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Growth and recruitment in *Vallisneria americana* as related to average irradiance in the water column

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Abstract

We investigated the relationships between average irradiance, \bar{I} , and the growth responses of *Vallisneria americana* over 102 days. \bar{I} was manipulated by changing the planting depth and turbidity of the water. Growth responses were indicated by the Relative Growth Rate (RGR), Net Assimilation Rate (NAR), Leaf Area Ratio (LAR) and the proportion of the canopy (B_e) exposed to irradiances above the daily average light compensation point. The relationship of \bar{I} and RGR ($r^2=0.894$) mirrored that between \bar{I} and NAR, an estimate of net plant photosynthesis ($r^2=0.934$). The compensation irradiance, \bar{I}_c , calculated from the NAR– \bar{I} relationship, was similar to the mean value for leaves measured in short-term laboratory experiments ($26 \mu\text{mol m}^{-2} \text{s}^{-1}$). Changes in LAR with \bar{I} were less than for NAR, showing that *V. americana* alters its canopy morphology with changes in turbidity. As \bar{I} influenced B_e , increases in RGR and shoot and leaf recruitment were accompanied by increases in B_e . An empirical RGR– \bar{I} relationship for *V. americana* accurately predicts biomass and colonised depth in turbid waters. The model suggests that growth does not occur at $B_e < 22\%$, and that shoot and leaf recruitment do not occur at $B_e < 80\%$, as resources then are diverted to leaf extension. © 1998 Elsevier Science B.V. All rights reserved

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1. Introduction

The relationship between photosynthesis and irradiance (P–I) in submersed macrophytes is well-documented (Adams et al., 1974; Madsen and Sand-Jensen, 1991; Schwarz and Howard-Williams, 1993; Schwarz et al., 1996). Less is known of the way that growth

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and irradiance interact to produce biomass at the whole-plant and seasonal time scales (Carter et al., 1996). One option is to measure net photosynthesis rates, biomass and light profiles in the canopy, and so construct a carbon-balance model for the whole plant (Van der Bijl et al., 1989; Zimmerman et al., 1994). This requires many repetitive measurements, particularly if light, turbidity and biomass change through the growing season. An alternative is to assess the relationship between light availability over an extended period and the growth of a plant.

Most clear-water studies consider incident Photosynthetically Active Radiation (PAR: 400–700 nm) and assume negligible attenuation due to depth or interception by the canopy (Barko and Smart, 1981; Sand-Jensen and Madsen, 1991; Madsen and Sand-Jensen, 1994; cf. Tanner et al., 1993). In turbid water, however, rapid light extinction compels a different approach. In this paper, the light available for growth is represented by the average irradiance (\bar{I}) between the water surface and sediment in the absence of plants (Riley, 1957; Oliver and Ganf, 1988). This is related to the mean daily subsurface irradiance \bar{I}'_o , the depth to the sediment z_r and the downwelling extinction coefficient K_d :

$$\bar{I} = \frac{\bar{I}'_o (1 - e^{-K_d \cdot z_r})}{K_d \cdot z_r} \mu\text{mol m}^{-2} \text{ s}^{-1} \tag{1}$$

Table 1 contains definitions of all symbols.

Where the canopy reduces the irradiance, the specific absorption coefficient K_s of leaf biomass B (per m^3 over z_r) may be introduced:

Table 1
Symbols and parameters referred to in the text

| Symbol | Definition | Units |
|------------------------|---|--|
| B | Biomass | g m^{-3} |
| B_c | Biomass exposed to irradiances above the daily average light compensation point | g m^{-3} |
| \bar{I} | Average irradiance between water surface and sediments in the absence of plants | $\text{mol m}^{-2} \text{ s}^{-1}$ |
| I'_o | Mean daily subsurface irradiance, averaged over daylight hours | $\mu\text{mol m}^{-2} \text{ s}^{-1}$ |
| \bar{I}_c | Minimum \bar{I} for growth (cf. Sand-Jensen and Madsen, 1991) | $\mu\text{mol m}^{-2} \text{ s}^{-1}$ |
| \bar{I}_k | Onset of light-saturated growth (RGR_{max}/α) | $\mu\text{mol m}^{-2} \text{ s}^{-1}$ |
| \bar{I}_{ini} | Mean noon irradiance at leaf tips at the start of the experiment | $\mu\text{mol m}^{-2} \text{ s}^{-1}$ |
| I_c | Light compensation point in leaf pieces | $\mu\text{mol m}^{-2} \text{ s}^{-1}$ |
| I_k | Onset of light-saturated photosynthesis in leaf pieces | $\mu\text{mol m}^{-2} \text{ s}^{-1}$ |
| K_d | Rate of downwelling extinction (or attenuation) coefficient | ln m^{-1} |
| K_s | Specific absorption coefficient | $\text{m}^2 \text{ g}^{-1}$ |
| z_r | Depth to sediment (cf. “mixed depth”) | m |
| α | Growth efficiency; linear slope of the light-limited portion of the RGR – \bar{I} curve | $\text{m g}^{-1} \text{ g}^{-1} \text{ d}^{-1} (\mu\text{mol m}^{-2} \text{ s}^{-1})^{-1}$ |
| RGR | Whole-plant relative growth rate as instantaneous growth per initial dry weight | $\text{mg g}^{-1} \text{ d}^{-1}$ |
| RGR_{max} | Maximum light-saturated RGR | $\text{mg g}^{-1} \text{ d}^{-1}$ |
| NAR | Net assimilation rate; assimilatory efficiency per unit leaf area | $\text{g cm}^{-2} \text{ d}^{-1}$ |
| LAR | Leaf area ratio; ratio of the assimilatory area of a plant per unit total dry weight | $\text{cm}^2 \text{ g}^{-1}$ |

$$\bar{I} = \frac{\bar{I}_o(1 - e^{-(K_d \cdot z_r + K_s B)})}{K_d \cdot z_r + K_s B} \mu\text{mol m}^{-2} \text{ s}^{-1} \quad (2)$$

Thus, the \bar{I} experienced by a plant depends on the depth distribution of B . Plants with a surface canopy will receive a higher effective \bar{I} , and those in deeper water a lower \bar{I} , than suggested by Eq. (1). The effects of K_d and K_s are assumed additive, given the relationship between the inherent and apparent optical properties of water (Kirk, 1983; Oliver, 1990). In turbid water, plants with most photosynthetic tissue close to the surface will maximise carbon assimilation. With increased turbidity (or depth), the photosynthesis: respiration ratio and rate of biomass accumulation will decline (in the absence of photoadaptation). This trend is reported for seagrasses (Dennison and Alberte, 1982; Zimmerman et al., 1994).

Growth is determined by the efficiency of carbon assimilation relative to total biomass. The former is estimated by the Net Assimilation Rate (NAR), and the latter by the Leaf Area Ratio (LAR). The product of NAR and LAR is the Relative Growth Rate (RGR) (Harper, 1977). NAR generally increases with irradiance, following a typical P–I curve (Kirk, 1983). Changes in LAR indicate a plant's capacity to alter its canopy morphology in a variable light environment. For example, at low irradiances the plant is likely to concentrate photosynthetic biomass at the surface by increasing leaf length and reducing leaf width, thereby increasing LAR. In shallow water, the plant may produce many short leaves to maximise light interception and reduce LAR. The effects of light-induced changes in NAR and LAR are revealed by plotting them against RGR (Poorter and Remkes, 1990).

Vallisneria americana Michaux is a perennial, dioecious monocotyledon with basal meristems. Murray populations were regarded as *V. spiralis* (cf. Black, 1980; Lowden, 1982), but Jacobs and Frank, 1997, refer them to *V. americana*. It typically occurs at 1–2 m depth in the Murray, but flows from the tributary Darling River may produce turbidities of 100–600 Nephelometric Turbidity Units (NTU) and downwelling extinction coefficients of 6–25 m⁻¹ (Mackay et al., 1988; Oliver, 1990). Growth is then limited to <1 m (Walker et al., 1994). In this study, the average irradiance is manipulated, via turbidity and depth, to determine its effects on growth and shoot and leaf recruitment in *V. americana* in a 102-day experiment involving three turbidities and five depths. The depth treatments effectively varied B_e , the proportion of the canopy receiving sufficient light for net photosynthesis. The turbidity treatments were intended to evaluate the hypothesis that plant performance declines with increasing turbidity regardless of depth, and to test whether or not the RGR– \bar{I} response follows the P–I curve described by Jassby and Platt, 1976. We consider also the utility of this response for modelling the growth of *V. americana* in the Murray.

2. Methods and materials

2.1. Collection and preparation

V. americana ramets 30–50 cm high were collected from the littoral zone of the River Murray at Blanchetown, South Australia (34°25'S, 139°40'W), in December 1995. To

standardise the initial conditions, stolons and roots were trimmed to 5 and 10 cm, respectively. Each shoot was transferred to a 10 l pot (30 cm diameter, 18 cm depth) containing sandy-loam and 3g l⁻¹ slow-release fertilizer (Osmocote, 9-month pellets), equivalent to about 100 g N m⁻² y⁻¹. The loam was capped with 2 cm of grey clay to reduce leaching and emulate the oxygen regime of littoral sediments. The shoots were grown for 3 months at 20–35 cm depth in a clear-water pond (water temperature 20–30°C, noon photon irradiance 1500–2500 μmol m⁻² s⁻¹). In mid-May, three vigorous, non-flowering, female shoots were selected, to reduce the effect of age and gender, and the remainder was discarded. One week before transfer to turbid water, the leaves were trimmed to 10 cm length, to standardise the canopy distributions and simulate the condition of plants with leaves trimmed by exposure in shallow water. The experiment was conducted in winter, when flooding often occurs in the lower Murray.

2.2. Pond turbidity

Suspensions of the powdered clay mineral bentonite were used to simulate the light regime in the Murray (Thoms and Walker, 1993). Bentonite was wetted and mixed in water with an electric paint stirrer. This stock suspension was added to water in three outdoor ponds (3×4×1.1 m deep, 13 m³ volume) stirred continuously by a submersible pump (Ebara Best-Zero, 33 mm outlet, pond turnover time 1.5 h). Settled sediment was re-suspended by stirring using a broom, and new suspension was added as necessary. Turbidity was measured every 1–3 days at several sites in each pond using a Hach 2100A meter, and used to estimate *K_d* from an empirical relationship.

2.3. Average irradiance

Levels of *Ī* were set by arranging plants so that their leaf tips received a mean initial irradiance (*I_{ini}*) of 450, 100, 20, 5 or 0.1 μmol m⁻² s⁻¹ over 1000–1400 h when first flooded with turbid water (Table 2). To determine *I_{ini}*, *Ī_o*, was set to 600 μmol m⁻² s⁻¹

Table 2
Initial experimental conditions in three ponds with differing turbidities corresponding to extinction coefficients of 6.5.17, 12.6 0.34 and 21.90.33 m⁻¹ and Secchi depths of 21, 13 and 7 cm

| Initial irradiance (μmol m ⁻² s ⁻¹) | Average irradiance (mol m ⁻² s ⁻¹) | | | Depth (m) | | |
|---|---|------------------|-------|----------------------|-------|-------|
| | Pond turbidity (NTU) | | | Pond turbidity (NTU) | | |
| | 90±2 | 209±6 | 504±8 | 90±2 | 209±2 | 504±8 |
| 450 | 141 | 111 ^a | 67.6 | 14 | 12 | 11 |
| 100 | 78.3 | 67.7 | 46.9 | 39 | 24 | 17 |
| 20 | 49.6 | 43.5 | 33.8 | 66 | 39 | 24 |
| 5 | 36.8 | 34.8 | 26.3 | 90 | 49 | 31 |
| 0.5 | NA | NA | 20.4 | NA | NA | 39 |
| 0.1 | 18.3 | 20.8 | 17.8 | 145 ^b | 82 | 46 |

^a Effect simulated using shade cloth to reduce irradiance.
^b Most plants grazed by ducks; excluded from most analyses.
Ranges are mean standard error (*n*=78). Initial irradiance and average irradiance represent initial measurements at leaf tips. Depth represents the distance to the sediment surface

and K_d to 6, 12 and 24 m^{-1} (Table 2). Laboratory oxygen-production data showed that light-saturated photosynthesis occurred at about 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$, with light compensation (I_c) at 20–25 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Thus, plants receiving 5 and 0.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$ initially had insufficient light for net photosynthesis. Values of z_r were determined from the Lambert–Beer equation:

$$I_z = I'_0 e^{-K_d z_r} \mu\text{mol m}^{-2} \text{s}^{-1} \quad (3)$$

Throughout the experiment (mid May to late August 1996), solar irradiance (I_0) was recorded at one-minute intervals and averaged hourly using a LiCor aerial quantum sensor and Li1000 logger. Daily I'_0 was estimated as incoming irradiance (I_0) corrected for surface reflection, over a range of I_0 for each $K_d I_0$, and I_0 were measured with aerial and underwater LiCor 2π quantum sensors. The daily mean I'_0 value, \bar{I}'_0 , for each K_d treatment was taken as the average over 800–1800 h.

Each combination of treatments accommodated six replicate plants. These were placed on racks in the ponds and aligned to minimise shading, with the sediment surfaces at depths shown in Table 2. The experiment commenced on 16 May and lasted 102 days, comparable with the duration of the longest floods in the Murray. For comparison, typical K_d and turbidity values in the Murray are 2–5 ln units m^{-1} and 20–100 NTU, respectively (Oliver, 1990).

2.4. Growth and recruitment

Leaf recruitment and senescence, width and extension were recorded on 15 May, 5 June, 25 June and 25 August for the plants in the pond with $K_d=12.59$. On 15 May, the youngest leaf on one randomly-selected shoot per pot was twice punctured using a needle near the sediment, providing a mark to indicate extension rates. Leaves were re-marked lower down as the tip senesced. As new leaves are produced in the middle of the plant, with older leaves pushed alternately to either side, older and newer leaves are readily identified.

Plants were harvested on 26–29 August. Sediments were removed by washing over a 1-mm sieve and roots, stolons and leaves (including leaf bases and the few female peduncles) were separated by flotation. Root loss was <1% by weight. Plants were dried at 80°C to constant weight (about 72 h).

2.5. Specific absorption coefficient

The specific absorption coefficient for *V. americana* was measured following Westlake, 1964. Shoots with 10–60 cm leaves were secured to crosswires on a 30 cm diameter wire frame. Four densities of shoots were chosen, with about 20% of leaves in each group reaching the surface. For each density, 25 measurements of irradiance were made at the base of the shoots (depth 0.30 m) with a LiCor 2π underwater quantum sensor. Readings were taken around the plant in a stratified random pattern, between 1200–1400 h on a cloudless day. The specific absorption coefficient, K_s , was calculated as the slope of the relationship between K_d and B (per m^3 over 0.30 m). Values of B used in Eq. (2) were leaf dry weight as per m^3 over z_r .

2.6. Part of the canopy receiving irradiances above light compensation

The portion of the canopy (g dry weight) receiving irradiances above the light compensation level (I_c) was estimated by averaging measurements over the daylight hours. The average I_c value for leaves of varying ages at different depths was $20 \mu\text{mol m}^{-2} \text{s}^{-1}$. The mean depth of \bar{I}_c for each K_d was calculated from mean daily \bar{I}'_o values and Eq. (3). At the end of the experiment, the length of each leaf above the mean daily \bar{I}_c depth was estimated as the total leaf length less the length below that depth (i.e. $z_r - \bar{I}_c$ depth). In leaves that contacted the surface, deviations from vertical were ignored below 10 cm depth.

The penetration of mean daily compensating irradiances rather than saturating irradiances was determined for two reasons (cf. Dennison and Alberte, 1982; Dennison, 1987). First, the laboratory-determined range of I_c was smaller ($2\text{--}35 \mu\text{mol m}^{-2} \text{s}^{-1}$) than that of I_k , the onset of photosaturation ($19\text{--}144 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Blanch, unpub.). Second, I_k values were high relative to maximal in situ irradiances, due to high turbidity: thus, most photosynthesis in the canopy occurred at irradiances $< I_k$.

The relationships of leaf length, dry weight and surface area were determined for plants at three depths ($z_r=11\text{--}24$, $31\text{--}49$ and $60\text{--}90$ cm). Plants were taken from several rooting depths in each range, and the areas of 20–30 leaves of diverse ages were measured with a Delta T meter. Leaves were then dried at 80°C to constant weight (about 72 h).

2.7. Modelling

Jassby and Platt's (1976) hyperbolic tangential model was fitted to RGR and NAR data by quasi-simplex estimation, using a loss function that minimised the squared difference between observed and expected values (Statistica, 1994). Fits were accepted only if the residuals were normally distributed. Thus,

$$\text{RGR} = \text{RGR}_{\max} \tanh\left(\frac{\alpha \bar{I}}{\text{RGR}_{\max}}\right) - R (\text{mg g}^{-1} \text{d}^{-1}) \quad (4)$$

where

| | | |
|---------------------|---|---|
| RGR_{\max} | = | Estimated maximum RGR ($\text{mg g}^{-1} \text{d}^{-1}$) (see below) |
| α | = | Slope of the initial, linear section of the model, indicating photosynthetic efficiency ($\text{g g}^{-1} \text{d}^{-1} (\mu\text{mol m}^{-2} \text{s}^{-1})^{-1}$) |
| R | = | A constant to adjust for respiration (Van der Bijl et al., 1989; Olesen and Sand-Jensen, 1993). |

2.8. Modelled biomass in different flooding and turbidity regimes

The $\text{RGR}-\bar{I}$ relationship established in the pond experiment was used to predict the effects of turbidity and various depths and durations of flooding on *V. americana* in the River Murray. \bar{I} was calculated from Eq. (1) for each combination of z_r and K_d . Values of K_d spanned the range observed for the river ($2\text{--}25 \text{m}^{-1}$) and flooding depths were 0.5, 1.0, 1.5 and 2.0 m. RGR data were determined from the $\text{RGR}-\bar{I}$ model (Fig. 6(a)). The

effect of flood duration on plant biomass was estimated by

$$\text{Biomass change} = \frac{W_f}{W_i} = e^{\text{RGR} \cdot t} \quad (5)$$

where RGR is in $\text{g g}^{-1} \text{d}^{-1}$ and W_i and W_f are the initial and final plant dry weights (g), respectively, after t days. RGR is assumed constant over t days (exponential, density-independent growth), although this is strictly applicable only for similar conditions of temperature, photoperiod, carbon and nutrient supplies. Plants are assumed to be mature initially, at 10–30 cm depth, with leaves of 10 cm length.

3. Results

3.1. Solar irradiance and water temperature

Day length declined from 10 h in late May to 9 h in July. Mean minimum and maximum water temperatures were 12°C and 13.5°C (range 10–14, 11–17°C, respectively). The mean daily I_o over 102 days was $303 \mu\text{mol m}^{-2} \text{s}^{-1}$, instantaneous irradiance peaked at $589 \mu\text{mol m}^{-2} \text{s}^{-1}$ between 1300–1400 h. Surface reflectance was 29% for the two lower K_d treatments and 41% for the highest. Mean daily subsurface irradiance (\bar{I}'_o) was $0.71 \times 303 = 215 \mu\text{mol m}^{-2} \text{s}^{-1}$ for $K_d = 6.48$ and 12.6, and $0.59 \times 303 = 179 \mu\text{mol m}^{-2} \text{s}^{-1}$ for $K_d = 21.9$. These values were used in Eqs. (1)–(3) to calculate \bar{I} and I_z .

3.2. Survival

No plants died during the experiment. Even those in the deepest treatments survived 3 months with irradiances that, given laboratory P–I data, were insufficient or barely sufficient for photosynthesis. This confirms other observations that *V. americana* can tolerate extended periods with little or no photosynthesis (Titus and Adams, 1979; Madsen et al., 1991; Harley and Findlay, 1994).

3.3. Effect of turbidity on growth, biomass and recruitment at constant z_r

At an initial $z_r = 39$ cm, RGR was negatively correlated with turbidity (Table 3):

$$\text{RGR} = 21 - 0.047 \cdot \text{Turbidity} \quad (r^2 = 0.933, P < 0.0001)$$

As turbidity increased there was a four-fold decrease in \bar{I} (78.3 – $20.4 \mu\text{mol m}^{-2} \text{s}^{-1}$). RGR and NAR declined, but LAR remained fairly stable. The decline of RGR with NAR indicates that the diminished performance of the plants in highly turbid water is due to depressed carbon assimilation. At low turbidity (90 NTU), the total and leaf biomass were 7.72 and 6.90 g; at high turbidity (504 NTU), the corresponding values were 0.94 and 0.74 g, but the above-/below-ground ratio fell only from 8.4 to 3.7 (Table 3). It appears that in highly turbid water *V. americana* maintains roots and stolons in preference to leaves, providing a reserve for rapid leaf production when turbidity declines. Thus, shoot recruitment was lower at 209 NTU than at 90 NTU, and zero at 504 NTU.

Table 3
Growth responses and morphological characteristics of *Vallisneria americana*

| Turbidity (NTU) | 90±2 | 209±6 | 504±8 |
|---|------------------------|------------------------|-------------------------|
| Average irradiance ($\mu\text{mol m}^{-2} \text{s}^{-1}$) | 78.3 | 43.5 | 20.4 |
| Extinction coefficient (m^{-1}) | 6.5 | 12.6 | 21.9 |
| RGR ($\text{mg g}^{-1} \text{d}^{-1}$) | 17.5±1.39 ^a | 109±3.07 ^b | 2.4±2.15 ^c |
| LAR ($\text{cm}^{-2} \text{g}^{-1}$) | 231±29.8 ^a | 309±51.3 ^b | 294±42.2 ^{a,b} |
| NAR ($\text{g cm}^{-2} \text{d}^{-1}$) | 77±14.4 ^a | 35.8±11.3 ^b | -8.4±7.4 ^c |
| Σ Biomass (g) | 7.7±2.21 ^a | 4±1.42 ^b | 0.9±0.22 ^c |
| Leaf biomass (g) | 6.9±1.98 ^a | 3.6±1.23 ^b | 0.7±0.2 ^c |
| Stolon biomass (g) | 0.3±0.12 ^a | 0.1±0.08 ^a | <0.1±0.01 ^b |
| Root biomass (g) | 0.5±0.15 ^a | 0.3±0.15 ^b | 0.2±0.03 ^c |
| Σ Below ground (g) | 0.8±0.25 ^a | 0.5±0.22 ^a | 0.2±0.04 ^b |
| Above/below ratio | 8.4±1.11 ^a | 7.8±1.6 ^a | 3.7±1.16 ^b |
| Number new shoots | 5.8±4.48 ^a | 1.3±1.21 ^b | 0 |
| Σ number leaves | 69.3±20.2 ^a | 37.2±9.04 ^b | 15.6±4.04 ^c |
| Plant leaf length (m) | 22.4±7.1 ^a | 12.5±3.1 ^b | 3.1±0.9 ^c |

Values with the same superscript are not different at $P=0.05$ (Tukey's HSD test for unequal n , following ANOVA: Zar, 1996). Data are mean±standard deviation ($n=5-6$).

A grown at a depth of 39 cm with increasing turbidities. Average irradiance was calculated from Eq. (1). Data were ln-transformed, except for root dry weight which were arcsine transformed and RGR, NAR and LAR which did not require transformation.

Numbers of leaves, total leaf length and surface area also declined with increasing turbidity. LAR increased from 231 to about $300 \text{ cm}^2 \text{g}^{-1}$ in the medium and high turbidity treatments, but the leaves were thinner and narrower than those in 90 NTU, and given a higher surface area to volume ratio may have been able to intercept more light (cf. Enriquez et al., 1995).

3.3.1. Relative growth rate, net assimilation rate and leaf area ratio

\bar{I} was manipulated via changes in z_r and K_d to investigate its influence on plant performance and resource allocation. The combined data for the relationships between RGR and \bar{I} fell on a single curve regardless of K_d . The relationship was similar to the P-I response of Eq. (4) (Fig. 1(a)), which explained 89% of the variance in RGR. This suggested that RGR was dependent upon average illuminance irrespective of the planting depth or the turbidity. It may be fortuitous that the \bar{I} value at which RGR is zero ($\bar{I}_c=26 \mu\text{mol m}^{-2} \text{s}^{-1}$) was similar to the mean compensation irradiance measured for leaf pieces in the laboratory (20–25 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Table 4).

RGR increased linearly at low \bar{I} , when most of the canopy was not photosaturated and growth efficiency, α , was $0.33 \text{ mg g}^{-1} \text{d}^{-1} (\mu\text{mol m}^{-2} \text{s}^{-1})^{-1}$. With increasing \bar{I} more of the canopy sustained net photosynthesis, and RGR increased. At \bar{I} values above the compensation point ($\bar{I}_k=58 \mu\text{mol m}^{-2} \text{s}^{-1}$), most of the canopy was photosaturated during the day and RGR approached an asymptote of $19.1 \text{ mg g}^{-1} \text{d}^{-1}$ (note that applies only to the photoperiod, but RGR is calculated over 24 h).

For a given \bar{I} , z_r became very shallow as turbidity increased (Eq. (1)), and the plant response was to form a dense canopy and further reduce \bar{I} (Eq. (2)). The mean maximal

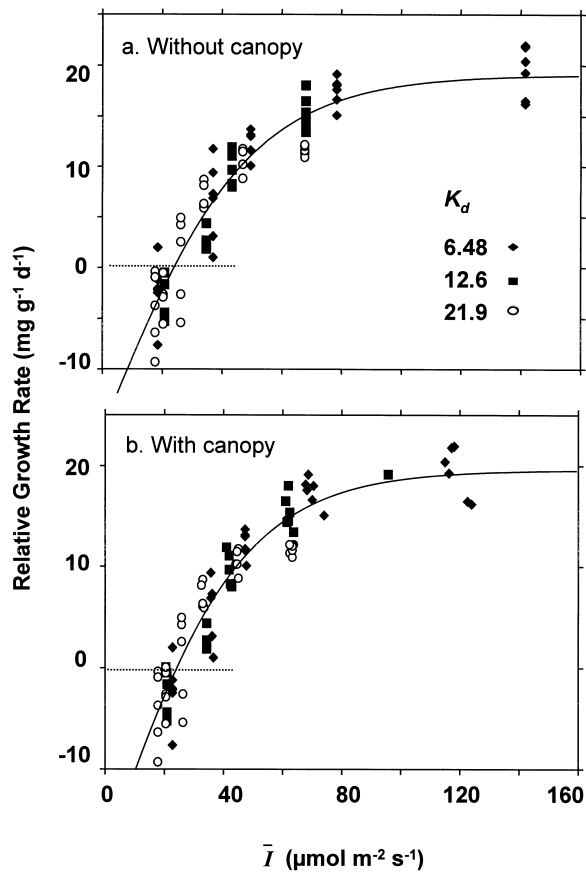


Fig. 1. Relationship of Relative Growth Rate (RGR) and average irradiance \bar{I} in *Vallisneria americana*. \bar{I} is calculated by (a) excluding and (b) including canopy absorption. The fitted model is the P-I relationship of Jassby and Platt, 1976. Parameters are in Table 4. The models are: (a) $\text{RGR (mg g}^{-1} \text{ d}^{-1}) = 35.13 \cdot \tanh(0.73 \cdot \bar{I} / 35.13) - 16.05$ ($r^2=0.894$, $n=81$); (b) $\text{RGR (mg g}^{-1} \text{ d}^{-1}) = 38.01 \cdot \tanh(0.83 \cdot \bar{I} / 38.01) - 18.43$ ($r^2=0.896$, $n=81$).

Table 4
Parameters describing relationships between RGR and NAR and the average irradiance \bar{I} between water surface and sediment

| | RGR _{max} or NAR _{max} | α (per $\mu\text{mol m}^{-2} \text{s}^{-1}$) | \bar{I}_c ($\mu\text{mol m}^{-2} \text{s}^{-1}$) | \bar{I}_k ($\mu\text{mol m}^{-2} \text{s}^{-1}$) |
|---|---|---|---|---|
| RGR (mg g ⁻¹ d ⁻¹) | | | | |
| (a) Without K_s (Eq. (1)) | 19.1 | 0.33 | 26 | 58 |
| (b) With K_s (Eq. (2)) | 19.6 | 0.36 | 24 | 54 |
| NAR (g cm ⁻² d ⁻¹) | 150 | 0.14 | 26 | 107 |

Effects with and without canopy absorption are shown (K_s =canopy extinction coefficient). Parameters were determined from the accompanying graphs and checked against model predictions. NAR_{max} was determined from the $\text{NAR}-\bar{I}$ model.

leaf length was 50 cm for plants at 11 m (Fig. 8), which placed about 75% of the leaf biomass at the surface. When absorption by the canopy was considered (Eq. (2); Fig. 1(b)), \bar{I} fell by up to 27% for plants in shallow water, but by <5% at depth, due to a smaller leaf biomass. \bar{I}_k and \bar{I}_c were lower (54 and 24 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively) and α was slightly elevated (0.36 $\text{mg g}^{-1} \text{d}^{-1} (\mu\text{mol m}^{-2} \text{s}^{-1})^{-1}$). This indicated more adaptation to shading than suggested by Eq. (1). Whilst light penetration to lower strata was reduced by the canopy, light interception by surface leaves increases the effective \bar{I} over the whole canopy permitting a higher carbon assimilation rate. Thus, RGR was influenced more by the depth distribution of B than B itself.

The RGR– \bar{I} response was due mainly to the influence of \bar{I} on NAR (Fig. 2). The NAR– \bar{I} relationship followed the theoretical P–I curve, accounting for 93% of the variance in NAR. The predicted NAR_{max}, 150 $\mu\text{g cm}^{-2} \text{d}^{-1}$, occurred at considerably higher \bar{I} than the maximum in this study. The value is nearly twice that for RGR (107 cf. 58 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Table 4), suggesting that changes in canopy leafiness, not assimilation efficiency, were responsible for RGR_{max} at high.

LAR ranged three-fold, from 146–406 $\text{cm}^2 \text{g}^{-1}$ (Fig. 3), whereas, NAR varied 17-fold, from –30 to 130 $\mu\text{g g}^{-1} \text{cm}^2 \text{d}^{-1}$. The reduced NAR at low \bar{I} was not countered by increased LAR, and RGR decreased in keeping with the reduction of \bar{I} with depth. The changes in LAR reflected morphological adaptations of *V. americana* to growth in turbid water. Relatively thick leaves (low unit leaf area per unit dry weight) were produced in high \bar{I} and thinner leaves were produced at low \bar{I} . Maximising leaf length per unit dry weight ensures that the plant is able to reach the surface sooner, and thin leaves there are likely to intercept more light (cf. Enriquez et al., 1995). LAR peaked at 25–40 $\mu\text{mol m}^{-2} \text{s}^{-1}$ within a narrow range of \bar{I} , regardless of K_d , again confirming that

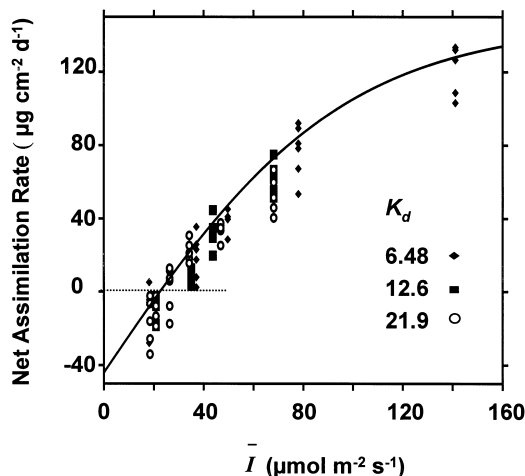


Fig. 2. Relationship between Net Assimilation Rate (NAR) and average irradiance \bar{I} in *Vallisneria americana*. The fitted model is the P–I relationship of Jassby and Platt, 1976. Parameters are in Table 4. The model is: $\text{NAR} (\text{cm}^2 \text{g}^{-1} \text{d}^{-1}) = 0.000191 \cdot \tanh(0.000002 \cdot \bar{I} / 0.000191) - 0.000042$ ($r^2 = 0.934$, $n = 81$).

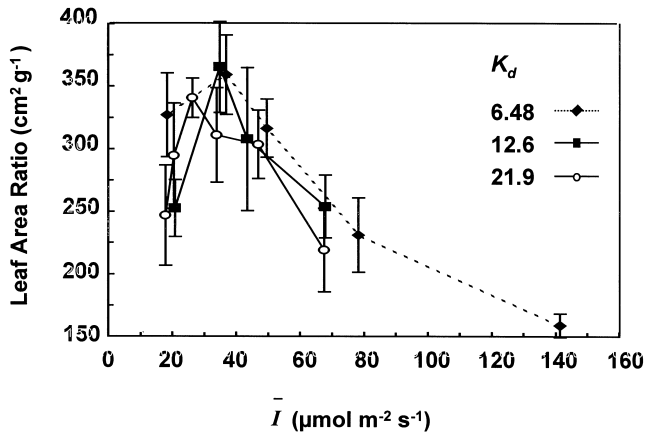


Fig. 3. Relationship between Leaf Area Ratio (LAR) and average irradiance \bar{I} in *Vallisneria americana*. Data are mean \pm standard deviation ($n=4-6$).

V. americana adjusted its canopy in response to changes in turbidity. At values of \bar{I} below \bar{I}_c , the production of young leaves was negligible (Table 6).

3.3.2. NAR and LAR as functions of RGR

NAR increased linearly as RGR rose from -5 to $10 \text{ mg g}^{-1} \text{ d}^{-1}$ (Fig. 4(a)), and above this value the net assimilation rate became more efficient as LAR decreased, thus, maintaining the growth rate. This relationship was similar to that between average irradiance and RGR (Fig. 1(a)), which suggested that \bar{I} was the over-riding, rate-limiting factor, irrespective of physical effects like light scattering due to increased turbidity and K_d . In comparison with the changes in NAR, LAR changed comparatively little (Fig. 4(b)), but was depressed at low and high RGR and had a broad peak at $0 < 7.5$.

3.3.3. Growth as a function of z_r and K_d

Fig. 5 shows the effects of z_r on RGR, NAR and LAR of plants grown in water of different clarity. RGR was maximal at the shallowest depth in the least turbid water, and decreased with z_r . The effect of high NAR on RGR in shallow water was partly offset by a reduction in LAR. The slope of the RGR– z_r curve was greatest at medium depths for each K_d , due to increasing NAR with z_r and high LAR. The decrease in NAR with z_r reflects downwelling light extinction, whereas, LAR increases with z_r due to morphological changes in the canopy under low light. Interpolation from Fig. 5(a) shows that depths at which no net growth occurred were about 130, 68 and 32 cm for $K_d=6.48$, 12.6 and 21.9, respectively. The maximal depth of colonisation, z_c (estimated as the depth where RGR is zero: cf. Schwarz et al., 1996) is given by

$$z_c = 8.89/K_d - 0.06 \text{ (m)} (r^2 = 0.99, n = 3)$$

This relationship is provisional, of course, and requires evaluation under field conditions.

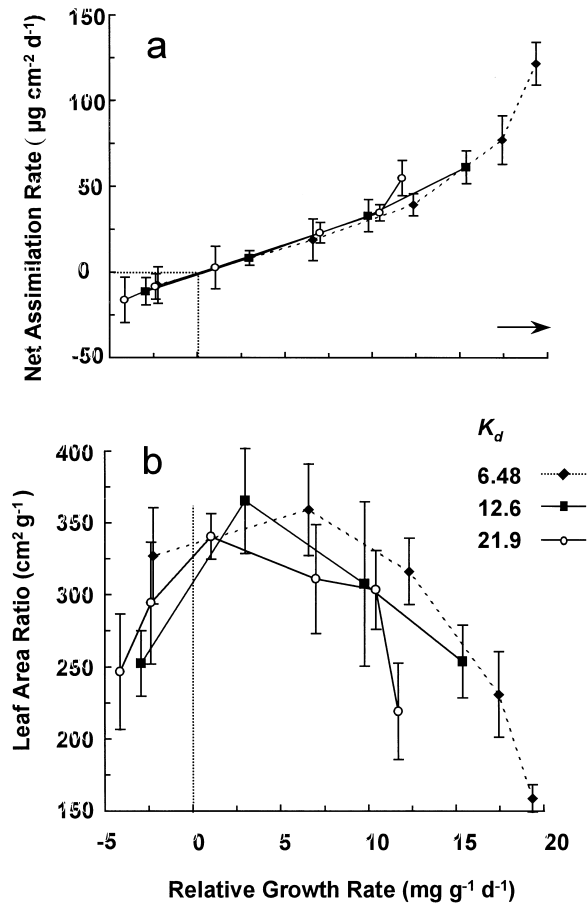


Fig. 4. (a) NAR and (b) LAR as functions of RGR in *Vallisneria americana* grown over a range of \bar{I} (the arrow shows the direction of increase in \bar{I}). Data are mean \pm standard deviation ($n=4-6$).

Similar expressions are reported for angiosperms, bryophytes and charophytes throughout the world (Spence, 1982; Chambers and Kalff, 1985; Vant et al., 1986).

The equation does not permit growth predictions at depths below z_c , and to overcome this a logistic model was constructed in terms of z_r and K_d (Fig. 5(b)). This accounted for 86% of the variance in RGR. Reductions in RGR for given z_r at high K_d are simulated by including K_d , with a negative exponent, in the denominator. When water clarity is high ($K_d=1$), RGR tends to a maximum at 1 m depth, but it declines rapidly toward zero as turbidity increases. A minimal RGR of $-5 \text{ mg g}^{-1} \text{d}^{-1}$ is predicted, regardless of K_d .

3.3.4. Shoot and leaf production

Shoot and leaf recruitment did not occur below $\bar{I}=35 \mu\text{mol m}^{-2} \text{s}^{-1}$, but leaf numbers increased linearly up to $\bar{I}=80 \mu\text{mol m}^{-2} \text{s}^{-1}$ (\bar{I}_k for the NAR- \bar{I} response), and levelled out as more of the canopy experienced photosaturation (Fig. 6). The alternative plot of shoot

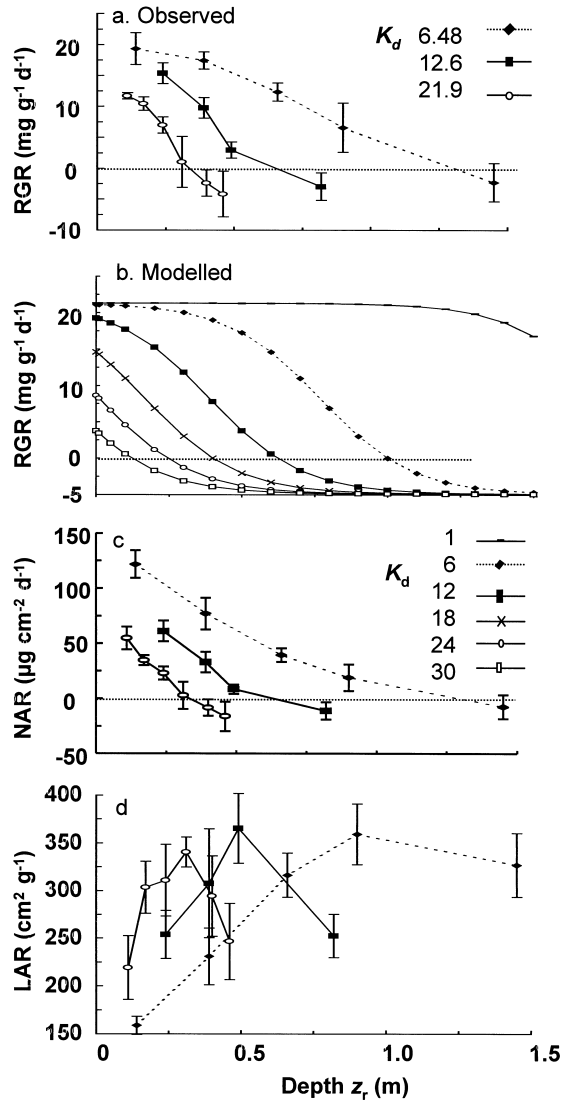


Fig. 5. (a) RGR, (c) NAR and (d) LAR in *Vallisneria americana* across a depth gradient, at three levels of turbidity (K_d). Data are mean \pm standard deviation ($n=4-6$). (b) RGR data were modelled by

$$RGR = 21.0 - \frac{25.8}{1 + K_d^{-3.34} e^{11.43 - 6.52 z_r}} (\text{mg g}^{-1} \text{d}^{-1}) (r^2 = 0.861, n = 81).$$

and leaf numbers against depth showed critical depths between 0.25 and 1.0 m, depending on water clarity.

Total plant leaf length was greatest in the shallowest, least-turbid water (Fig. 7). The longest leaves, though few in number (typically 1–2 per plant), were produced at the

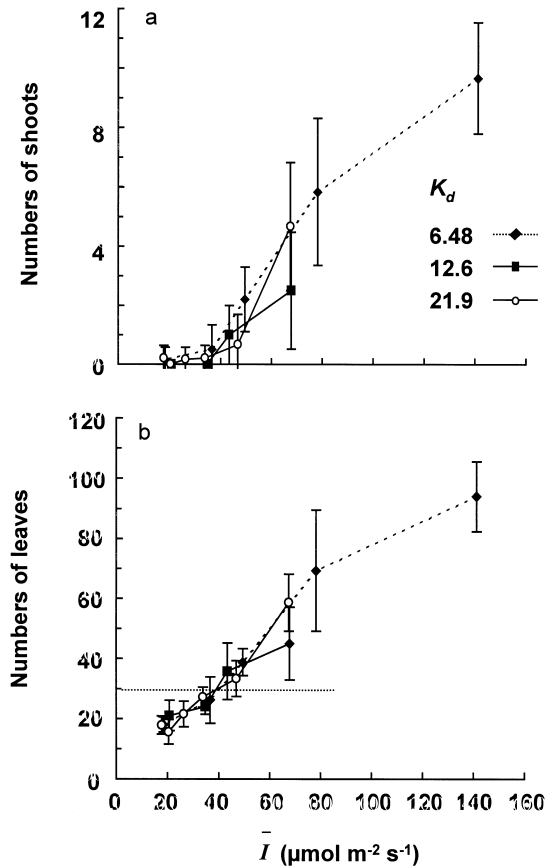


Fig. 6. (a) Shoot and (b) leaf numbers as functions of \bar{I} in *Vallisneria americana* at three values of K_d . The mean number of leaves in plants at commencement of the experiment was 29, shown by a dashed line. Data are mean \pm standard deviation ($n=4-6$).

greatest depth, and had been the youngest leaves at the start of the experiment. The older leaves were physiologically unable to extend, even when \bar{I} was artificially reduced.

The relationship between maximal leaf length and plant depth is independent of K_d ($P>0.22$; Fig. 8). At 14 cm depth, the maximal length was 50 cm, increasing to about 1.1 m at 90 cm depth. Regardless of depth or turbidity, new leaves were produced after one leaf had reached the surface, albeit slowly in deeper plants. Thus, most leaves that reached the surface from deeper water were initiated after flooding.

3.3.5. Biomass distribution among tissues

Maximum total, leaf, root and stolon dry weights occurred in the most turbid water at the shallowest depths (Fig. 9). Total plant and leaf dry weights decreased in sigmoidal fashion with depth. The linear decline of root dry weight was similar at for each K_d . The above-/below-ground dry weight ratio was 3.8–11, and highest at medium depths. Above-

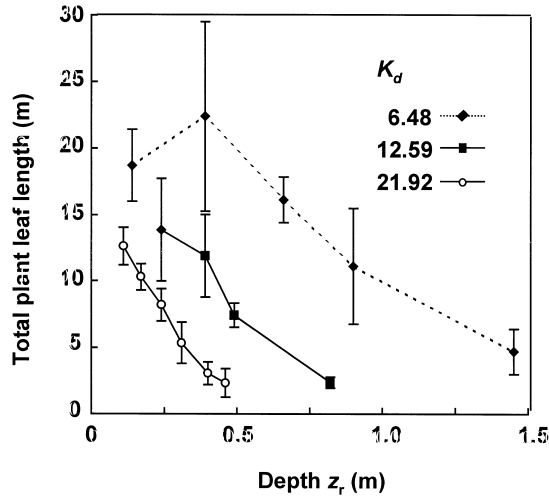


Fig. 7. Total leaf length per plant in *Vallisneria americana* with increasing depth at three values of K_d . Data are mean \pm standard deviation ($n=4-6$).

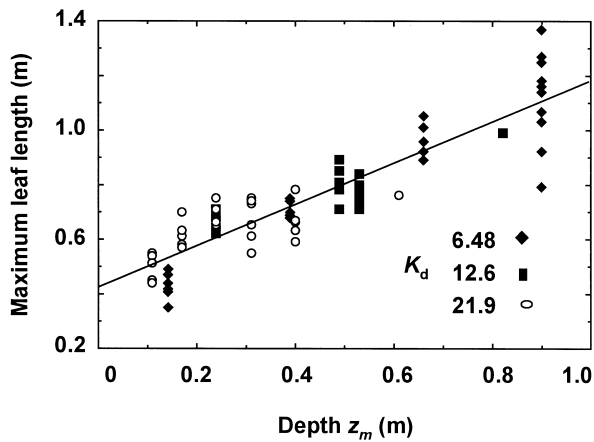


Fig. 8. Relationship between maximum leaf length per plant and depth to sediment in *Vallisneria americana* ($r^2=0.819$, $P<0.0001$). The value of K_d did not influence the relationship ($P=0.23$).

ground allocations peaked at 17 cm in $K_d=21.9$, and peaked at greater depths as light penetration increased.

Leaves and leaf bases were 86–91% of total dry weight in shallow water and 77–80% at depth, and corresponding root dry weights were 7–8% and 13–16% (Table 5). Stolon dry weight varied from 1–9%. Below-ground tissues in deeper water increased proportionately as leaf production slowed and only 1–2 thin, weak leaves were produced. Senescence of old leaves reduced the respiratory drain on the plant. Some old leaf bases

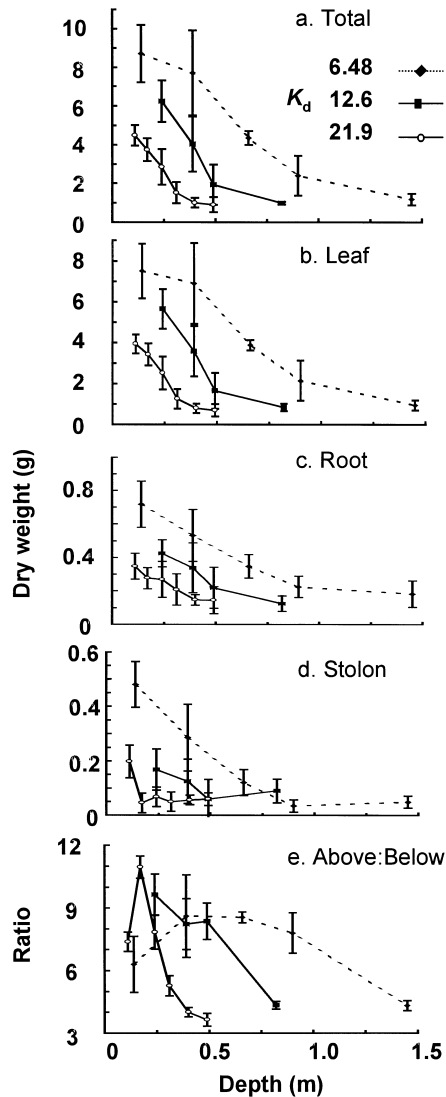


Fig. 9. Biomass allocation in *Vallisneria americana* across a depth gradient at three turbidity levels (K_d). Data are mean \pm standard deviation ($n=4-6$).

were retained, however, in each shoot; these had much lower light compensation points than young leaves (5 cf. $35 \mu\text{mol m}^{-2} \text{s}^{-1}$; Blanch, unpub.). One or two young leaves were maintained, but these grew slowly or not at all.

3.3.6. Leaf turnover, extension and width

Leaf recruitment was highest in shallower water ($0.53-0.55 \text{ week}^{-1}$) and lowest (0.03 week^{-1}) at 82 cm depth in $K_d=12.59$ ($F_{4,19}=33.2$, $P<0.0001$; Table 6). Senescence rates

Table 5

Mean percent tissue dry weights ($n=4$) across depth gradients at three extinction coefficients

| Extinction coefficient (m) | Depth (cm) | Dry weight (% of total) | | |
|----------------------------|------------|-------------------------|--------|------|
| | | Leaves | Stolon | Root |
| 6.5 | 14 | 86.2 | 5.5 | 8.3 |
| | 39 | 89.4 | 3.7 | 6.9 |
| | 66 | 89.3 | 2.7 | 8.0 |
| | 90 | 89.3 | 1.4 | 9.3 |
| | 145 | 80.3 | 4.2 | 15.5 |
| 12.6 | — | — | — | — |
| | 24 | 90.5 | 2.7 | 6.8 |
| | 39 | 88.6 | 3.1 | 8.3 |
| | 49 | 85.6 | 3.1 | 11.3 |
| | 82 | 78.7 | 9.2 | 12.1 |
| 21.9 | 11 | 87.9 | 4.4 | 7.7 |
| | 17 | 91.4 | 1.2 | 7.4 |
| | 24 | 88.1 | 2.1 | 9.2 |
| | 31 | 83.1 | 3.2 | 13.7 |
| | 46 | 77.2 | 6.6 | 16.2 |

Data are tabulated by depth and cannot be compared directly with extinction coefficients.

Table 6

Leaf recruitment and senescence across a depth gradient in water with light attenuation coefficient $K_d=12.59$ (209 NTU)

| Depth (cm) | \bar{I} ($\mu\text{mol m}^{-2} \text{s}^{-1}$) | Recruitment rate (week^{-1}) | Senescence rate (week^{-1}) |
|------------|--|---|--|
| 12 | 110.9 | 0.55 ± 0.03^a | 0.38 ± 0.12^a |
| 24 | 67.7 | 0.53 ± 0.03^a | 0.42 ± 0.05^a |
| 39 | 43.4 | 0.34 ± 0.05^b | 0.32 ± 0.05^a |
| 49 | 34.8 | 0.18 ± 0.05^c | 0.25 ± 0.08^a |
| 82 | 20.8 | 0.03 ± 0.01^c | 0.33 ± 0.10^a |

Data with the same superscript are not different at $P=0.01$ (Tukey's HSD test for unequal n following ANOVA: Zar, 1996). Data are mean \pm standard error ($n=4-6$).

were $0.25-0.42 \text{ week}^{-1}$, but did not differ significantly with depth ($P=0.64$) and balanced recruitment at 39–49 cm depth.

The maximal extension rate at $K_d=12.6$ was 1.1 cm d^{-1} . Peak rates occurred early in plants in shallow water (12, 24 and 39 cm depth, from 5 May to 5 June), but slowed when the lengths of leaves at the surface were 1–2 times the water depth. Plants at 49 cm initially grew at 0.3 cm d^{-1} , increasing to 0.95 cm d^{-1} as exposure to light increased, and slowed again to 0.36 cm d^{-1} after contacting the surface. The leaves marked at 82 cm did not grow, although they were initiated prior to flooding. Leaves produced immediately before this did grow, but older leaves did not. Leaf width decreased from 19.3 mm at 12 cm depth to 9.5 mm at 49 cm depth, and did not change below 39 cm (Table 7).

Table 7

Mean widths of leaves measured 15 cm above the sediment along a depth gradient ($K_d=12.59$)

| Depth (cm) | Leaf Width (mm) | <i>n</i> |
|------------|-----------------------|----------|
| 12 | 19.3±0.6 ^a | 28 |
| 24 | 16.2±0.5 ^a | 69 |
| 39 | 10.6±0.6 ^b | 33 |
| 49 | 9.5±0.5 ^b | 38 |
| 82 | 9.8±0.5 ^b | 6 |

Only mature leaves, initiated following flooding with turbid water and having since reached the surface, were included. Data with the same superscript are not different at $P=0.01$ (Tukey's HSD test for unequal n following ANOVA: Zar, 1996). Data are mean±standard deviation ($n=4-6$).

3.4. Relationship between plant performance and effective photosynthetic leaf biomass

Depths estimated to receive a daily average irradiance equivalent to I_c ($20 \mu\text{mol m}^{-2} \text{s}^{-1}$) were 37, 19 and 10 cm for $K_d=6.48$, 12.6 and 21.9, respectively, and were used to calculate B_e .

RGR was correlated with the effective photosynthetic leaf biomass, B_e (Fig. 10(a)). This explained the $\text{NAR}-\bar{I}$ response, underlying the $\text{RGR}-\bar{I}$ relationship, and indicates that plants with more of their canopy able to sustain net photosynthesis will produce more biomass. The model suggests that growth does not occur at $B_e < 22\%$, and that shoot and leaf recruitment do not occur at $B_e < 80\%$, as resources then are diverted to growing longer leaves rather than more leaves (Fig. 10(b)–(c)). The linear relationship between \bar{I} and B_e ($r^2=0.661$, $P<0.0001$) was similar to that for RGR and B_e , suggesting that over the long term average irradiance was the variable controlling plant growth.

4. Discussion

4.1. Growth and recruitment as functions of average irradiance

The objective of this study was to determine whether there was a relationship between the long-term (102 days) mean average water column irradiance, \bar{I} , and the growth performance of *V. americana*. The results suggest that 89% of the variation in RGR could be explained by \bar{I} . Given this relationship, and given also that \bar{I} is a complex variable dependent on the vertical extinction coefficient (itself a function of turbidity) and the rooting depth (Eq. (1)), it is not surprising that RGR data from all three pond experiments followed a predictable pattern. It is surprising, however, that this pattern is best represented by the P–I curve of Jassby and Platt, 1976, originally developed to model short-term photosynthesis in well-mixed phytoplankton communities. The inclusion of a term for the absorption of light by the plant canopy (Eq. (2)) had little effect on the model parameters.

The similarity of the responses of RGR and NAR to \bar{I} suggest that the assimilatory efficiency per unit leaf area had most influence on RGR. For comparison, maximal RGR values reported for other macrophytes include $40 \text{ mg g}^{-1} \text{d}^{-1}$ for *Egeria densa* in turbid

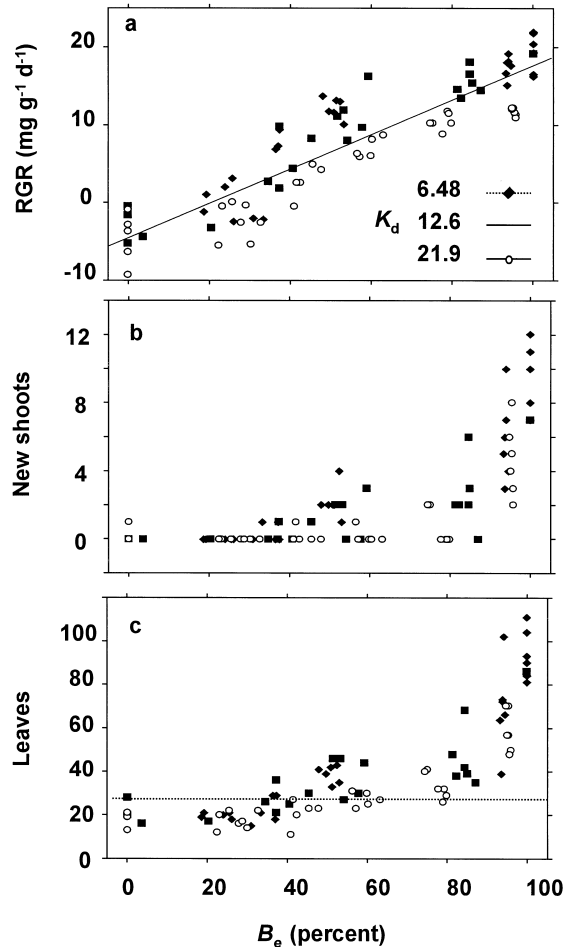


Fig. 10. (a) RGR and (b) shoot and (c) leaf recruitment as functions of B_e , the photosynthetically effective canopy biomass. The relationship between RGR and B_e is significant ($r^2=0.830$, $P<0.0001$). The mean number of leaves at the commencement of the experiment was 29 per pot, indicated by a dashed line in the lower panel.

water (Tanner et al., 1993) and $30\text{--}70 \text{ mg g}^{-1} \text{d}^{-1}$ for *Callitriche cophocarpa* and *Elodea canadensis* (Madsen and Sand-Jensen, 1994). RGR depends on the depth distribution of B relative to the light gradient, rather than the magnitude of B . When a high proportion of B is at the surface, light interception is maximised. In contrast, a plant in deeper water with most of the canopy close to the sediments will experience a lower \bar{I} than predicted by Eq. (1). The estimated specific absorption coefficient (K_s), $0.0051 \text{ m}^2 \text{g}^{-1}$, is 2–4 times lower than reported for *V. americana* by Titus and Adams, 1979, or for *Potamogeton pectinatus* ($0.024 \text{ m}^2 \text{g}^{-1}$; Van der Bijl et al., 1989), and may reflect the high turbidities used here.

Some 66% of the variation in leaf biomass receiving irradiances above I_c was explained by \bar{I} . Average irradiances above $35 \mu\text{mol m}^{-2} \text{s}^{-1}$ were strong determinants of shoot and leaf recruitment, and below this value no recruitment occurred. Similarly, shoot and leaf recruitment ceased at $B_c < 80\%$, and growth ceased at $B_c < 22\%$. Similar responses for angiosperms and charophytes. A similar trend is reported for other freshwater and marine species (Dennison and Alberte, 1982; Barko and Smart, 1981; Goldsborough and Kemp, 1988; Olesen and Sand-Jensen, 1993).

Although NAR was the main factor affecting RGR, the role of LAR also was important. At low \bar{I} , *V. americana* was unable to increase LAR sufficiently to offset the reduction in NAR (and so maintain RGR), but the changes in LAR indicated that morphological plasticity was a key adaptation to growth in turbid water (as for other submersed macrophytes: Madsen, 1991).

The growth relationship here is comparable to that reported by Dennison and Alberte, 1982 and Dennison, 1987 for the seagrass *Zostera marina*. For *V. americana*, however, the main determinant is B_c rather than the quantum flux at the leaf tips and leaf bases. The flux differential between leaf tips and bases, governed by z_r , K_d and leaf length, is significant for long-leaved, submersed species, and particularly so in turbid water. In deeper, less turbid water the differential is less and the quantum flux at the leaf tips is an reasonable estimate of available light.

The \bar{I}_c values determined from the RGR– \bar{I} curve and the P–I responses for leaf pieces in the laboratory were similar (26 cf. 20–25 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for leaves of different ages at different depths at 12°C: Blanch, unpub.). This is remarkable as the P–I measurements do not account for night-time leaf respiration and 24 h below-ground. Photosynthesis might be expected to balance respiration over 24 h at a higher \bar{I} , but this appears to be prevented by high rates of carbon assimilation at the surface, where most biomass is concentrated. I_c values from 3.5–47.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$ are reported for charophytes (*Chara vulgaris*, *Nitella translucens*) and angiosperms (*Callitriche cophocarpa*, *Elodea canadensis*, *Fontinalis antipyretica*, *Littorella uniflora*, *Ranunculus peltatus*, *Zostera marina*) (Sand-Jensen and Madsen, 1991; Olesen and Sand-Jensen, 1993; Madsen and Sand-Jensen, 1994). Although these data refer to ambient irradiance at the surface, they approximate \bar{I}_c as the plants were grown in clear water.

In deep water, *V. americana* allocated 77% of its biomass to leaves, compared to 91% in shallow water (Table 5). Allocation to stolons was <10%, and maximal when growth was very high (vegetative reproduction) or low (negligible leaf recruitment). As turbidity increased, leaf biomass declined more rapidly than root and stolon biomass (Table 3). In very low light, *V. americana* retained a comparatively strong below-ground structure to anchor the basal meristems, and the canopy consisted mainly of moribund leaves and 1–2 young leaves. The old leaves had a comparatively low and respiration rate (Blanch, unpub.). They harvested photons at very low flux densities and thereby supported extension by the young leaves.

4.2. Applications of average irradiance

\bar{I} averaged the differences in instantaneous irradiance between the water surface and sediments. It was calculated from an estimate of mean daily subsurface irradiance

($I'_0=303 \mu\text{mol m}^{-2} \text{s}^{-1}$), representing irradiances from 40 to $>1600 \mu\text{mol m}^{-2} \text{s}^{-1}$. Although it is a crude estimate of the light environment, it proved to be strongly correlated with growth and recruitment in *V. americana*. Part of its utility is that it is a single number derived from easily-determined parameters. RGR could be expressed as a function of z_r and K_d (Fig. 5(b)). It would be interesting to determine if leaf and whole-plant light compensation points coincide for other species. If so, growth could be predicted by assuming that RGR is zero at an \bar{I} corresponding to short-term measurements of \bar{I}_c for leaf pieces.

Once the RGR– \bar{I} relationship for a species is known, predictions of relative performance can be made by determining \bar{I} from I'_0 , z_r and K_d . The relationship will depend on the supply of inorganic carbon (Madsen and Maberley, 1991; Sand-Jensen and Madsen, 1991), nutrients (Chambers and Kalff, 1987) and temperature (Barko and Filbin, 1983). Future studies could determine RGR as a function of \bar{I} and one or more of these factors. For example, Madsen and Sand-Jensen, 1994 determined the relationship between RGR, irradiance and inorganic carbon for *Callitriche cophocarpa* and *Elodea canadensis*. \bar{I} may be appropriate only if a plant's photosynthetic tissues reach the surface, as shorter plants will experience less irradiance than suggested by Eq. (1). It may prove most useful in turbid waters, where plants experience a wide range of light conditions. If confirmed, these relationships could provide simple, testable empirical models (cf. Peters, 1990).

4.3. Modelled growth in *Vallisneria*

The RGR– \bar{I} relationship in this experiment (Fig. 1(a)) may be used to model the growth of *V. americana* relative to z_r , K_d and flood duration (Table 8). It may also be useful as a format for modelling morphologically similar species although not applicable to elodeid species. Values of z_r and K_d are assumed constant over time, although the same relationship could be used to model different combinations of z_r and K_d . Further, the percent change in biomass is assumed to be independent of pre-flood biomass.

The model predicts growth (positive RGR) for flooding depths up to 2 m for values of $K_d < 5 \text{ m}^{-1}$. This coincides with the maximum observed colonised depth of *V. americana* in the River Murray when K_d is 2–5 m^{-1} (Walker, unpub.). If the water rises 0.5 m for 1 week when $K_d=2 \text{ m}^{-1}$, a 14% increase in plant biomass is predicted. If the rise is 2 m, the biomass increase is 11%, reflecting a reduction in RGR from 19.0 to 15.0 $\text{mg g}^{-1} \text{d}^{-1}$ as \bar{I} falls from 172.4 to 66.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$. A 0.5 m rise in the water level, given $K_d=2 \text{ m}^{-1}$, is likely to double biomass in about 5 weeks, and to quadruple it in 12 weeks.

As K_d or z_r increase, \bar{I} decreases causing a lower RGR. Plants flooded to 2 m with water of $K_d=5 \text{ m}^{-1}$ are likely to show virtually no growth (a 2% increase over 12 weeks) because \bar{I} then approaches 24.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$, near \bar{I}_c , the minimum light required for growth (Table 4). A reduction in biomass (3% after 1 week, 27% after 12 weeks) is predicted for plants flooded to 1.5 m when $K_d=8 \text{ m}^{-1}$, as \bar{I} then is $< \bar{I}_c$ (17.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Table 8). With increasing K_d , the depth at which no net growth occurs becomes shallower. A net loss of biomass is predicted at $z_r=1.0 \text{ m}$ when $K_d=11 \text{ m}^{-1}$, but $z_r=0.5 \text{ m}$ when $K_d=20 \text{ m}^{-1}$.

Table 8
Modelled growth in field populations of *Vallisneria americana*

| K_d (m^{-1}) | Depth (m) | $\bar{I}^{a,b}$ ($\mu mol\ m^{-2}\ s^{-1}$) | RGR ($mg\ g^{-1}\ d^{-1}$) | % Change in plant dry weight | | | | | | |
|-----------------------|--------------|--|---------------------------------|------------------------------|-----|-----|-----|-----|-----|-----|
| | | | | Flood duration (weeks) | | | | | | |
| | | | | 1 | 2 | 3 | 4 | 6 | 8 | 12 |
| 2 | 0.5 | 172.4 | 19.0 | 14 | 31 | 49 | 70 | 122 | 190 | 394 |
| | 1.0 | 117.9 | 18.6 | 14 | 30 | 48 | 68 | 118 | 183 | 375 |
| | 1.5 | 86.4 | 17.2 | 13 | 27 | 43 | 62 | 106 | 162 | 324 |
| | 2.0 | 66.9 | 15.0 | 11 | 23 | 37 | 52 | 88 | 131 | 252 |
| 5 | 0.5 | 89.0 | 17.4 | 13 | 28 | 44 | 63 | 108 | 165 | 331 |
| | 1.0 | 48.2 | 10.7 | 8 | 16 | 25 | 35 | 57 | 82 | 146 |
| | 1.5 | 32.3 | 4.5 | 3 | 7 | 10 | 14 | 21 | 29 | 46 |
| | 2.0 | 24.2 | 0.3 | 0 | 0 | 1 | 1 | 1 | 2 | 2 |
| 8 | 0.5 | 52.1 | 11.8 | 9 | 18 | 28 | 39 | 64 | 94 | 170 |
| | 1.0 | 26.5 | 1.6 | 1 | 2 | 3 | 4 | 7 | 9 | 14 |
| | 1.5 | 17.7 | -3.7 | -3 | -5 | -7 | -10 | -14 | -19 | -27 |
| | 2.0 | 13.3 | -6.6 | -5 | -9 | -13 | -17 | -24 | -31 | -43 |
| 11 | 0.5 | 38.4 | 7.2 | 5 | 11 | 16 | 22 | 36 | 50 | 84 |
| | 1.0 | 19.3 | -2.7 | -2 | -4 | -5 | -7 | -11 | -14 | -20 |
| | 1.5 | 12.9 | -6.9 | -5 | -9 | -13 | -18 | -25 | -32 | -44 |
| | 2.0 | 9.6 | -9.1 | -6 | -12 | -17 | -23 | -32 | -40 | -53 |
| 15 | 0.5 | 28.3 | 2.5 | 2 | 4 | 5 | 7 | 11 | 15 | 23 |
| | 1.0 | 14.1 | -6.0 | -4 | -8 | -12 | -15 | -22 | -29 | -40 |
| | 1.5 | 9.4 | -9.3 | -6 | -12 | -18 | -23 | -32 | -40 | -54 |
| | 2.0 | 7.1 | -10.9 | -7 | -14 | -21 | -26 | -37 | -46 | -60 |
| 20 | 0.5 | 19.7 | -2.4 | -2 | -3 | -5 | -7 | -10 | -13 | -18 |
| | 1.0 | 9.9 | -9.0 | -6 | -12 | -17 | -22 | -31 | -39 | -53 |
| | 1.5 | 6.6 | -11.3 | -8 | -15 | -21 | -27 | -38 | -47 | -61 |
| | 2.0 | 4.9 | -12.5 | -8 | -16 | -23 | -29 | -41 | -50 | -65 |
| 25 | 0.5 | 14.5 | -5.7 | -4 | -8 | -11 | -15 | -21 | -28 | -38 |
| | 1.0 | 7.3 | -10.8 | -7 | -14 | -20 | -26 | -36 | -45 | -60 |
| | 1.5 | 4.9 | -12.5 | -8 | -16 | -23 | -30 | -41 | -50 | -65 |
| | 2.0 | 3.6 | -13.4 | -9 | -17 | -25 | -31 | -43 | -53 | -68 |

^a Estimated % surface reflectance for K_d =2, 5, 8, 11, 15, 20 and 25 m^{-1} is 10, 20, 30, 30, 30, 35 and 40%, respectively.

^b =303 $\mu mol\ m^{-2}\ s^{-1}$.

RGR was calculated from Fig. 6(a), and \bar{I} was calculated for a range of flooding depths (z_r) and downwelling extinction coefficients (K_d) Eq. (1)). Growth is percent change in whole plant dry weight. For each combination of K_d and z_r , growth over t days was determined as $e^{RGR \times t}$.

In the late 1980s, declines were observed in the range and abundance of submersed macrophytes, particularly of *V. americana*, in the lower Murray, due to turbid inflows from the Darling River (Walker et al., 1994). Turbidity was frequently 30–160 NTU and occasionally 450 NTU (Mackay et al., 1988). Few records exist of K_d in this period, but data from Oliver, 1990 and the present study suggest that it would have been in the range 3–20 m^{-1} . Submersed macrophytes did not occur below about 1 m, and were largely

absent from river reaches below weirs, where daily level fluctuations typically were equivalent to the photic depth. The model predictions are consistent with these observed changes.

Kimber et al. (1995) reported that *V. americana* produces tubers at depths up to 0.8 m at a mean $K_d=4.64\text{ m}^{-1}$ in Lake Onalaska, Wisconsin. From their data, the minimal \bar{I} for tuber production was $225\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$ (assuming $\bar{I}_o=912\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$ from the given mean daily irradiance of 39.4 mol m^{-2} , day-length 12 h and 6% surface reflectance). This is well above the \bar{I}_c determined here ($26\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$), and may reflect the energetic cost of tuber production. Tuber production appears not to occur in *V. americana* in the lower Murray, presumably because the winters are less severe.

The model is provisional, and should be applied cautiously to field populations of *V. americana*. Losses in biomass to grazing and waves or turbulence are unaccounted, and would reduce actual biomass accrual below predicted levels. This may be more likely at low \bar{I} , as the leaves are more fragile and prone to tearing.

Canopy-forming macrophytes are configured for optimal light interception in turbid water (Titus et al., 1975; Titus and Adams, 1979). In the River Murray, *V. americana* forms dense, monospecific stands with a semi-continuous surface canopy. Its ribbon-like leaves are resilient to wave motion, and its basal meristems permit development of young leaves near the sediment, where wave energy is least. Other common plants in the lower Murray, notably *Potamogeton crispus*, *P. tricarinatus* and *Myriophyllum* spp., favour more protected areas, perhaps due to their less robust structure.

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