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EFFECT OF FLOWERING ON VEGETATIVE GROWTH AND FURTHER REPRODUCTION IN *FESTUCA NOVAE-ZELANDIAE*

Summary: Flowering intensity and plant size were monitored in 155 *Festuca novae-zelandiae* individuals over four years to determine if trade-offs exist between inflorescence production and vegetative growth, and between inflorescence production in different years. Less than half of the population flowered in any one year, 36% of individuals did not flower at all, and only 17% flowered in all four years of the study. Mean number of inflorescences per individual per year varied from 1.54 to 5.53 (maximum = 85). No trade-offs were detected between flowering frequency and intensity; individuals that flowered more frequently also produced more inflorescences in each flowering episode. No trade-off was detected between current and future reproduction, rather flowering intensity was positively correlated between years. Growth, as measured by diameter increment, was positively related to flowering frequency and flowering intensity, both across all individuals studied and within 1m x 1m plots. The presence of a positive relationship between growth and reproduction within plots argues against meso-scale variability in environment factors being the cause of the results from analyses involving all individuals. Clearly reproduction in *F. novae-zelandiae* does not incur a marked cost in growth or future reproduction. The assumptions underlying theoretical expectations of such trade-offs may not be valid for long-lived clonal plants such as *F. novae-zelandiae*.

Keywords: *Festuca novae-zelandiae*; Poaceae; New Zealand; growth; reproduction; trade-off.

Introduction

When an organism has only a fixed amount of resources to expend, costs incurred in one activity should be at the expense of investment in another activity. Life history theory predicts that an increase in reproductive effort should result in an increase in current reproductive output and a reduction in somatic growth (Williams, 1966; Harper and Ogden, 1970; Harper, 1977; Cockburn, 1991). There are many animal examples of trade-offs between reproduction and demographic parameters such as growth, survival and residual reproductive value (Partridge and Harvey, 1985; Reznick, 1985; Bell and Koufopanou, 1986; Cockburn, 1991), however a cost of reproduction has been detected in surprisingly few plant species (Table 1). More often vegetative growth and reproductive effort in plants are positively correlated (Harper, 1977; Watkinson and White, 1985; Thompson *et al.,* 1991; Aarsen and Taylor, 1992; Bazzaz and Ackerley, 1992). A trade-off between reproduction and vegetative growth should be particularly conspicuous in determinate-flowering plants such as perennial grasses (Watson, 1984; Cockburn, 1991). When the apical meristem of a grass tiller forms a floral primordium, the tiller is no longer available for vegetative growth, and dies after reproduction. It could be expected that intense flowering should have a detectably negative impact on vegetative growth as reproduction involves a loss of existing meristems.

Life history theory also predicts that when increased allocation to reproduction affects survival, a trade-off should exist between current reproductive output and residual reproductive value (Williams, 1966). A trade-off between current reproductive effort and future reproduction has been demonstrated less often (Law, 1979; Bell and Koufopanou, 1986). In *F. novae-zelandiae* new tillers are frequently initiated in late summer following seed maturation (Lord, 1992), therefore conditions exist for current reproduction to affect future reproduction, as energy allocated to flowering and fruiting could be at the expense of allocation to new vegetative meristems.

This study examines flowering frequency and intensity, and plant growth over four years in *Festuca novae-zelandiae* in order to determine if trade-offs exist either between reproduction and growth or between reproductive frequency and reproductive intensity. The study seeks specifically to answer four questions: (1) do all plants flower in all years? (2) do plants that flower less than annually compensate by flowering more heavily in reproductive years? (3) does the intensity of

Table 1: *Some studies of costs of reproduction. RA = proportion of total resources devoted to reproductive, RO = total quantity of reproduction, RE = reproductive biomass / (reproductive biomass + net annual growth). References not cited in the text are from a literature search for the term "cost of reproduction".*

Source	Organism	Relationship examined	Result
Cost detected			
Law, 1979	*Poa annua*	current vs future reproduction	negative
Martinez-Ramos *et. al,* 1988[1]	palm	current vs future reproduction	negative
Muir, 1995	clonal herb	reproduction vs storage/growth	negative
Primack and Hall, 1990	orchid	reproduction vs growth	negative
"	"	current vs future reproduction	negative
Thoren *et. al,* 1996	carnivorous spp	reproductive vs somatic resources	negative
Watkinson and White, 1985	"many trees"	reproduction vs growth	negative
Costs not detected			
Antlfinger and Wendel, 1997	orchid	reproduction vs growth	no relationship
"	"	current vs future reproduction	no relationship
Bouzille *et. al,* 1997	*Juncus*	reproduction vs shoot production	no relationship
Dudash and Fenster, 1997	perennial herb	reproduction vs survival	no relationship
"	"	current vs future reproduction	no relationship
Horvitz and Schemske, 1988	perennial herb	bud removal on growth/survival	no relationship
Parker, 1997	*Cytisus*	current vs future reproduction	no relationship
Pfister, 1992	macroalga	RA vs total biomass	no relationship
Reekie and Bazzaz, 1987	perennial grass	Reproduction vs growth	no relationship
"	"	current vs future reproduction	no relationship
Aberg, 1996	macroalga	RE vs plant size	positive
Ackerley and Jasienski, 1990[1]	perennial herb	RO vs plant weight	positive
Cunningham, 1997	palm	current vs future reproduction	positive
Harper and Ogden, 1970	perennial herb	RO vs plant weight	positive
Mark, 1965	perennial grass	current vs future reproduction	positive
Oyama and Dirzo, 1988[1]	palm	RA vs plant size	positive
Pinero *et. al,* 1982[1]	palm	RA vs plant size	positive

[1]Cited in Bazzaz and Ackerley (1992).

flowering in the current year affect flowering in subsequent years? (4) do plants that flower frequently or heavily show a reduction in vegetative growth?

Methods

Study area

The study was conducted in the University of Canterbury Experimental Area at Cass, South Island, New Zealand (43°02'S, 171°45'E). The climate at Cass is characterized by wet springs and dry summers. Summer temperatures tend to be temperate (mean January temperature 15 °C, maximum recorded temperature 40°C), but winter temperatures are relatively mild (Greenland, 1977). Most of the experimental area supported *Nothofagus* forest until approximately 500 years BP (Molloy, 1977).

Data collection

Festuca novae-zelandiae (Hack.) Cockayne is an endemic tussock which lives for at least 50 years (Moore, 1976). Flowering occurs from November to January and fruiting in February and March (Connor, 1963). Previous years' inflorescences persist on the plant for at least a year and are distinguishable from current years' inflorescences by the degree of weathering that has occurred.

In September 1989, fourteen 1 m x 1 m plots were randomly located in a 20m x 20m area of dense short-tussock grassland at 670m a.s.l. in the Cass experimental area. All 155 *Festuca* tussocks within these plots were permanently tagged, and in September 1989 and again in January 1992, measurements were made of mean basal diameter using a diameter tape. The proportion of individuals flowering and the number of inflorescences per individual produced during the previous (summer) flowering season were recorded in September 1989, March 1990, March 1991 and January 1992.

Table 2: *Flowering intensity among 155* Festuca novae-zelandiae *tussocks over four years. Mean inflorescences m^{-2} were analysed using one-way ANOVA. Mean number of inflorescences tussock^{-1} were analysed by repeated measures ANOVA, using SAS Proc GLM (SAS Institute, 1990).*

	1988/89	1989/90	1990/91	1991/92	*F*	*p*	df
% of plants flowering	37.4	29.0	42.6	50.3			
mean inflorescences m^{-2}	30.1	17.1	51.3	45.8	2.35	NS	
mean inflor. tussock^{-1}	2.72	1.54	4.64	4.13	12.2	0.0001	3;459

The change in plant diameter from September 1989 to January 1992 was used as a measure of plant growth. As change in diameter is not a particularly accurate measure of growth, daughter tiller production was monitored over 1990 and 1991 for 75 tillers in 30 tussocks of various sizes to provide an, admittedly limited, quantitative comparison to overall diameter increment. Tillers were selected at 2cm intervals along transects through the middle of each tussock and banded with small lengths of plastic coated wire. For tussocks with a basal diameter of 2cm or less, only the centre-most tiller was banded. The production of daughter tillers by these original tillers was recorded every three months.

Analysis

In case diameter increment was not independant of initial basal diameter, the relationship between reproduction and vegetative growth was examined using partial correlation coefficients, whereby the correlation between two variables can be examined independantly of their relationship to a third variable, and analysis of covariance, in which the effect of initial basal diameter was extracted as a covariate. These, and all other analyses were performed using Statistix for Windows 1.0 (Analytical Software, 1996) except where stated otherwise. For all analyses of variance Bartletts test was used to test for homogeneity of variance. If variances were unequal, data were either transformed, or non-parametric Kruskal-Wallis tests were used, which perform one-way analyses of variance on ranked, rather than raw data.

Results

Do all plants flower in all years?

The proportion of individual *Festuca* tussocks that flowered in a given year varied from 29% to 50% (Table 2). Over a third (36%) of individuals surveyed produced no inflorescences at all during

the four year census period; only 17% of individuals flowered in all four years (Table 2). Those plants that did not flower during the census period were significantly smaller in basal diameter than those that did (Kruskal-Wallis ANOVA: $H = 62.2$, $n=155$, $p_{approx}<0.001$). Inflorescences per tussock varied significantly between years (Table 2).

Do intermittent flowerers flower more heavily in reproductive years?

In light of the less-than-annual flowering of most of the population, it is logical to ask whether plants that reproduce less than annually produce more inflorescences when they do flower. To examine this I divided the total number of inflorescences produced by each plant during the study period by the number of years each plant flowered. I found no tradeoff between frequency and intensity of reproduction; individuals that flowered more frequently also tended to produce more inflorescences per flowering episode. Frequently-flowering plants were also significantly taller and wider (Table 3).

Does current flowering intensity affect subsequent flowering intensity?

Flowering intensity was relatively consistent among years; when individuals were ranked by the number of inflorescences produced each year, rank scores were highly positively correlated between years (Table 4).

Does flowering frequency and intensity affect growth?

The majority of individuals (115 / 155 = 74%) increased in diameter over the study period, 15% decreased in size and 11% remained the same size. Mean diameter increased from 4.52cm to 5.45cm over the four year study period. Large plants grew more, in absolute terms, than small plants (linear regression: change in diameter = 0.478 + 0.065 initial diameter, $R^2 = 0.047$, $F = 7.53$, $n = 155$, $p<0.01$). However small plants grew proportionately more than large plants (linear regression: change in

Table 3: *Means and results of Analysis of Variance (ANOVA) for* Festuca novae-zelandiae *tussocks in five flowering frequency classes (years flowering out of four). "Infl. flowering yr^{-1}" is inflorescences produced over four years / no. of reproductive years. Standard deviations are in brackets. Superscripts indicate means are significantly different (p<0.05) according to T-tests of general contrasts.*

| | Flowering frequency | | | | | | |
	0/4	1/4	2/4	3/4	4/4	*F*	*p*
(a) mean values for all 155 tussocks							
% individuals	36.1	17.4	14.8	14.2	17.4		
Infl. flowering yr^{-1}	0	1.41	3.00	9.68	10.7	315.2*	0.001*
	(0)	(0.797)	(4.51)	(11.0)	(6.72)		
Height (cm)	31.9	36.5	41.2	46.4	50.7	38.99	0.001
	(7.21)	(5.09)	(7.03)	(9.20)	(6.98)		
Basal diameter (cm)	1.44	2.51	4.71	7.85	10.6	56.77	0.001
	(1.53)	(2.44)	(2.21)	(4.12)	(4.05)		
Change in diameter	0.434	0.267	0.829	1.625	1.367		
1989-1992	(0.82)	(1.59)	(1.30)	(1.83)	(1.57)		
Change in diameter		0.05[a#]	0.71[ab#]	1.72[c#]	1.60[bc#]	4.02[#]	0.01[#]
corrected for initial diameter							
(b) mean values for 32 tussocks in Plots 7 and 9 only							
Change in diameter		0.84[ab#]	0.82[a#]	1.67[b#]	1.45[ab#]	4.06[#+]	0.01[#+]
corrected for initial diameter							
Infl. flowering yr^{-1}		1.50	1.81	6.83	8.97	13.5+~	0.001+~

*Kruskal-Wallis H and P$_{approx}$ results.
[#]Results of analysis of covariance controlling for initial diameter, reproductive plants only.
[+]F and P values are for reproductive frequency classes nested within plots.
[~]Analysis performed on log-transformed data, but untransformed mean values given.

diameter/initial diameter = 0.568 - 0.044 initial diameter, $R^2 = 0.088$, $F = 14.7$, $n = 155$, $p<0.001$). No new tillers were produced by banded tillers in 9 of the 30 tussocks in which tiller production was monitored, but all of these plants were less than 4 cm in diameter in 1990 and one died during the study period. For the remaining 21 tussocks, the total number of new tillers produced by the original banded tillers was significantly correlated with diameter increment over the study period (Pearsons Correlation, $r = 0.435$, $n = 21$, $p<0.05$), providing some validation for the use of diameter increment as a measure of growth.

Analyses of change in diameter showed no trade-off between growth and either total flowering effort, or flowering frequency. The partial

correlation between change in diameter and total inflorescence production over the study period, controlling for initial diameter, was significant positive ($r = 0.389$, $n = 155$, $p<0.001$). This did not appear to be due to flowering stimulating tillering; in the four tussocks in which banded tillers flowered, flowering tillers produced no more daughter tillers than nonflowering tillers (Paired T-test, flowering vs nonflowering tillers within each tussock: $T = 1.53$, $df = 3$, $p>0.2$). Analysis of covariance, using only plants that flowered during the study period, was performed to determine whether change in diameter differed significantly between reproduction frequency classes (number of flowering years out of four) whilst controlling for the effect of initial plant diameter. A significant difference was found between reproduction frequency classes, but in the direction of a positive relationship between growth and flowering frequency (Table 3).

Table 4: *Pearson's Correlation coefficients for inflorescence production in different years. N=155 and P<0.001 in all cases.*

Flowering season	1989/90	1990/91	1991/92
1988/89	0.5469	0.7031	0.6682
1989/90	—	0.5768	0.4992
1990/91		—	0.7491

Discussion

Moore (1976) noted that mature plants of *Festuca novae-zelandiae* flowered in most years on Molesworth Station in North Canterbury. In each

year of this study some plants flowered, however individuals that flowered regularly were in the minority in the population and a significant proportion of the population did not flower at all during the study period. No trade-off was detected between flowering frequency and flowering intensity; plants that flowered more often produced more inflorescences in any one reproductive episode and were also generally larger. This study also detected no trade-off between growth and reproduction. Larger plants flowered more frequently and produced more inflorescences per flowering episode and there was a consistent positive relationship between vegetative growth and both flowering frequency and intensity. This concurs with findings from many different plant species, and especially long-lived perennials, that reproductive output is often positively correlated with size (Harper, 1977; Pinero *et. al,* 1982; Watkinson and White, 1985; Ackerley and Jasienski, 1990; Bazzaz and Ackerley, 1992; Pfister, 1992). As a result of this correlation between size and fecundity in *F. novae-zelandiae*, the same few individuals dominated the reproductive output of the population over several years; the top 10% of individuals in terms of fecundity over the study period (16 plants) accounted for 56% (1135 / 2020) of inflorescences produced. Such a fecundity imbalance is likely to have a profound and long-lasting influence on the genetic structure of the local population (Watkinson and White, 1985).

In many animals (*e.g.* studies cited in Partridge and Harvey 1985; Reznick, 1985) and some plants (*e.g.* Law, 1979; Martinez-Ramos *et. al,* 1988; Primack and Hall, 1990; Geber, 1990), current reproductive effort has been shown to affect subsequent reproductive effort and residual reproductive value. In contrast, this study detected no trade-off between current and future reproduction; flowering intensity in *F. novae-zelandiae* showed a positive correlation between years, over the four years of the study, agreeing with findings for *Chionochloa* species (Mark, 1965; D. Kelly, *pers. comm*), which are also long-lived tussock-forming grasses.

What factors might account for the absence, in this study, of the expected negative relationship between growth and reproduction? In the remainder of the discussion I will consider two types of explanations: (1) environmental effects and (2) the inapplicability of theoretical assumptions. Variation in both plant size and reproductive allocation can arise from fine-scale spatial variability in environmental factors within the range of a population (Bazzaz and Ackerley, 1992). Microenvironmental differences between adjacent

areas can have a profound impact on both the liklihood and intensity of reproduction (*e.g.* Kelly, 1993) and on overall plant growth, thus potentially producing a positive correlation between reproduction and growth (Samson and Werk, 1986; Bazzaz and Ackerley, 1992). If the area of grassland sampled in this study encompassed sufficient site variability then the positive relationship between reproduction and growth obtained could be due to this factor. Unfortunately no environmental measurements were made at the time of the study, however analyses of variances not presented here found significant differences between plots in initial plant diameter, diameter increment, and total culm production, suggesting spatial variation in site favourability. To test whether these spatial differences could account entirely for the results of this study, I repeated key analyses for the two plots (7 and 9) containing the most reproductive individuals. In all cases within-plot analyses confirmed the results from analyses involving all individuals. Individuals that flowered more frequently also tended to produce more inflorescences per flowering episode (Table 3b). The partial correlation between change in diameter and total inflorescence production over the study period, controlling for initial diameter, was significantly positive for Plot 9 ($r = 0.473$, $n = 14$) and positive in direction but not significantly so for Plot 7 ($r = 0.138$, $n = 37$). A nested analysis of covariance showed that while a difference existed in diameter increment between reproductive frequency classes within plots, this was of the nature of a positive relationship between growth and reproduction (Table 3b). These analyses show that the positive relationship found between growth and reproductive in this study is not simply due to meso-scale spatial differences in site favourability.

In the introduction I suggested that a trade-off between growth and reproduction should be especially noticeable in perennial grasses where flowering is determinate at the shoot-level and results in the loss of a meristem. Clearly such a trade-off is not a feature of *F. novae-zelandiae*. Other studies testing for costs of reproduction, either in terms of vegetative growth and survival, or future reproduction, have produced conflicting results, and there are a growing number of examples where theoretically expected costs of reproduction have not been detected (Table 1). The assumptions that underlie the measurement of trade-offs between vegetative growth and reproduction are (a) that the resource supply is fixed, and (b) allocation to structures reflects competing allocation to functions (Williams, 1966; Harper and Ogden, 1970; Reekie

and Bazzaz, 1987; Primack and Hall, 1990; Bazzaz and Ackerley, 1992). It is likely that neither of these assumptions are valid for many (or possibly any) plants (Bazzaz and Ackerley, 1992). Long-lived perennial plants, in particular, may not suffer any demographic costs (i.e. to growth, survival) of reproduction (Horvitz and Schemske, 1988). Photosynthetic reproductive structures can contribute as much as 64% of carbohydrate needs for production of flowers and fruit, and reproduction can be associated with changes in leaf physiology that affect photosynthesis rates (Bazzaz and Ackerley, 1992; Reekie and Bazzaz, 1987). Also structures cannot be easily assigned to either reproduction or growth; stems may be involved in both functions so do not represent a diversion of resources away from one function towards another (Bazzaz and Ackerley, 1992). Long-lived clonal plants such as tussock- or sward-forming grasses may be even less likely to meet these assumptions. In contrast with unitary organisms which reach a fixed size at reproductive maturity, growth in clonal plants is indeterminate and unbounded, and fecundity can increase exponentially with size (Watkinson and White, 1985). In unitary organisms, the resources available for producing offspring are obtained through a single mouth, whereas proliferation in clonal organisms continually generates new mouths (Cockburn, 1991). Within one growing season the resources available for allocation to growth or reproduction are thus themselves increasing as the majority of new structures, both vegetative and reproductive, can contribute to resource acquisition. Furthermore, large clonal plants, due to their many physiologically active modules may be particularly able to absorb reproductive costs by increasing resource uptake or by storage. Tuomi *et al* (1983) suggest that such physiological resistance to somatic costs can lead to reproduction without any detriment to growth or survival. It may be, then, that the Demographic Theory of Optimal Reproduction, which predicts trade-offs between growth and reproduction, and current and future reproduction (Williams, 1966), is simply inappropriate for long-lived clonal plants like *Festuca novae-zelandiae*.

Acknowledgments

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