Journal of Ecology (1989), **77**, 1093–1110

REGENERATION AND ESTABLISHMENT STRATEGIES OF EMERGENT MACROPHYTES

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SUMMARY

(1) The covariation within, and the relationship between, seven juvenile (seed/seedling) and thirteen adult traits of twenty-five species of emergent macrophytes occurring along the Ottawa River, Canada, is described.

(2) Contrary to r–K selection, but in accordance with C–S–R theory, there was no association between these two sets of traits.

(3) The major axis of variation within the juvenile traits consisted, at one end, of large, slowly germinating seeds with seedlings possessing a low relative growth rate, and at the other end of small, rapidly germinating seeds with seedlings possessing a high relative growth rate. The regeneration strategies of these species are interpreted as consisting of fugitive vs. stress-tolerant juveniles.

(4) The adult traits showed two major trends. The largest was associated with the ability to occupy space and consisted of correlated variation in above-ground biomass, canopy diameter, rhizome thickness and rhizome or stolon length; this trend is interpreted as consisting of fugitive vs. competitive adults. A subordinate trend consisted of an uncoupling of height from above-ground biomass and was associated with the 'leafless' morphology of a subset of species; this trend was related to environments in deeper water but having infertile soil and was interpreted as a stress-tolerant strategy.

(5) These trends in trait variation were found to be related to environmental gradients of soil fertility and water depth.

INTRODUCTION

A central goal of community ecology is to predict changes in species composition in time (succession) and in space (gradient analysis). Yet, given the vast numbers of species and the even greater range of possible environments, reductionist studies of selected species and specific environments are not, of themselves, likely to produce general predictive models of plant community composition. To develop such models it will be necessary to abandon taxonomic units as the standard variables and instead use those attributes of plants (for instance, height or relative growth rate) that are generalizable beyond taxonomic boundaries. This leads naturally to the notion of ecological 'strategies', i.e. groups of morphological, physiological or phenological traits that vary predictably with environmental gradients (*sensu* Grime 1979; Southwood 1988).

By concentrating on strategies rather than on species, it may be possible to identify general processes by which environments, plant traits and local species pools interact to determine the types of communities that form in particular environments (Grime 1979; Southwood 1988). One approach would be to explore the relationship between a selected trait and a chosen environmental variable. However, since it is plants, not individual traits, that live or die, the covariation among traits must be studied as well as variation between traits and environments.

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Current concepts of life-history strategies provide competing predictions concerning the way in which traits should covary. Consider the concept of r–K selection (MacArthur & Wilson 1967) in which particular traits are hypothesized to vary with the relative degrees of density-dependent and density-independent mortality (Pianka 1978). In environments that impose high rates of density-independent mortality are found r-selected species. In plants, such species should possess juvenile (seed/seedling) traits such as large numbers of small seeds capable of wide dispersal, inhibition of germination under an established canopy or in the dark, but rapid germination under favourable conditions (Gadgil & Solbrig 1972; McNaughton 1975; Harper 1977). Adult traits should be those associated with early maturity (small size, phenotypic plasticity, lack of vegetative spread) and poor competitive abilities.

In K-selected species, associated with environments lacking large scale episodes of density-independent mortality, are found the opposite suite of traits: small numbers of large seeds that are not widely dispersed, seedlings capable of survival under a closed canopy, large adult size and strong competitive abilities. Notice that juvenile and adult traits are consistently coupled: given a list of juvenile traits of a species it should be possible to predict the types of adult traits that it possesses. The 'bet-hedging' model (Murphy 1968; Stearns 1976), although differing in the particular association between juvenile and adult traits, also implicitly assumes that an association exists.

In Grime's C–S–R model of plant strategies (1974, 1977, 1979), this association between juvenile and adult traits does not exist. Thus, although intra-correlated juvenile and intra-correlated adult traits exist, the juvenile and adult subsets themselves may vary independently.

These suggested relationships between plant traits, environments, and the plant communities that result, suggest three questions. The first two will be addressed using a sample of twenty morphological traits on twenty-five plant species occurring on freshwater shorelines. The last question will be explored in the Discussion section by relating the trait data presented in this paper with the distributional data presented in Day *et al.* (1988). The questions are: (i) Are the traits possessed by juveniles (seed/seedlings) of an assemblage of twenty-five emergent macrophyte species independent of the traits possessed by adults of these species? (ii) What are the patterns of covariation among twenty morphological traits of these species of widely different taxonomy? (iii) Is there any predictable relationships between these traits and the environments in which the species occur?

The study system

In order to answer these questions a system is required that has two properties. First, there must be recognizable physical gradients. Second, there must exist appreciable variation in the traits possessed by the component species. The emergent zone of rivers and lakes has both of these properties.

There are two obvious environmental gradients in this system, the water-depth gradient and the exposure gradient (Hutchinson 1975; Spence 1982; Keddy 1982, 1983, 1985). The water-depth gradient goes from high on the shore, where the soil is inundated for only a short period of the year, to lower on the shore, where the soil is inundated for most of the growing season. Below this depth are found floating-leaved and submerged species; these are not discussed in this paper. The exposure gradient runs perpendicular to the water-depth gradient and involves correlated changes in soil fertility and direct exposure to wave action. One extreme of the exposure gradient consists of sandy, nutrient-poor shores which experience the full force of incoming waves while the other extreme is found in sheltered bays having organic, nutrient-rich soil.

Equally important, there is a wide range of morphologies found among the emergent plants in this habitat. Above-ground dry weight per ramet varies from 0·02 g to 20·53 g in the set of species examined in this study. Seed dry weights range from 1×10^{-5} g to $5{\cdot}2 \times 10^{-2}$ g; this covers the entire range of seed sizes found in herbaceous species (Harper, Lovell & Moore 1970). Morphologies vary from leafless photosynthetic stems (e.g. *Scirpus acutus*) to graminoid forms (e.g. *Carex crinita*) and branching forbs (e.g. *Penthorum sedoides*).

METHODS

Average values for twenty morphological traits (Appendix 1) were measured on each of twenty-five species. Species names are listed in Appendix 2; nomenclature follows Gleason & Cronquist (1963) unless otherwise indicated, except for the grasses which follow Dore & McNeill (1980). Seven of these traits are properties of seeds or seedlings and are therefore termed juvenile traits. The remaining thirteen traits are properties of adult plants and are termed adult traits.

Juvenile traits

Seed collection and storage

Seeds of the twenty-five species were collected during September 1985. Most were collected in Breckenridge Marsh (45°48′00″N, 45°57′30″W) Canada, along the Ottawa River, but those of *Dulichium aurundinaceum* and *Scirpus americanus* were collected in Luskville Marsh, 5 km upstream. The trait values reported here are probably underestimates of within-species variation.

All seeds were kept in porous nylon bags and stored in 75% saturated sand at 4 °C, from October 1985 until the various experiments were begun. This storage treatment has been shown to maintain viability and subsequent germination in a wide variety of wetland species (Moore 1985).

Seed weight

All appendages (wings, pappus, etc.) were removed from the seeds before weighing. Fifty seeds of each species were chosen at random, excluding those that were obviously inviable, dried to a constant weight at 60 °C, and weighed individually to within 10 μg. A few species had seeds too light to weigh individually; for these species (Appendix 1) samples of fifty seeds each were measured and then transformed to average individual weights. For all statistical analyses, seed weights were transformed to their natural logarithms to insure linearity with respect to other variables. A large negative number is therefore indicative of a small seed weight.

Germination trials

Growth chamber. Seeds were removed from cold storage and counted into each of 176 (two treatments × four replicates × twenty-two species) 5-cm diameter Petri dishes, twenty-five seeds per dish. Each petri dish contained two Whatman No. 1 filter papers that were saturated with 4 ml of distilled water. Temperature was held constant at 20 °C. Petri dishes were arranged at random in the growth chamber. The light treatment involved a regime of 14 h light followed by 10 h of darkness. In the dark treatment, seeds were removed from cold storage in the dark, counted using a dim neutral green light to avoid disturbing the phytochrome system of the seeds, and then covered with aluminum foil. Even brief illumination of seeds by low-intensity green light may eventually cause germination in certain species (Grime & Jarvis 1975; Blom 1978). Since the seeds in this experiment were only exposed for approximately 5 min, it is unlikely that any germination would be due to this effect. The experiment began on 19 June 1986 and was terminated on 5 July 1986.

Glasshouse. This experiment was similar to the light treatment described above except that the Petri dishes were placed in a glasshouse that had natural fluctuations in temperature (from 10 °C to 30 °C) and light conditions. There was no dark treatment because this experiment was meant to approximate conditions likely to be experienced by seeds in vegetation gaps on the shoreline when water levels drop. The experiment began on 1 April 1986 and was terminated on 16 April 1986.

Germination rate and percentage. Germination rate was estimated as a weighted mean according to the formula:

$$r_{ij} = \Sigma_j (p_{ij} \times j)$$

where p_{ij} is the proportion of all seeds of species i germinating on the day j, relative to the total number of seeds of species i germinating during the experiment. Thus the average seed of species i germinates r days from the beginning of the experiment. Germination percentage was the proportion of seeds germinating during the experiment. These two variables were used to differentiate between two potentially different attributes: the speed with which seeds can germinate and the number of seeds which can germinate in a given time period.

Maximum relative growth rate

For twenty-three species (Appendix 1) the relative growth rate of seedlings from Day 10 to Day 30 was measured; this time period was chosen because most of the species studied by Grime & Hunt (1975) have maximal relative growth rates between these times. Each seedling was grown in a separate container with 500 cm^3 of soil. This quantity of soil was shown by Grime & Hunt (1975) to be sufficient to allow even large seedlings such as sunflowers to grow unhindered for up to four weeks. The rooting medium was a 2:1 mixture of fertile potting soil and vermiculite; this was augmented with 50 ml of RX-15 commercial fertilizer (NPK ratios of 15:30:15) before the experiment began. Soil analyses were carried out on the rooting medium by the Ontario Ministry of Agriculture and Food; the results are shown in Table 1. Because these nutrient values are higher than those found naturally along the Ottawa River, it may be assumed that the plants were less limited by nutrient conditions in this experiment than when growing in the field. Whether the resulting relative growth rates would be maximal in any absolute sense is unknown but

TABLE 1. Quantities (mg kg^{-1}) of three macronutrients and soil pH in a marsh in Luskville, Quebec, dominated by *Typha angustifolia*, and the rooting medium for the $\mathbf{R}_{\max}$ experiment

Soil provenance	Phosphorus	Potassium	Magnesium	Soil pH
Luskville	5	107	254	5·8
Experiment	82	372	700	6·3

they are probably maximal relative to the field gradient. The relative growth rates will therefore be referred to as maximum relative growth rates ($\mathbf{R}_{\mathbf{max}}$) in accordance with Grime & Hunt (1975). Relative growth rates (in weeks^{-1}) were calculated according to the formula (Fisher 1920):

$$\mathbf{R}_{\mathbf{max}} = 7(\ln b_{30}) - \ln(b_{10})/(30-10),$$

where b_i is the average dry weight per seedling on Day *i*.

Species were planted in a complete randomized design on the glasshouse bench. The experiment contained twenty 'blocks'. Each block consisted of twenty-three pots, one for each of the twenty-three species. The position of each species within each block was randomized. Seeds of a particular species were placed in the appropriate pot and the first seedling to emerge was marked and its date of emergence noted. Unless this seedling died soon after emergence, it was used and all other seedlings emerging later were removed.

Of the twenty blocks, ten were randomly chosen for the first harvest, independently for each species. The individual of each species within each of the ten chosen blocks was then harvested ten days after it had emerged, dried to a constant weight at 60 °C, and weighed to within 10 μg. The same procedure was followed with the remaining ten blocks and the individuals in these pots were harvested thirty days after emergence.

Seedling organic fraction: mineral element ratio

The weight of mineral elements in a known dry weight of tissue was determined to within 10 μg by ashing the thirty-day-old seedling tissues obtained from the relative growth rate experiment at 600 °C for 4 h. The weight of the organic fraction was calculated by subtracting the ash weight from the dry weight. The ratio of the organic fraction to the weight of inorganic minerals were included because it has been suggested that stress-tolerant species have larger nutrient concentrations per gram of tissue than fast-growing species, when grown in fertile conditions (Chapin 1980).

Adult traits

The remainder of the traits listed in Appendix 1 were measured on adult plants growing in Breckenridge Marsh during late August and early September 1986. At this time, all species had already flowered and were at their maximum seasonal height. The marsh is described in detail by Shipley & Keddy (1987). It is located in a sheltered, organic bay and is minimally exposed. All reported adult traits are averages over five individuals measured in the field, chosen using a random number table. As these traits were measured in the field they should not be interpreted as genotypic potentials.

The shortest and longest distance between successive shoots on a rhizome or stolon were used to measure the degree of clumping of a genet. Canopy diameter was the widest diameter of the canopy of a single ramet. Canopy form for individual ramets was classified into five types: (i) 'monolayer', such as *Onoclea sensibilis*, in which the photosynthetic tissues are all displayed in a single plane; (ii) 'multilayer', such as *Lythrum salicaria*, in which photosynthetic tissues are displayed in many planes; (iii) 'graminoid', such as *Carex crinita*, in which all of the leaves originate from a common origin on the rhizome and form a canopy with a conical shape; (iv) 'single stem', such as *Scirpus acutus*, in which a single, leafless photosynthetic stem emerges from the rhizome; and (v) a 'tussock of stems', such as *Juncus filiformis*, in which a group of leafless photosynthetic stems emerge from a common origin on the rhizome. Finally, growth form was classified

TABLE 2. Pearson correlation coefficients between all quantitative traits measured; values of 0·5 or higher are marked in bold type. Juvenile and adult traits are separated by dashed lines. See Appendix 1 for details of the trait name abbreviations

	rlf	rlc	plf	plc	pdc	cn	$\mathbf{R}_{max}$	rt	sd	ld	rd	b	h	d	lt	lw
w	**0·7**	**0·6**	**−0·5**	−0·2	0·2	−0·1	**−0·7**	0·1	0·2	0·3	0·2	0·1	0·1	0·1	0·4	0·0
rlf		**0·5**	**−0·7**	**−0·6**	−0·1	−0·3	**−0·5**	−0·1	0·2	0·4	0·0	−0·2	−0·2	−0·1	0·1	0·3
rlc			−0·4	**−0·6**	−0·2	−0·3	0·4	−0·1	0·2	0·2	0·3	−0·1	−0·1	−0·2	**0·5**	−0·3
plf				0·3	−0·2	0·2	**0·5**	−0·1	−0·2	−0·3	−0·2	−0·1	−0·2	0·1	−0·2	−0·3
plc					0·3	**0·6**	0·1	0·0	−0·3	−0·2	−0·1	0·1	0·2	0·3	−0·3	−0·4
pdc						**0·8**	−0·3	0·1	−0·1	0·0	−0·1	0·2	**0·5**	0·2	−0·2	−0·1
cn							0·1	−0·1	−0·2	−0·1	−0·3	0·1	0·3	0·3	−0·3	**−0·5**
$\mathbf{R}_{max}$								0·2	0·2	0·3	−0·1	0·4	0·0	0·0	0·2	−0·1
rt									0·3	**0·6**	**0·5**	**0·6**	0·4	0·4	0·3	0·4
sd										**0·6**	0·0	0·3	−0·1	0·2	**0·5**	**0·7**
ld											0·3	**0·5**	0·2	0·0	**0·6**	**0·5**
rd												**0·5**	**0·5**	0·1	**0·6**	−0·1
b													**0·8**	**0·5**	**0·8**	−0·1
h														0·4	**0·5**	−0·3
d															0·3	−0·2
lt																−0·1

as either (i) creeping, (ii) upright, or (iii) rosette. Measurement and interpretation of the other adult traits listed in Appendix 1 are self-evident.

Statistical analysis

Association between juvenile and adult traits

The biological hypothesis to be tested is the following: species that are similar to each other based on one set of traits (juvenile or adult) are also similar to each other based on the other set of traits. In other words, it is possible to predict one set of traits from knowledge of the other set.

Most statistical tests of correlation between dissimilarity matrices (Gower 1971; Sneath & Sokal 1973; Hubert 1978) actually test the more restrictive hypothesis of a linear relationship between dissimilarities in the two matrices (Lefkovitch 1984). There are a number of computational and conceptual problems with this more restricted hypothesis, and a more appropriate test is described in Lefkovitch (1984), based only on those dissimilarities which contain the most pair-wise information and derived from the relative neighbourhood graph of Toussaint (1980). This non-parametric test is therefore used here. Thus, the statistical null hypothesis assumes independence of nearest neighbours in the two sets of traits.

Relationship between traits

Principal coordinates analysis (PCO) was used to identify the major axes of variation in the matrices of juvenile and adult traits (Gower 1966). Similarity was calculated using Gower's similarity coefficient (Gower 1971). This method is appropriate when the data contain dichotomous or unordered multistate variables. The percentage of the total squared length in the matrix accounted for by a particular eigenvalue is analogous to the percentage of variation in the data accounted for by an eigenvalue in principal components analysis, and can be interpreted in the same way.

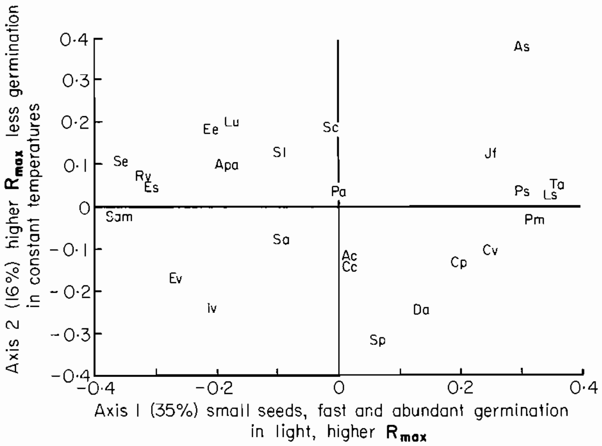

FIG. 1. Axes 1 and 2 of the principal coordinate analysis of seven juvenile traits in twenty-five species of emergent macrophyte. Also shown are those traits that correlated most strongly with the two axes. Mnemonic codes corresponding to species names are listed in Appendix 2. Percentages refer to the percentage of the total length accounted for by that axis.

RESULTS

Uncoupling of juvenile and adult traits

Gower's similarity coefficients based on all attributes show no evidence for an association between juvenile and adult traits for the twenty-five species examined (Lefkovitch's non-parametric test, $G_2 = 2{\cdot}103$, $P > 0{\cdot}1$) (Table 2).

Juvenile traits

The first axis of the principal coordinate analysis identified the major trend for species with small seeds to germinate rapidly and abundantly and to have high seedling $\mathbf{R}_{\mathbf{max}}$; this accounted for 35% of the total squared length (Fig. 1). The second axis represented a subordinate trend of species having above average seedling $\mathbf{R}_{\mathbf{max}}$ but below average quantities of seeds germinating under constant temperatures for a given rate of germination, and accounted for a further 16% of the total squared length. There was also some indication that the ability to germinate in the dark was important in defining this second axis. Thus, 51% of the total squared length was accounted for by these first two axes. The third axis (not shown) identified the ability to germinate in the dark, but accounted for only 8% of the total squared length. The Pearson correlations between the juvenile traits and the first two axes are shown in Table 3.

Adult traits

The first axis of the principal coordinate graph for adult traits accounted for 25% of the total squared length (Fig. 2a). Species that weighed heavily on this axis were those with ramets that were heavy (i.e. those that produced large quantities of above-ground biomass), had a wide canopy diameter, thick rhizomes and thin leaves. The second axis identified a component of size independent of biomass, and species that weighed heavily on this axis tended to be tall irrespective of how heavy they were. This second axis accounted for a further 20% of the total squared length (Fig. 2b). The third axis, which accounted for a further 13% of the total squared length, identified those species that were

TABLE 3. Pearson correlations between all quantitative traits and the first three DCA axes of Day *et al.* (1988), the first two PCO (principal coordinate analysis) axes based on juvenile traits, and the first three PCO axes based on adult traits. Values of 0·5 or larger marked in bold type. See Appendix 1 for details of the trait name abbreviations

	Vegetation data			Juvenile PCO		Adult PCO		
	DCA1	DCA2	DCA3	PCO1	PCO2	PCO1	PCO2	PCO3
w	−0·5	−0·0	0·2	−0·7	−0·4			
rlf	−0·3	**0·6**	**0·8**	**−0·9**	0·2			
plf	0·1	−0·4	**−0·7**	**0·9**	−0·2			
plc	0·1	**−0·5**	**−0·7**	**0·7**	**−0·7**			
pdc	−0·1	**−0·5**	−0·2	0·0	−0·4			
cn	0·2	**−0·5**	**−0·6**	0·2	0·3			
R_{max}	**0·5**	**0·5**	−0·4	**0·6**	**0·7**			
rt	0·2	0·1	**−0·5**			0·4	0·1	**−0·5**
sd	0·1	0·4	0·2			0·4	−0·2	−0·1
ld	−0·1	0·4	0·0			0·1	0·1	**−0·5**
rd	0·3	0·3	0·0			−0·1	0·4	**−0·7**
b	0·3	0·3	**−0·6**			**0·5**	0·3	**−0·7**
h	0·2	−0·1	**−0·6**			0·3	**0·7**	**−0·5**
d	0·3	0·2	**−0·5**			**0·8**	0·1	−0·1
lt	−0·2	0·4	−0·2			**−0·7**	−0·1	**−0·7**
lw	−0·1	0·3	**0·8**			0·1	−0·3	−0·1

both short and light, had thin rhizomes or none at all, roots close to the surface of the soil and thin leaves (Fig. 2c). Table 3 gives the Pearson correlations between the species scores on the first three axes and those traits that were continuous; no measure of association could be calculated for the dichotomous or unordered multistate variables.

Appendix 3 gives the average trait values for all species.

DISCUSSION

There was no association between the juvenile and adult subsets of traits and so there is no evidence that these two collections of traits are coupled. The discussion of ecological strategies in this group of species must therefore deal with these two life-history stages separately. This conclusion is in contradiction to most models of life-history stages, as mentioned in the Introduction. Grime's (1974, 1977, 1979) C–S–R model explicitly describes uncoupling of juvenile and adult traits and therefore coincides better with the observed covariation in plant traits. Grime, Hunt & Krzanowski (1987) found the same result based on a clustering of 273 species of British plants using fifteen adult traits and nine juvenile traits, although no inferential tests of significance were done. A subsequent study, using the same methodology but based on a larger data set, found similar trends (Grimes, Hodgson & Hunt 1988). As their study was done on different species, in a different geographical region, involved different habitats and included different attributes, such as concordance provides strong empirical evidence for such a generality.

An adaptive trait must (by definition) vary predictably with an environmental gradient. Examples are the relationship between seed size and shade (Salisbury 1942), seed size and drought (Baker 1972), relative growth rate and soil fertility and disturbance (Grime & Hunt 1975), germination characteristics and disturbance (Grime *et al.* 1981), or nuclear DNA content and temperature (Grime 1983). Presumably such traits vary predictably because possession of them by a plant increases the probability that the plant will successfully establish itself at that point on the gradient. A number of studies have shown

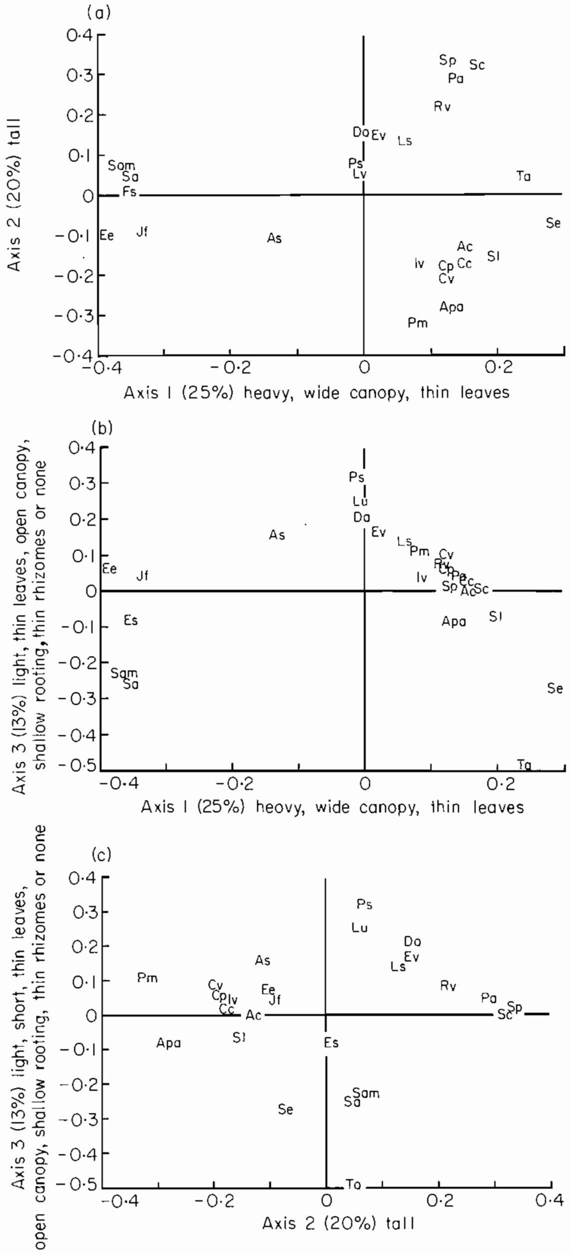

FIG. 2. (a, b, c) Axes 1, 2 and 3 of the principal coordinate analysis of thirteen adult traits in 25 species of emergent macrophyte. Also shown are those traits that correlated most strongly with the three axes. Mnemonic codes corresponding to species names are listed in Appendix 2. Percentages refer to the percent of the total length accounted for by that axis.

this to be true, at least for seed size (Fenner 1978; Rabinowitz 1978; Gross 1984; Fenner 1985), relative growth rate (Fenner 1978; Gross 1984; McConnaughay & Bazzaz 1987), height (Smith 1982; Newman 1983; Benjamin 1984; Mitchley & Grubb 1986; Weiner 1986; Weiner & Thomas 1986) and vegetative spread (reviewed in Grime 1979). This body of experimental and correlational evidence can be used to interpret the covariation of traits identified in this paper. It must be emphasized that these results and interpretations are strictly applicable only to the species and traits chosen. The traits were chosen because they were expected to be important in the context of plant strategies by the authors cited below.

Regeneration strategies

Competition, as this concept is used in the ecological literature, actually consists of two distinct abilities: the ability to suppress the growth of other individuals and the ability to resist being suppressed by others (Goldberg & Fleetwood 1987). These two abilities need not always be closely associated, and may actually vary independently at different stages in a life history. In particular, seedlings are not likely to suppress the growth of established vegetation and are therefore dependent on vegetation gaps of varying dimensions either to germinate or to survive and attain reproductive size (Pickett & White 1985). There are therefore two ways that a juvenile plant can increase the probability that it will survive to reproduce in the presence of established vegetation: either it avoids suppression by escaping in time or space (a fugitive strategy) or it resists excessive suppression due to details of its physiology (a stress-tolerant strategy) (Grime 1979; Fenner 1985).

These two different ways of dealing with competitive suppression are reflected in the intra-correlated juvenile traits included in this study. At one end of the first axis in Fig. 1 is a suite of juvenile traits consisting of large, slowly germinating seeds and seedlings having a low $\mathbf{R}_{\mathbf{max}}$, and at the other end of this axis is a suite of juvenile traits consisting of small, rapidly germinating seeds and seedlings having high $\mathbf{R}_{\mathbf{max}}$.

There is some experimental evidence that these traits affect the ability of a seedling to establish under a closed canopy. Gross (1984) found that, in the absence of established vegetation, small-seeded species had a higher relative growth rate and quickly occupied space. In the presence of established vegetation the large-seeded species had the more rapid relative growth rate because they were less severely suppressed. Similar conclusions were drawn by McConnaughay & Bazzaz (1987). In a correlative study, Salisbury (1942) showed that the average size of seeds of different species increased with the degree of shading in the habitats that they normally occupied.

Plants with large numbers of very small seeds are generally better able to disperse to new locations (Harper, Lovell & Moore 1970; Fenner 1985), are better able to enter the seed bank (Fenner 1985) and are subsequently dormant until they encounter the high light intensities, red:far-red ratios and fluctuating temperatures indicative of a gap in the vegetation. In a large comparative study Grime *et al.* (1981) found that the germination characteristics of a large number of species accorded well with their known regeneration patterns in the field. One can therefore interpret the covariation of juvenile traits identified in this study as a continuum of strategies ranging from fugitive juveniles that require large gaps in the vegetation in order to establish, to stress-tolerant juveniles that can establish in the smaller gaps of a less disturbed canopy. Thus the juvenile strategies are reminiscent of the r–K continuum when considered independently of the adult traits.

Strategies of established plants

While the regeneration strategy was presumably involved with the range of responses to different kinds of gaps in the canopy, the strategies of established plants are apparently involved principally with the ability to occupy space. Apart from those species with a leafless morphology (Ec, Es, Jf, Sam and Sa; Fig. 2) the species low on the first two principal coordinate analysis axes and highest on the third axis (Fig. 2) are small plants, with ramets containing little above-ground biomass, and with small rhizomes or stolons or no basal structures except roots. There were no annuals in this data set, but there was a number of facultative annuals potentially capable of completing their life cycle in one growing season, based on personal observations of plants grown from seed in the glasshouse. All of these species were located in this part of the ordination (*Agrostis stolonifera*, *Juncus filiformis*, *Lycopus uniflorus*, *Lythrum salicaria*, *Penthorum sedoides*, and *Plantago major*). This was an interesting observation because generation time was not included as a variable in the ordination.

High on axis one and low on axis three of the coordinate analysis (Fig. 2a,b) were the more massive species capable of aggressive vegetative spread (*Typha angustifolia*, *Sparganium eurycarpum* and *Acorus calamus*). Those species that were lowest on axis 1 were those with a leafless morphology (Ee, Es, JF, Sam, Sa), characterized by height but little above-ground biomass and a very thin canopy.

It may at first appear surprising that height was not one of the important traits on this first axis, since height is definitely of adaptive advantage in thick vegetation (Givnish 1982; Smith 1982; Newman 1983; Benjamin 1984; Mitchley & Grubb 1986; Weiner 1986; Weiner & Thomas 1986) where light attenuation through the canopy decreases exponentially (Smith 1982; Fitter & Hay 1983). This may be because in shoreline vegetation height has another, and conflicting, function, which weakens the correlation between height and above-ground biomass.

In order to survive, emergent plants must get above the water surface, which implies a requirement for height quite apart from the necessity to compete for light when growing in deeper water. Failure to get above the surface for an extended period of time results in the death of emergent plants (Harris & Marshall 1983; Hutchinson 1975; Van der Valk 1981; Lieffers & Shay 1981). Some plants, however (*Scirpus americanus*, *Scirpus acutus*, *Eleocharis smallii*), are found in deeper water but in relatively infertile soil (Hutchinson 1975; Day *et al.* 1988) and have, as predicted by Grime (1979), low $\mathbf{R}_{\mathbf{max}}$ values. These plants have leafless, hollow, photosynthetic stems that are tall but contain little biomass—a necessary consequence of height, herbaceous habit, and a low relative growth rate.

An hypothesis to explain the uncoupling of juvenile and adult traits

Generally, the regenerative strategies coincide with the r–K categorization when considered in isolation, yet there is no association between juvenile and adult traits, an important assumption of r–K selection. Thus the r–K selection model breaks down when both juvenile and adult traits are considered together: species having r-selected juvenile traits can have either r-selected or K-selected traits as adults, and *vice versa*. An excellent example is *Typha augustifolia*. As an adult it is tall, heavy, has thick rapidly growing rhizomes and is a long-lived perennial. As a juvenile its features are those of a fugitive species because it produces very large numbers of very small wind-dispersed seeds showing rapid germination in the light with fluctuating temperatures, inhibition of

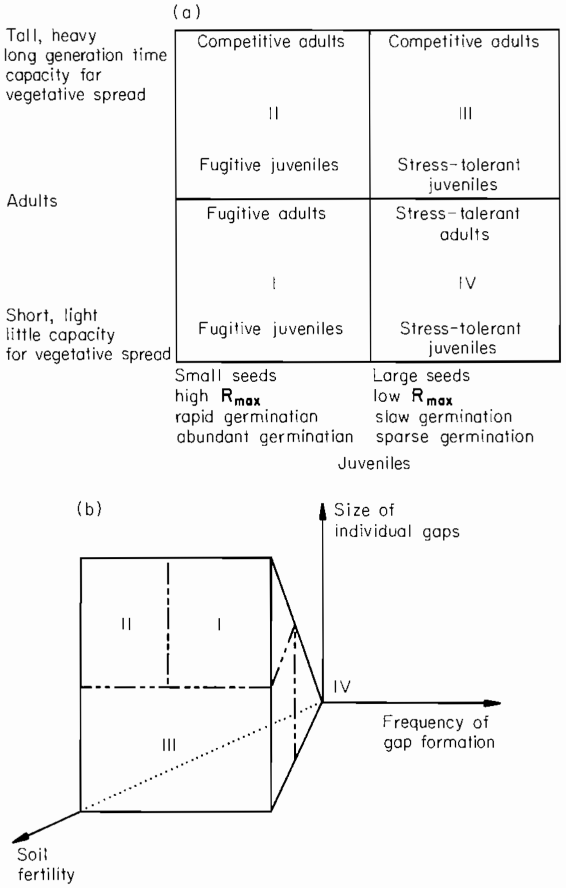

FIG. 3. (A) The major trends in adult and juvenile traits of 25 species of emergent macrophyte. Since these two sets of attributes are independent, the two orthogonal axes result in four types of herbaceous strategies. (b) Speculative relationships between environmental characteristics (soil fertility, frequency of gap formation, and the size of individual gaps) and the four strategies described in (a).

germination in the dark, and seedlings with the highest $\mathbf{R}_{\mathbf{max}}$ values of the twenty-three species studied.

This uncoupling of juvenile and adult traits, and the resulting contradiction with r–K selection, can be explained by considering two properties of disturbance (density-independent mortality): frequency and size (Miller 1982). The frequency of disturbance is the rate at which new gaps are formed in the vegetation, and the size of a disturbance is the amount of bare ground exposed (i.e. gap size) after an individual disturbance event (Fig. 3b).

Consider areas having fertile soil but differing in the frequency and size of disturbance events. In areas with large gaps forming frequently there will be sparse vegetation cover most of the time. Competition intensity will presumably be low (Wilson & Keddy 1986a,b) and because of the frequent and intense density-independent mortality, the probability of survival of long-lived perennials will also be low. Thus, typical r-selected traits will be favoured (Pianka 1978; Roughgarden 1979), both for juveniles and for adults. This corresponds to Grime's (1974, 1977, 1979) ruderal strategy, and to type I traits (Fig. 3a). In areas in which disturbance in neither intense nor frequent, typical K-selected traits will be favoured (type III traits; Fig. 3a), both for juveniles and adults. Thus, so long as the frequency and intensity of disturbance are correlated, the r–K continuum holds.

Conversely, in fertile areas with large gaps forming very infrequently, there will be a thick vegetation cover most of the time, interrupted by infrequent episodes in which intense density-independent mortality destroys large areas of adult vegetation. This occurs in emergent plant communities when, for example, unusually high or low water levels kill off most of the established vegetation, or when an explosion of muskrat populations causes large gaps (up to 5 m in diameter) to form. In such conditions r-selected adult traits would not be favoured because of the intense competition that would exist most of the time, yet K-selected juvenile traits would not be selected either because of an inability to repopulate after the disturbance. Species with K-selected adult traits but with r-selected juvenile traits would be best adapted to these environments (type II; Fig. 3a). These conclusions are mirrored in Chesson's (1982) theoretical studies on the 'storage effect', relevant to populations with overlapping generations and variable juvenile recruitment.

Following Grime (1974, 1977, 1979) the assumption is that in habitats with inherently low productivity, vegetation can only exist when disturbance, either its frequency or size, is minimal. In such habitats the expected suite of juvenile traits is not obvious, although there is some evidence (Baker 1972) that stressful conditions (at least drought) select for large seeds and therefore the other correlated traits that vary with seed size. In Fig. 3 these speculative relationships are summarized.

Plant traits and environmental gradients

It is possible to relate the morphologies of the plants to the environments in which they normally occur by using the data presented by Day *et al.* (1988), who produced a multivariate description of the emergent plant communities and environmental conditions along the Ottawa River using detrended correspondence analysis (DCA) and the clustering algorithm TwinSpan (Hill & Gauch 1980). In this study, a series of stepwise multiple regressions were performed using the species' scores on the first three DCA axes as dependent variables and all of the continuous traits as independent variables. This analysis included only the thirteen species common to both data sets. The stepwise regressions consistently chose three traits as best predicting species position along the indirect gradients identified by the DCA scores: (i) above-ground ramet biomass, (ii) germination rate in fluctuating temperatures and light conditions, and (iii) seedling relative growth rates. A canonical analysis (Gittins 1985) was used to identify the relationship of these three traits to the indirect gradients. The canonical correlation between these two sets of data was highly significant ($R^2 = 0{\cdot}89$, $P < 0{\cdot}001$ Wilk's Lambda).

Low on the first two DCA axes and high on the third DCA axis is found the least fertile sites characterized by low soil organic content (a general index of soil fertility), high percentages of sand and gravel, and low-standing crop. This environment contains species with large slow-germinating seeds, low $\mathbf{R}_{\mathbf{max}}$, and light adults. These traits correspond with Grime's (1979) description of stress tolerators. Higher on the first two DCA Axes and lower on the third DCA axis is found the more fertile, less disturbed environments characterized by high soil organic content and a higher percentage of silt/clay. Species that occur in this environment possess typical competitor (*sensu* Grime 1979) traits, such as height, large amounts of above-ground biomass, high $\mathbf{R}_{\max}$ and a large capacity for vegetative spread. In the centre of the three-dimensional space defined by the DCA axes are species closer to Grime's (1979) ruderal strategy. These plants had adult traits of small to intermediate size, little capacity for vegetative spread, rather small seeds, and intermediate $\mathbf{R}_{\max}$.

The description of plant strategies given above is concordant with environment–trait relationships given by other authors for emergent macrophytes. Van der Valk (1981) attempted to predict the cyclical succession found in prairie potholes by using functional groups, and recognized regeneration strategies similar to those described in this paper. Day *et al.* (1988) proposed five functional groups based mostly on adult traits: competitive dominants, gap colonizers, reeds, stress tolerators and ruderals.

Obviously, the environment–trait relationships described in this paper are only crude first approximations which ignore any ecotypic variation within species and many of the subtleties described, for instance, in Grubb (1977). However, it seems reasonable to develop a good understanding of the major trends in trait variation and trait–environment correlation before embarking on more species-specific details. A broad general understanding of ecological strategies has already progressed from deductive, almost intuitive, relationships (r–K selection) to qualitative empirical ones. Future studies that explicitly relate predictor (environmental) variables to response (trait) variables should provide more exact, and falsifiable, predictions concerning plant strategies.

The distribution and abundance of species, as taxonomic entities, are strongly affected by historical and stochastic factors. This, combined with the fact that plant communities are dynamic entities, means that studies relating the distribution of taxonomic entities (species) to environmental gradients are only relevant locally, both in time and space. Instead, the emphasis should be on the traits possessed by species, whatever their scientific bionomial. Such attributes, however, will have to include both adult and juvenile traits because these two sets of traits apparently vary independently.

ACKNOWLEDGMENTS

We thank L. Lefkovitch for help with the statistical analyses and for suggesting improvements to the text. R. van Hulst, L. Maillette and R. Reader improved the manuscript with their critical comments. This research was funded by the Natural Sciences and Engineering Research Council of Canada.

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(*Received 30 June 1988; revision received 18 March 1989*)

APPENDIX 1

Traits measured and their mnemonic codes.

Trait	Abbreviation
Log$_e$ of seed weight(g)*	w
Average time to germination in the light under fluctuating temperatures (10-30 °C) (days)	rlf
Average time to germination in the light under constant temperatures (20 °C) (days)	rlc
Percentage germination in the light under fluctuating temperatures (20 °C)	plf
Percentage germination in the light under constant temperature (10–30 °C)	plc
Percentage germination in the dark under constant temperatures (20 °C)	pdc
Ratio of organic to inorganic fraction in seedling tissues (g/g)	cn
Maximum relative growth rate of seedlings aged 10 to 30 days (g/g week)	$\mathbf{R}_{\mathbf{max}}$
Thickness of rhizomes or stolons (where present) (mm)	rt
Shortest distance between successive shoots on a rhizome or stolon (where present) (cm)	sd
Longest distance between successive shoots on a rhizome or stolon (where present) (cm)	ld
Depth from soil surface to rhizome, stolon or roots (cm)	rd
Dry weight of above-ground biomass of a single ramet (g)	b
Maximum height above ground of photosynthetic tissues of a single ramet (cm)	h
Maximum diameter of the canopy of a single ramet (cm)	d
Maximum leaf thickness (mm)	lt

Maximum leaf width (cm)	lw
Presence of rhizomes or stolons	vp
Canopy type: (i) leafy—monolayer (1) —multilayer (2) —graminoid (3) (ii) leafless—single stem (4) —tussock of stems (5)	ct
Growth form—creeping (1) —upright (2) —rosette (3)	gf

* The following species had seeds too light to weigh accurately individually: *Agrostis stolonifera*, *Juncus filiformis*, *Lythrum salicaria*, *Penthorum sedoides*, *Scirpus cyperinus* and *Typha angustifolia*.

APPENDIX 2

Species names and mnemonic codes.

Species	Number
Acorus calamus L.	Ac
Agrostis stolonifera L.	As
Alisma plantago-aquatica L.	Apa
Carex crinita Lam.	Cc
Carex projecta Mack.	Cp
Carex vulpinoidea Michx.	Cv
Dulichium aurundinaceum (L.) Britton	Da
Eleocharis erythropoda Stud.	Ee
Eleocharis smallii Britton	Es
Elymus virginicus L.	Ev
Iris versicolor L.	Iv
Juncus filiformis L.	Jf
Lycopus uniflorus Mochx.	Lu
Lythrum salicaria L.	Ls
Penthorum sedoides L.	Ps
Phalaris arundinacea L.	Pa
Plantago major L.	Pm
Rumex verticillatus L.	Rv
Sagittaria latifolia Willd.	Sl
Scirpus americanus Pers.	Sam
Scirpus acutus Muhl.	Sa
Scirpus cyperinus (L.) Kunth	Sc
Sparganium eurycarpum Engelm.	Se
Spartina pectinata Link	Sp
Typha angustifolia L.	Ta

APPENDIX 3

Average trait values for all measured traits. See Appendix 1 for units. Also given are the standard errors of the measured $\mathbf{R}_{\mathbf{max}}$ values. Species names are given in Appendix 2 and trait names in Appendix 1. One exception is seed weight, symbolized in this table as sw, which gives the actual average seed weights (μg) and standard deviations, not their natural logarithms

Species	sw	rlf	rlc	plf	plc	pdc	vp	t	sd	ld	rd	b	h	d	$\mathbf{R}_{\mathbf{max}}$	cn	ct	gf	lt	lw
Ac	91 ± (17)	7·7	10·4	71	28	0	Yes	6·1	2·0	6·0	1·5	4·7	77·6	30·8	1·00 ± (0·12)	7·43	3	2	1·2	1·0
As	5	—	—	—	—	—	Yes	0·2	2·0	4·0	0·5	0·1	14·2	10·0	1·52 ± (0·13)	13·35	1	1	0·1	0·3
Apa	33 ± (13)	16·0	3·9	0	25	0	No	—	—	—	2·0	2·9	27·6	23·0	1·05 ± (0·25)	2·00	3	3	0·3	6·1
Cc	63 ± (1)	11·2	10·5	68	58	0	Yes	6·0	0·5	2·0	2·5	0·9	57·2	84·8	1·04 ± (0·05)	—	3	2	0·3	0·7
Cp	19 ± (4)	8·0	6·4	63	81	0	Yes	3·2	0·5	1·0	2·5	0·4	55·0	33·4	1·07 ± (0·08)	10·39	3	2	0·2	0·5
Cv	20 ± (4)	7·7	7·2	78	93	0	Yes	2·7	0·5	1·0	2·5	0·4	46·6	35·0	1·17 ± (0·06)	8·53	3	2	0·1	0·3
Da	53 ± (11)	6·6	9·8	71	82	0	Yes	3·0	3·0	5·0	5·0	0·8	48·0	20·0	0·89 ± (0·08)	6·94	2	2	0·1	0·5
Ee	31 ± (5)	12·9	10·3	16	4	0	Yes	0·7	0·1	4·0	0·5	0·1	36·0	0·1	—	4·79	5	2	—	—
Es	145 ± (18)	12·8	16·0	9	2	0	Yes	1·2	1·0	10·0	3·0	0·4	72·2	0·3	0·92 ± (0·32)	5·06	4	2	—	—
Ev	307 ± (63)	16·0	8·7	0	57	6	Yes	2·4	—	—	2·0	0·9	73·2	32·8	0·74 ± (0·13)	8·15	2	2	0·1	0·9
Iv	1364 ± (529)	7·5	10·5	2	40	7	Yes	7·6	5·0	5·0	2·2	1·7	57·2	24·8	0·76 ± (0·17)	8·25	3	2	0·4	1·8
Jf	2	5·3	6·6	93	23	0	Yes	0·3	0·3	5·0	1·0	0·1	52·0	0·1	1·30 ± (0·09)	—	5	2	—	—
Lu	17 ± (7)	14·5	10·3	16	7	0	No	—	7·0	25·0	1·3	0·3	37·0	12·8	1·18 ± (0·12)	6·86	2	2	0·2	1·8
Ls	5	4·4	4·2	64	80	13	No	—	—	—	2·5	5·5	85·0	15·4	1·42 ± (0·10)	7·96	2	2	0·2	1·4
Pa	31 ± (11)	—	—	—	—	—	Yes	2·0	0·8	6·0	6·0	4·5	120·0	50·7	1·12 ± (0·10)	7·91	2	2	0·1	1·4
Pm	16 ± (7)	6·1	—	98	—	—	No	—	—	—	1	0·1	12·0	16·6	1·16 ± (0·10)	5·09	3	2	0·2	2·7
Ps	1	4·0	6·7	91	54	0	No	—	13·0	4·5	0·5	0·6	25·0	—	1·25 ± (0·22)	—	2	2	0·1	2·0
Sl	29 ± (10)	9·8	10·0	20·0	10·0	3	Yes	7·1	25·0	25·0	5·0	3·2	51·4	37·6	1·21 ± (0·10)	6·74	3	3	0·4	3·5
Sam	263 ± (45)	13·0	15·0	1	2	0	Yes	4·0	2·0	5·0	13·0	0·4	76·4	0·3	0·76 ± (0·25)	2·08	4	2	—	—
Sa	161 ± (33)	11·3	12·1	48	38	0	Yes	8·4	1·0	30·0	7·5	1·8	72·2	0·3	—	—	4	2	—	—
Sc	1	5·5	8·1	2	1	0	Yes	5·6	1·0	1·0	5·0	7·9	153·2	39·8	1·18 ± (1·18)	6·33	2	2	0·7	0·9
Se	5204 ± (1418)	7·2	6·1	30	0	0	Yes	4·7	21·0	27·0	—	13·7	100·4	47·0	1·16 ± (0·13)	5·83	3	2	3·6	1·0
Sp	161 ± (38)	7·2	6·1	30	90	47	Yes	2·9	1·0	11·0	3·0	7·8	161·8	42·0	0·77 ± (0·09)	16·62	2	2	—	1·2
Ta	4	3·3	5·6	66	85	0	Yes	14·0	4·0	25·0	10·0	20·5	167·2	49·2	1·63 ± (0·10)	6·89	3	3	1·8	0·7
Rv	249 ± (34)	16·0	11·0	0	2	18	Yes	13·1	2·0	—	5·0	5·73	71·8	33·0	1·05 ± (0·07)	9·84	2	2	0·2	1·9