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EPHEMERAL CLONAL INTEGRATION IN *CALATHEA MARANTIFOLIA* (MARANTACEAE): EVIDENCE OF DIMINISHED INTEGRATION OVER TIME[1]

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A major advantage of clonal growth forms is the intergenerational transfer of resources through vascular connections (clonal integration). Connections linking ramets can be persistent or ephemeral. For species with ephemeral connections, whether the extent of clonal integration changes over time is unclear. To address this issue, we tracked water movement using an isotopic label and assessed the demographic performance of parent and offspring ramets over time in a severing experiment. Our study system was the understory herb *Calathea marantifolia*, which has parent ramets that produce vegetative bulbils (clonal offspring) that pass through distinct pre- and post-rooting stages. Little water was transported between parents and offspring, and the direction of movement was primarily from parent to pre-rooting offspring. Anatomical observations of inter-ramet connections showed that vascular bundles were twice as abundant in parent stems compared to inter-ramet connections. Severing inter-ramet connections reduced the growth of offspring ramets but not parents. Survival of pre-rooting offspring was reduced by 10% due to severing, but post-rooting offspring were not affected. Our results suggest that offspring ramets of *C. marantifolia* are weaned from their parent as they progress from pre- to post-rooting stages.

Key words: bulbil; *Calathea marantifolia*; clonal integration; clonal phenology; deuterium labeling; Marantaceae; physiological integration; stable isotopes; water transport.

One of the principal differences between sexual and clonal reproductive strategies is the timing and amount of resources transferred from the parent to the reproductive offspring. Sexual offspring receive a relatively small, one-time investment of endosperm and cotyledon tissue. By contrast, clonally produced offspring can potentially receive a relatively large maternal investment over a long period through vascular connections (clonal integration). Across species, clonal plants form a continuum in terms of the spacing of ramets along vascular connections, with one end occupied by clumped growth forms (phalanx) and the other by spreading (guerilla) growth forms (Lovett-Doust, 1981; White, 1984). Phalanx growth forms typically occupy late successional environments, while the guerilla strategy is found in early successional sites (Schmid and Bazzaz, 1987; Adachi et al., 1996). In tropical secondary forests and disturbed areas of primary forests, a type of guerilla growth form with ephemeral vascular connections is common among members of the Zingiberales (e.g., *Calathea donnell-smithii*, Marantaceae; *Costus scaber*, Costaceae; *Alpinia purpurata*, Zingiberaceae). In this growth form, clonal bulbils are produced atop reproductive shoots. These shoots eventually fall to the ground where bulbils root directly and remain connected to their parent for some time before becoming independent. To our knowledge, this type of guerilla growth form has received no attention in the clonal plant literature, and the extent to which clonal bulbils are physiologically integrated with the parent ramet before and after they root in the soil is unknown.

One of the main advantages of the clonal life-history strategy is hypothesized to be the presence of vascular connections linking ramets. Some inter-ramet connections are persistent, lasting longer than an individual ramet's lifespan, while others are ephemeral, decaying shortly after a ramet is produced (Jónsdóttir and Watson, 1997; Tamm et al., 2002). Persistent connections can transport resources between ramets increasing the probability of ramet establishment (e.g., Hartnett and Bazzaz, 1983; Peltzer, 2002). For species with ephemeral connections, it is not known wether the extent of clonal integration or its influence on ramet demography decreases as the connections age.

Physiological integration—resource sharing between interconnected ramets—may allow for transport of water and mineral nutrients through the xylem and carbohydrate transport through the phloem (Alpert and Mooney, 1986; Stuefer and Hutchings, 1994; Alpert, 1996; Wijesinghe and Hutchings, 1997). The directionality and intensity of resource transport depends on both source–sink dynamics and anatomical continuity between ramets (Pitelka and Ashmun, 1985), which can change over time (e.g., Marshall and Sagar, 1968). The directionality of resource movement in the majority of species and conditions studied is from parent (or "mother") ramets to offspring (or "daughter") ramets (acropetal; Pitelka and Ashmun, 1985). Acropetal transport benefits offspring by increasing their growth and survival, often at a cost to their parent's growth or survival (Pitelka and Ashmun, 1985; Salzman and Parker, 1985; de Kroon and Schieving, 1990). The extent of integration is variable across species, with some having no integration (Price and Hutchings, 1992) while others are highly integrated (Hartnett and Bazzaz, 1985).

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Clonal integration has been investigated by tracing the movement of resources between ramets or through experimental manipulations that test for ramet interdependence in terms of growth or survival (Pitelka and Ashmun, 1985), but only rarely have both methods been combined (Jónsdóttir and Callaghan, 1989; de Kroon et al., 1996, 1998). Most commonly, isotopes such as ^{14}C, ^{15}N, and ^{32}P (reviewed in Pitelka and Ashmun, 1985; Marshall, 1990; Jónsdóttir and Watson, 1997) and more recently deuterium-labeled water (de Kroon et al., 1996, 1998) are used as tracers in clonal plant studies. Isotope experiments can be used to quantify the transport of resources between labeled and recipient ramets at a specific point in time, but not to assess the demographic consequences of resource sharing. The importance of resource integration for plant fitness can be evaluated by comparing the demographic performance (survival and growth) of ramets with intact and severed inter-ramet connections (Jónsdóttir and Watson, 1997).

We investigated the phenology of ephemeral physiological integration in the neotropical understory herb *Calathea marantifolia* Standl. (Marantaceae). We investigated the degree of resource sharing and its associated influence on ramet demography before and after offspring ramets root in the soil. Our hypothesis is that offspring ramets are more integrated with their parent prior to rooting compared to post-rooting; therefore, the demographic consequence of severing inter-ramet connections will be more severe before rooting. Specifically, we addressed the following questions: (1) Does the connection linking parent and offspring ramets have the structural capacity for water transport? (2) In which direction is water transported; from parent to offsrpring or vice versa? (3) Does the proportion of translocated water decrease after offspring ramets root? (4) Does severing inter-ramet connections reduce the demographic performance (survival and growth) of parent and offspring ramets? (5) Are offspring ramets affected by severing their inter-ramet connections before rooting more than after they root?

MATERIALS AND METHODS

Study system—Field experiments were conducted on *Calathea marantifolia* (Marantaceae) located in secondary forest and abandoned plantations at the La Selva Biological Station of the Organization for Tropical Studies (10°28′N, 83°59′W). La Selva is in the Atlantic lowlands of Costa Rica and has primary and secondary forest classified as premontane wet tropical forest according to the Holdridge vegetation classification system (Hartshorn, 1983).

Calathea marantifolia is an herb reaching 2.3 m in height and occurs in wet to semideciduous forests from central Ecuador to Honduras (Kennedy, 1978). During the rainy season, *C. marantifolia* begins its reproductive phenology by producing a single terminal inflorescence from a reproductive shoot. After the infructescence has senesced, an offspring ramet develops from the axil of the terminal leaf subtending the inflorescence. On average, by 7.5 months postfruiting, nearly all parent plants (>98%) have produced a clonal offspring (D. P. Matlaga and C. C. Horvitz, University of Miami, unpublished manuscript). The offspring increases in leaf area and develops roots atop the parent's reproductive shoot. On average, by the time clonal offspring are 2 months old, the parent's shoot has lowered to the ground, and the offspring have rooted in the soil (D. P. Matlaga, unpublished data). Offspring remain connected to the parent for 1–12 months after rooting in the soil (D. P. Matlaga, unpublished data). We refer to offspring ramets that have not rooted in the soil as "pre-rooting" and those that have as "post-rooting." Parents typically produce one offspring ramet per shoot, but may have several shoots at a time.

Anatomical characteristics of inter-ramet connections—Plant material was collected at Fairchild Tropical Botanic Garden (Coral Gables, Florida, USA). We compared the appearance and quantity of vascular bundles between the stem connecting parent and offspring ramets (herein, connection) and the stem of the parent ramet (herein, parent stem) (Fig. 1). To investigate the abundance of the vascular bundles, we used cultivated plants from the garden. We collected six pre-rooting and six post-rooting offspring, each with its connected parent ramet stem. Cross-sections of the connection and parent stem were cut by hand with a single-edge razor blade. Concentrated HCl-phloroglucinol was used to visualize lignin (Ruzin, 1999). To estimate the number of vascular bundles, we visually divided cross sections into eight equal pie-shaped pieces. We counted the number of vascular bundles for three randomly chosen pieces using a stereomicroscope. The average number of bundles was calculated for each pie-shaped piece and was multiplied by eight to estimate the total number of vascular bundles per cross section. We examined the difference in the total number of vascular bundles between connection and parent stem using a Mann–Whitney *U* test. The vascular tissue was photographed with a Nikon Coolpix 4500 digital camera (Nikon, Tokyo, Japan).

Inter-ramet water transport—To examine reciprocal transport of water between parents and offsping (pre-rooting and post-rooting), we conducted a field experiment in natural populations. We traced the movement of deuterium-enriched water between a labeled ramet (provided with enriched water) and a recipient (not provided with enriched water). We located 40 parent–offspring pairs with intact connections, 20 with offspring that had not yet rooted (Fig. 1A) and 20 with offspring that had already rooted (Fig. 1B). In each group, the parent–offspring pairs were randomly assigned to one of two treatments: (1) the parent was labeled, and the offspring was the recipient; or (2) the offspring was labeled, and the parent was the recipient. Thus, the fully crossed experiment included two factors: rooting stage of the offspring (unrooted or rooted) and which ramet was labeled (parent or offspring).

We provided labeled water to parents and offspring that had already rooted by dripping 700 ml of deuterium-enriched water 2 cm from the base of the ramet, over 6 h (1000–1600 hours) each day for 5 d (18–22 May 2007). Water was quickly absorbed by the soil and did not pool on the surface. Offspring that had not yet rooted were sprayed with 10 ml of deuterium-enriched water on their exposed roots twice a day (1000 and 1300 hours) each day for 5 d (18–22 May 2007). Several studies have shown that fractionation does not occur during water uptake by roots or during xylem transport (e.g., White et al., 1985). Because leaf water can lose label by equilibration with atmospheric humidity, we sampled petioles. Sections of leaf petiole (4 cm) were harvested from parents and offspring on 22 May 2007 between 1600 and1700 hours. A 5-ml sample of soil was taken at the base of the recipient ramet (unlabeled) to verify that enriched water had not moved through the soil. All samples were immediately placed in BD Vacutainer 7 ml serum tubes (BD Franklin Lakes, NJ), sealed with parafilm, and stored at −18°C until processed.

Samples were taken to the Stable Isotope Laboratory, Department of Biology, University of Miami (Coral Gables, FL) for water extraction and determination of deuterium content. Water was removed from leaf petiole samples by squeezing for all samples except five, for which distillation was used (Vendramini and Sternberg, 2007). For all soil samples, water was removed by distillation. The hydrogen isotope ratio for a sample is expressed as a deviation (δD) in parts per thousand (‰) from the international standard VSMOW (Vienna-Standard Mean Ocean Water) by

$$\delta D_{sample}\ (‰) = \left[\frac{\left(D/H\right)_{sample}}{\left(D/H\right)_{VSMOW}} - 1 \right] \times 1000, \qquad (1)$$

where D/H, the ratio of deuterium (D) to hydrogen (H), is calculated for the extracted sample water and compared to that for the standard water (VSMOW). The precision of the analysis is ± 3‰. The δD value of the water provided to the ramets was ~5000‰ and was produced by mixing 1 L of local water with 1 mL of 99.8% D_2O.

Water samples were analyzed in a Multiflow system connected to an Isoprime mass spectrometer (GV, Manchester, UK). We used ~5 mg of platinum black powder (Sigma-Aldrich, St. Louis, Missouri, USA) to equilibrate hydrogen with water vapor for 24 h, then analyzed the equilibrated gas to derive the hydrogen isotope ratio of the water using a modification of Prosser and Scrimgeour (1995) as follows. Water samples (0.5 mL), and similarly, the internal laboratory standards, were placed in 5.9 mL vials (Exetainer vials; Labco, High Wycombe, UK) with cuvettes containing the platinum black catalyst and sealed with screw caps that had a pierceable rubber septum (Exetainer cap; Labco). Isotope analysis of the equilibrated gas proceeded as in Vendramini and Sternberg (2007).

We evaluated the effectiveness of our labeling protocol by comparing δD values of labeled ramets in different groups using Kruskal–Wallis tests.

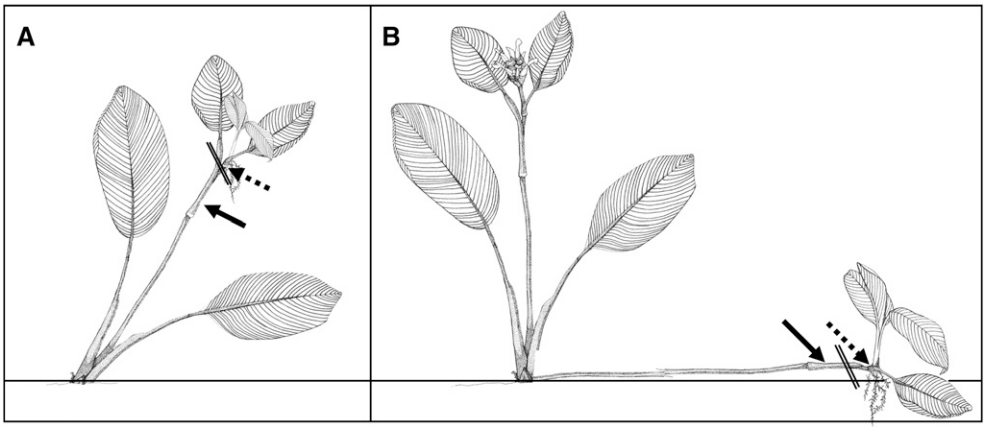

Fig. 1. Severing treatments and points of anatomical comparison of *Calathea marantifolia*. Offspring that had not yet rooted (A) were severed (parallel lines) and reconnected to the parent shoot. Offspring that had already rooted (B) were severed at the same location (parallel lines) but not reconnected. Anatomical comparisons were made between the parent stem (solid arrow) and connection point between offspring and parent (dashed arrow). Illustration by Erin Kuprewicz.

To determine if recipient ramets had received enriched water through inter-ramet connections from the labeled ramet, we compared δD values of recipient ramets to background samples using a single sample comparison with a population mean (Sokal and Rohlf, 1995) and displayed the results graphically. Because we did not have samples from untreated ramets, we used parent recipient ramets connected to pre-rooting offspring as background for analyses because their δD was on average the lowest (Table 1), did not have outliers (Fig. 2), and was not significantly different from soil samples taken from the base of the parent ramet ($Z = 0.456$, $P = 0.742$). In addition, of the recipient ramets, δD values for parent recipient ramets connected to pre-rooting offspring were closest to the mean δD (17. 6) found in precipitation in the month of May in the study region (Estrada Meteorological Station; IAEA/WMO, 2006).

For the recipient ramets that did receive enriched water, we calculated the proportion of water transported between labeled and recipient ramets as

$$\text{Proportion of water transported} = \frac{\delta D_{RR} - \delta D_{bkgd}}{\delta D_{LR} - \delta D_{bkgd}}, \quad (2)$$

where δD_{RR} is the mean δD value for recipient ramets, δD_{LR} is the mean δD value for labeled ramets and δD_{bkgd} is the mean value for the background ramets (parent recipient ramets connected to pre-rooting offspring). The standard error of this index was calculated using the error propagation method of Taylor (1997).

Demographic consequences of physiological integration—To determine the demographic consequences of physiological integration, we conducted a field experiment in natural populations. During 5–31 July 2006, we haphazardly located parent–offspring pairs with offspring that had not yet rooted ($N = 170$) and with offspring that had already rooted ($N = 170$). Parent and offspring were individually marked, and all leaf lengths were measured. Area of each leaf was estimated from a previously determined regression relationship between leaf length and area (Horvitz and LeCorff, 1993), and areas of all leaves per ramet were summed to calculate total leaf area. Parent–offspring pairs were randomly assigned to one of two treatments; severing or leaving the inter-ramet connection intact. Offspring that had not yet rooted were severed and reattached to the parent's reproductive shoot, 2 cm below the original point of attachment, using two plastic cable ties to allow severed offspring to remain at the same height (and thus receive the same amount of understory light) as unsevered offspring, but prevented sap flow. Offspring are attached to the terminal node of the parent's reproductive shoot, which is enclosed in the sheath of the axillant leaf. Therefore, to sever the connection, we needed to remove the parent's axillant leaf. To standardize damage to the parent, we removed the axillant leaf on parents in the nonsevering treatment as well. Parent ramets in the severing treatment had all their offspring removed at 90, 150, 240, and 360 d after treatment began. Survival and growth of offspring was censused at 90, 150, 240, and 360 d after treatment. Survival and growth of parents was censused one year after the treatment began.

No parent ramets died during the study. We analyzed the effects of severing the inter-ramet connection on offspring survival using a Kaplan–Meier survival analysis (Fox, 2001; Levesque, 2007) to estimate cohort survivorship ("survival function"), mean survival time, and the survival probability at the end of the study. We analyzed the effects of severing the inter-ramet connection on the growth of offspring (change in leaf area) with a repeated-measures ANOVA. The main effects of the model were severing (yes or no), developmental stage of offspring (not yet rooted or already rooted) and time. The effect of severing on the growth of parents (change in leaf area) was evaluated with a *t* test.

TABLE 1. Mean abundance of deuterium (±SE), expressed as δD, in parent and offspring ramets of *Calathea marantifolia*. Values for labeled ramets that received enriched water by spraying are in boldfaced type, and those for labeled ramets that received enriched water by dripping are in regular face.

	Role of ramet		δD (±SE)	
Stage of offspring	Parent	Offspring	Parent	Offspring
Rooted	Labeled	Recipient	422 ± 82	−19 ± 2
Not rooted	Labeled	Recipient	399 ± 93	−2 ± 9
Rooted	Recipient	Labeled	−24 ± 6	381 ± 69
Not rooted	Recipient	Labeled	−21 ± 1	**129 ± 49**

RESULTS

Anatomical characteristics of connections—We did not observe resin or other materials filling vessels in the inter-ramet connections or parent stem. There were significantly more vascular bundles in the stems of the parent (Fig. 3B) than in the tissue connecting parents to offspring (Fig. 3A; Mann–Whitney $U = 5.50$, $P = 0.0001$; parent stem: 200.8 ± 12.1, connection: 90.4 ± 4.2; mean ± SE). We observed a difference in the directionality of the vascular bundles between the parent stem and inter-ramet connection. All the vascular bundles in the parent stem ran parallel to one another (Fig. 3D). In contrast, vascular bundles in the inter-ramet connection were not parallel and instead formed a plexus (Fig. 3C).

Effectiveness of labeling—*Abundance of deuterium in labeled ramets*—The labeling protocol was effective, with labeled ramets having abundant deuterium. The amount of deuterium in ramets that received enriched water by dripping was high and equal across groups (Table 1; $H = 0.111$, df = 2, $P = 0.946$). By comparison, ramets that received enriched water by spraying

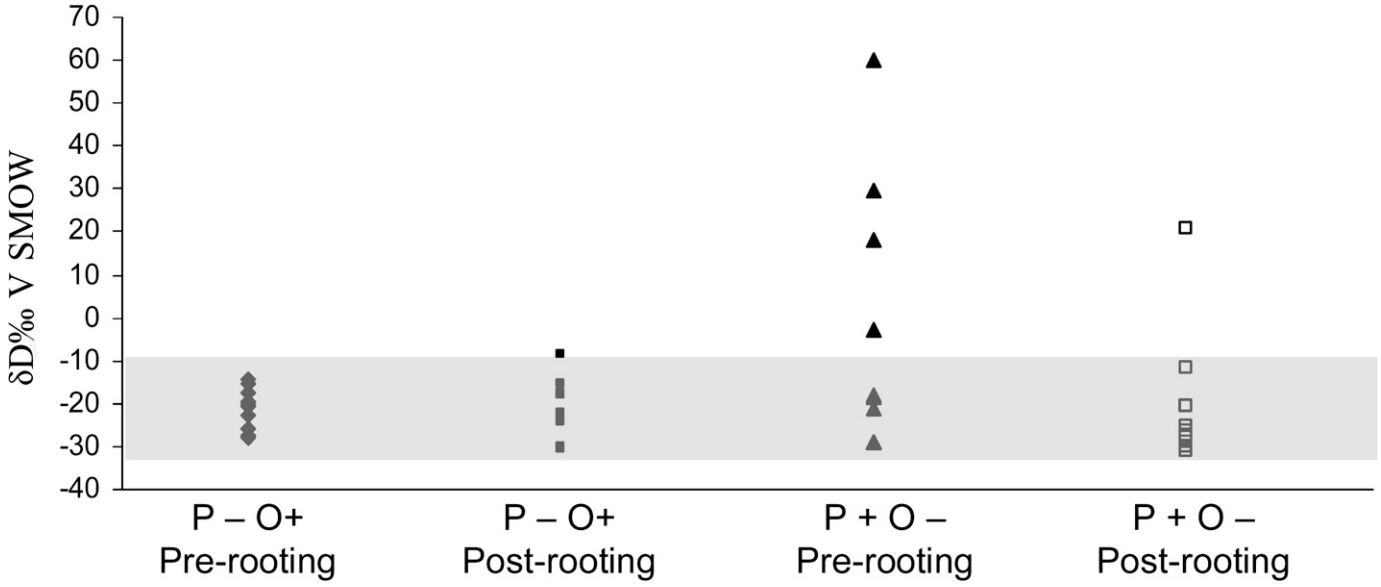

Fig. 2. Deuterium (δD) values for recipient ramets (P, parent; O, offspring; +, labeled ramet; –, recipient ramet) of *Calathea marantifolia*. Rooting status of the offspring ramet (pre- or post-rooting) is noted below parent and offspring labeling. Ramets with petiole water having δD values within the gray area are not significantly different from background levels; those outside the gray area are significantly different at $P < 0.05$ according to a single-sample comparison with the background population (Sokal and Rohlf, 1995).

had less deuterium, although they had much more deuterium than recipient ramets (Table 1).

Soil samples from the base of the recipient ramets had very low deuterium (δD = −31.8 ± 8.8, mean ± SE), indicating that deuterium did not move through the soil from labeled to unlabeled ramets.

Inter-ramet water transport—*Abundance of deuterium in recipient ramets*—Overall, we observed very little water transport between parents and offspring. Deuterium was higher than background levels in a few recipient ramets (Fig. 3), and the proportion of water translocated was below 5% for all treatments (Fig. 4). The abundance of deuterium in recipient ramets was

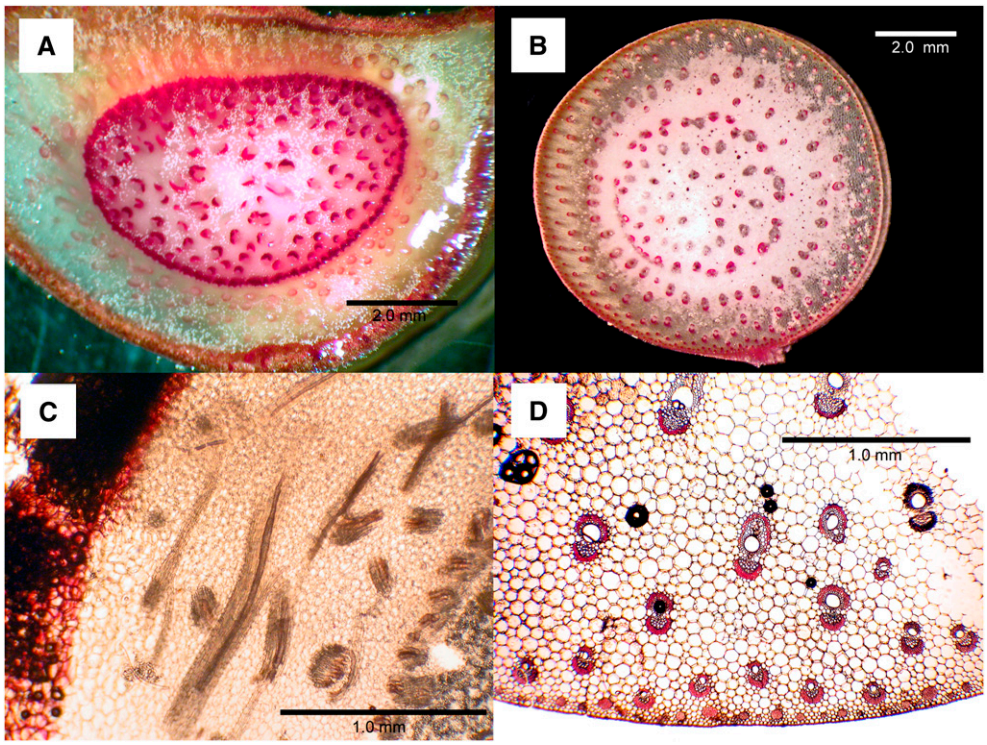

Fig. 3. Vascular anatomy of (A and C) the inter-ramet connection and (B and D) the parent stem of *Calathea marantifolia* under different magnification. Photographs by Jay Horn.

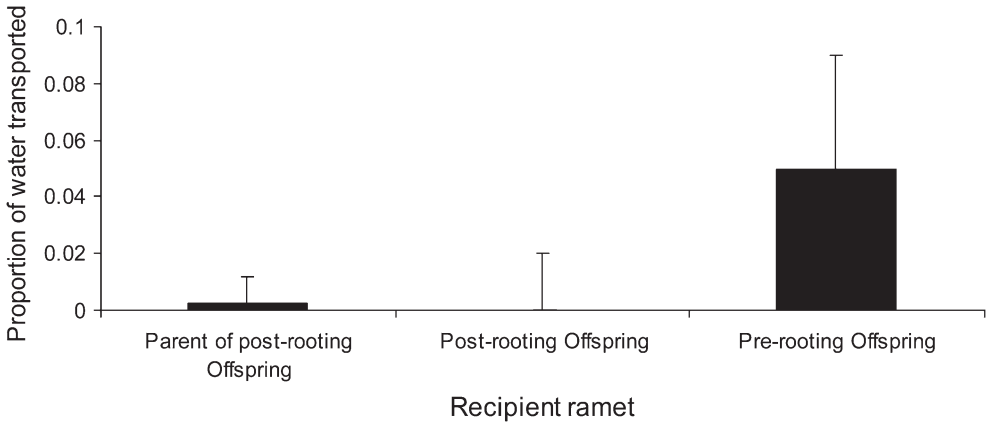

Fig. 4. Mean proportion (±SE) of water transported from labeled to recipient ramets of *Calathea marantifolia*. Parent of pre-rooting offspring was used as background to allow for the calculation of the proportion of water transported in the other recipient ramets.

unequal across treatments ($\chi^2 = 9.911$, df = 3, $P = 0.019$). Translocated water moved predominantly from parent to offspring. Offspring that had not yet rooted had significantly more deuterium and a greater proportion of water transported than those that had already rooted (Figs. 2, 4; Mann–Whitney, $U = 15.00$, $P = 0.009$).

Demographic consequences of physiological integration— Severing connections reduced the survival of offspring that had not yet rooted, but did not affect the survival of offspring that had already rooted (Fig. 5; log-rank test of homogeneity of survival between treatments; pre-rooting offspring: $\chi^2 = 9.334$, df = 1, $P = 0.002$; post-rooting offspring: $\chi^2 = 4.04$, df = 1, $P = 0.525$). On average, severing the connections reduced the estimated days until death by 46 d for offspring that had not yet rooted. In contrast, offspring that had already rooted survived equally as long with intact or severed connections (Fig. 6A). Severing reduced the probability of surviving to the end of the year-long study by 10% for offspring that had not yet rooted, but rooted offspring were not affected (Fig. 6B).

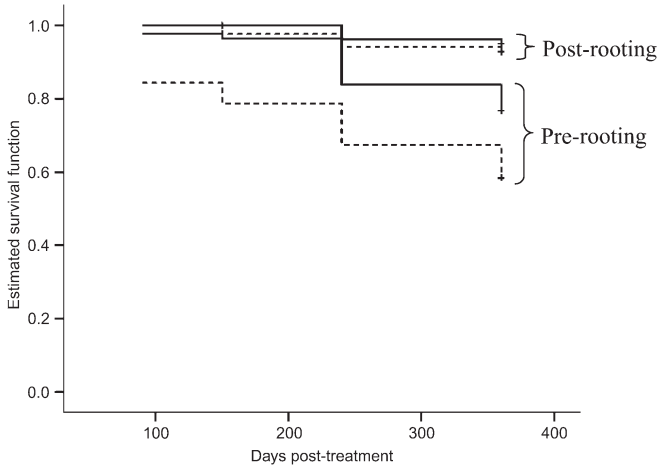

Fig. 5. Cohort survivorship for *Calathea marantifolia* of offspring in pre-rooting and post-rooting stages having either an intact (unbroken lines) or severed (dashed lines) connection to the parent. Survival functions are Kaplan–Meier estimates.

Offspring growth was reduced by the act of severing connections, but growth of parents was not. The growth of offspring was influenced by whether they had already rooted, by whether the connections to their parents had been severed, and by a rooting × severing interaction (Table 2). Offspring who had not yet rooted lost leaf area over the study period, although the loss was more dramatic when connections to parents were severed (Fig. 7). Offspring who had already rooted with intact connections added a small amount of leaf area over the study period, and those with severed connections maintained nearly constant leaf area (Fig. 7). The leaf area of parents was unaffected by severing, both initially ($t = 0.152$, df = 333, $P = 0.879$) and one year later ($t = 0.676$, df = 332, $P = 0.500$).

DISCUSSION

Our results show that water transport and the demographic consequences of clonal integration in *Calathea marantifolia* diminish before connections between parent and offspring are lost. Data from our isotope and severing experiments suggest that resource sharing in *C. marantifolia* is acropetal (moving from the parent to offspring) and that offspring receive fewer resources from their parent after they have rooted in the soil. Before rooting, offspring receive a small amount of water from their parents, and severing their connections reduces their demographic performance. After offspring root in the soil, however, they receive no water from their parent, and severing their connection has little effect on their demography. It is surprising that parents showed no demographic cost of supporting offspring considering that offspring appear to use their resources; however, several other studies have also found no cost associated with acropetal resource transfer (e.g., Stuefer and Hutchings, 1994; Van Kleunen and Stuefer, 1999).

Overall, we found that very little water is transported between parents and offspring. This lack of water translocation could be the result of several mechanisms. Initially, we suspected that a barrier to xylem flow may be present in the inter-ramet connection linking parent and offspring, preventing water transport. However, in the connection, we observed seemingly functional vascular bundles, with both xylem and phloem similar to those in the parent's stem, without any evidence of resin-filled vesicles that could obstruct water movement. However, both the number and directionality of bundles differed between connections

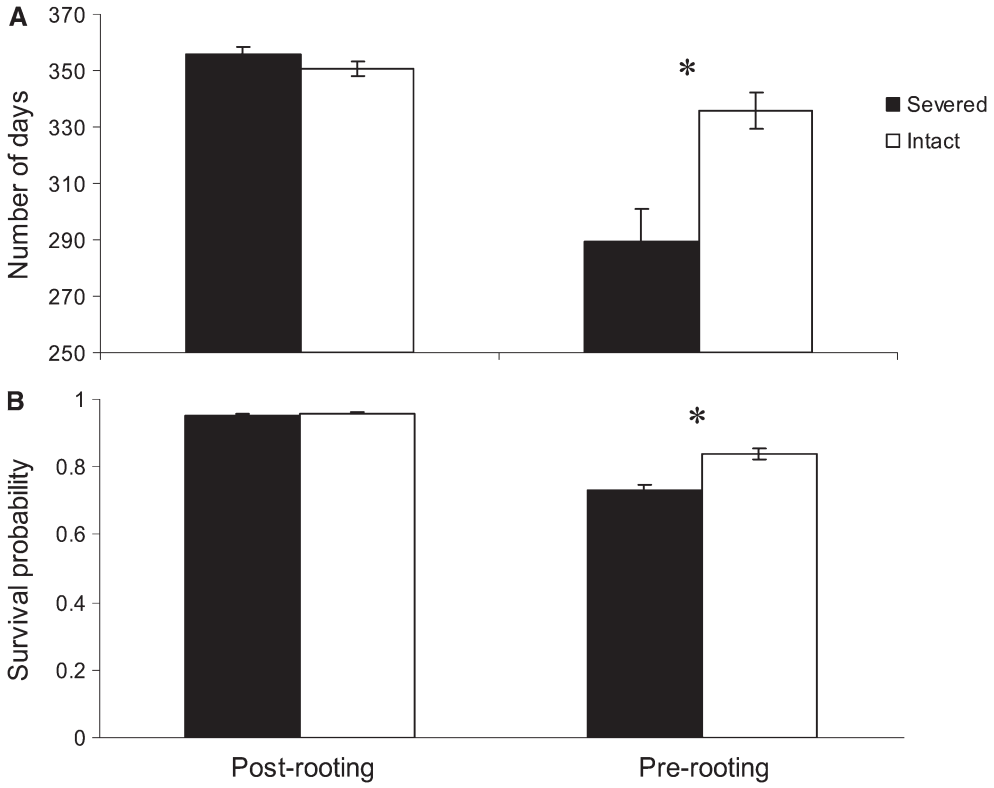

Fig. 6. Mean (A) number of days until death (±1 SE), estimated by the product-limit method of Kaplan–Meier and (B) cumulative mean probability of survival (±1 SE) at the end of the study for severed (connection to parent severed) and intact (connection to parent intact) offspring ramets of *Calathea marantifolia*. Significant differences at $P < 0.05$, indicated with an asterisk (*), were determined using a *t* test.

and parent stem. Compared to the parent stem, inter-ramet connections had fewer vascular bundles, and these bundles formed a plexus. The near absence of water translocation we observed may be related to a lack of sufficient vascular plumbing linking parent and offspring ramets.

An alternative explanation is that the low levels of water translocation were the result of source–sink dynamics. Water transport depends on the strength of the water potential gradient and the distances between sources (sites of high water potential) and sinks (low water potential; Pitelka and Ashmun, 1985). The gradient in water potential between ramets is created by transpiration at the leaf surface and water uptake by the roots (Pitelka and Ashmun, 1985). If the leaves of *C. marantifolia* offspring have low transpiration rates, little water would be moved from the parent. Similarly, if the roots of offspring are as efficient at water uptake as those of the parent and if water availability is the same for parents and offspring, little water will be moved from the parent. Previous work has shown that when parents and offspring receive the same watering regime, water translocation levels are low (de Kroon et al., 1996). Therefore, in our study, water may not have been transported between parents and rooted offspring because parents and offspring were rooted in soils with similarly high moisture contents. Our isotope experiment was conducted during the rainy season with 56 mm of rain during the 2 weeks before our experiment, and 75 mm fell during the experiment (D. A. Clark, University of Missouri–St. Louis, personal communication). Offspring that had not yet rooted could only access water vapor from the air and water that

TABLE 2. Repeated measures two-factor ANOVA for the effects of severing treatments (connection severed or intact), stage of offspring (pre- or post-rooting), and time on ramet size (log of leaf area) for *Calathea marantifolia*.

Source of variation	df	SS	*F*	*P*
Between-subject effects				
Stage of offspring	1	86.083	136.037	0.0001
Severing	1	25.737	40.672	0.0001
Severing × Stage of offspring	1	8.677	13.712	0.0001
Error	245	155.035		
Within-subject effects				
Time	3	10.160	30.60	0.0001
Time × Stage of offspring	3	14.812	44.728	0.0001
Time × Severing	3	15.864	47.905	0.0001
Time × Stage of offspring × Severing	3	6.478	19.561	0.0001
Error	735	81.135		

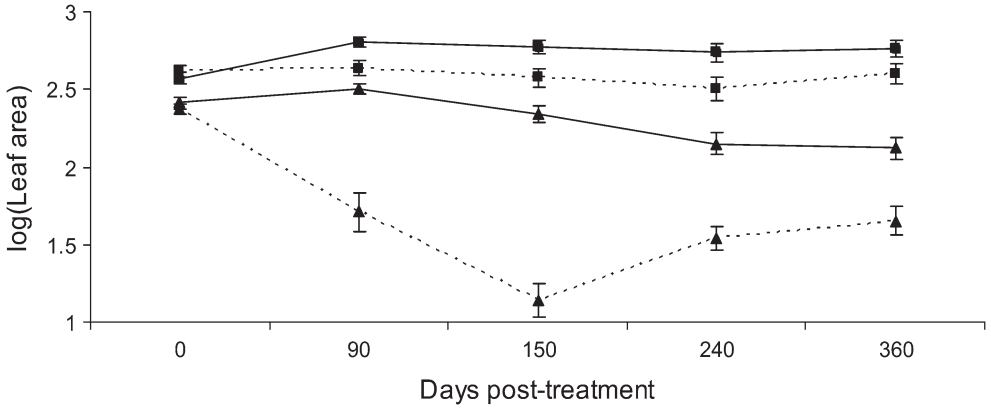

Fig. 7. Mean (±SE) leaf area of pre-rooting (triangles) and post-rooting (squares) offspring of *Calathea marantifolia* having either severed (dashed) or intact (unbroken) connections to their parent.

drips onto their roots, explaining why they received more transported water from their parent than post-rooting offspring. These results agree with previous work showing an increase in water transport when offspring have access to less water than parents (de Kroon et al., 1996).

The directionality of water transport we observed was primarily from parent to offspring (acropetal). Our results showing that severing the inter-ramet connections reduces the demographic performance of offspring but not parents, also supports that resource transport is acropetal. Our results are in contrast to some clonal species with persistent connections, where parents experience a cost, typically a reduction in growth, associated with sharing resources with offspring (Pitelka and Ashmun, 1985; Salzman and Parker, 1985; de Kroon and Schieving, 1990). *Calathea marantifolia* may undergo no, or little, cost of supporting offspring because of the large size difference between parents and offspring. In terms of leaf area, parents are nearly an order of magnitude larger than their offspring.

The demographic consequences of severing connections for offspring depended greatly on whether the offspring was rooted in the soil. Both the survival and growth of pre-rooting ramets were reduced by severing. However, the survival of post-rooting ramets was not affected, and their growth was only slightly reduced. These results agree with results from our isotope experiment showing that pre-rooting offspring received translocated water from their parents, but post-rooting offspring did not. Together, these results suggest that offspring are gradually cut off from their parent's resources over time as inter-ramet connections age.

It is unclear how *C. marantifolia* offspring receive parental resources, which increase their demographic performance, in the virtual absence of water transport. Because the same transport system (xylem) translocates water and mineral nutrients, the movement of these resources is positively correlated (i.e., Stuefer et al., 1996; de Kroon et al., 1998). We observed little water movement during our study; therefore, it is likely that few mineral nutrients were transported. Photosynthates, which are transported in the phloem, are typically associated with increased growth (Evans, 1991). The increase in offspring growth and survival we observed when connections to the parent are not severed may be the result of offspring receiving photosynthates from their parent. Therefore, the pattern of carbohydrate translocation may differ from that of water translocation. Offspring ramets may receive a large proportion of their carbohydrates from the parent, in contrast to receiving a small proportion of water. Additionally, resource transfer between parents and offspring may be seasonal with more integration during the dry season. Our isotope study took place during the rainy season, while our severing experiment spanned wet and dry seasons. Further study is needed to understand which resources are shared between ramets and whether integration is seasonal.

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