats by native versus introduced species (especially eurasian water milfoil, *Myriophyllum spicatum*), e.g: what is the effective dispersal unit for submersed aquatic plants in rivers, what is the potential role of seed banks in recolonization, and what are the physiological requirements for seedlings to survive and produce overwintering tubers?

To address these questions we developed three studies. In the first, sediment was sampled to determine the distribution and density of seeds of *Vallisneria* and of other submersed aquatic species. In the second, seed germination under shade regimes was compared in greenhouse and pond settings to determine whether light availability affected germination. In the third, seedlings germinating from the seed bank were grown under replicated shade treatments to determine seasonal light requirements for production of overwintering tubers.

Study Area

Pool 7, Lake Onalaska, was chosen for these studies because of its historical importance as a staging area for canvasback ducks and because long-term monitoring studies of *Vallisneria americana* populations (Korschgen and Green, 1988, Korschgen, unpublished data) enable comparisons between previous *Vallisneria* populations and the current distribution of the seedbank.

Lake Onalaska is a large (2,835 hectares), shallow (mean depth 1.43 m) backwater area of the Upper Mississippi River, inundated in 1937 during the construction

of a 9-foot navigation channel and associated locks and dams (Korschgen et al. 1987). Water flows into the lake through two chutes from the Mississippi River channel running along the west side of the Pool. From the southern chute, Sommer's chute, the lake may receive up to 80% of its water (Pavlou et al., 1982). From the north and the east, Black River water enters the lake. The lake has three sediment types, based on physical characteristics (Figure 2). During 1990-1992 the following submersed species were observed in the lake: *Ceratophyllum demersum*, *Chara*, *Elodea canadensis*, *Heteranthera dubia*, *Myriophyllum spicatum*, *Najas flexilis*, *Potamogeton crispus*, *P. foliosus*, *P. natans*, *P. pectinatus*, *P. richardsonii*, *P. zosteriformis*, and *Vallisneria americana*. Sediment was sampled from 103 sites in Pool 7, Lake Onalaska, of the Upper Mississippi River (Figure 1).

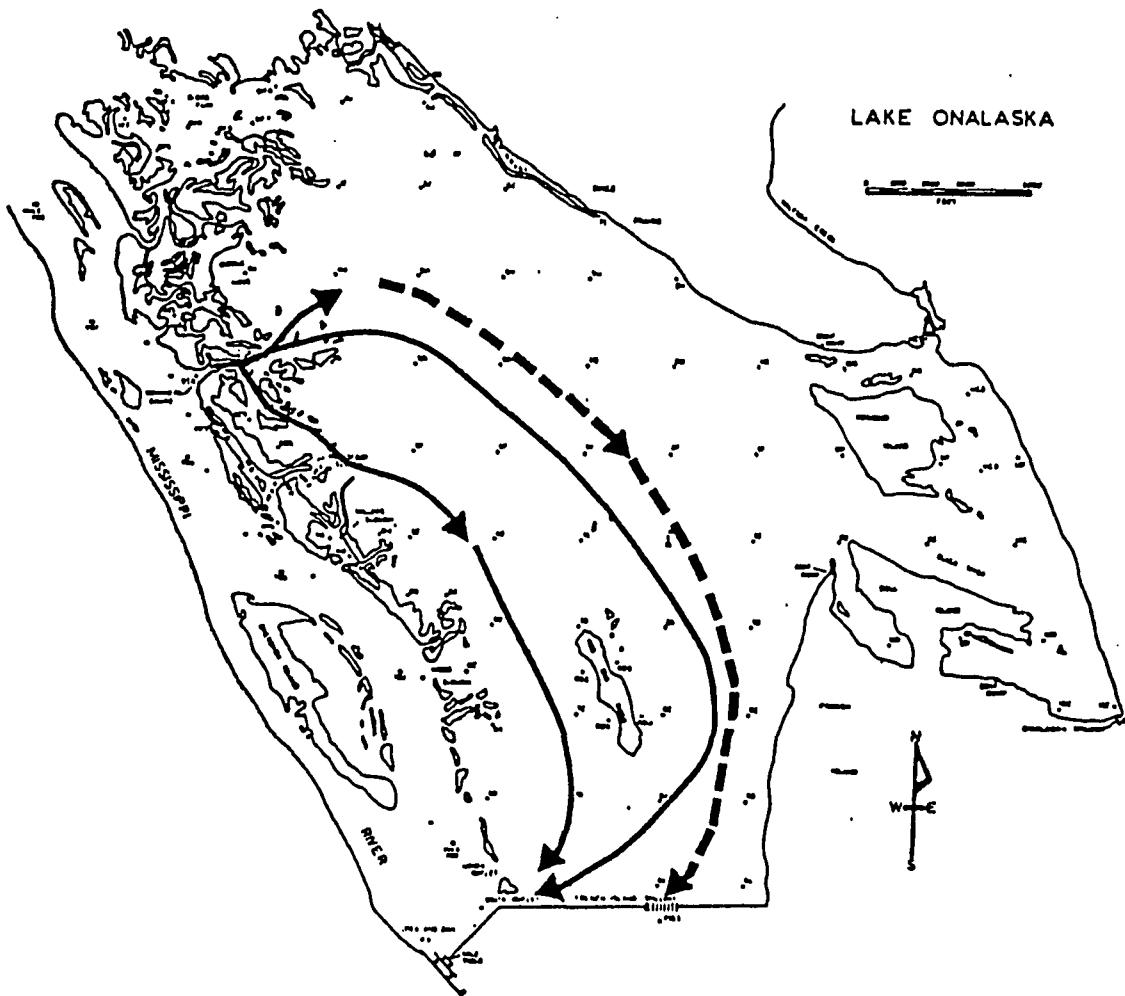


Figure 1. Lake Onalaska predominant flow patterns. Solid line indicates primary trajectory; dashed lines indicate secondary trajectory. From Pavlou et al., 1982

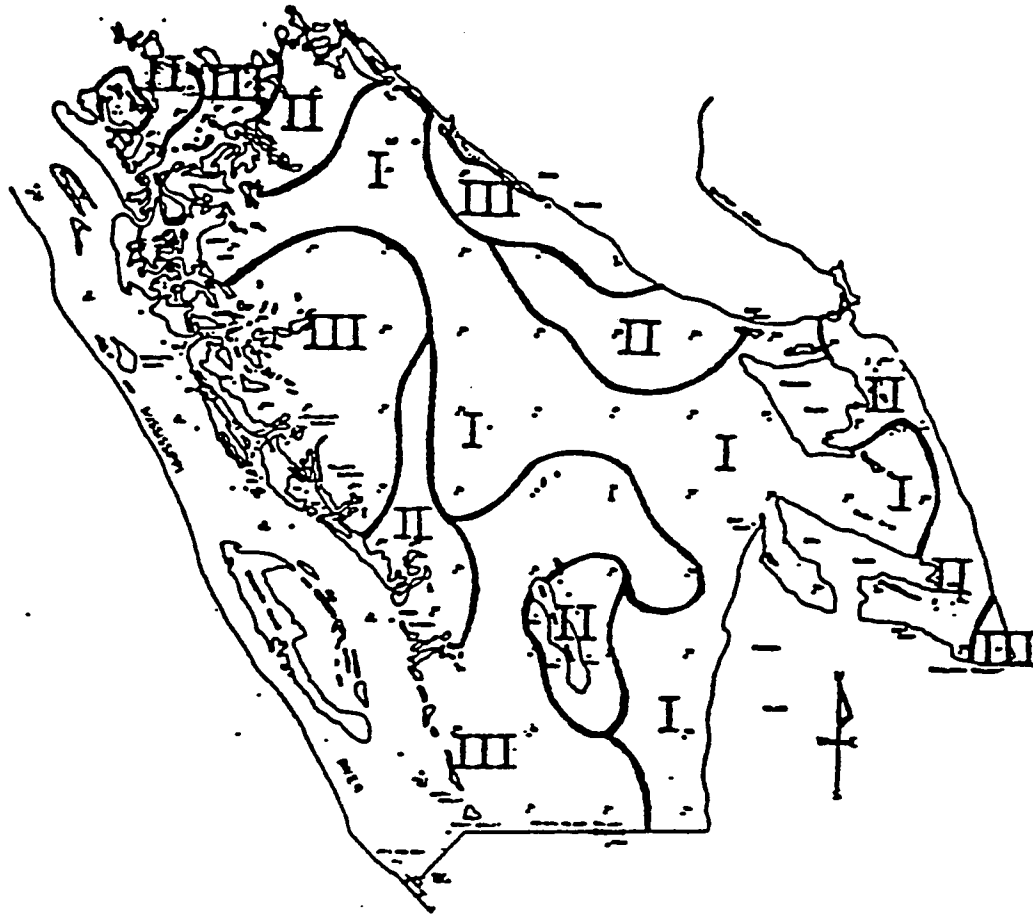


Figure 2. Lake Onalaska. Sediment types. I = fine; II = medium; III = coarse. From Pavlou et al., 1982

METHODS

Seed Bank Study

From May 28 to June 1, 1990, sediment cores were collected at 103 uniformly spaced grid points in Lake Onalaska. A LORAN positioning system was used to locate sites previously mapped using a grid system developed by Korschgen et al. (1987). Depth and all aquatic plant species were recorded at each site. A four-inch diameter clear PVC coring device was used to collect five sediment cores to a depth of 5 cm at each site (total volume per site 2 l). After roots, turions and tubers were removed, the cores were mixed and separated into three equal samples and each sample was placed in a bucket (266 cm² surface area) which was then placed in an outdoor concrete pond (4.9m by 9.5 m, mean depth 1.1 m) at 0.4, 0.8 or 1.2 m depth. Depths were chosen to determine whether germination was affected by light availability. The pond was located at the U.S. Fish and Wildlife National Fisheries Research Laboratory, on an island between the Mississippi and Black Rivers, near La Crosse, Wisconsin. Pond water came from a shallow (23 m deep) Black River aquifer.

Germination was monitored every two weeks until buckets were harvested at the end of August. This seedling assay method provided an estimate of the viable seeds present in the seed bank (the "ecologically active" portion of the seed bank, Haag, 1983), but did not provide information about the total numbers of seeds of species present. Species nomenclature is based on Fassett (1957). Depths of sampling points, species distributions and seed densities were mapped using a GIS system (Arc-Info, Version 6.1, 1992) on a GIS base map provided by the U.S. Fish and Wildlife Service Environmental Management Technical Center, La Crosse, Wisconsin. Sampled depths were divided into 11 depth classes (Table 1) . A two-factor nested analysis of variance (SAS Institute, 1987) was used to determine if seedling distributions were random or were significantly related to depth and location within depth.

Light Requirements for Seed Germination

Vallisneria fruits were collected in October and stored wet for one month at 4 C in a cold room. Seeds were washed from the fruits, sorted, and counted into lots of 20

Table 1. Depth classes for Lake Onalaska

Class	Depth
1	$x < 0.50 \text{ m}$
2	$0.50 \text{ m} \leq x < 0.75 \text{ m}$
3	$0.75 \text{ m} \leq x < 1.00 \text{ m}$
4	$1.00 \text{ m} \leq x < 1.25 \text{ m}$
5	$1.25 \text{ m} \leq x < 1.50 \text{ m}$
6	$1.50 \text{ m} \leq x < 1.75 \text{ m}$
7	$1.75 \text{ m} \leq x < 2.00 \text{ m}$
8	$2.00 \text{ m} \leq x < 2.25 \text{ m}$
9	$2.25 \text{ m} \leq x < 2.50 \text{ m}$
10	$2.50 \text{ m} \leq x < 2.75 \text{ m}$
11	$2.75 \text{ m} \leq x$

using a dissecting microscope. Seeds were sown on sterilized sand in 500 ml opaque plastic cups that were then filled with distilled water and either uncapped (full light), capped with black plastic shade cloth screens rated to reduce light by 47, 55, 63 or 92%, or covered with black plastic (dark). Cups were arranged on a greenhouse bench in two Latin Squares of six rows and columns each to control for position effects (twelve replicates of each shade treatment). Natural light was augmented by metal halide lamps with 14 hr light/ 10 hr dark photoperiod. Seedlings were counted three weeks after planting. Instantaneous light levels in the cups under each treatment were measured in place using a LiCor underwater quantum sensor.

To examine the responses of overwintering seeds, fruits that had not been used for the greenhouse study were stored wet at 4 C until the following April. Forty seeds each were sown in buckets on washed sand in outdoor concrete ponds 1 m deep, in randomized blocks of cells 1 m² with no shade cloth, or under shade cloth rated to reduce light by 47, 63, 73, 80 or 92 %. Seed germination was counted after six weeks.

Light and Seedling Growth and Tuber Production-1992

Seedling emergence and seedling tuber production were monitored as part of a 1992 study on the light requirements for tuber production from plants grown from overwintering tubers (Kimber and van der Valk, 1994). Sediment was collected in mid-April, 1992, from Pool 7, Lake Onalaska, Wisconsin from an area of a former *Vallisneria* bed. It was mixed and placed in buckets in two concrete ponds (4.9 m by 9.5 m) at the U.S. Fish and Wildlife Service National Fisheries Research Laboratory in La Crosse, Wisconsin. Each pond ranged in depth from 0.9 m to 1.1 m. Two submersible pumps in each pond circulated and aerated water such that the turnover rate was once every 2.4 days. Five buckets of sediment were placed in each of 48 shade cells (24 cells in each of two ponds), that were arranged in rows (randomized blocks) of four shade treatments each. Each cell (surface area 1 m by 1 m) was isolated from the next by black plastic side walls that extended down to approximately 20 cm from the bottom of the ponds. The bottom was left free to increase water flow between cells and decrease temperature differences between light treatments. The tops of the cells were covered

with removable frames having either no shade cloth (open cell), or black plastic shade screen, resulting in a reduction of light to 25, 9, 5, or 2 % of ambient, averaged over the growing season (Kimber and van der Valk, 1994).

The experiment was planted on April 26. On June 24, all buckets were observed and seedling emergence recorded. Eight harvests were made over the growing season. In June, July and August, buckets were harvested approximately every two weeks. On June 17, July 15 and August 15 one bucket of was harvested from odd-numbered rows (six replicates of each treatment); on June 30, July 27 and August 29, even-numbered rows were harvested (six replicates). On September 23 one bucket of sediment from each cell was collected (twelve replicates). At harvest the number of seedlings of each species present was recorded for each bucket. For each *Vallisneria* seedling, the numbers and lengths of leaves and the presence of tubers were recorded. Data were analyzed statistically by one-way analysis of variance for unequal sample sizes (General Linear Models procedures, SAS Institute, 1987).

RESULTS

Seed Bank

The depth at which buckets were placed had no effect on germination or seedling survival; the analyses presented here are based upon the number of seedlings or sporelings found of each species at a site, pooled for all three buckets. Seeds generally had germinated by six weeks after the experiment started. Viable seedlings were found in 90 of the 103 sites sampled (Table 2) comprising species of rooted submersed, floating submersed, emergent and floating plants. *Vallisneria americana* was the most common and widespread species (Figure 3), present in 62 of the sites, followed by *Najas flexilis*, a species that reproduces only by seed (Fassett, 1957). Seedlings of *Potamogeton pectinatus* were the rarest encountered in this survey.

A mean depth of 1.35 m was calculated for the sampled locations. Around the mean, the distribution of sampled locations with depth (Figure 4) indicates that changes in depth are gradual, with most sites between 0.5 and 2.0 m deep. The total number of species that occurred at a given depth declined slightly with increasing depth (Figure 5) and individual species distribution varied with depth (Table 2).

Vallisneria and *Heteranthera* seedlings had the widest distribution, being found in all depth classes where seedlings were found (Table 2 and Figure 6). In contrast, viable seedlings of *Ceratophyllum* and *Elodea* appeared to be restricted to shallow depths (less than 1.5 m for *Ceratophyllum* and less than 1.0 m for *Elodea*). *Pontederia* seedlings appeared to be restricted to emergent community locations: six of the seven sites where *Pontederia* seedlings were found were in *Typha*, *Sagittaria* or *Pontederia* beds. *Sagittaria* seedlings were not restricted to the same degree: beds of emergents were present at only five of the twelve sites where seedlings were found. Species diversity was highest in three regions of the lake (Figure 7): the shallow emergent beds fringing inflows at Sommer's chute; sites north of Sommer's chute receiving inflows from the Mississippi River and the Black River, and shallow sites along the eastern shore of the lake.

Table 2. Aquatic seedling species composition from Lake Onalaska

Species	Number of sites	Density ² Mean	Density SD	α depth	α row within depth
<i>Ceratophyllum demersum</i>	14	32.12	43.00	0.0001	0.0238
<i>Chara sp.</i>	26	46.12	69.62	0.0002	0.0509
<i>Elodea canadensis</i> ³	5	120.00	93.00	0.0002	0.0007
<i>Heteranthera dubia</i>	25	17.50	8.12	0.4011	0.2304
<i>Lemna minor</i> ¹	--				
<i>Myriophyllum spicatum</i>	16	18.75	13.75	0.0038	0.0339
<i>Najas flexilis</i>	46	32.62	30.00	0.7675	0.5280
<i>Pontederia cordata</i>	7	12.50	0	0.0053	0.0002
<i>Potamogeton crispus</i> ³	15	200.88	241.62	0.6965	0.4777
<i>P. foliosus</i>	24	12.50	0	0.0659	0.6721
<i>P. pectinatus</i>	3	12.50	0	0.0180	0.0422
<i>Sagittaria sp.</i>	13	39.38	37.12	0.0001	0.0001
<i>Vallisneria americana</i>	62	36.75	27.25	0.5396	0.4560

¹ Sites could not be determined for *L.minor*

² Density (plants/m²) for sites where species present

³ From fragments

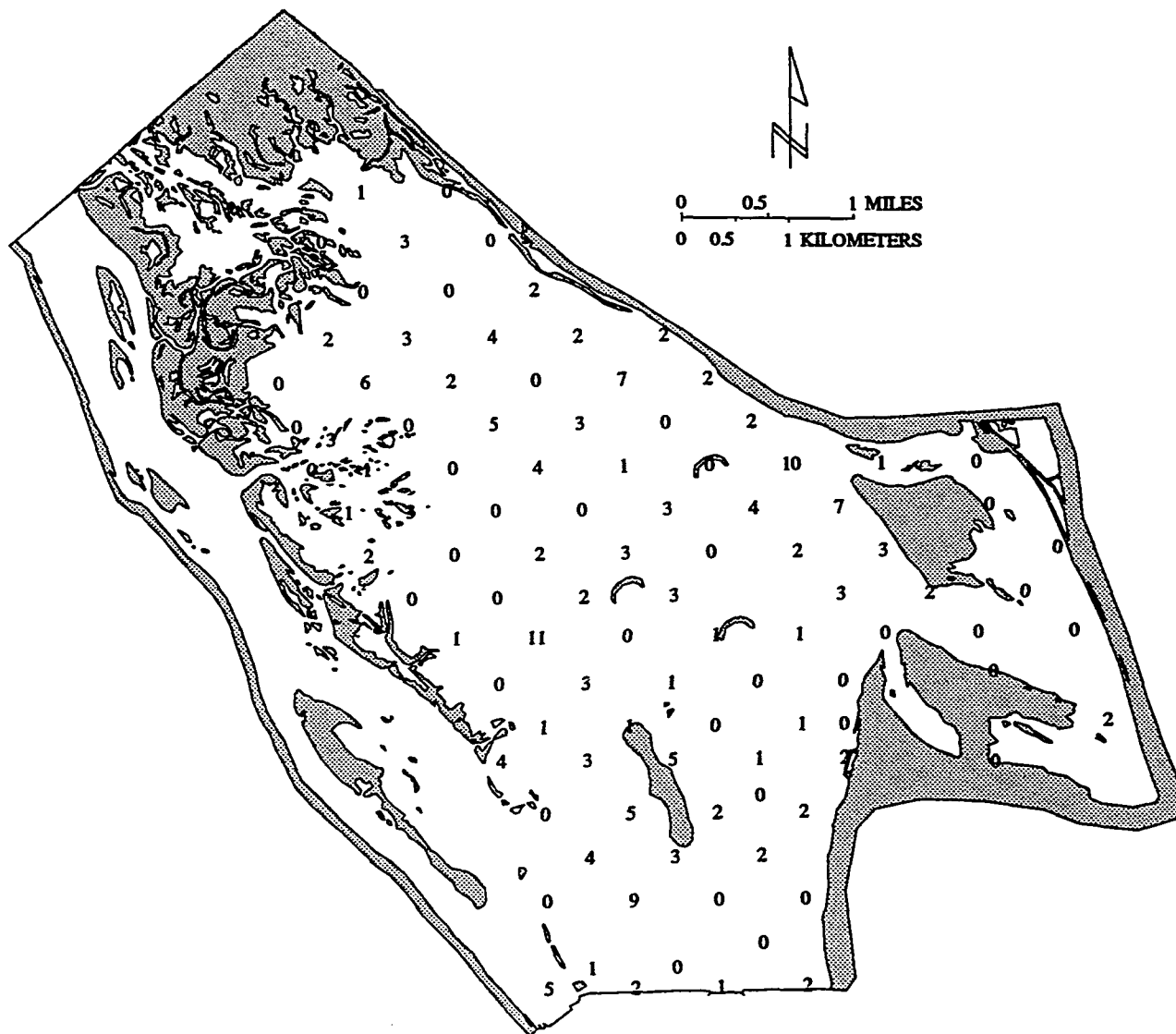


Figure 3. Distribution of *Vallisneria* seedlings in Lake Onalaska. Numbers are seedling densities

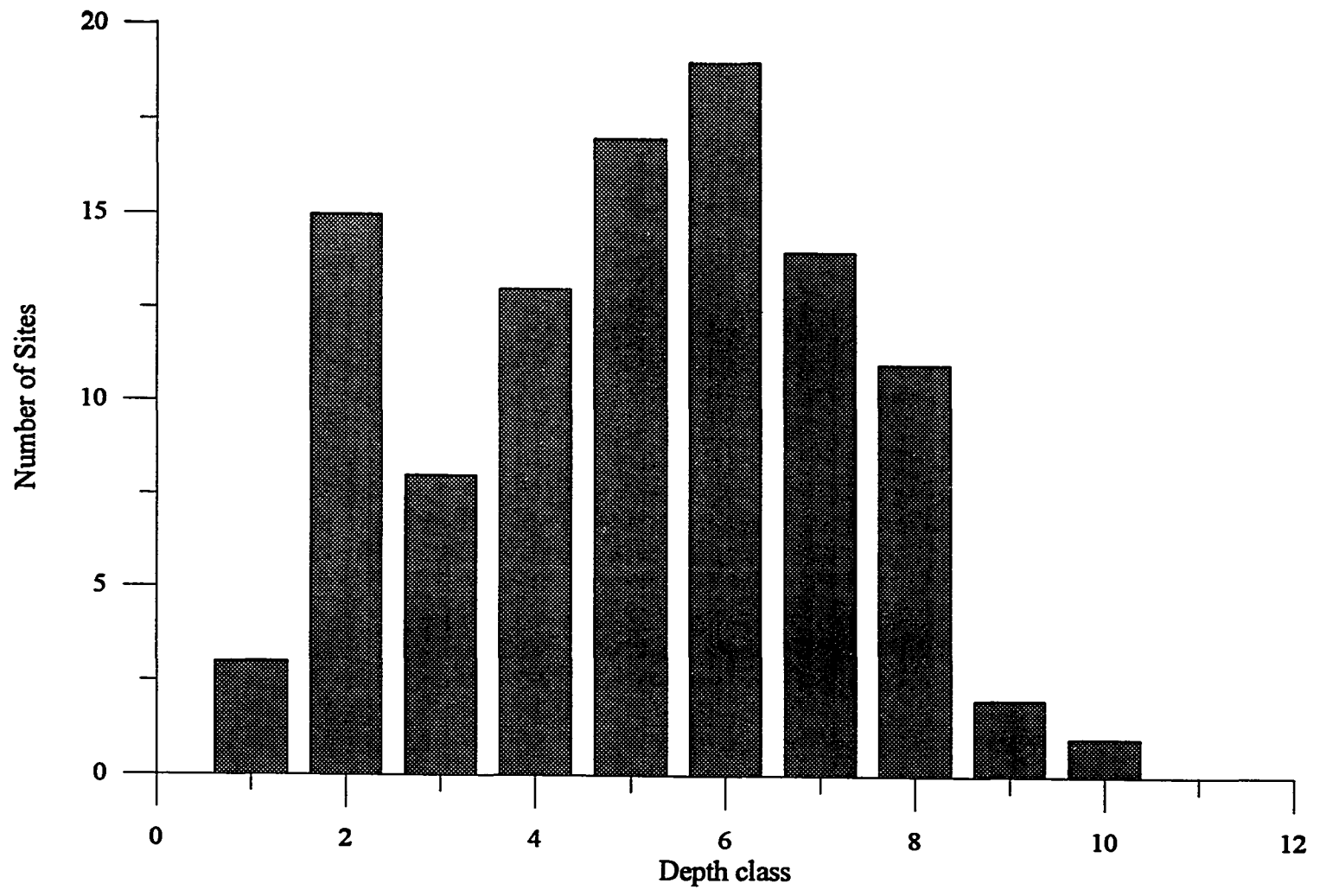


Figure 4. The distribution of depth classes for sampled sites in Lake Onalaska

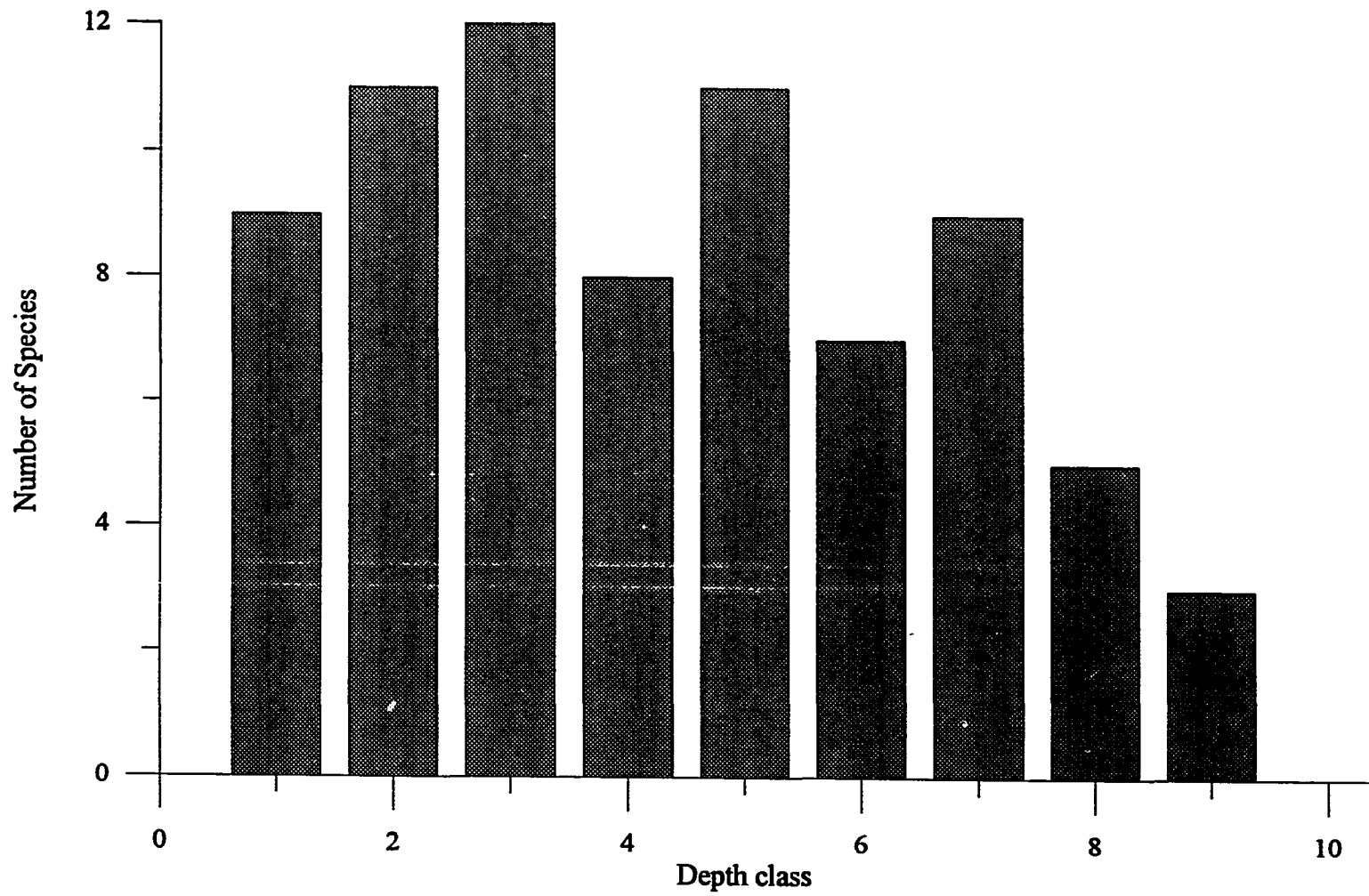


Figure 5. The distribution of the total number of species with depth class in Lake Onalaska

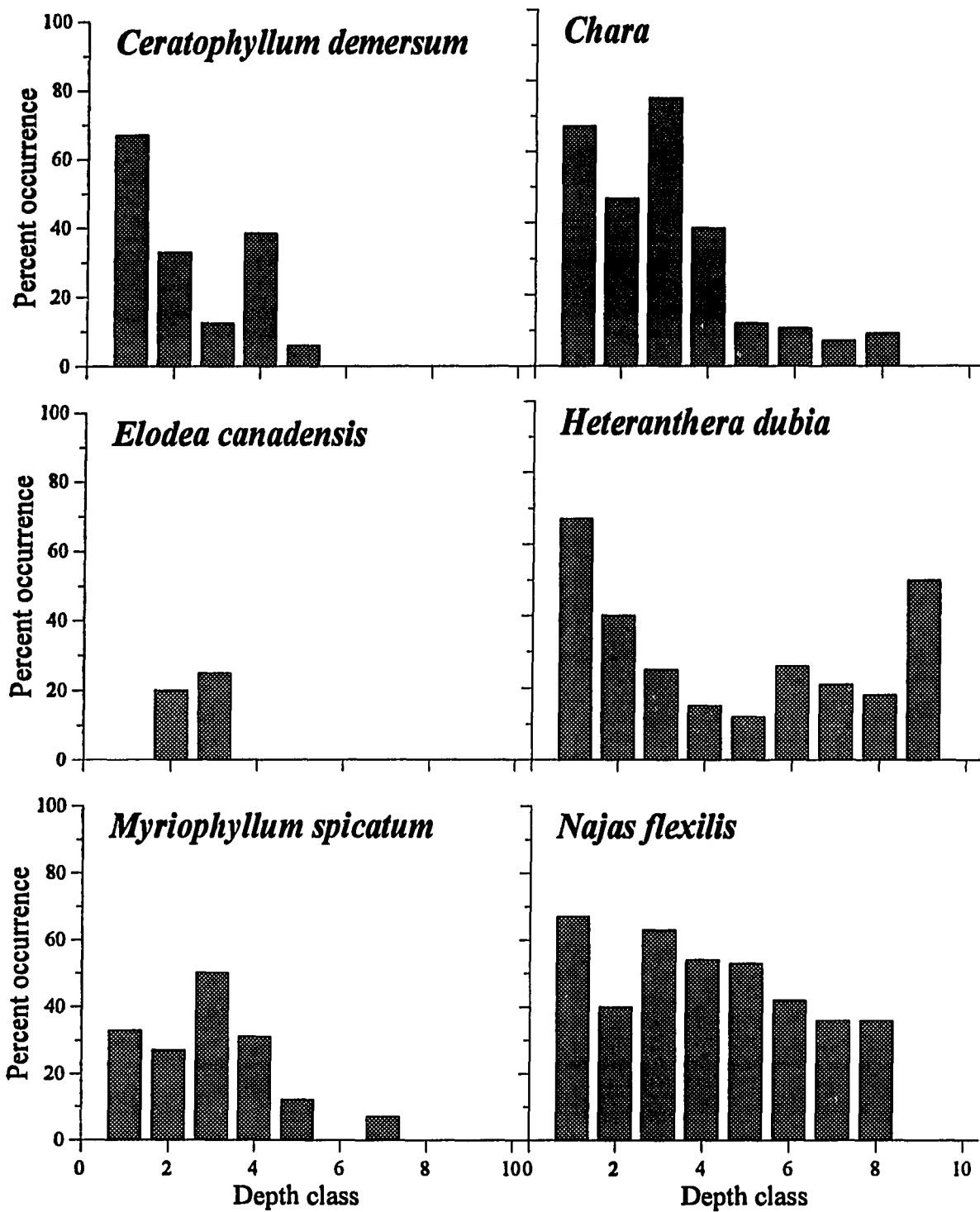


Figure 6. The distribution of each species with depth class

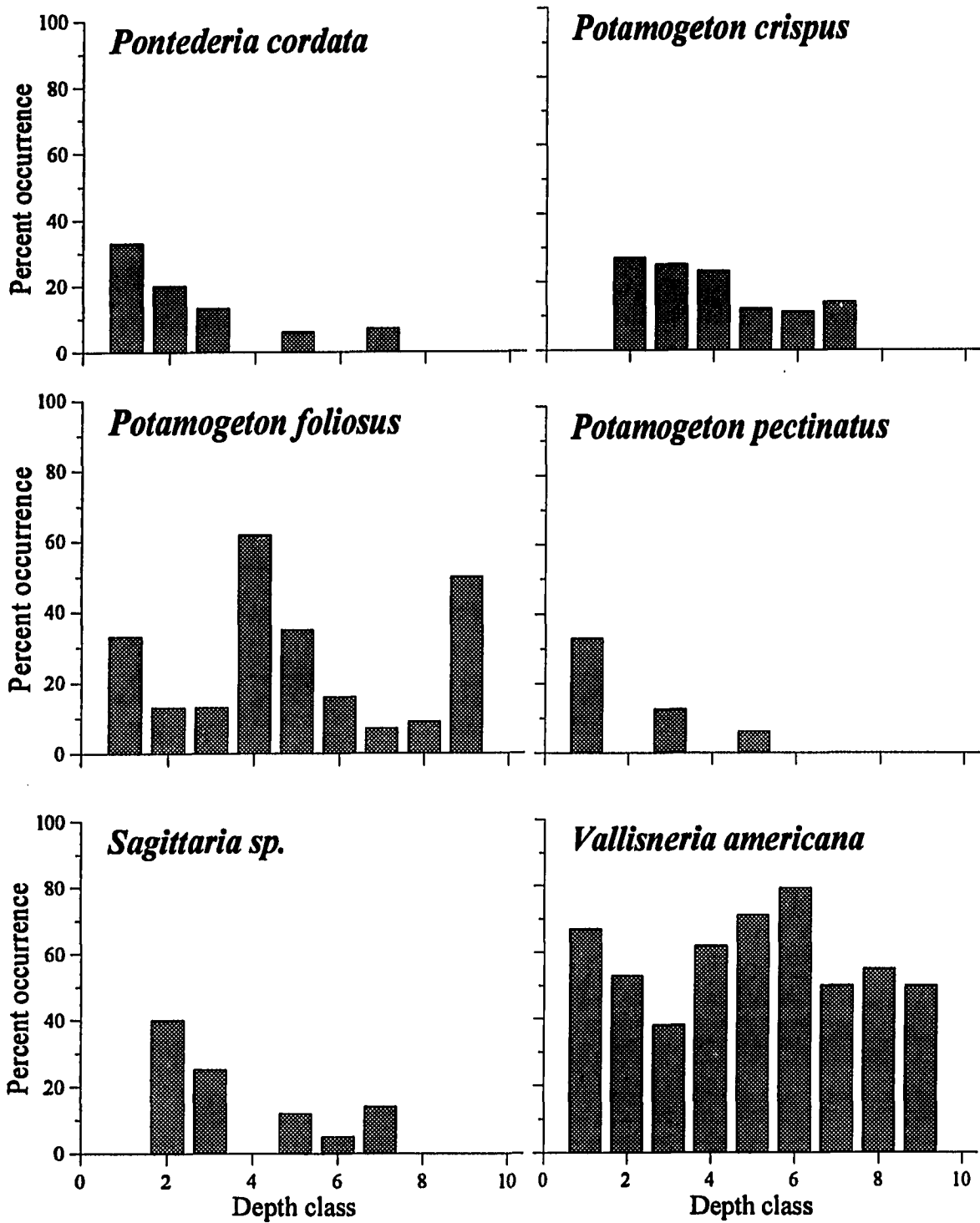


Figure 6. continued.

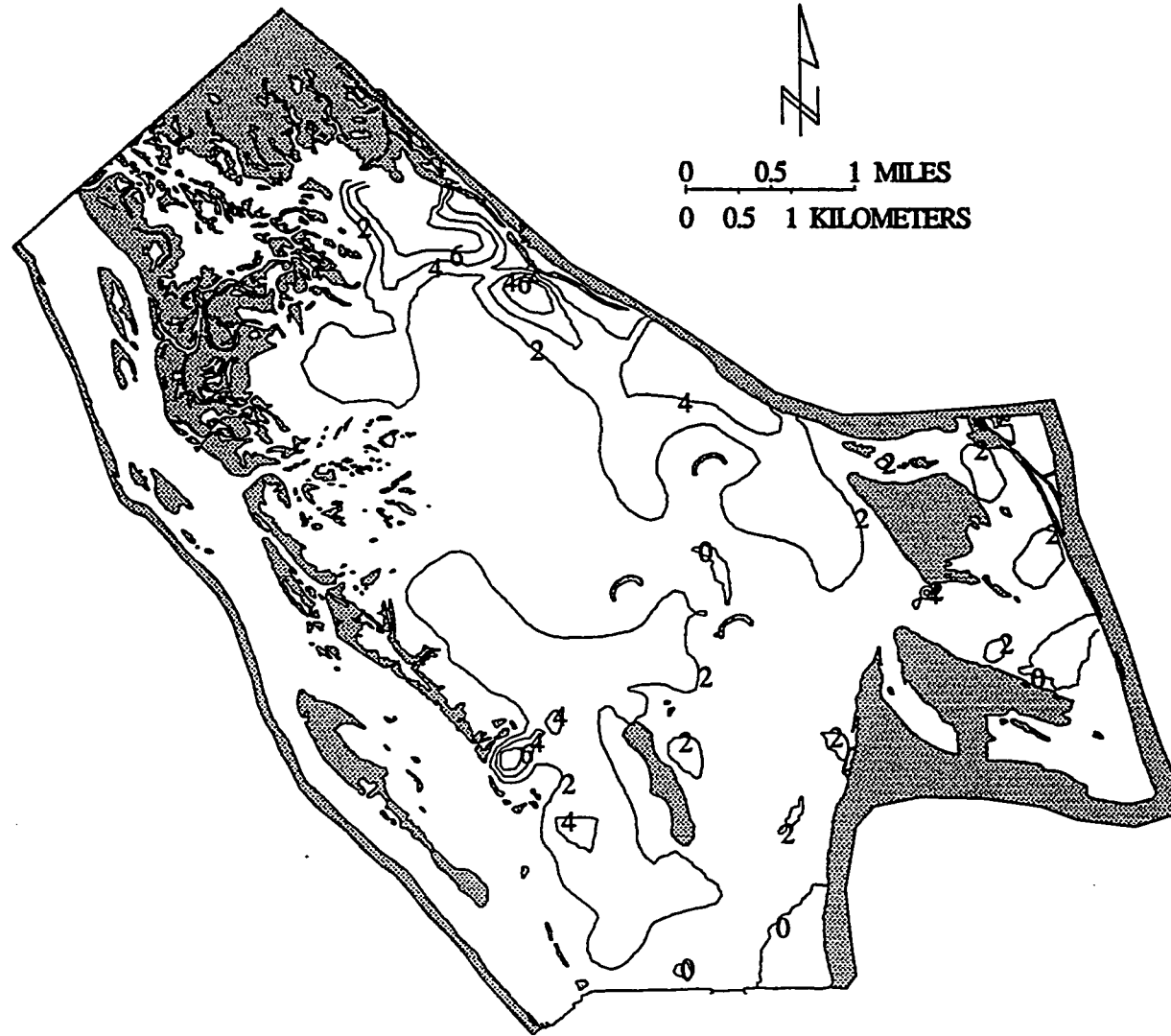


Figure 7. Contours of species diversity of seedlings in Lake Onalaska

Light Requirements for Seed Germination

Seeds germinated in all treatments in the greenhouse study (Table 3). The percentage of germination was not different between any of the light treatments, but was significantly higher in the dark treatment. Seeds from the same source also germinated in all treatments in the outdoor pond experiment conducted the following spring, and there was no significant effect of shading on seedling germination (Table 3).

Light and Seedling Growth and Tuber Production-1992

As observed during the earlier seed bank survey, seedlings in this experiment germinated approximately six weeks after the experiment was initiated. Seedling germination for all species, observed for all buckets on June 24, was not significantly affected by the three higher light treatments imposed (Table 4), but was significantly lower in the 2 % light treatment.

In subsequent harvests, new seedlings appeared that had not been observed in the June 24 census (Table 4), indicating that seeds continue to germinate throughout the summer, and especially towards the end of the summer (note September 23 and October 12 harvests). In spite of new recruitment, overall numbers of *Vallisneria* seedlings at the end of the summer were dependent on light availability (Tables 4 and Table 5). The mean numbers of seedlings from the 25% and 9% light treatments as measured on September 23 were higher than the numbers of seedlings found in the June 24 census for the same light treatments (Table 5), and were also higher than the September 23 harvests of seedlings in the 5% and 2% light treatments. Seedlings from the two higher light treatments also produced tubers (Table 4); these were not found in seedlings from the 5% and 2% treatments. Tuber production by *Vallisneria* seedlings was also observed in the 1990 seed bank study. In both studies, seedlings produced single, short rosettes of four to eight leaves (mean length 5 cm) and, after growing to that stage, stored net photosynthate in belowground overwintering tubers (mean fresh weight, 0.07 g). *Sagittaria* seedlings, which resemble those of *Vallisneria*, also produced single, short rosettes and tubers by the end of the seed bank study. In addition, *Chara* produced gametangia, *Najas* flowered and set seed, and *Heteranthera* produced corms.

Table 3. Germination of *Vallisneria* seeds as a function of light availability

Treatment	Greenhouse						Pond			
	N	Midday Light ($\mu\text{moles}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)		Percent Germination		T-Test ($\alpha = 0.05$)	Percent Germination			T-Test ($\alpha = 0.05$)
		Mean	SD	Mean	SD		N	Mean	SD	
Open	12	228	104	37	24	A	6	34	17	A
55 %	12	108	40	34	25	A				
63 %	12	75	28	39	28	A	3	19	11	A
80 %	12	48	22	48	23	A	4	49	14	A
92 %	12	11	5	30	26	A	7	36	18	A
0 %	12	0	0	68	27	B				

Table 4. Seed bank germination and survival dynamics (total seedbank)

Percent light transmission	N	Harvest Date	Initial ¹ Census	-----Harvest ² -----			Number of <i>Vallisneria</i> seedlings	
				New Survived	Died	Total		
25	12	30 Jun	5	1	2	3	3	2
	12	27 Jul	6	4	3	3	7	2
	12	15 Aug	4	2	2	2	4	3
	12	29 Aug	1	6	0	1	6	1
	24	23 Sep	6	18	4	2	22	17
	24	13 Oct	12	5	8	4	13	10
	Mean	96		0.354 A ³				
9	12	30 Jun	0	3	0	0	3	3
	12	27 Jul	4	2	2	2	4	2
	12	15 Aug	2	4	2	0	6	3
	12	29 Aug	9	5	1	8	6	3
	24	23 Sep	4	12	1	3	13	10
	24	13 Oct	4	15	1	3	16	12
	Mean	96		0.240 A				
5	12	30 Jun	0	2	0	0	2	2
	12	27 Jul	3	4	1	2	5	4
	12	15 Aug	3	3	1	2	4	4
	12	29 Aug	5	4	0	5	4	4
	24	23 Sep	12	12	5	7	17	7
	24	13 Oct	5	7	5	0	12	7
	Mean	96		0.292 A				
2	12	30 Jun	1	2	0	1	2	1
	12	27 Jul	4	1	2	2	3	1
	12	15 Aug	2	2	1	1	3	3
	12	29 Aug	2	0	0	2	0	0
	24	23 Sep	5	8	2	3	10	7
	24	13 Oct	3	2	0	3	2	2
	Mean	96		0.177 B				

¹ Numbers of seedlings found in each treatment counted in each bucket on June 24.

² On each harvest date after the initial census, seedlings were counted in harvested buckets of both sediment treatments.

³ Means: percentages of buckets with seedlings of all species. Means with the same letter are not significantly different at $\alpha = 0.05$.

Table 5. *Vallisneria* presence as a function of light availability, September 23 census

Percent light transmission	N	Mean ¹	T grouping	Mean total Fresh weight (g)	% seedlings with tubers	Mean tuber Fresh wt (g)
25	12	1.000	A	0.22	33.3	0.10
9	12	0.583	A B	0.08	25.0	0.04
5	12	0.250	B	0.03	0	
2	12	0.167	B	0.02	0	

¹ The mean represents the fraction of total buckets which contained seedlings

² Means with the same letter are not significantly different at $\alpha = 0.05$

DISCUSSION

The seed bank did not reflect the composition of the vegetation within the lake. For example, extensive beds of *Potamogeton pectinatus* were observed in the lake in 1991, but *P. pectinatus* was the rarest species in the seed bank. Similarly, no seedlings of *P. richardsonii* and *P. zosteriformis* were found, even though adult plants have been observed in the lake (Sohmer, 1975). In a study of Lake Wabamun, Haag (1983) found these species to be rare in the germinating seed bank though they were common in the adult population and attributed the lack of germination to strong dormancy or a long time requirement for germination.

Species diversity was higher in the sandy sediments of areas found either in the northern part of the lake, close to the eastern shore, or near Sommer's chute. Sandy sediments are associated with stronger currents or with greater exposure or wave action (Keddy, 1982). Seeds may be carried into these areas, especially the area near Sommer's chute, from the main channel of the Mississippi River or the Black River. Total species distribution patterns also reflected the previous distribution of adult *Vallisneria* beds (Figure 8), indicating that the beds may trap seeds or other propagules of other species. The lower species diversity in the central and southern portions of Lake Onalaska may be explained by depth limitations for some species. Alternatively, seedlings may be less viable due to burial by silt and clay in the middle of Lake Onalaska. Hartleb et al. (1993) reported that seeds of *Myriophyllum spicatum* had lower percentages of germination when buried by more than 2 cm of sediment.

Germination of *Vallisneria* seeds occurred regardless of storage time or light (Table 3). This is similar to results reported by Muenscher (1936), in which *Vallisneria*, stored either at 1-3 C in the dark or at 18-20 C in diffuse light, germinated regardless of treatment, in contrast to many of the other species examined. This may imply that *Vallisneria* has no inherent dormancy or germination requirements. Muenscher (1936) also reported that *Vallisneria* had higher rates of germination when protected from direct sunlight. The insensitivity of *Vallisneria* seed germination to light level and the greater germination percentage in darkness are similar to the responses of

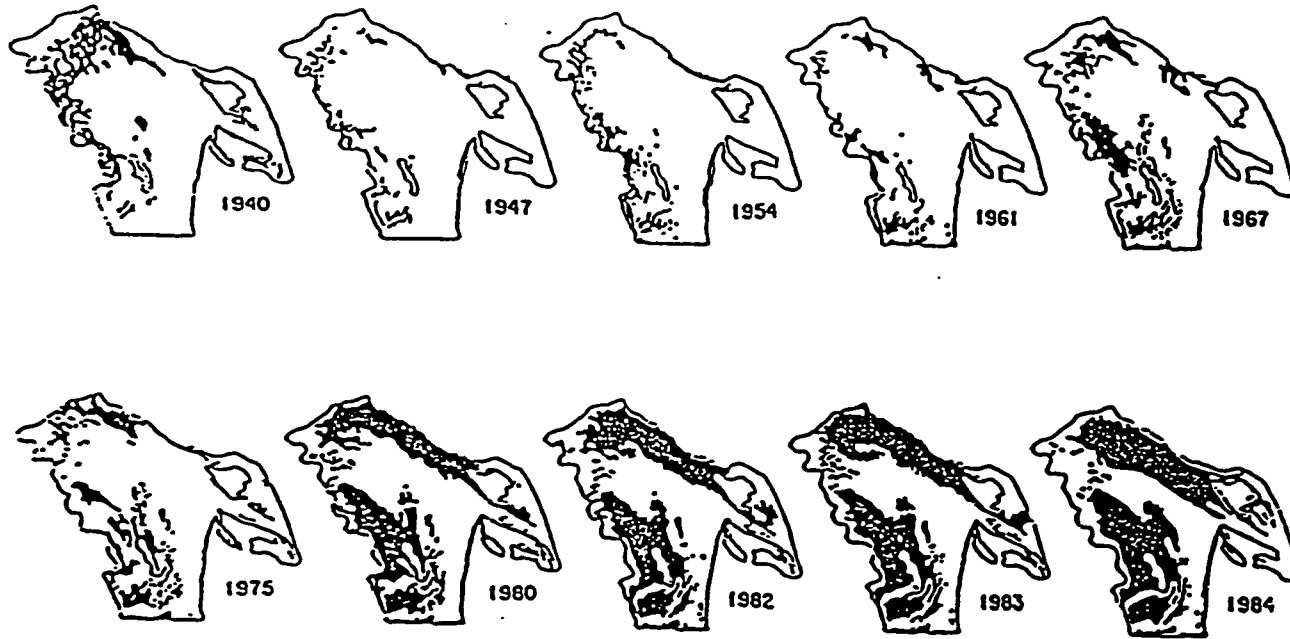


Figure 8. Historical distribution of *Vallisneria* in Lake Onalaska mapped by C.E. Korschgen (unpublished data)

Najas marina (Forsberg, 1965, Agami and Waisel, 1984); *Najas marina* had greater germination in darkness than at any light level. In contrast, Choudhuri (1966) reported 89 % germination of *Vallisneria spiralis* seeds in an alternating day/night regime as compared with 10 % germination in continuous darkness.

Seedling survival, growth and reproduction was significantly greater in treatments with at least 9% of surface light availability over the growing season. These light requirements are the same as those for plants grown from tubers (Kimber and van der Valk, 1994) and are in agreement with field studies in the Potomac River indicating that minimal seasonal light availability of 10% is necessary for *Vallisneria* clonal reproduction (Carter and Rybicki, 1990). Light levels in Lake Onalaska were monitored during the summer of 1990 (Owens, 1993) and indicate that the depth for 10% light availability was less than 0.5 m. In the seed bank study, 3 sites were less than 0.5 m and *Vallisneria* occurred at 2 of those locations. Based on the results of this study, the viable *Vallisneria* seedlings present in shallows should be able to survive and produce overwintering tubers. While tuber production by seedlings of *Vallisneria* may provide a mechanism for reestablishment of populations after disappearance, the extent and frequency to which this occurs is unknown.

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GENERAL SUMMARY

Vallisneria americana declined in the Upper Mississippi River after a drought in 1988. A hypothesis for the decline was that record high water temperatures coupled with low light levels increased respiration rates and thus light requirements for growth. Seasonal light requirements for growth and tuber production of approximately 9% of surface light were estimated from field studies of *Vallisneria* growth at 0.5, 1.0 and 1.5 m depth. Pond studies where plants from tubers were grown in lake sediment and sand-amended low fertility lake sediment in 2, 5, 9 or 25 % light in outdoor ponds produced similar results. Sediment fertility effects on growth were increasingly important ($\alpha = 0.05$) at average light intensities greater than $110 \mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, but low sediment fertility did not prevent plants in high light from producing tubers.

Instantaneous light compensation points were typically between 9 and 18 $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Net photosynthesis decreased with temperature increases from 20 to 30 C; these effects were greater at lower light levels.

Vallisneria americana germinated from sites throughout the lake and produced tubers. Twelve other species of aquatic plants germinated from the seed bank. To determine the light requirements for seedling survival and tuber production, sediment from Lake Onalaska was incubated in ponds under 2, 5, 9 or 25 % light. Seedlings germinated under all shade treatments but survival was significantly higher at 9% and 25% light availability, and tuber production was restricted to these light levels.

For both seedling and plants growing from tubers, light requirements were similar, and light was the primary factor limiting growth. Light compensation points were low and similar to those reported for other submersed macrophytes (Sand Jensen and Madsen, 1991), indicating that *Vallisneria americana* is adapted to low light levels.

Increased water temperatures decreased net photosynthesis up to 30 % at low light levels. These results imply that *Vallisneria* growing in turbid water will be more productive in cooler temperatures. These results may also have implications for management: Bulthuis (1983b and 1987) proposed that summer dredging operations would have more deleterious effects on seagrasses due to turbidity increases occurring at

the same time that plant respiratory demands were increasing as water temperatures rose. This would also be true for *Vallisneria*, a rosette species with similar growth form to many seagrass species.

The potential for *Vallisneria* to recolonize Lake Onalaska appears to be limited by the availability of depths where light is adequate, which are not colonized by eurasian water milfoil, now present in the lake. Restoration efforts should focus on areas less than 1.0 m deep, and on areas receiving higher flow from the Mississippi River or the Black River. These areas would have more constant temperatures, and decreased boundary layers for gas exchange.

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