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Clonal growth and sexual reproduction: tradeoffs and environmental constraints

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Clonal growth confers a number of benefits on plants, but involves some costs as well. We examined whether seed reproduction is reduced in clonal plants due to these costs. Further, we investigated whether this relationship differs for species with optima at stressful or low-productivity sites, as a possible indication that clonality acts as insurance against reduced seed reproduction in such conditions. We evaluated 472 species for which seed production per unit area had been determined, and employed this information together with data on seed mass, height at maturity, clonal traits and optimum habitat conditions (using Ellenberg indicator values). There was a strong hyperbolic relationship between seed output and seed mass, with a scaling coefficient of –1, indicative of a simple tradeoff relationship. We performed analyses both with and without taking phylogeny into account.

Reproductive output (i.e. the product of seed output and seed size) of was lower in clonal than in non-clonal plants (in both with and without phylogeny incorporated in the analyses); within non-clonal species, it was high in annuals and monocarpic plants relative to nonclonal perennials. Reproductive output was lower in clonal plants with extensive lateral spread. This may be due to lower mortality of such plants, which should favor reduced reproductive output, but direct resource tradeoff may also be involved. Reproductive output in all clonal and non-clonal plants increased with the nutrient status and light level of the species' optimum, and decreased with moisture. Because the proportion of clonal plants in vegetation is known to decrease along the same gradients, we can infer that as sexual reproduction becomes increasingly difficult in terms of these characteristics, clonal plants may capitalize on their capacity to bypass it. However, the relationships with habitat parameters disappeared in the phylogenetically corrected analysis, indicating that habitat preferences and reproductive output evolved together.

Ever since clonality has been identified as one of the key strategies of plants, ecologists have been asking about the benefits and costs implicated (Ashmun et al. 1982, Eriksson 1997). Clonal growth involves massive turnover of tissues, repeatedly during the plant lifespan. Such turnover has both energetic and ecological costs. Energetic costs arise because new resources are required to form new tissue; ecological costs are due to the uncertainty whether a vegetative offspring will be placed in favorable conditions, as well as the potential for increased selfing (Vallejo-Marín et al. 2010). On the other hand, clonality provides a plant with a number of benefits. It makes it possible to forage for limiting resources, share them among connected ramets, and escape sites where some limiting resource might have been exhausted (Hutchings and de Kroon 1994). It also provides the option to form multiple descendants of a zygote vegetatively, spreading mortality risks among them (Eriksson and Jerling 1990).

Clonality has appeared repeatedly during the evolution of vascular plants (van Groenendael et al. 1996), indicating that its costs are often outweighed by its benefits. Better understanding these costs and benefits has thus become a challenge in the study of the evolution of clonality (Eriksson 1997). The key issue in this respect is the link between clonality and sexual reproduction (note that henceforth we use 'sexual reproduction' to denote reproduction by seed, ignoring the possibility that in some plants seeds may be formed by asexual means). By increasing the number of descendants of a given zygote, clonality provides the clone an effective tool to reduce per-zygote mortality rates, which should favor delayed reproduction (Gadgil and Bossert 1970, Reznick 1985) and hence lower sexual reproductive investment in clonal plants. However, clonality might have been favored as a response to reduced fertility and failure to reproduce by seed due to other, unrelated causes. It has been hypothesised that clonality evolved as such a response in smaller plants that fail to reproduce sexually under competition from taller neighbours, either conspecific or heterospecific (Aarssen 2008). Alternatively, Eckert (2001) found that some plants may become clonal after increasing environmental harshness makes sexual reproduction

impossible. This has been demonstrated to occur in several taxa (Dorken et al. 2004).

All these hypotheses involve putative negative correlations between clonality and seed reproduction. There is some evidence that, across a number of plant species, sexual reproduction and clonal spreading are negatively correlated at the level of maternal plant resource investment (Söyrinki 1938) or at the level of population dynamics (Boedeltje et al. 2008, Herben et al. 2012). This can be, due, e.g. to slower development of seedlings of clonal plants than perennial non-clonal plants (Šmilauerová and Šmilauer 2007), or reduced capability of clonal plants to establish from seeds in their own stands (Eriksson 1992).

However, we are not aware of any study that has compared reproductive effort of clonal plants with that of non-clonal species. It is well known that in a single reproductive event, annual and monocarpic perennials have higher fecundity than polycarpic perennials (Karlsson and Méndez 2005); hence, it may be assumed that clonality, being common in polycarpic perennials, might have contributed to this difference. Observations on the intraspecific level suggest that clonal reproduction is at the expense of sexual reproduction (Harper 1967), but interspecific comparative data showing how clonal and non-clonal plants differ in their resources investment into sexual reproduction are lacking.

Collection of such data is also hindered by the fact that investment in seed reproduction involves two variables which are traded off against each other, seed mass and seed number. Whereas seed mass is easily measurable much information is available for various growth forms and biomes (Kleyer et al. 2008, Hintze et al. 2013), data on seed numbers are much more difficult to obtain and therefore rather scarce. Additionally, seed number can be expressed in two ways, viz. per individual and per unit canopy area, with these measures having rather different ecological meanings (discussed by Moles and Westoby 2006). While most of the data show consistent negative correlations between seed size and seed production per area (Henery and Westoby 2001, Šerá and Šerý 2004), seed production per plant individual depends on its size and plant age (Moles et al. 2004). Available data on seed production per individual are therefore biased towards unitary plants, namely annuals and trees, where individuals, and hence their fecundities, can be reasonably defined. Because clonal plants are subject to fragmentation, it is difficult to assign the number of seeds produced to an individual fragment. Seed number is therefore best assessed on a per unit area basis. Thus, a comprehensive analysis across clonal and nonclonal plants should be based on seed number per unit canopy area, which can be employed regardless of how an individual is defined.

Such comparative data on seed reproduction and clonality can also be used to approach identification of possible selective forces by examining how investment into seed reproduction changes with habitat parameters that are the putative drivers of clonality (Eckert 2001, Aarssen 2008, see overview for intraspecific level in Abrahamson 1980). In particular, it could enable examination of whether plant species with their optima in unfavorable conditions (low productivity, low light availability, high or low moisture) have different reproductive outputs in comparison with those dwelling in more suitable conditions, and whether such environmental effects differ between clonal and nonclonal plants. In addition, it allows investigation of whether and how reproductive output in clonal plants varies with the type of clonal growth they possess. For example, plants with long rhizomes invest more energy in non-photosynthetic tissues than do plants with short rhizomes, suggesting that clonal plants with extensive lateral spread may have lower fecundity than those with short lateral spread.

In this paper, we ask specifically whether herbaceous clonal plants differ from non-clonal herbs in their reproductive output and whether reproductive output in these groups changes with parameters of their habitats. The relationship between clonality, habitat, and reproductive output should indicate whether reproductive output is constrained by stressful or low productive conditions, and whether such constraints operate differently in clonal and non-clonal plants. For the subset of clonal plants, we also ask whether these constraints are affected by their clonal growth parameters, in order to determine whether reproductive output is traded against investment into clonal structures.

In order to answer these questions, we reanalyzed a published dataset on single-reproductive-event seed number and seed production per square meter of 472 herbs in central Europe (Šerá and Šerý 2004). We classified species according to their life history as clonal perennials, non-clonal polycarpic perennials, monocarpic perennials and annual plants. These categories express differences in their relative investment into belowground non-photosynthetic tissues, age at first reproduction, number of reproductive events, and clonality. We used Ellenberg indicator values to get information on parameters of typical habitats of these species. To disentangle possible effects of shared phylogenetic history, we used both non-phylogenetic and phylogenetic regressions.

Methods

Trait data

Data on seed mass and reproductive output of populations were taken from Šerá and Šerý (2004). In that study, data on seed production were collected from 472 species using the following approach. First, for each species, the mass per seed was estimated by weighing a defined number of seeds. A seed is understood here as a functional generative element. Then, for each species, the numbers of seeds produced in an area of 1 m^2 were counted at three well-developed stands at the fruiting stage. Each count was divided by the estimated cover of the species to recalculate seed production for hypothetical 100% cover. This value would be averaged over all the stands of the given species. Following Henery and Westoby (2001), we refer to this variable as seed output per area (shortened as seed output).

Data on plant lifespan were taken from Kubát et al. (2002), with the support of other sources (LEDA traitbase, Kleyer et al. 2008; CLOPLA database, Klimešová and de Bello 2009). Plants species were classified into four lifespan categories: 1) annuals, i.e. species that usually complete their whole reproductive cycle within one year; 2) monocarpic (non-clonal) perennials, i.e. species that typically live more than one year, but flower only once during their lifetime

(typically at the end); 3) polycarpic (non-clonal) perennials, i.e. species that typically live more than one year, flower repeatedly during their lifetimes, but do not possess organs of clonal growth or vegetative multiplication; 4) clonal polycarpic perennials, i.e. species that typically live more than one year and possess organs of clonal growth and multiplication. Further, we used data from Kubát et al. (2002) to get information on plant height. Clonal growth data were taken from CLOPLA ver. 3.2 (Klimešová unpubl.). For the subset of clonal species, we further extracted data on an additional five traits of clonal growth (Table 1). Values of Ellenberg indicator values for nutrients, moisture and light were taken from Ellenberg et al. (1992). Whereas moisture values are known to correlate rather well with average soil water content, nutrient values are primarily approximations of overall site productivity (Schaffers and Sýkora 2000). Phylogenetic data were obtained from Durka and Michalski (2012).

Data analysis

Relationships between seed output per m^2 and seed mass were analysed using standard major axis (SMA) regression (package lmodel2 from R Development Core Team) on logarithmically transformed values of both variables. The exponent for relationships between seed output and seed mass was calculated as the slope of such an SMA regression. SMA regression is preferred to ordinary least squares when both variables are measured with error, and the choice of dependent and independent variables is arbitrary. We calculated confidence intervals for these exponents. Average reproductive output was calculated as the predicted number of seeds for a plant with seeds weighing 1 mg; these numerical values were obtained by back-transformation of the values predicted by the functional form obtained from the SMA regression. The same set of analyses was done for individual subsets of data, divided into individual lifespan categories.

We fitted linear statistical models using type 1 sum of squares: *seed output* ~ *seed mass* × *lifespan,* and examined the individual terms of the model with the *F*-statistic. We interpreted a significant main effect of *lifespan* as a difference in reproductive output that depends on lifespan values, and a significant interaction as differences in lifespan categories in their relationships between reproductive output and seed mass variation.

Further, we defined *reproductive output* for individual species as the product of seed output and seed mass. This variable represents the absolute amount of energy invested in reproduction per unit area (i.e. canopy). Using this definition, we examined the relationships between reproductive output and plant height, and the moisture, light and nutrients Ellenberg indicator values, as well as their interaction with lifespan category. First, we built a best model using stepwise regression. All these variables and their interactions with lifespan were available for inclusion/deletion. We started both from the model log(*reproductive output*) ~ log(*height*), and from the full model with all three indicator values as predictors. Plant height was used as a covariate to account for differences in canopy height and hence in leaf area index. We identified the best-fitting model using the AIC (Akaike information criterion) by a bidirectional stepwise procedure implemented in the step function in R ver. 2.15.1. To examine separate effects of individual predictors we fitted the linear model log(*reproductive output*) ~ *tested variable* × *lifespan*, and examined the significance of individual terms of the model using the *F*-statistic.

For the subset of clonal plants, we further examined traits of clonal growth (bud bank size, mean bud bank depth, connection persistence, multiplication rate and lateral spread) using stepwise regression. All these variables were available for inclusion/deletion. We started both from the model log(*reproductive output*) ~ log(*height*), and from the full model with all traits of clonal growth. We identified the best-fitting model by using the AIC in a bidirectional stepwise procedure implemented in the step function in R ver. 2.15.1. In all regression analyses, traits that had strongly skewed distributions (height, seed mass, seed output, and reproductive output) were log-transformed before the analysis.

Phylogenetic models were fitted using phylogenetic generalized least squares assuming Brownian model evolution of the trait (i.e. setting $\lambda = 1$) using the pgls function from the caper package for R and using the same set of models as in the nonphylogenetic regressions.

The phylogenetic signals of continuous traits were assessed using Pagel's λ (Freckleton et al. 2002). We fitted λ using a

Table 1. Clonal growth traits used in the analyses. [1)]trait defined only for plants with clonality = 1.

Abbreviation	Units	Definition	No. of species for which data are available
Life span		annual/perennial monocarpic/perennial polycarpic/ clonal polycarpic	472
Clonality	yes/no	whether the plant possesses organs of clonal growth	472
Bud bank size	no. of buds	no. of stem-derived buds in the soil and at the soil surface	472
Mean bud bank depth	cm	weighted mean depth of stem-derived buds	448
Conection persistence	yes/no	whether clonal connections between ramets persist two or more years[1)]	244
Multiplication rate	no. of offspring	no. of offspring shoots per parent shoot per year, including offspring of small size. Small offsprings are defined as those clonal offsprings for which it would take more years to attain size comparable with other clonal offspirng of the plant; they usually resemble seedlings[1)]	246
Lateral spread	meters	lateral spreading distance of clonal growth organs[1)]	245

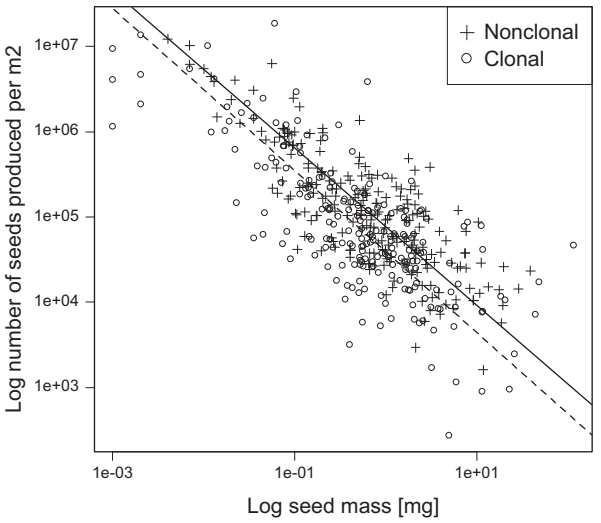

Figure 1. Relationship between seed output and seed mass for clonal plants versus all non-clonal species. Solid line = non-clonal plants; dashed line = clonal plants. Lines were fitted by standard major axis regression. For values of slopes and intercepts see Table 2.

maximum likelihood approach employing the pgls function from the caper package for R and calculated their upper and lower confidence limits. For categorical traits such as clonality, we used the D statistic of Fritz and Purvis (2010) and tested the likelihood of the estimated value based on two extreme hypotheses: 1) hypothesis $\lambda = 0$ (no phylogenetic signal); and 2) hypothesis $\lambda = 1$ (Brownian model of trait evolution across the phylogenetic tree, i.e. complete phylogenetic signal). The fitting and tests were done using the phylo.d function from the caper package.

Results

Analysis of the whole data set showed a strong relationship between seed output and seed mass (Seed output = 55 271, Seed mass$^{-0.943}$, $R^2 = 0.581$; Fig. 1). The slope of the relationship in the log-log plot was not significantly different from –1 (Table 2), indicating tradeoff of one variable against the other. The interaction between seed mass and lifespan category was not significant ($F = 0.09$, DF = 3, 426, $p = 0.965$), indicating lifespan categories did not differ in their slopes. In SMA analyses split by lifespan categories, all confidence intervals of the slope contained –1, indicating seed mass/seed number tradeoff independently in each of these categories (Table 2).

Although individual points showed large scatter (Fig. 1), there was a highly significant difference among individual lifespan categories in the values (Table 2, Fig. 2; $F = 14.9$, DF = 3, 429, $p < 0.001$; $R^2 = 0.088$), indicating differential reproductive output among lifespan categories. The highest reproductive output was shown by monocarpic perennials, followed by annuals; clonal species had the lowest reproductive output (47% of the annuals). Nonclonal perennials and clonals are marginally significantly different ($F = 3.575$, DF = 1, 259, $p = 0.059$). The difference among individual lifespan categories was significant also in the phylogenetic analysis ($F = 9.21$, DF = 3, 429, $p < 0.001$; $R^2 = 0.060$).

Stepwise selection using AIC identified all three Ellenberg indicator values as well as plant height as predictors of reproductive output after having accounted for lifespan (lifespan: DF 4, $p = 0.008$, difference in adjusted $R^2 = 0.025$; height: DF 1, $p < 0.001$, difference in adjusted $R^2 = 0.052$; moisture: DF 1, $p = 0.001$, difference in adjusted $R^2 = 0.024$; nutrients: DF 1, $p = 0.011$, difference in adjusted $R^2 = 0.014$; light: DF 1, $p = 0.132$, difference in adjusted $R^2 = 0.003$; residual DF 320; all effects are positive except for moisture); none of the interactions was included in the model. When individual predictors (height and Ellenberg indicator values) were tested separately, only plant height, Ellenberg indicator value for nutrients and (marginally) Ellenberg indicator value for moisture had significant effects on reproductive output (Table 3, Fig. 3). Only Ellenberg nutrients showed significant interaction with lifespan category. None of these relationships was significant when phylogenetic regression was used.

Within the group of clonal plants, stepwise selection using AIC identified ramet height (difference in adjusted $R^2 = 0.043$, positive effect), bud bank depth (difference in adjusted $R^2 = 0.007$, positive effect) and lateral spread (difference in adjusted $R^2 = 0.012$, negative effect) as predictors of reproductive output.

All reproductive traits were rather strongly phylogenetically conserved (Table 4). While both seed mass and seed output were close to the Brownian motion model (i.e. strong phylogenetic dependence); reproductive output had a much weaker phylogenetic signal. Clonality also had a rather strong phylogenetic signal ($1 - D = 0.634$, $n = 433$), although its phylogenetic dependence was significantly different (weaker) than that expected by the Brownian motion model.

Discussion

Analysis of the whole data set showed a strong relationship between seed output and seed mass (see also Šerá and Šerý 2004), which is compatible with a simple tradeoff. Our

Table 2. SMA regressions of seed output and seed mass (after log transformation). Values of the intercept are back-transformed to seed mass units (mg).

			Slope			Intercept		
Group	n	R^2	Estimate	2.5% CI	97.5% CI	Estimate	2.5% CI	97.5% CI
All plants	472	0.581	−0.943	−1.003	−0.887	55271	53104	56954
Annuals	131	0.649	−0.920	−1.021	−0.828	80822	75358	84965
Monocarpic perennials	36	0.777	−0.867	−1.024	−0.734	115844	114691	115844
Polycarpic perennials	61	0.606	−0.953	−1.124	−0.809	54176	50514	56954
Clonal plants	244	0.573	−0.949	−1.037	−0.868	39340	36680	41357

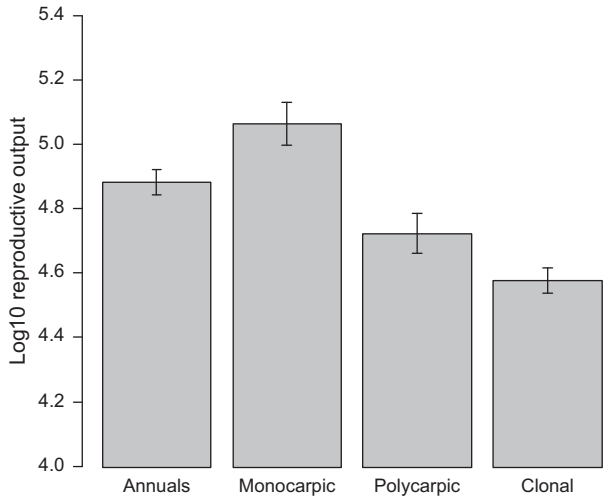

Figure 2. Reproductive output in individual lifespan categories. Bars indicate standard errors.

results thus complement findings of Henery and Westoby (2001) and Moles and Westoby (2006), who have demonstrated similar relationships for woody species. Existence of such a relationship between these two variables means that, independently of the differences in seed size in the examined species, reproductive output of a plant can be defined (Lloyd 1987) as a product of seed output and seed size. In the present study, reproductive output defined in this way was lower in clonal than in non-clonal plants; within nonclonal species, it was high in annuals and monocarpic plants relative to nonclonal perennials. While differences in reproductive output between annuals and perennials is a well-known phenomenon (Karlsson and Méndez 2005), low reproductive output in clonal species relative to nonclonal species has not previously been reported.

Low reproductive output in clonal plants may be due to several mechanisms. High reproductive output is selected for when adult or juvenile mortality is high (Gadgil and Bossert 1970). Clonal plants have low per-genet mortality due to mortality risks being spread among multiple ramets (Eriksson 1997), which may lead to lower reproductive allocation and higher allocation to survival. However, such a relationship should arise only when there is a resource tradeoff between sexual reproduction and survival. There is limited support for such a tradeoff in monocarpic herbs (Sosnová and Klimešová 2009).Our present data show that reproductive output is reduced by increased lateral spread also in clonal plants, indicating that such a tradeoff may to some extent operate in them as well. An additional explanation could be that large clones could hinder crossfertilization and hence seed production (Jacquemyn and Honnay 2008, Vallejo-Marín et al. 2010), namely if inter-genet competition is strong and can prevent mixing among stands comprising several genets. In our study, this is supported by the effect of lateral spread, with lower sexual reproduction found in plants with greater lateral spread.

Clonal growth also makes plants more abundant on the local scale (Herben et al. 2014), implying that a lower reproductive output could be sufficient to maintain viable populations. In extreme cases, high local dominance found in clonal plants may make sexual reproduction unnecessary for local population maintenance, further reducing selection for high reproductive output or increasing selection for long-distance seed dispersal and the ability to produce viable seeds after selfing (Jacquemyn and Honnay 2008, Vallejo-Marín et al. 2010).

The key role in the low mortality of clonal plants is played by the (typically belowground) connections between ramets and associated belowground storage. In monocarpic plants, storage organs contain resources that are ultimately used for seed reproduction, and investment in them thus only delays use of the resources in a reproductive event. In contrast, perennial plants produce and maintain belowground organs continuously, with important consequences for the total resource availability of individual ramets and reduced potential for growth (Suzuki and Hara 2001). This may underlie, essentially due to resource limitation, lowered reproductive output in clonal plants, such as shown by our data. Resource tradeoff may also underlie the negative correlation between reproductive output and the extent of lateral spread. This relationship is fairly weak (difference in adjusted R^2 only slightly greater than 1%), but appears even after plant height has been partialled out; thus, it is a size-independent effect of investment in structures involved in clonal spread.

Reproductive output along environmental gradients

In addition to differing among individual lifespan categories, reproductive output varied systematically along environmental gradients of moisture, productivity and, to a lesser degree, light availability. Interestingly, all lifespan categories showed

Table 3. Statistical tests of model terms in models with log reproductive effort as response variable and lifespan category, one additional predictor and their interaction as predictors. Adjusted R^2 represents the difference in adjusted R^2 due to the inclusion of the term.

	Lifespan category			Predictor tested			Interaction			
Predictor in the model	Adjusted R^2	F	p	Adjusted R^2	F	p	Adjusted R^2	F	p	Residual DF
Non-phylogenetic analysis										
Height	**0.086**	**11.7**	**<0.001**	**0.059**	**29.9**	**<0.001**	−0.008	0.1	0.993	419
Nutrients	**0.069**	**8.7**	**<0.001**	**0.019**	**9.3**	**0.002**	**0.013**	**2.9**	**0.034**	392
Moisture	**0.065**	**7.5**	**<0.001**	0.006	3.4	0.064	−0.008	0.2	0.923	362
Light	**0.074**	**9.3**	**<0.001**	<0.001	1.2	0.280	−0.003	0.7	0.592	410
Phylogenetic analysis										
Height	**0.061**	**10.1**	**<0.001**	0.003	2.4	0.124	−0.002	0.7	0.532	418
Nutrients	**0.058**	**9.0**	**<0.001**	−0.002	0.2	0.683	0.005	1.7	0.173	392
Moisture	**0.061**	**8.9**	**<0.001**	0.001	1.2	0.269	−0.006	0.3	0.835	360
Light	**0.045**	**7.6**	**<0.001**	0.004	2.6	0.108	0.002	1.3	0.284	409

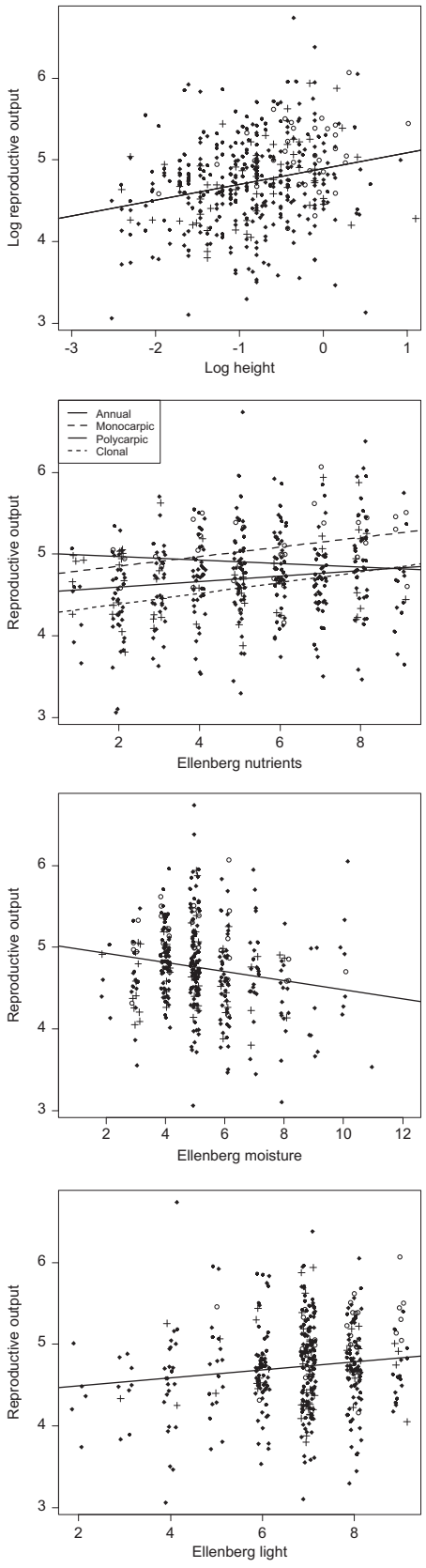

Figure 3. Relationships between reproductive output, and plant height (top pane) and Ellenberg indicator values for nutrients (upper middle pane), moisture (lower middle pane) and light (bottom pane). Reproductive output is the predicted number of seeds per 1-m^2 per year (seed output of species) of a plant species with seed mass equal to 1 mg. Solid circles – annuals, empty circles – monocarpic nonclonal, crosses – polycarpic non-clonal, diamonds – clonal plants. To improve visibility, Ellenberg indicator values were jittered. Lines were fitted using ordinary least squares regression. One line was fitted if the interaction of the predictor and lifespan category was not significant; four separate lines (one for each lifespan category) were fitted if the interaction was significant. For tests of these relationships, see Table 3.

Table 4. Phylogenetic signal in continuous traits. Values of lambda close to unity indicate that the trait has been evolving randomly, but along the topology of the phylogenetic tree, i.e., it has a strong phylogenetic signal; values close to zero indicate absence of phylogenetic signal in the trait.

	n	Pagel's lambda	95% confidence interval of lambda
Seed mass	433	0.981	0.958 – 0.994
Seed output	433	0.935	0.889 – 0.963
Reproductive output	433	0.687	0.525 – 0.801
Plant height	423	0.741	0.594 – 0.846
Ellenberg nutrients	397	0.586	0.422 – 0.722
Ellenberg moisture	365	0.483	0.231 – 0.700
Ellenberg light	413	0.452	0.238 – 0.646

essentially the same response to environmental parameters, viz. reducing their reproductive output in stressful environments (low light, low nutrients and high moisture). This is likely because of simple resource limitation in the cases of light and nutrients, and limitation by stress from excessive moisture.

It has been shown that the proportion of clonal plants in vegetation changes along these gradients in a fashion that parallels the decrease in reproductive output (Klimeš et al. 1997, Ye et al. 2014, Klimešová and Herben unpubl.). In particular, clonal plants nearly completely replace non-clonal plants in aquatic and waterlogged habitats and forest understory, i.e. wet and dark ends of environmental gradients (Klimeš et al. 1997, Klimešová and Herben 2014). Clonal growth can provide insurance against low reproductive output, with low proportions of nonclonal species in these environments simply resulting from greater difficulties of non-clonal plants in maintaining positive population growth rates there, due to strong resource limitation on sexual reproduction. Clonal growth is much less constrained in these environments: adventitious rooting is easy in wet soil, and low carbon availability forces plants to build short-lived tissue which they must keep replacing. It is likely that this relationship would be even stronger if we include plants from fully aquatic environments, where clonal reproduction largely prevails and sexual reproduction is strongly suppressed (Grace 1993).

However, prevalence of clonal reproduction and reduced reproductive output is not the case in all stressful conditions. For example, dry habitats are dominated by non-clonal plants, and fecundity is not reduced in dry habitats. Therefore, in these conditions, clonality is not particularly favored and reproductive output is higher. As our data do not contain species from the extremely dry conditions found in semideserts or deserts, we cannot say how general this phenomenon is.

Limitations of the approach

There are two methodological limitations to our data set. First, seed output was typically determined at plots of well-developed and fruiting plants. This is likely to result in

overestimation of seed production relative to the overall population of the species and thus the values reported are better seen as upper limits than true estimates. However, it is likely that this approach will overestimate seed production more in clonal than in non-clonals plants, as clonal plants, which do not necessarily rely on sexual reproduction, typically have large numbers of sterile ramets in their populations. It is thus likely that the true difference between reproductive output in clonal and non-clonal plants may be even larger than our data show.

More exact data on this could be provided by using seed number data per shoot. While such data have been collected for many species (Söyrinki 1938, Kleyer et al. 2008, Hintze et al. 2013), they are of little use in determining reproductive output unless they are accompanied by data on the proportions of fruiting versus sterile shoots, such as collected by plant demographers (Burns et al. 2010). We advocate combining both approaches, taking into account variations in density that all populations show (Hartley et al. 2004, Gastner et al. 2009) and using demographic data to estimate lifelong reproductive output (Moles and Westoby 2006).

Second, we assume that reproductive output can be expressed by the product of seed output and seed size per unit canopy. However, reproductive output as an absolute measure is not fully informative, due to its potential dependence on total resources available to the plant. As reproductive effort is defined as the proportion of resource invested in reproduction (Thompson and Stewart 1981, Samson and Werk 1986), our approach would be fully correct if all species in the set would have identical canopies, namely identical leaf area indexes. However, this is unlikely to be the case. Leaf area index is known to vary across habitats as well as across and within plant species and to vary systematically as a function of plant height (Gower et al. 1999, Falster et al. 2011). This is likely to be the reason for the significant positive relationship between reproductive output and plant height, a relationship which is identical for clonal and non-clonal plants and systematically explains about 5% of the variation in (log) reproductive output. As the relationship between leaf area index and plant height is known to follow a power law, and height typically explains a high proportion of variation in leaf area index (Gower et al. 1999), we assume that using log height as a covariate in analyses involving log reproductive output should remove a major part of variation due to this effect and that height-corrected reproductive output could be a good approximation of reproductive effort.

Conclusions

Both reproductive output and clonality are fairly strongly phylogenetically conserved and probably evolved together as a response to environments in which resource limitation hindered sexual reproduction. The present data cannot answer the question whether clonality evolved as insurance in plants with already poor reproductive output or whether clonal plants reduced their reproductive output to gain energy for clonal growth. Low reproductive output of clonal plants is due not only to a direct resource tradeoff between clonality and sexual reproduction (although there is an indication of it), but also falls into the more general category of ecological costs to sexual reproduction associated with clonality. Our data do show, however, that seed reproduction becomes increasingly difficult in some types of stressful habitats and that clonal plants may capitalize on their capacity to bypass it.

It should further be stressed that clonality as reproductive insurance should be examined in the context of other mechanisms that can insure against failed or reduced sexual reproduction. Plants in stressful environments could save resources not only by producing lower number of smaller seeds, but also by investing less in flowering and fruiting structures such as flowers, nectar, or fleshy fruits. They also could save energy by allowing self-fertilization or cleistogamy, or by forming agamospermous seeds. As these mechanisms are available to a number of plant species, lower reproductive output of clonal plants is likely to be a consequence of the clonal growth habit, and is unlikely to be the prime driver of clonality. Clonality affects too wide an array of plant traits to be explained only as a response to reduced fertility.

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