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Architectural and physiological heterogeneity within the synflorescence of the pseudoviviparous grass *Poa alpina* var. *vivipara* L.

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Abstract

Many biotypes of the northern-hemisphere Arctic-Alpine grass *Poa alpina* L. reproduce asexually via prolification of the spikelet axis to produce dehiscing shoots. Although capable of photosynthesis, the source–sink characteristics of these synflorescence systems are unknown, including the degree to which plantlets from different regions of the synflorescence are capable of providing for their own carbon requirements, or contributing to other sinks. Photosynthetic rates within the paracladial zone, as determined by infrared gas analysis (IRGA), exceeded respiratory rates by 3–4-fold. $^{14}CO_2$ tracer studies determined that the paracladial zone was not only as efficient at fixing carbon as the youngest fully expanded leaf (per unit dry weight), but that both organs exported carbon mainly basipetally (cf. extensive acropetal export from this leaf in seminiferous grasses). Distal plantlets of the paracladial zone fixed approximately 20% more $^{14}CO_2$ than did proximal plantlets. This was by virtue of their greater dry weight. At dehiscence, 'distal' plantlets were more likely to become established, and possessed relative growth rates more than 10 times those of 'proximal' plantlets. Paracladial heterogeneity was also apparent as an increased proportion of aborted spikelets on proximal paracladia. The possible causes of this heterogeneity are discussed.

Key words: Photosynthesis, carbon, partitioning, source–sink relationships, inflorescence, heterogeneity.

Introduction

Pseudoviviparous grasses have the ability to reproduce asexually by means of vegetative 'plantlets'. After dehiscing from the parent plant, plantlets root and establish quickly in short growth seasons (Lee and Harmer, 1980). Each plantlet represents the continued growth of an indeterminate spikelet. The axis (rachilla) has reverted from a phase of reproductive growth (producing florets, in some instances with seed) back to vegetative growth (producing miniature, morphologically complete leaves).

The spikelets of many grasses are capable of fixing carbon, and are of considerable importance to the development of caryopses (Porter *et al*., 1950; Thorne, 1966). Indeed, in the case of *Poa annua* L., it was determined that 20–25% of $^{14}CO_2$ incorporated into the caryopses at 14 d after inflorescence exertion was initially fixed within the inflorescence (Ong and Marshall, 1975). Ong *et al*. stated that the inflorescence of *P. annua*, and that of *Lolium perenne* L., was the most active assimilatory organ of the reproductive tiller (Ong *et al*., 1978), with all parts of the inflorescence (except caryopses) fixing $^{14}CO_2$; 40–50% of which was accounted for by the lemmas and paleas. Nomenclature of grasses follows Hubbard (Hubbard, 1984).

It was previously determined that pseudoviviparous plantlets of *Festuca vivipara* (L.) Sm. do photosynthesize (Lee and Harmer, 1980). However, the extent to which pseudoviviparous plantlets are self-sufficient in terms of carbon supply remains poorly understood.

The concept of carbon fixation by plantlets poses further questions: (a) is assimilation by plantlets the sole

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source of carbon for plantlet development after their exertion from the surrounding leaf sheath? (b) are rates of carbon fixation in plantlet leaves equivalent to those of homologous parent plant leaf-blades? and (c) does export of carbon occur from the paracladial zone (i.e. the region of repeated inflorescence modules, or paracladia, comprising the reproductive synflorescence; Vegetti and Anton, 1995)?

Any investigation of the physiological relationships between organs such as paracladia must first determine their spatial and temporal relationships. For example, in three varieties of rice (*Oryza sativa*) the pattern of development within the paracladial zone was hierarchical, with distal paracladia being further developed than proximal paracladia—there being a gradient in physiological time along the rachis (Mohapatra and Sahu, 1991; Mohapatra *et al.*, 1993). This was also observed in grasses in general (Arber, 1934). In addition, the architecture of the paracladial zone in rice differed spatially, with larger numbers of spikelets being produced by proximal paracladia (and caryopses from these being 'quite poor' [*sic*]). An initial aim of the present study was, therefore, to describe the reproductive architecture in order to provide a physical context in which to consider the physiology of this structure.

Materials and methods

Plant growth

The biotype of *Poa alpina*, cultivation and inflorescence-induction methods used were identical to those detailed recently (Pierce *et al.*, 2000). Briefly, plants were grown in washed silver sand in 1.0 l capacity pots with nutrients supplied as a one-fifth strength Long Ashton Nutrient Solution modified to provide phosphorus and nitrogen at 0.6 and 1 mg equivalent l^{-1}, respectively.

Structure of the synflorescence

Morphological maps were made of the paracladial zone of six replicate synflorescences, the presence and relative position of plantlets and aborted spikelets being noted. The synflorescence of the main axis from separate plants, 20 d after exertion of the distal florescence from the sheath of the youngest leaf on the axis, was used.

Gas exchange within the paracladial zone

Gas exchange within the paracladial zone was determined by infrared gas analysis (IRGA) using an ADC LCA 4 and a reconfigured 'conifer-type' leaf cuvette (PLC 3; ADC Bioscientific, Pindar Road, Hoddesdon, Herts., UK). The entire paracladial zone was enclosed within the cuvette, with no culm tissue included. Light was provided using 250 W metal-halide lamps (model HGI/NDL; FGL Lighting Ltd., Pinewood Studios, Bucks., UK), and plant tissue temperature measured using an independent thermistor, placed in direct contact with plant tissue. Instantaneous net photosynthetic rate was measured at a photosynthetic photon flux density (PPFD) of 500 μmol m^{-2} s^{-1} incident at the plant tissue surface, and at a temperature of 20 °C. Air flow within the cuvette was maintained at a constant rate of 300 ml min^{-1}. Respiratory rates were measured by enclosing the cuvette in aluminium foil to exclude light, at 19 °C. Leaf area within the paracladial zone was determined by analysis (Delta-Tscan; Delta-T Devices Ltd., Burwell, Cambridge, UK) of leaf images created using a flatbed scanner (ScanJet 4c; Hewlett-Packard Ltd., Bracknell, Berks, UK).

Measurements were made from a population of plants at various stages of development up to 21 d after exertion, but not before 7 d, as proximal paracladia had not yet emerged at this time.

C-14 pulse-labelling experiments

Pulse labelling of tissue was conducted using the protocol of Farrar (Farrar, 1993*a*), in which various organs (detailed below) were supplied with $^{14}CO_2$. The source of activity was $Na_2{}^{14}CO_3$ (Amersham Life Sciences Ltd., Little Chalfont, Bucks., UK), with an activity per feed of 10 μCi≡370 kBq.

A pulse-feed of 20 min duration was applied to the chosen plant part using either the PLC 3 IRGA cuvette, or a smaller hand-built cuvette (G Gunn and JF Farrar, unpublished results), at 20 °C and a PPFD of 700 μmol m^{-2} s^{-1}. The pulse feed was followed by a 2 h chase period at 20 °C and a PPFD of 700 μmol m^{-2} s^{-1}. Four unfed control plants directly neighbouring the pulse-fed plants were used to monitor possible refixation of respiratory $^{14}CO_2$.

Following the chase period, pulse-fed plants were dissected into their component organs (depending on the particular experiment) and each component dried to constant weight in a forced-air oven at 70 °C. Dried tissue samples were later oxidized (OX400 Biological Sample oxidizer; Lab. Impex Systems, Wimborne, Dorset, UK). The $^{14}CO_2$ evolved was trapped in Oxosol™ C^{14}scintillant (National Diagnostics, Hessle, Hull) and radioactivity counted (liquid scintillation counter; WinSpectral 1414; EG and G Wallac Ltd., Milton Keynes, UK). A blank containing scintillant was used to remove the background activity from all data. The following experiments were conducted:

(1) *Feeding of $^{14}CO_2$ to first leaf or entire paracladial zone of parent plant*: The first leaf (the distal leaf on the peduncle, including the blade, sheath and sheathed internode) of plants at 20 d from paracladial exertion, and also the entire paracladial zone of a further group of plants, were pulse-fed using the PLC 3 cuvette.

(2) *Feeding of $^{14}CO_2$, following physical manipulation of the paracladial zone*: Also at 20 d from exertion, the distal half (by spikelet number) of the paracladial zone of six replicate plants was removed with a razor blade under water, discarded, and the cut rachis of the parent plant sealed with silicon grease, leaving only the proximal half of the paracladial zone attached to the parent plant. In a further six replicates the paracladia from the proximal two rachis nodes (i.e. proximal half by spikelet number) were removed, discarded, and stumps on the parent rachis sealed. Six control plants were left intact. Treated plants were left for 24 h before pulse-feeding of the first leaf using the PLC 3 cuvette.

(3) *Feeding of $^{14}CO_2$ to the culm of the parent plant*: A portion of the distal internode of the culm was pulse-fed at 20 d from paracladial exertion. Manipulation treatments identical to those detailed in Experiment 2 were also imposed on the paracladial

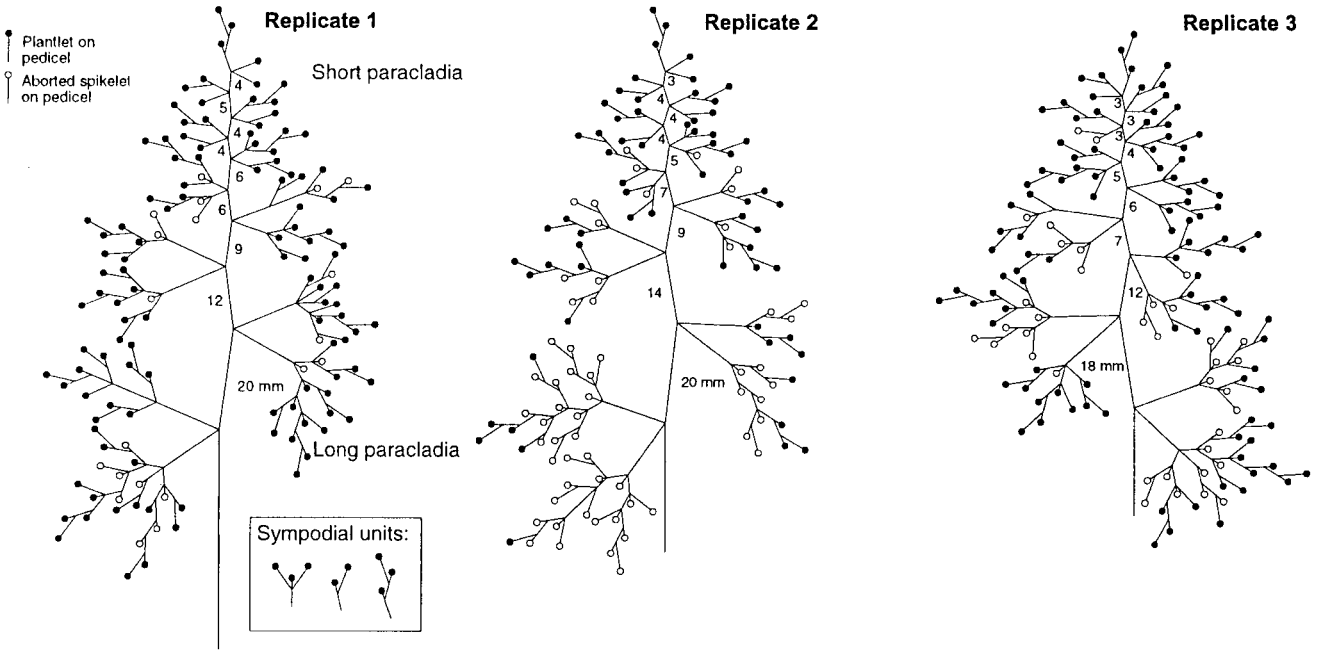

Fig. 1. Two-dimensional diagrammatic representations of the paracladial zone of the biotype of *Poa alpina* studied. Paracladia possessed monochasial units supported on dichasial units. The synflorescence was monotelic. Numbers refer to the lengths of rachis internodes (mm). Solid circles represent entire spikelets (each with a plantlet present); open circles represent aborted, withered spikelets. Three plants, representative of the natural variability in the population, are presented.

zones of a second group of plants at 7 d after paracladial exertion (i.e. when proximal paracladia had emerged and were available for manipulation), with either the distal or proximal half removed. Control plants were left intact. Eight replicate plants of each treatment were harvested destructively at 7 d from exertion, and at two subsequent harvests, each 7 d apart. Relative growth rate (RGR) of attached plantlets was then determined (using the equation of Hunt, 1990).

Establishment of plantlets, post-dehiscence from the parent plant

Plantlets were removed from 20 plants at the time of cessation of culm elongation growth (i.e. when plantlets first readily dehisced; Pierce *et al*., 2000). From each plant a plantlet from the distal end of the paracladial zone, and a single plantlet from the proximal end were removed; providing 20 plantlets from each position. Ten plantlets from each position were placed immediately in labelled sealed envelopes and dried in an oven at 60 °C for 24 h, and dry weights taken. The remaining 10 plantlets from each position were 'sown' (pedicel down) in seed trays containing washed silver sand, and covered with a sheet of glass to prevent excessive water loss. Trays were placed in an alpine greenhouse (maximum temperature 21.9 ± 0.9 °C, minimum 8.8 ± 0.4 °C averaged over the course of the experiment, with natural illumination of approximately 16 h daily duration) and watered on alternate days with distilled water. After 30 d the number of plantlets surviving was recorded, material was dried and dry weights obtained.

Root growth in dehisced plants

Six distal and six proximal plantlets were divided between three Petri dishes. Petri dishes each contained 10 layers of Whatman No. 1 filter paper (8.5 cm diameter), moistened with distilled water on which plantlets were placed each with their basal end in contact with the filter paper (modified from Harmer and Lee, 1978). Petri dishes were placed in a growth room at 15 °C with a PPFD of 450 μmol m^{-2} s^{-1} for 20 d with further distilled water added on alternate days using a wash bottle. On the emergence of roots, the oldest root was marked with a spot of red indelible marker ink. Every third or fourth day the number of roots was counted and the length of the oldest root measured.

Results

Architecture of the paracladial zone of P. alpina

The main axis was hapaxanthic (terminating with the reproductive structures), and paracladia were ultimately monotelic (terminating in a spikelet), i.e. it was a 'closed system' (Cámara-Hernández and Rua, 1991; Fig. 1). Two first-order paracladia were borne on each node of the rachis. Paracladia were arranged in a sympodial fashion, but were not completely monochasial (i.e. with unbranching chains of units) or dichasial (branching), but a combination of both. Paracladia were observed to revert to their original unspread position after the cessation of culm elongation growth.

The proportion of the total number of spikelets borne on each node decreased acropetally along the rachis, with $48.6 \pm 1.2\%$ of spikelets being borne on the proximal two rachis nodes (Fig. 2b), defining these two nodes as the proximal half of the paracladial zone by spikelet number.

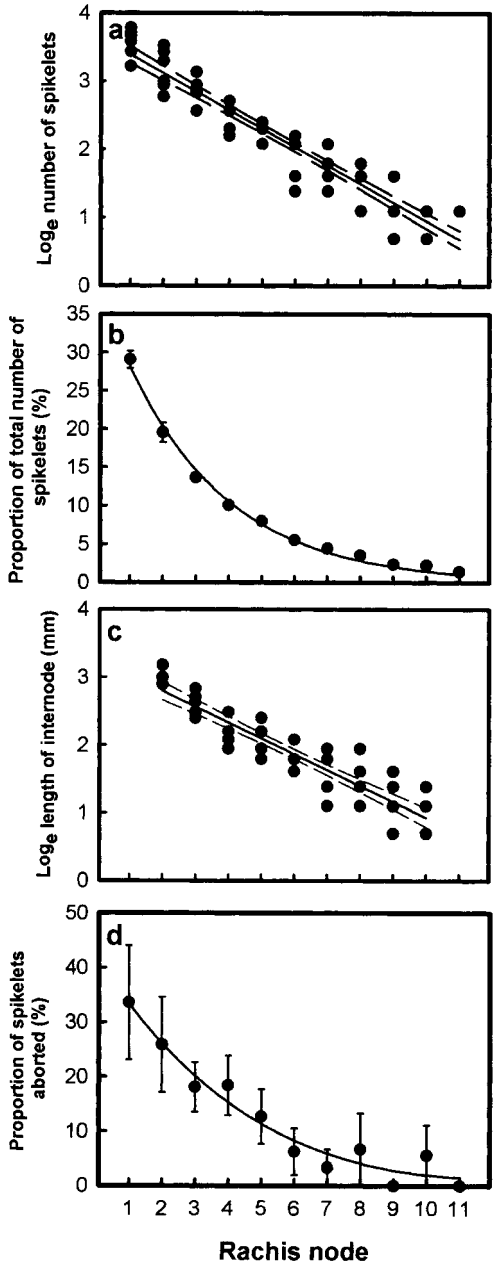

Fig. 2. The morphology of the paracladial zone, showing (a) number of spikelets borne on each main rachis node (data Log_e transformed; $r^2=0.91$, $b=-0.27$, $P\leq0.001$; dashed line represents 95% confidence interval for the plotted linear regression), (b) proportion of spikelets borne on each rachis node, expressed as a percentage of the total number of spikelets, (c) internode lengths along the rachis of the paracladial zone ($r^2=0.84$, $b=-0.23$, $P\leq0.001$) and (d) proportion of aborted spikelets borne on paracladia at each rachis node (equation of fitted line: $y=ae^{-bx}$; $r^2=0.95$, $P\leq0.001$). Data in (b) and (d) represent the mean $\pm$1SE of six replicates (where large enough to be shown). Rachis node one was the proximal node.

There was a strong exponential relationship between rachis node number and the number of spikelets borne on the node; the number of spikelets decreasing towards the distal end of the rachis (Fig. 2a; $r^2=0.91$, $P\leq0.001$). An equivalent relationship was seen between internode number and the length of the internode, with internodes becoming shorter with distance acropetally along the rachis (Fig. 2c; $r^2=0.84$, $P\leq0.001$).

A number of spikelets were aborted (i.e. did not possess florets or plantlets). Such spikelets were represented by either a pair of green glumes (identical in external appearance to a young spikelet in which florets were not yet visible), a pair of withered brown glumes or by a withered mass. The proximal node possessed the greatest proportion of aborted spikelets (Fig. 2d).

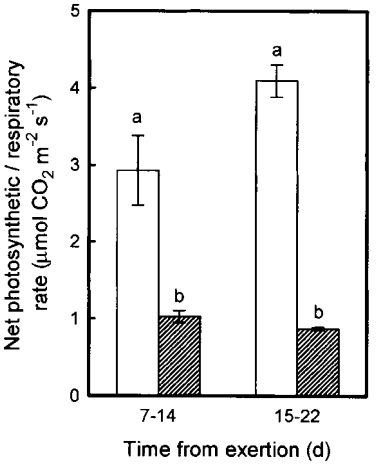

Fig. 3. Net photosynthesis (open bars) and respiration (hatched bars) in the paracladial zone, 14 d and 21 d after exertion of the culm. Data represent the mean $\pm$1SE of five separate determinations. Different letters represent significant differences between means at the $P\leq0.05$ level, determined by Fisher's multiple comparison procedure (ANOVA).

Carbon fixation

Net photosynthetic rate of the paracladial zone was three to four times that of the respiratory rate ($P\leq0.001$; Fig. 3), with the difference between these rates increasing over time ($P=0.018$).

During the ^{14}C pulse-feeding experiment 1, unlabelled control plants had a ^{14}C content of 0.02 ± 0.005 Bq mg^{-1} DW, with unfed regions of pulse-fed plants exhibiting ^{14}C contents two orders of magnitude higher (4.8 ± 0.8 Bq mg^{-1} DW with the first leaf pulse-fed, or 5.9 ± 0.9 Bq mg^{-1} DW with the panicle pulse-fed, i.e. reassimilation of respiratory derived $^{14}CO_2$ was minimal and values in unfed parts of pulse-fed plants represent export from pulse-fed regions). Of the ^{14}C fixed by the first leaf on the main axis, 83% was retained in the leaf after a 2 h chase period (Fig. 4a), with 3.1% of the remaining ^{14}C exported acropetally and 13.9% exported basipetally (Fig. 4a). When the paracladial zone was pulse-labelled with $^{14}CO_2$, 4.5% of ^{14}C was exported after 2 h (Fig. 4b). The specific ^{14}C content of three portions of the fed paracladial zone were not significant from one another ($P\leq0.05$; Table 1a).

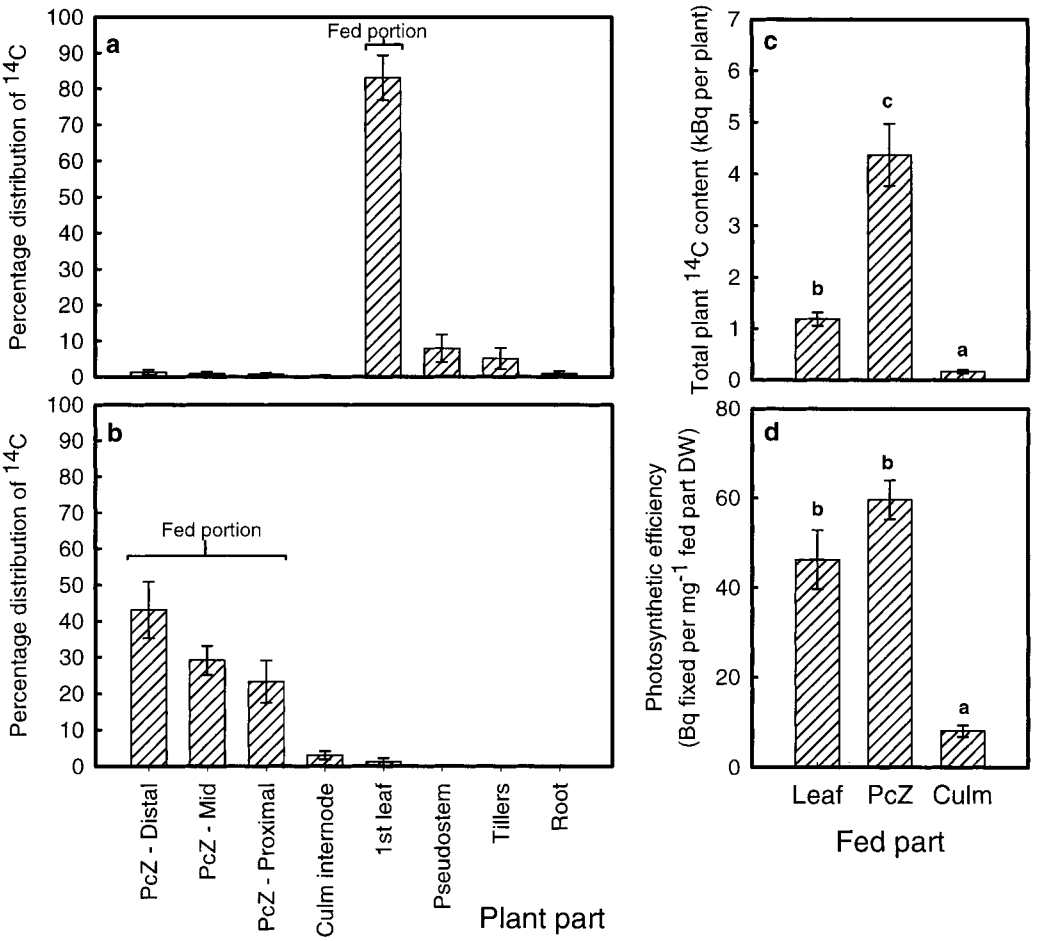

Fig. 4. (a, b) The percentage distribution between plant parts of ^{14}C when (a) the first leaf and (b) the entire paracladial zone (PcZ) were pulse-fed $^{14}CO_2$. (c, d) The results of feeding $^{14}CO_2$ to the first leaf, paracladial zone and culm; (c) total plant ^{14}C content and (d) photosynthetic efficiency (total amount of ^{14}C fixed per unit fed organ dry weight) of photosynthetic organs after pulse-chasing. Data represent the mean $\pm$1SE of either eight (a, b) or 6 (c, d) separate determinations. Different letters represent significant differences between means at the $P \leq 0.05$ level, determined by Fisher's multiple comparison procedure (ANOVA).

The absolute ^{14}C content of plants pulse-fed via the paracladial zone (4.4 ± 0.6 kBq per plant) was approximately four times that of plants fed via either the first leaf (1.2 ± 0.1 kBq per plant) or the culm (Fig. 4c). Taking the amount of ^{14}C fixed per unit dry weight as an estimate of photosynthetic efficiency, the first leaf and paracladial zone showed no significant difference in efficiency of carbon fixation (Fig. 4d). The higher total amount of ^{14}C fixed by the paracladial zone compared to the first leaf (Fig. 4c) was due to the larger mass of the former compared to the latter. The culm had a much lower photosynthetic efficiency than either the first leaf or the paracladial zone.

Development and establishment of plantlets post-dehiscence

In the treatment with intact parent plants, plantlets from the distal region of the paracladial zone attained a higher dry weight than did plantlets from the proximal region (Fig. 5a, b; Table 2a). Plantlets from both distal and proximal regions exhibited decreasing RGRs with increasing time from exertion (Fig. 5c; $P \leq 0.05$).

In treatments where proximal plantlets were excised from the parent plant paracladial zone, the remaining distal plantlets showed no difference to their counterparts, on intact plants, with respect to final dry weight attained or RGR of distal plantlets (Fig. 5a, c, d). However, in plants in which the distal plantlets were removed, proximal plantlets maintained a high RGR (Fig. 5d) and after 21 d had attained the same dry weight as distal plantlets of intact plants (Fig. 5a, b). Manipulation (excision of the proximal half) resulted in a significant increase in the amount of ^{14}C imported into the distal half of the paracladial zone from the pulse-fed first leaf of *P. alpina* after 2 h ($P=0.048$, Student's *t*-test; Table 1b), with excision of the distal half resulting in a similar, but non-significant, tendency to increase import into the proximal half of manipulated synflorescences ($P=0.067$).

Table 1. *(a) Specific ^{14}C content of different regions of the paracladial zone when the entire paracladial zone was pulse-fed $^{14}CO_2$ and (b) specific ^{14}C content of distal and proximal halves of the paracladial zone after pulse-feeding the first leaf with $^{14}CO_2$*

The paracladial zone was either intact (control) or manipulated by removal of all spikelets in the reciprocal half of the paracladial zone. Data represent the mean ± 1SE of (a) eight and (b) five replicates, respectively. Different letters represent significant difference between means at the P ± 0.05 level determined by Tukey's multiple comparison procedure (ANOVA).

(a)	Position in paracladial zone	^{14}C content (Bq mg^{-1} DW)
	Distal	57.9 ± 4.2 a
	Mid	58.6 ± 4.9 a
	Proximal	55.7 ± 4.8 a

(b)	Specific ^{14}C content (Bq mg^{-1} DW)	
	Manipulated	Control
Proximal	1.38 ± 0.2 a	0.93 ± 0.1 ab
Distal	1.42 ± 0.2 a	0.97 ± 0.1 b

Adventitious roots arose extra-vaginally through the leaf-sheaths at the base of plantlets. The number of roots produced by distal plantlets was not significantly different from the number produced by proximal plantlets (Fig. 6a). However, the length of the oldest root produced by distal plantlets was arithmetically, and at three time points significantly, greater than that of proximal plantlets ($P \leq 0.05$; Fig. 6b; see also Table 2b). The final dry weight of these plantlets was 5.3 ± 0.4 mg (distal) and 3.1 ± 0.5 mg (proximal); significantly different as determined by Student's *t*-test ($P \leq 0.001$). The relative growth rate of distal plantlets (0.042 ± 0.004 g g^{-1} d^{-1}) on establishment in sand culture was over 10 times that of proximal plantlets (0.004 ± 0.002 g g^{-1} d^{-1}, $P \leq 0.001$). In addition, proximal plantlets expressed a mortality rate of 30% over this 30 d period, whereas all the distal plantlets survived.

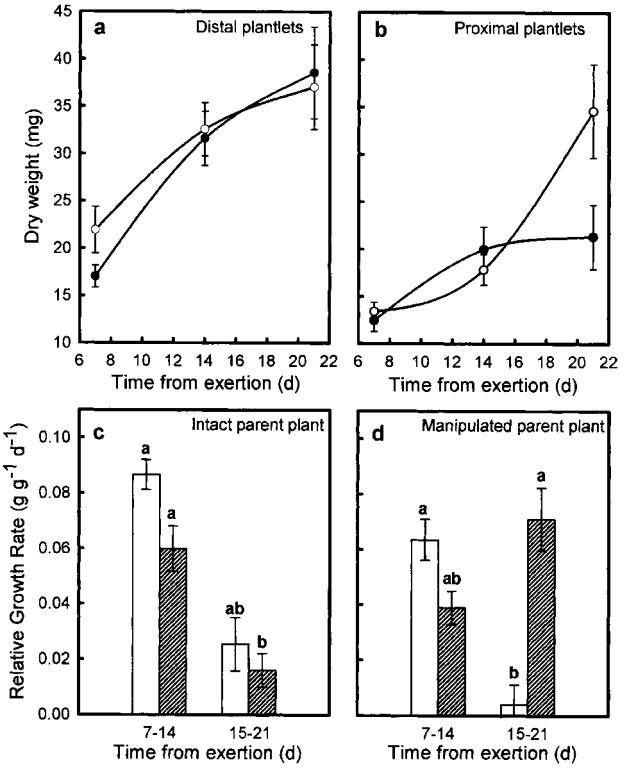

Fig. 5. (a, b) The absolute growth (mg DW basis) of (a) distal and (b) proximal plantlets from either control (intact paracladial zone; solid circles) or manipulated plants (distal or proximal half of the paracladial zone removed; open circles). (c, d) The relative growth rate (RGR) of plantlets from distal (open bars) and proximal (hatched bars) positions within the paracladial zone: (c) intact, control parent plant (d) manipulated parent plant. Data represent the mean ± 1SE of 10 separate determinations in all cases. Different letters represent significant differences between means at the $P \leq 0.05$ level, determined by Fisher's multiple comparison procedure (ANOVA).

Discussion

Gas exchange data disclose that the respiratory requirements of the paracladial zone could be met by photosynthesis within the paracladial zone itself. As pseudoviviparous plantlets do not accumulate storage compounds (Lee and Harmer, 1980), the excess carbon fixed is likely to be used in the growth of new plantlet tissues or be available for export. Indeed, the paracladial zone possessed a photosynthetic efficiency equal to that of parental leaf tissue, was able to fix nearly four times the absolute amount of ^{14}C as the first leaf on the parent plant, and was shown to export carbon basipetally.

Although the paracladial zone in general exhibits efficient photosynthesis, this may be consolidated mainly in the leaves of plantlets, which possess the high surface area/volume characteristics of parent leaves and are ideal for efficient gas exchange. Other organs, such as the rachis, may well be chlorenchymatous, but possess morphological characteristics suited to their mechanical role, rather than for optimizing gas exchange. For example, photosynthesis does occur in the culm, but with an efficiency approximately a fifth of parent leaf or general paracladial photosynthesis (Fig. 4d), perhaps subsidizing, but not necessarily fulfilling this organ's requirements for carbon.

Photosynthetic activity *per se* of plantlets from all regions of the paracladial zone was equal at 20 d (Table 1a). However, in absolute terms more carbon was fixed by plantlets in the distal half by virtue of the higher dry weights of these plantlets. At this point in time, distal plantlets had been exposed to an environment suitable for gas exchange and light capture for a longer period, and were conceivably at a more advanced developmental stage than proximal plantlets, the paracladial zone exhibiting the gradient in physiological time along the axis observed previously (Mohapatra *et al.*, 1993).

Table 2. *Summary of statistical significance of Analysis of Variance*

*, **, *** indicate significance at the $P \leq 0.05$, 0.01 and 0.001 levels, respectively. NS, not significant. (a) Influence of position of propagule, manipulation of paracladial zone and time upon absolute growth of plantlets from either intact or manipulated plants (cf. Fig. 5). (b) Influence of position at either end of the paracladial zone of parent plant upon the length of the oldest root following dehiscence and establishment of plantlets (cf. Fig. 6).

Source		Significance
(a)	Position	***
	Time	***
	Manipulation	NS
	Position × Manipulation × Time	*
(b)	Time	***
	Position	***
	Position × Time	**

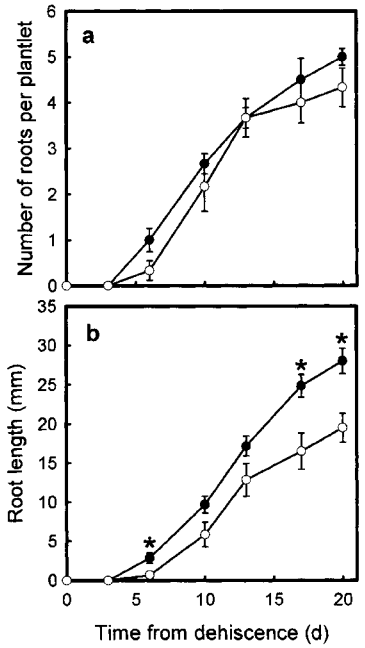

Fig. 6. Growth of roots of plantlets; (a) plantlet root number and (b) length of the oldest root (mm) after dehiscence of plantlets from either end of the paracladial zone (●, 'distal plantlets'; {cir}, 'proximal plantlets'). Data represent the mean ± 1SE of six separate determinations. * indicates a significant difference between means (at each time point) at the $P \leq 0.05$ level, determined by Student's *t*-test.

However, this cannot explain why attached proximal plantlets only achieved comparable RGRs to distal plantlets if distal plantlets were removed from the system (and not vice versa), RGRs of proximal plantlets remaining low throughout development in intact synflorescences (Fig. 5c). Manipulation and ^{14}C feeding experiments show that limited allocation of carbon from parental sources had a similar tendency to increase to both distal and proximal paracladial regions when the reciprocal region was removed (Table 1b). Thus competition for parental carbon is unlikely to explain the observed RGR response (conceivably organs other than plantlet leaves form paracladial sinks dedicated to parental sources, perhaps accounting for the small amounts of acropetal transport in the system). Equally, heterogeneity is unlikely to result from competition for nutrient resources, as *P. alpina* grown at different nutrient regimes retains paracladial heterogeneity, which thus appears to be inherent to the system (Pierce, 1998). Such heterogeneity, also in terms of the frequency of the observed spikelet abortion, may result from a hierarchy of phytohormonal dominance in the synflorescence systems of other grass species (Patel and Mohapatra, 1992).

The heterogeneity observed is somewhat analogous to fruit production in many seminiferous plants that initiate more fruits than can be supported by the available resources. A proportion of these fruits grow in a typical fashion, with the remainder being relatively undeveloped. Underdeveloped fruits are viewed as a reserve which may rapidly resume development should either more resources become available or the more highly developed fruits dehisce (Lee, 1980). Should distal plantlets of *Poa alpina* be lost due to dehiscence, proximal plantlets may then attain an equivalent dry weight (Fig. 5a, b) and will presumably become as effective as propagules. Thus the organization of the synflorescence system results in a proportion of plantlets which are vigorous and well able to establish (i.e. distal plantlets), with the remainder held in reserve for rapid growth, rather than all of the plantlets being water-stressed to a relatively high degree (plantlets in all pseudoviviparous species tested experience water stress if they remain attached to the parent plant; Lee and Harmer, 1980) and less likely to establish and compete effectively.

The architectural study of the paracladial zone revealed that the length of rachis internodes was proportional to the number of spikelets borne on each rachis node, with 49% of plantlets being borne on the proximal two nodes. This arrangement in seminiferous grasses (from which pseudovivipary is the derived condition) would allow for effective spacing of the denser proximal paracladia, possibly facilitating air movement for pollination. The selective advantage of possessing a larger proportion of spikelets on proximal paracladia which requires spacing remains unclear. One possible advantage may be a lower centre of gravity, which would effectively reduce the bending moment acting on the culm and aid the mechanical support of the paracladial zone whilst maximizing caryopsis production. Another possibility is that spikelets are more evenly distanced from parental sources, acting to equalize flux between the source and numerous sinks and therefore resource allocation between caryopses (Cook and Evans, 1983; Farrar, 1993*b*). Retained by pseudoviviparous biotypes, this architecture is likely to be beneficial for other reasons, the spacing of proximal paracladia ensuring less shading between plantlets and thus maximizing photosynthesis. However, the

relationship between space and shading is dynamic as plantlets are indeterminate, with further leaves being produced (Pierce, 1998).

Regarding the whole plant, the majority of ^{14}C exported from the first leaf after 2 h was exported basipetally, indicating that the paracladial zone was not in itself as important a source of carbon for parental sinks as parental sources were. In seminiferous *Poa annua* the first leaf mainly allocated ^{14}C acropetally to the developing caryopses, with only older leaves supplying roots and developing tillers (Ong and Marshall, 1975). Therefore the data indicate that photosynthesis in the paracladial zone results in a whole-plant source–sink hierarchy in which the leaves on the main axis provide photoassimilate primarily for roots and developing tillers, rather than for propagules.

The small proportion of ^{14}C exported from labelled organs in the present study was no doubt the result of the short chase period employed, although this was intended to provide a clearer picture of carbon fixation patterns, and also respiratory loss and refixation of ^{14}C was minimised (Atkinson and Farrar, 1983; Farrar, 1993*a*). A more detailed study could precisely determine the location of sink tissues within the synflorescence and give a more extensive account of the source–sink hierarchy of the whole plant.

In conclusion, the paracladial zone of a pseudoviviparous biotype of *Poa alpina* was a source of ^{14}C that was as efficient as the youngest leaf on the axis, capable not only of providing for its own carbon requirements but also of exporting photoassimilate. In addition, carbon allocation from the youngest leaf on the main axis was mainly basipetal; a source of carbon for parental sinks not usually available to seminiferous grasses. Heterogeneity was observed within the paracladial zone, with distal plantlets possessing higher relative growth rates and hence higher dry weights, resulting, at dehiscence, in more rapid root growth and a higher likelihood of establishment and survival than proximal plantlets. Further heterogeneity was noted with regard to paracladial architecture and to the degree of spikelet abortion, which was greater in the proximal region.

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