

OBSERVATIONS ON THE CLONAL PARENTAGE OF CULMS IN WILD STANDS OF A CLUMPING BAMBOO FROM NORTHERN AUSTRALIA

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HOGARTH NJ & FRANKLIN DC. 2009. Observations on the clonal parentage of culms in wild stands of a clumping bamboo from northern Australia. Culms and culm shoots harvested from bamboo are the primary products of multi-generational sequences of clonal parents and offspring. However, very little is known about the contribution of clonal parent–offspring relationships to productivity. We investigated age and size relationships and the impact of disturbance on clonal parent–offspring relationships for 491 culm recruits in wild clumps of the monocarpic bamboo, *Bambusa arnhemica*, from monsoonal northern Australia. Although one-year-old parents were the most common, we found considerable flexibility in parent–offspring relationships, with variation among years in the age of parents. Moreover, rhizomes with senescent or dead culms still produced new ramets. Offspring were generally of similar size to their parents although this varied among years and was influenced by disturbance. The age of the parent did not markedly affect the size of the offspring provided that the parent was leafy. Parent rhizomes with senescent or dead culms produced much smaller offspring. We argue that the suggested prominent role of first-year ramets as parents has little or nothing to do with their contribution to clump resources. A management emphasis on retaining one-year-old culms as the immediate drivers of productivity may be misplaced.

Keywords: *Bambusa arnhemica*, monsoonal northern Australia, management, harvest, culm size, shoot, ramet, clonal

HOGARTH NJ & FRANKLIN DC. 2009. Pencerapan keturunan klon kulma dalam dirian liar rumpun buluh dari utara Australia. Kulma dan pucuk kulma yang dituai daripada buluh merupakan hasil primer jujukan berbilang generasi bagi induk serta anak klon. Bagaimanapun, tidak banyak yang diketahui tentang sumbangan hubungan induk klon dengan anak terhadap produktiviti. Kami menyiasat hubungan antara usia dan saiz serta impak gangguan terhadap hubungan induk klon dengan anak bagi 491 penokokan kulma dalam rumpun liar buluh monokarpa, *Bambusa arnhemica* yang berasal dari utara Australia. Walaupun induk yang berusia satu tahun sangat biasa, kami mendapati fleksibiliti yang agak ketara dalam hubungan induk dengan anak, dengan variasi dalam usia induk. Tambahan lagi, rizom yang mempunyai kulma yang tua atau yang telah mati masih menghasilkan ramet baru. Anak umumnya sama saiz dengan induk walaupun terdapat variasi antara tahun dan dipengaruhi gangguan. Usia induk tidak begitu mempengaruhi saiz anak asalkan induk adalah berdaun. Rizom induk yang mempunyai kulma yang tua atau yang telah mati menghasilkan anak yang jauh lebih kecil. Kami menghujahkan bahawa peranan ramet yang berusia setahun sebagai induk hanya sedikit atau tiada langsung mempengaruhi sumber rumpun. Justeru penekanan pihak pengurusan dalam mengekalkan kulma yang berusia satu tahun sebagai pendorong produktiviti mungkin tidak tepat.

INTRODUCTION

The primary resources harvested from bamboos, namely, culms and culm shoots, are products of clonal growth. Li *et al.* (2000) and Saitoh *et al.* (2002, 2006) demonstrated the importance of clonal integration in influencing culm recruitment in running (leptomorph) bamboos, but little is known about the contribution of clonal parent–offspring relationships to productivity in clumping species. The oft-repeated observation that most parent ramets are one year old

(reviewed by Kleinhenz & Midmore 2001) has prompted the suggestion that productivity in bamboo stands depends on maintaining many young ramets (Prasad 1987, Chaturvedi 1988, Lakshmana 1990, Kleinhenz & Midmore 2001). Yet, near-complete removal of an annual cohort of culms in *Bambusa arnhemica* had no measurable effect on productivity in the following year (Franklin 2006), suggesting flexibility in the age relationship between parents and offspring.

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Offspring size in clumping bamboos is related to the quality of parents, but supporting data are lacking (Ueda 1960).

Genets of pachymorph (clumping) bamboos begin life as a single ramet produced from seed, the ramet consisting of a rhizome and culm with associated roots, branches and foliage (McClure 1966). The seedling ramet may be no more than 15 cm tall and soon stops growing, and instead reproducing clonally by expansion of rhizome buds. In the early years of life, a genet grows by two processes, namely, an increase in the number of ramets and an increase in their size (Banik 1988). After a period that may be as long as 15 years (Pearson *et al.* 1994), ramet cohorts reach adult or mature size, with growth of the genet continuing solely by the recruitment of additional ramets (Ueda 1960). However, the lifespan of ramets (and especially culms) is less than that of the genet, even in monocarpic (semelparous) species (Taylor & Qin 1993, Pearson *et al.* 1994). As a result, mature bamboo genets in wild or unmanaged stands comprise many culms of various ages including some that are senescing or dead.

Bamboo ramets are recruited by the expansion of rhizome buds in annual cohorts and the subsequent rapid elongation of culms (Ueda 1960). Thus, each ramet has a clonal parent ramet, and each culm has a corresponding parent culm (McClure 1966). Throughout this manuscript we use the terms ‘parent’ and ‘offspring’ to describe these sequential clonal connections, a usage consistent with other literature on clonal plants (Gardner & Mangel 1999, Chesson & Peterson 2002).

We examine parent–offspring relationships in wild stands of the clumping, monocarpic bamboo *B. arnhemica* (Poaceae: Bambuseae) from monsoonal northern Australia. We considered two questions. First, what were the age and size relationships between parent and offspring culms? Second, what were the impacts of disturbance on these relationships?

MATERIALS AND METHODS

Study species and area

Bambusa arnhemica is a medium size (12–18 m tall, culm diameter mostly 6–8 cm), pachymorph (clumping) and monocarpic bamboo endemic to the monsoonal tropics in the Top End of

the Northern Territory of Australia (Franklin 2003). It mostly occurs in mono-dominant stands or mixed with other riparian vegetation along watercourses (Franklin & Bowman 2004).

Culm parentage in *B. arnhemica* was examined in mature, wild and essentially unmanaged, even-aged stands at two sites—on the bank of a lagoon in the floodplain of the Mary River at Mary River Park (12° 54' S, 131° 39' E) and on the bank of the Adelaide River near Owens Lagoon (12° 59' S, 131° 15' E). The Mary River site was first assessed in April and May 2001 and the Owens Lagoon site, in May and June 2001. The climate at both sites is tropical with high temperatures and solar radiation throughout the year (McDonald & McAlpine 1991). Seasonal rainfall is reliable and heavy, with 95% of the mean annual rainfall of about 1500 mm falling between October and April (McDonald & McAlpine 1991). The bamboo stand on the Mary River was burnt by an intense wildfire in August 2001 and was subject to prolonged flooding in the 2003/04 wet season. The Adelaide River stand flowered in 2004 and subsequently died and was also subject to prolonged flooding in the wet season prior to flowering.

Field work

Data were collected in the course of a demographic study in which every culm on every clump in the two study sites was individually tagged, its diameter at the internode nearest to 1.3 m height measured to 0.1 cm, year of recruitment recorded, and its state examined annually. Culm states recognized were leafy, senescent (some green in culm but no foliage) and dead. In total 38 clumps and 1947 culms were monitored for five years at Mary River Park and 30 clumps and 1229 culms for four years at the Owens Lagoon site.

From the second year of the demographic study onwards, where possible we identified the parentage of new culms by tracking the rhizome connection using a geologist’s pick as a probe for underground rhizomes (most were underground).

Data analysis

We evaluated the possibility that offspring diameter (y) reflects the diameter of its parent (x) graphically, evaluating the fit of $y = x$ using the formula:

$$r^2 = 1 - (\text{residual sum of squares} / \text{total sum of squares}).$$

We investigated processes influencing the relationship between offspring and parent diameter using generalized linear models and the Akaike Information Criterion (Burnham & Anderson 2002). Generalized linear models allow the inclusion of both continuous and categorical variables. The Akaike Information Criterion provides an alternative to probability-based evaluation of data, which is preferable in multivariate modelling for two reasons—it facilitates the appraisal of multiple hypotheses and it avoids the problem of spurious critical values that is inherent in step-wise regression.

The analysis was performed using the software Statistica 7 (StatSoft 1984–2006). The ratio was modelled with a normal distribution and log link function, with the deletion of four cases in which damage to the parent at the time of assessment was such that their diameter at 1.3 m did not reflect the size of their rhizomes. Explanatory variables considered were the state of the parent culm, age difference and site \times year, all of which were treated as categorical. Parental state categories were leafy and senescent/dead, the latter combined for reasons of sample size. Also, as a result of sample size considerations, we recognized three age-difference categories, namely, 0–1 years, 2–4 years and ‘unknown’; exclusion of unknown cases would have greatly reduced the sample size and, thus, the power of the analysis to discriminate other effects. Since sites were subject

to disturbances (fire, flood, flowering) that were a feature of years and differed between sites, we created a categorical variable ‘site \times year’, with seven categories (four years at Mary River and three at the Adelaide River) to represent these features.

RESULTS

The parent culms of 491 culm recruits were identified (403 at Mary River and 88 at Adelaide River), 47% of the 1049 recruits for which assessment was attempted. Many rhizomes were too deep underground, or the rhizomes too crowded, to confidently identify parents.

Most parent culms were one or two years old at the time of offspring recruitment, but the age of recruiting parents ranged from the same year to more than four years older than offspring, with a moderate amount of variation among years (Figure 1). With n being the sample size, annual mean \pm SD (n [no. of years]) frequencies of parent age at the time of recruitment were: same year as offspring = $0.65 \pm 0.47\%$ (4), one year old = $47.7 \pm 6.3\%$ (4), two years old = $30.7 \pm 6.2\%$ (3), three years old = $10.4 \pm 10.5\%$ (2), four years old = 1% (1), and greater than four years old = 4% (1). Parents that produced more than one offspring did so most often in successive years but numerous other combinations were recorded (Table 1). At the time of recruitment, the parent culms of 443 offspring ramets were leafy (90.2%), 4 were senescent (0.8%) and 44 were dead (9.0%).

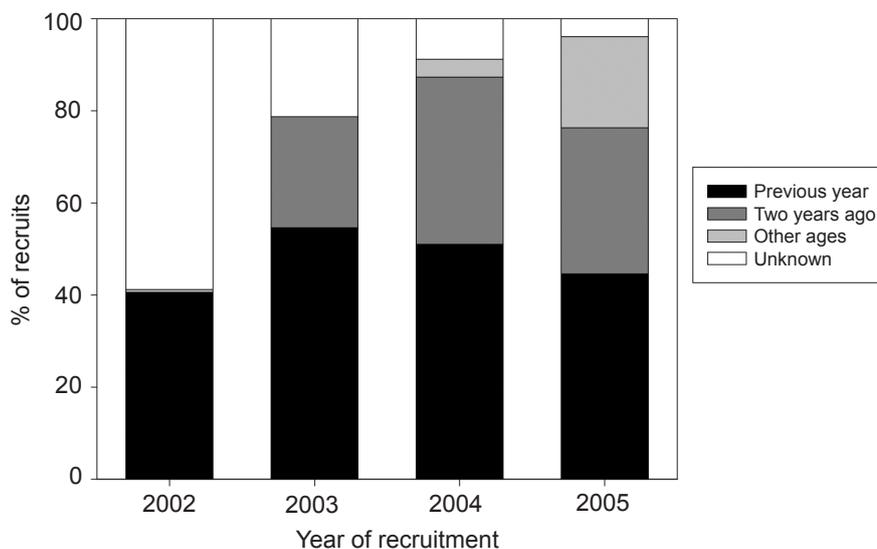


Figure 1 The age relationship between parents and 491 offspring recruits over the course of the study

Table 1 Parent–offspring age relationships for parent culms that were recorded producing more than one offspring culm

Age relationships	n
Two offspring recorded	
0, 1	1
1, 1	7
1, 2	20
1, 3	6
2, 2	4
2, 3	1
3, 3	1
Unknown	7
Three offspring recorded	
1, 1, 1	1
1, 1, 2	2
1, 2, 3	1
Unknown	1

Year codes: 0 = recruited in same year, 1 = parent recruited in the previous year, 2 = parent recruited two years prior, 3 = parent recruited three years prior

Most culms had a similar diameter to that of their parent, though a semi-discrete group had offspring:parent diameter ratios of less than 0.5 (Figures 2 and 3). The median offspring:parent diameter ratio was 0.94. Most of the explained model deviance in the analysis of diameter ratios was contributed by the state of the parent (leafy compared with senescent/dead) and secondarily by the interaction of site and year, with the well-supported additive effect of age difference accounting for an additional 1.9% of the deviance (Table 2). Leafy parents tended to have offspring close to their own diameter, whereas senescent/dead parent culms tended to have offspring about one-third their diameter (Figure 4). Median diameter ratios were severely depressed at Adelaide River in 2004 and somewhat depressed at Mary River in 2002 but were otherwise close to 1:1 (Figure 5). Model parameters and further analysis of the age difference effect showed it to be primarily attributable to contrasts between known and unknown age differences rather than between

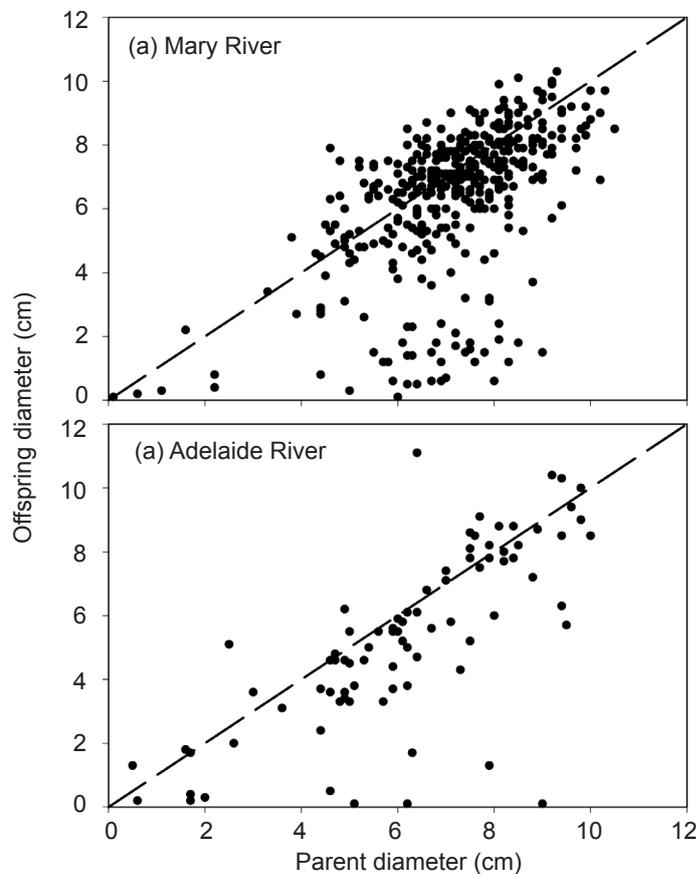


Figure 2 The relationship between parent and offspring culm diameters for 487 culm recruits at two sites in northern Australia. The dashed line indicates a 1:1 relationship (for Mary River, $n = 400$, $r^2 = 0.169$, for Adelaide River, $n = 87$, $r^2 = 0.456$).

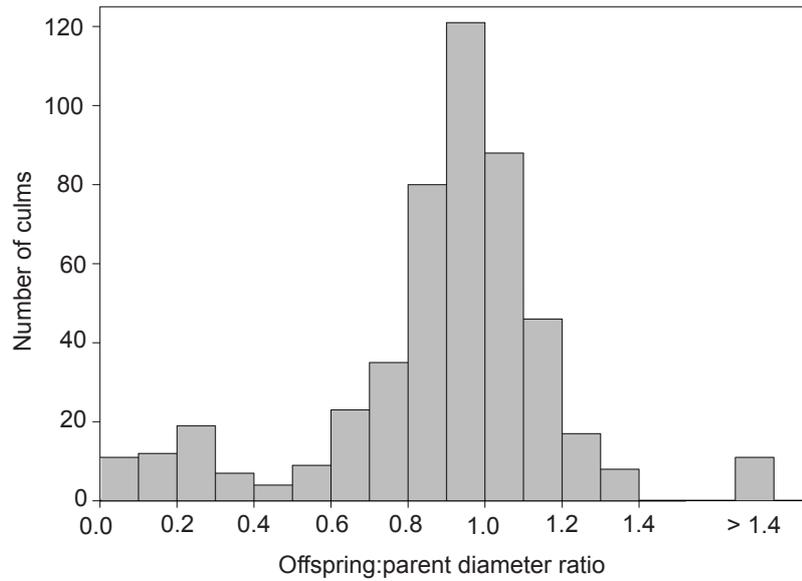


Figure 3 Distribution of offspring:parent diameter ratios for 487 bamboo culms

Table 2 Evaluation of potential explanators of the ratio between diameter of offspring and parent culms using generalized linear modelling

Model	Δ_i	K	%DE
Parent state + site \times year + age difference	0	10	36.8
Parent state + site \times year	10.06	8	34.9
Parent state + age difference	38.22	4	29.8
Parent state	42.92	2	28.5
Site \times year + age difference	111.20	9	20.1
Site \times year	139.80	7	14.5
Age difference	169.61	3	7.6

Δ_i = the difference between AIC_c scores for a given model and the best supported model, K = the number of parameters in the model, %DE = the percentage of deviance explained by the model, n = 487. The model with the most support is that with the lowest AIC_c score. As a rule of thumb, models with $\Delta_i < 2$ are well-supported and those with $\Delta_i > 10$ have no support (Burnham & Anderson 2002).

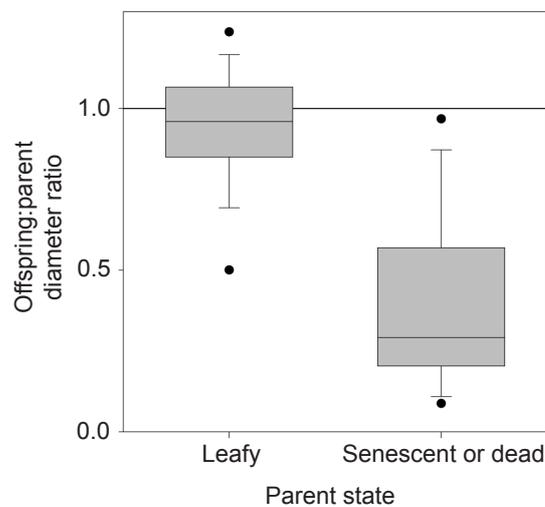


Figure 4 Culm offspring:parent diameter ratios for parent culms which were leafy and senescent/dead at the end of the season of recruitment. Data are median (horizontal line), 25th and 75th percentile (box), 10th and 90th percentile (whiskers) and 5th and 95th percentile (dots).

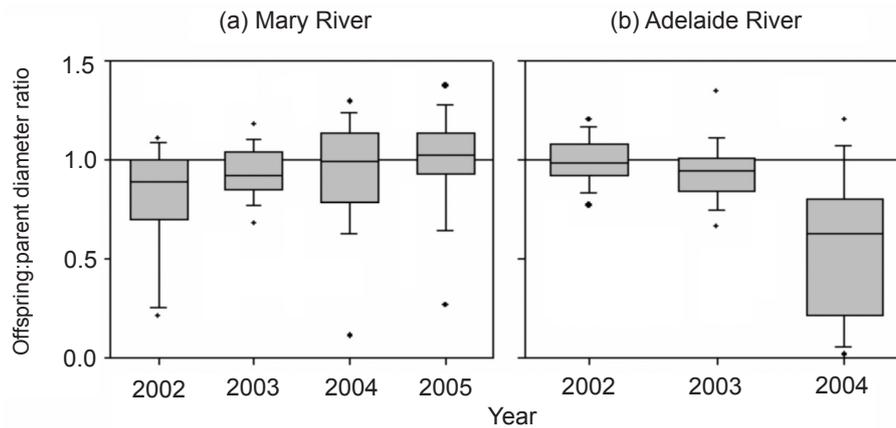


Figure 5 Variation among years and sites in culm offspring:parent diameter ratios in a clumping bamboo from northern Australia. Years are those that offspring were recruited. Data are median (horizontal line), 25th and 75th percentile (box), 10th and 90th percentile (whiskers) and 5th and 95th percentile (dots).

known age classes, with inconclusive evidence of a slight decline in ratios with increasing age differences.

DISCUSSION

We have shown that there is considerable flexibility in parent–offspring relationships in *B. arnhemica*. Three results support this finding: (1) parent age when recruiting varied from less than one year to more than four years old, with a mean of 48% of parents being one year old, (2) among years, there was a variation in the age structure of the parent population, and (3) rhizomes whose associated culms were senescent or dead were still able to produce new ramets. Offspring were generally of similar size to their parents although this varied among years. Offspring were proportionately smaller in the wet season following the severe fire at Mary River and, especially, in the year prior to flowering at Adelaide River. The parent age did not markedly affect the size of the offspring provided that the parent was leafy. Parent status (leafy, senescent or dead) was the strongest proximal factor influencing offspring size, with parents that were senescent or dead producing proportionately smaller offspring than did leafy parents, though not invariably so. This result was not restricted to the 2001/02 recruitment season at the Mary River site which was affected by fire in the year prior (DC Franklin *et al.*, personal observation).

The age relationships we have documented are broadly consistent with those previously reported

in clumping bamboos (reviewed in Kleinhenz & Midmore 2001) although the proportion of parents that were one year old is lower in *B. arnhemica*. This may reflect high levels of natural disturbance at our study sites. In particular, fire may destroy culms whilst the rhizomes, being under the ground, are protected from its direct effects (Trabaud 1987). The low diameter ratio at Adelaide River in 2004 occurred immediately before the mass flowering and subsequent death of all culms and rhizomes (resource allocation to sexual reproduction), but may also have been related to severe flood damage in the 2003/04 wet season (Franklin & Hogarth 2008). Flexible recruitment may help bamboo survive disturbances such as fire and flood.

The relationship between parent age and productivity

Upon emergence from the bud on a parent rhizome (especially during the phase of rapid elongation), a new ramet is a net consumer of carbohydrates that are supplied by one or more generations of parent ramets (Li *et al.* 1998, 2000). At some point in its subsequent development, a ramet acquires sufficient foliage and roots to generate the resources needed for its own maintenance and further development, and switches to being a net contributor of resources to other ramets. To our knowledge there are no studies that identify the timing of this important transition in bamboos and the state of root and canopy development associated with it.

In some bamboos, branch and foliage development does not commence until the second year (Waheed-Khan 1962, Banik 1993, Pearson *et al.* 1994) and in others may be poorly developed in the first year, with development continuing until the second to fourth year (Waheed-Khan 1962, Banik 1993, Lakshmana 1994) or even longer (Taylor & Qin 1993). In *B. arnhemica*, branch and foliage development commences in either the first or second year, with no more than limited canopy development in the first year (Franklin 2005). Although the young foliage of first-year culms may have photosynthetic rates up to 40% higher than 1–3-year-old culms (Kleinhenz & Midmore 2002), this may be insufficient to overcome limited canopy development. Thus, in *B. arnhemica* and perhaps in many other wild bamboos, one-year-old culms are unlikely to be net contributors to clump productivity because they have not yet developed the necessary photosynthetic capacity.

This raises intriguing and important questions about the prominent role first-year ramets play as parents of ramet recruits. Suggestions that older culms contribute little to clump vigour (see Introduction) are not supported by observations of resources being transferred among bamboo ramets (Li *et al.* 2000, Saitoh *et al.* 2002, 2006, though these studies were conducted with leptomorph species). Derner and Briske (1998) demonstrated the redirection of resources to up to the fourth generation of offspring in a clonal, perennial grass, and also that the clump functioned as a series of discrete ‘sectors’ that share resources (see also Briske & Derner 1998).

The suggested prominent role of first-year ramets has little or nothing to do with their contribution to clump resources. First-year ramets are simply the growing points of functional clump sectors with the youngest rhizome bud meristematic tissue. Apical dominance by mature culms may also favour recruitment from young ramets with incompletely developed canopies—apical dominance demonstrably plays a role in ramet recruitment in clonal grasses (Briske & Derner 1998, Tomlinson & O’Connor 2004). Recruitment from older culms occurs when a clump sector failed to recruit in the previous year or if the younger rhizome is damaged. The generally strong relationship we noted between parent and offspring size occurs because both

reflect the vigour of the clump sector, in part due to the intense competition among sectors (Briske & Derner 1998). Similarly, the frequent but far from universal depression of offspring size when the parent culm was senescent or dead reflects the state of the clump sector, which may or may not match that of the immediate parent. These propositions, however, along with a remarkable range of other fundamental bio-mechanistic issues in the growth of clumping bamboos—including the longevity of rhizome connections and extent of resource sharing amongst ramets—remain to be examined.

The concentration of ramet recruitment in the vicinity of one-year-old culms may facilitate clump expansion as well as the concentration of growth in areas where soil resources have not been depleted. They also facilitate the optimal occupation of canopy space by ramets, as noted in other clumping, clonal plants (Wikberg & Svensson 2006, Lanta *et al.* 2008). However, if our interpretation of the processes involved in ramet recruitment in clumping bamboos is correct, then underlying assumptions about retaining first-year culms because they are immediate drivers of productivity may be misplaced. In bamboo management situations, culm retention strategies that place a strong emphasis on retaining first-year culms at the expense of retaining older culms may need to be reconsidered.

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