

Seed yield and biomass allocation in *Sorghum bicolor* and F₁ and backcross generations of *S. bicolor* × *S. halepense* hybrids

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The Land Institute is developing perennial grains to be grown in prairie-like mixtures. One approach involves the development of a perennial grain sorghum by crossing tetraploid *Sorghum bicolor* with wild *S. halepense* to combine high seed yield with overwintering ability via rhizome production. We grew tetraploid *S. bicolor*, F₁ hybrid (BC₀), and two backcross generations (BC₁ and BC₂) in a randomized block design to examine total biomass, seed yield, and allocation to plant parts within and across generations. Root, rhizome, stem and leaf, and total biomass decreased from the BC₀ to BC₂ to *S. bicolor* generations, whereas panicle mass, seed mass, and reproductive allocation were lowest in the BC₀ generation ($p < 0.05$, ANOVA). Mean seed mass ($\text{g} \cdot \text{plant}^{-1}$) was 39.1 in the BC₀, 107.3 in the BC₁, 84.1 in the BC₂, and 92.7 for the *S. bicolor* parent, which translated into yields of 171.9, 471.6, 396.7, and 407.5 $\text{g} \cdot \text{m}^{-2}$, respectively. Reproductive allocation varied from 14.7% in BC₀ to 28.9% in BC₂ compared with 33.5% in *S. bicolor*. Mean allocation to rhizomes was 2.71% in BC₀ but negligible in BC₁ and BC₂. There was no relationship between rhizome mass and seed mass within any generation, but there was a positive correlation between total plant mass and rhizome mass in BC₀. We divided the BC₀ population into four groups with respect to rhizome production and found no significant differences among the groups in plant size or seed yield. Within each generation, reproductive allocation was inversely related to culm mass. The lack of an apparent trade-off between allocation to rhizome versus allocation to seed within any generation supports the possibility of combining within a population high seed yield and production of perennating belowground organs.

Key words: backcross, hybrid, perennial grains, reproductive allocation, rhizome, seed mass, *Sorghum bicolor*, *Sorghum halepense*.

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Le Land Institute développe des graminées pérennes pour la culture en mélange dans des sites de type prairie. Une des approches consiste à développer un sorgho à grains, pérenne, en croisant le *Sorghum bicolor* tétraploïde avec le *S. halepense* sauvage, afin de combiner le fort rendement en grains avec la capacité d'hivernage par la production de stolons. Les auteurs ont cultivé le *S. bicolor*, le F₁ hybride et les rétrocroisements avec deux descendances (BC₁ et BC₂) dans un dispositif expérimental au hasard, et ils ont examiné la biomasse totale, le rendement en grains et l'allocation des réserves aux différentes parties de la plante, à l'intérieur et entre les générations. Les biomasses de la racine, du rhizome, de la tige, de la feuille ainsi que la biomasse totale diminuent, des descendants de BC₀, à BC₂ à *S. bicolor*, alors que la masse du panicule, la masse des graines et l'allocation à l'appareil reproducteur sont plus faibles dans la descendance BC₀ ($p < 0,05$, ANOVA). La masse moyenne des semences ($\text{g} \cdot \text{plant}^{-1}$) est de 39,1 chez le BC₀, 107,3 chez le BC₁, 84,1 chez le BC₂, et 92,7 chez le parent *S. bicolor*, ce qui se traduit par des rendements respectifs de 171,9, 471,6, 396,7 et 407,5 $\text{g} \cdot \text{m}^{-2}$. L'allocation pour la reproduction varie de 14,7% chez le BC₀ à 28,9% chez le BC₂, comparativement à 33,5% chez le *S. bicolor*. L'allocation moyenne au rhizome est de 2,71% chez le BC₀ mais négligeable chez les BC₁ et BC₂. Il n'y a pas de relation entre la masse du rhizome et la masse des graines pour une génération donnée, mais il y a une corrélation positive entre la masse totale de la plante et la masse du rhizome chez le BC₀. Les auteurs divisent la population BC₀ en quatre groupes quant à leur production de rhizomes, sans pour autant trouver de différences significatives entre les groupes quant à la dimension du plant ou au rendement en grains. À l'intérieur de chaque génération, l'allocation à la reproduction montre une relation inverse avec la masse du chaume. L'absence apparente de compensation entre l'allocation au rhizome vs. l'allocation aux semences pour une génération donnée, confirme qu'il serait possible de combiner, dans une population, une forte production de graines avec la production d'organes souterrains pérennes.

Mots clés : rétrocroisement, hybride, graminées pérennes, allocation à la reproduction, rhizome, masse des graines, *Sorghum bicolor*, *Sorghum halepense*.

[Traduit par la rédaction]

Introduction

The development of herbaceous perennials as grains may alleviate some of the environmental problems that can arise from agricultural practices comprising annual crops grown on erodible soils (Wagoner 1990; Soule and Piper 1992). Mixtures of perennial grains could reduce energy expenditures on tillage, reduce soil erosion, provide much of their own nitrogen fertility, encourage and harbor biological control agents, and minimize weed growth. One approach involves domesticating wild perennials (e.g., *Tripsacum dactyloides*, *Agropyron intermedium*, *Desmanthus illinoensis*) to produce seeds

for human or livestock consumption. Another strategy involves the development of perennial grains via crossing annual crops with perennial relatives. In this paper, we focus on work to develop a perennial grain sorghum by crossing tetraploid *Sorghum bicolor* with wild *S. halepense* to combine high seed yield with overwintering ability via rhizome production. The theoretical arena for this work involves considerations of seed yield, resource allocation, and effects of enhanced reproduction on subsequent growth and survivorship.

One of the challenges raised against the feasibility of perennial grains is an assumed trade-off between seed production and subsequent plant growth and survival. Such a trade-off between resources devoted to reproduction versus vegetative

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growth would lead to predictions that plants are more likely to die after reproducing (e.g., Law 1979) and a large reproductive output in 1 year should be negatively correlated with growth that year or in the following year (e.g., Sohn and Policansky 1977). Whether reproduction results in a demographic cost has been tested in plant populations by examining correlations between reproduction in 1 year and growth, survival, and reproduction in the following year (e.g., Piper 1992).

Bazzaz and Ackerly (1992) defined reproductive allocation (RA) as the proportion of total resources devoted to reproduction. Overall, RA can increase, decrease, or remain constant in relation to size variation within a species, depending on the allometric relationship between reproduction and total biomass (e.g., Samson and Werk 1986; Bazzaz et al. 1987; Weiner 1988). In many cases, RA is a linear function of total plant mass.

The purpose of this study was to examine the relationship between plant size and reproduction, and possible trade-offs between seed production and perennation in *S. bicolor* parental lines, and BC₀, BC₁, and BC₂ hybrid and backcross generations of *S. bicolor* × *S. halepense* crosses. To determine whether costs of reproduction exist, it is important to measure whether individuals differing in RA, but similar with respect to age and environment, differ in growth or overwintering potential (Horvitz and Schemske 1988). Thus, the experimental population consisted of even-aged individuals. Specifically, we addressed three questions.

First, how does the pattern of biomass allocation change among generations varying for rhizome production across annual to more perennial generations? A major assumption of allocation theory is that resource allocation among functions is mutually exclusive, thus generating trade-offs among plant parts (Bazzaz and Ackerly 1992). This assumption may not be observed, however, because reproduction itself can lead to an increase in the total resource supply (e.g., through photosynthesis of reproductive parts) and plant structures can simultaneously contribute to more than one function such that measures of allocation to structures do not always reflect investment in function. In general, annuals generally have higher seed output and RA than perennial congeners (Warwick et al. 1984, 1986; Bazzaz et al. 1987; Hancock and Pritts 1987).

Second, what is the relationship between reproduction and total biomass? In herbaceous plants, reproduction is often a direct function of plant size (e.g., Wolfe 1983; Pitelka et al. 1985; Piper 1989). If sorghum hybrid generations vary in overall growth, this could have important consequences for seed yield.

Third, is there a trade-off between seed and rhizome production? To distinguish it from RA, reproductive effort (RE) may be defined as investment of a resource in reproduction that results from its diversion from vegetative activity (Bazzaz and Ackerly 1992). RE can be defined physiologically by examining changes in vegetative biomass resulting from reproduction (Tuomi et al. 1983; Reekie and Bazzaz 1987a, 1987b). To develop a successful perennial grain sorghum, we must optimize simultaneously seed yield and rhizome production. We are interested in the balance or interplay among these functions. Here, because we were concerned about traits linked to overwintering ability, we examined whether there were negative correlations between such traits as high seed yield and ability to produce rhizomes, the basis for perennation in *Sorghum halepense* and its hybrids.

Materials and methods

Description of crosses and experimental design

Sorghum halepense (L.) Pers., Johnsongrass, is a rhizomatous perennial that grows up to 3 m tall. The inflorescence is an open panicle 15–49 cm long bearing spikelets. It is a tetraploid with a chromosome number of $2n = 40$. A native of southern Eurasia to India, in North America *S. halepense* is a common weed of roadsides, ditches, and agricultural fields. It was introduced into the southeastern United States in the early 1800s (McWhorter 1971) and by 1900 was a serious weed in much of the U.S.A., reaching southern Canada (southwestern Ontario) by the late 1950s (Alex et al. 1979). Weedy traits include extensively creeping rhizomes, which allow overwintering in temperate climates, large numbers of small seeds, shattering of seed heads, seed dormancy, vigorous growth rate, and large variability (Warwick and Black 1983). Horowitz (1973) reported a mean seed production of $84 \text{ g} \cdot \text{plant}^{-1}$, with a maximum of $243 \text{ g} \cdot \text{plant}^{-1}$.

Sorghum bicolor (L.) Moench is a cultivated annual grown from Texas to South Dakota. Mean dryland grain yield for Saline County, Kansas, 1980–1992, is $2780 \text{ kg} \cdot \text{ha}^{-1}$ (range = $680\text{--}4850 \text{ kg} \cdot \text{ha}^{-1}$; Kansas State Board of Agriculture 1980–1992). Most crop varieties are diploid ($2n = 20$). To increase the likelihood of producing fertile hybrids we used tetraploid lines of *S. bicolor* derived from earlier work by Doggett (1988). Two sets of hybrids were made in 1983 and 1986 using different *S. halepense* and tetraploid *S. bicolor* parental lines. The first set of crosses used a taller grain sorghum parent ("2004") with an open panicle type. These crosses were used to derive a BC₀F₃ composed of BC₀F₂ plants that had survived one winter in Salina, Kansas (Jones 1991). This population on average would be composed of 50% *S. bicolor* genes and 50% *S. halepense* genes. The second set of crosses used a set of tetraploid *S. bicolor* parents ("6727") with better agronomic qualities including shorter plant height, increased stalk strength, more compact panicles, larger seed size, and higher seed yield in previous trials. Two backcross generations were derived from these hybrids by crossing F₁ hybrid plants to a cultivated recurrent plant then self-pollinating to derive a BC₁F₄ population with an average of 75% *S. bicolor* genes and a BC₂F₄ population with an average of 87.5% *S. bicolor* genes (Jones 1991). Backcrosses were made without selection for rhizome production or overwintering ability.

We grew the two *S. bicolor* parents, hybrid (BC₀), and two backcross generations (BC₁ and BC₂) in a randomized complete block design to examine total biomass, seed yield, and allocation to plant parts. In early May 1992, plants were established from seed in a $24 \times 11.8 \text{ m}$ field plot on a Tobin silt loam, 0–2% slope (fine-silty, mixed, Mesic Cumulic Haplustolls). Seedlings were thinned to a spacing of 25 cm apart within 6 m long rows, with rows 91 cm apart. There were 12 rows in four blocks; the outer rows were border rows. In August, we randomly selected and marked 5–10 plants per row for harvest. At the end of the growing season, but prior to seed shattering, we removed the marked plants from the field, dividing them into roots, rhizomes, culms (stem and leaves), panicles, and seeds. Root balls were soaked in 15-L plastic buckets of water, then carefully washed to minimize root loss. Plant parts were air-dried in a greenhouse to constant mass and weighed.

Data on absolute and relative biomass between generations were compared by one-way ANOVA. Relationships among total biomass and plant parts within generations were examined by multiple correlation. Within-population variability was estimated using coefficients of variation (CVs).

Results

Differences across generations

Root, rhizome, stem and leaf (culm), and total biomass decreased from the BC₀ to BC₂ generations, whereas panicle mass and seed mass increased from BC₀ to BC₁, then declined in BC₂ (Table 1). Mean seed mass ($\text{g} \cdot \text{plant}^{-1}$) was

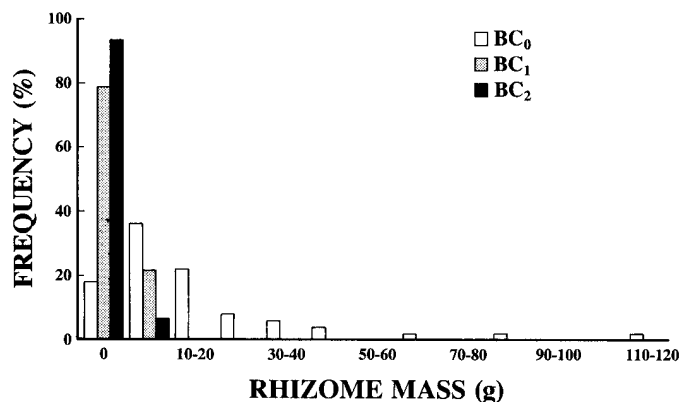


FIG. 1. Distributions of rhizome mass for BC₀, BC₁, and BC₂ hybrid generations.

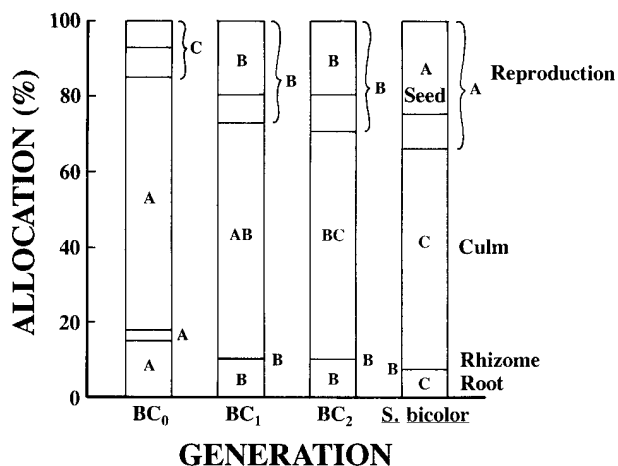


FIG. 2. Mean biomass allocation (%) for *Sorghum bicolor* and three generations of *S. bicolor* × *S. halepense* crosses. The reproductive portion (panicle) is further divided into seed and accessory reproductive structures (e.g., pedicels). Bar sections with the same letter do not differ at $p < 0.05$ (ANOVA; Duncan's multiple range test).

39.1 in the BC₀ ($n = 50$), 107.3 in the BC₁ ($n = 70$), 84.1 in the BC₂ ($n = 89$), and 92.7 g in the *S. bicolor* parental lines. These translated into yields of 171.9, 471.6, 396.7, and 407.5 g · m⁻², respectively. Seed size, measured as 100-seed mass, increased fivefold from the BC₀ to BC₁ generation, and increased from the BC₁ to the BC₂ generation (Table 2). There was no difference in seed size between BC₂ and *S. bicolor* plants, however.

There was a wide range of rhizome production within the BC₀ generation, but rhizome expression was largely lost from the other hybrid generations. Nevertheless, one BC₁ plant produced 8.5 g rhizomes and one BC₂ plant produced 5.0 g rhizomes (see Fig. 1).

Reproductive allocation varied from 14.7% in BC₀ to 30.3% in BC₂ (Fig. 2). RA was significantly higher in *S. bicolor* than in BC₁ and BC₂ generations, which in turn had significantly higher RA than the BC₀.

There were differences in some variables between the 2004 (parent of BC₀) and 6727 (parent of BC₁ and BC₂) *S. bicolor* parents. The 2004 line had higher root mass (38.9 vs. 24.2 g, $p < 0.05$), reproductive mass (156.6 vs. 94.1 g, $p < 0.01$), seed mass (122.8 vs. 62.6 g, $p < 0.001$), total mass (500.4

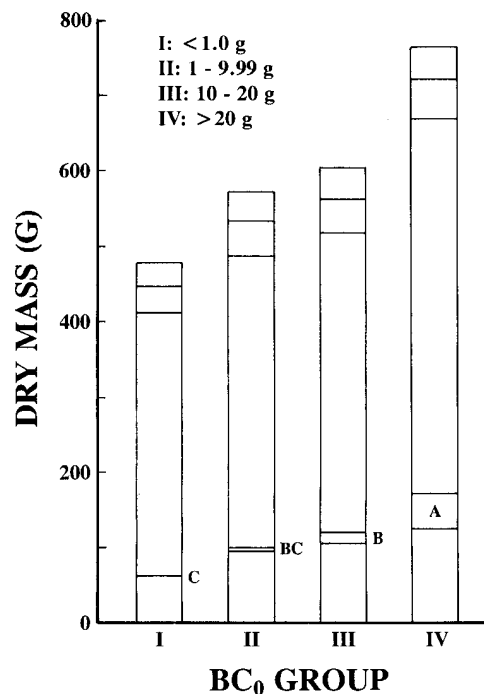


FIG. 3. Mean biomass distribution (g) for four groups of BC₀ plants differing in rhizome mass. Bar designations as in Fig. 2. Bar sections with the same letter do not differ at $p < 0.05$ (ANOVA; Duncan's multiple range test).

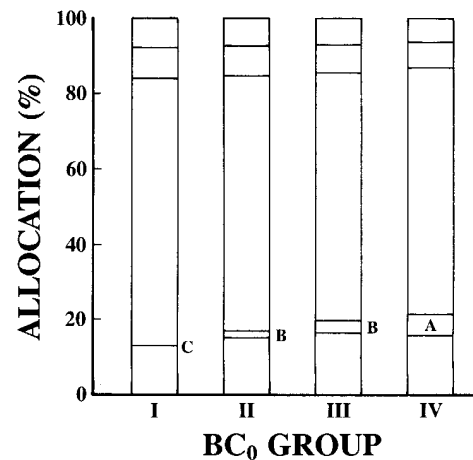


FIG. 4. Mean biomass allocation (%) for four groups of BC₀ plants differing in rhizome mass. Bar designations as in Fig. 2. Bar sections with the same letter do not differ at $p < 0.05$ (ANOVA; Duncan's multiple range test).

vs. 305.0 g, $p < 0.05$), and RA (36.2 vs. 30.8%, $p < 0.05$). The higher seed yield of 2004 was contrary to our previous experience with these lines.

Within each generation, rhizome mass was the most variable plant component (Table 3). CVs for all plant parts were high, however. A similar pattern occurred for variability in percentage allocation (Table 4), although overall CVs were lower than for absolute biomass. Among generations, the BC₀ population was generally more variable than the other populations for such important reproductive measures as total seed mass, mean seed mass, and RA.

TABLE 1. Biomass distribution (g) for plants of *Sorghum bicolor* and three generations of *S. bicolor* × *S. halepense* crosses

Plant part	BC ₀ (n = 50)	BC ₁ (n = 70)	BC ₂ (n = 89)	<i>S. bicolor</i> (n = 40)
Seeds	39.1 ± 32.8c	107.3 ± 77.5a	84.1 ± 66.0b	92.7 ± 60.9ab
Total reproduction	83.5 ± 57.1b	141.5 ± 89.2a	116.3 ± 84.9a	125.3 ± 74.0a
Culms	408.3 ± 264.6a	349.5 ± 227.3ab	265.2 ± 221.4bc	245.8 ± 194.0c
Rhizomes	15.9 ± 22.5a	0.4 ± 1.2b	0.1 ± 0.6b	0.0 ± 0.0b
Roots	98.3 ± 88.7a	54.3 ± 37.7b	43.0 ± 49.0bc	31.6 ± 23.2c
Total	606.0 ± 398.5a	549.2 ± 319.2a	424.6 ± 323.0b	402.7 ± 277.4b

NOTE: Values are means ± SD. For each variable, means followed by the same letter do not differ at $p < 0.05$ (ANOVA; Duncan's multiple range test).

TABLE 2. One-hundred seed mass (g) for *S. bicolor* and three *S. bicolor* × *S. halepense* hybrid generations

Generation	n	100-seed mass
BC ₀	18	0.51 ± 0.12c
BC ₁	18	2.51 ± 0.54b
BC ₂	14	3.58 ± 0.40a
<i>S. bicolor</i>	16	3.79 ± 0.78a

NOTE: Values are means ± SD. Means followed by the same letter do not differ at $p < 0.05$ (ANOVA; Duncan's multiple range test).

TABLE 3. Coefficients of variation (%) for biomass distribution in *Sorghum bicolor* and three generations of *S. bicolor* × *S. halepense* crosses

Plant part	BC ₀ (n = 50)	BC ₁ (n = 70)	BC ₂ (n = 89)	<i>S. bicolor</i> (n = 40)
Seeds	83.9	72.2	78.5	65.7
Total reproduction	68.4	63.0	73.0	59.1
Culms	64.8	65.0	83.5	78.9
Rhizomes	142	343	502	—
Roots	90.2	69.4	114.0	73.4
Total	65.8	58.1	76.1	68.9

TABLE 4. Coefficients of variation (%) for percentage biomass allocation in *Sorghum bicolor* and three generations of *S. bicolor* × *S. halepense* crosses

Plant part	BC ₀ (n = 50)	BC ₁ (n = 70)	BC ₂ (n = 89)	<i>S. bicolor</i> (n = 40)
Seeds	71.4	48.7	57.4	42.4
Total reproduction	45.6	39.1	43.9	35.5
Culms	11.3	18.1	20.7	20.3
Rhizomes	104	324	529	—
Roots	32.7	43.1	61.8	30.4
Harvest index*	69.4	49.5	56.0	42.2

*Harvest index = seed mass / aboveground mass.

Reproduction versus total biomass

Within each generation, seed and total reproductive mass increased with culm mass. Culm mass and seed mass were positively correlated in each generation (BC₀, $r = 0.61$; BC₁, $r = 0.56$; BC₂, $r = 0.51$; *S. bicolor*, $r = 0.77$; all $p < 0.0001$). Reproductive allocation (%), however, was inversely related to culm biomass in both BC₁ ($r = -0.30$, $p < 0.05$) and BC₂ ($r = -0.36$, $p < 0.0001$) generations. Consistently, there was an inverse relationship between percent allocation to culm and percent allocation to seed (BC₀, $r = -0.66$; BC₁, $r = -0.83$; BC₂, $r = -0.88$; *S. bicolor*, $r = -0.94$; all $p < 0.0001$). In all of the generations, seed yield was positively correlated with plant size (BC₀, $r = 0.70$; BC₁, $r = 0.73$; BC₂, $r = 0.65$; *S. bicolor*, $r = 0.86$; all $p < 0.0001$). Thus, depending on the generation, anywhere from 42 to 74% of the variation in seed yield was attributable to plant size. Similarly, root mass and seed mass were consistently positively correlated (BC₀, $r = 0.70$; BC₁, $r = 0.48$; BC₂, $r = 0.32$; *S. bicolor*, $r = 0.72$; all $p < 0.001$). Within each generation, the biggest plants produced the largest seed yields.

Seed versus rhizome production

Although rhizome production decreased from the BC₀ to BC₂ generations, there was no inverse relationship between rhizome mass and seed mass within any generation. Instead, the main trade-off seemed to be allocation to culm versus seed. Only in BC₂ was there an inverse relationship between percent allocation to seed and percent allocation to roots ($r = -0.26$, $p < 0.05$).

Patterns within the BC₀ generation

Because the BC₀ generation was the only population that retained a high rate of rhizome expression, we examined more closely the patterns of seed yield and rhizome expression

within the BC₀. We divided the BC₀ plants into four categories based on rhizome mass: group I (rhizome mass < 1.00 g) were essentially annual plants; group II (rhizomes 1.00–9.99 g) showed a tendency to produce rhizomes but were probably only weakly perennial; group III (10.00–20.00 g) displayed stronger rhizome expression and were more likely perennial; and group IV (rhizomes > 20.00 g) were probably strongly perennial. We compared differences among the groups by ANOVA.

The only significant difference among these groups was in absolute and percentage rhizome production (Figs. 3 and 4). Larger plants produced more rhizome mass and allocated a greater percentage of their biomass to rhizomes, but other plant parts did not differ among groups. This analysis showed that biomass devoted to seed did not decline significantly with increased biomass devoted to rhizome. There was no significant difference in seed yield between "annual type" and

“perennial type” BC₀ hybrids. Instead, rhizome production was associated with increased overall growth.

Discussion

Biomass allocation across generations

The results demonstrate some differences in biomass allocation between more “perennial type” (plants that produce more rhizomes) and “annual type” (plants that produce few or no rhizomes) sorghum and sorghum hybrids. From the BC₀ generation to the *S. bicolor* parents, RA more than doubled, percent culm declined somewhat, and percent belowground (roots plus rhizomes) biomass in the annual types (BC₂, BC₁, *S. bicolor*) was one-half that in the BC₀. Moreover, the annual types featured higher seed yield and larger seeds, the increase in seed yield seeming to arise primarily from lower allocation to culms. Retention of rhizomes by some BC₁ and BC₂ plants was a positive trait in these generations, although overall rhizome production was rare in these populations.

Our results were similar to those of Warwick et al. (1984, 1986) on annual versus overwintering *S. halepense* biotypes in Canada. In their studies, total plant mass was similar between biotypes. Annual type plants, however, produced larger seeds and allocated greater percentage biomass to reproduction (21 vs. 11%) and culms. In contrast, overwintering types devoted more biomass, absolutely and relatively (28.6 vs. 18.9%), to underground organs.

Overall, masses of inflorescences, culms, rhizomes, and total plant were smaller for the BC₀ of the present study than for field-grown perennial *S. halepense* reported by Warwick et al. (1986). Mean root mass, however, was nearly identical in the two studies. Percentage allocation to root and rhizome was lower in our BC₀ plants than in their perennial *S. halepense* (15.3 vs. 41.9%). In their study, annual populations had higher panicle biomass and RA (17.8 vs. 11.3%).

Seed size of our BC₀ was somewhat higher than that reported by Warwick et al. (1984) for overwintering types of *S. halepense* from southern Ontario (0.51 ± 0.12 vs. 0.38 ± 0.27 g/100 seeds). Seed size is directly related to both grain quality and, in many species, likelihood of seedling establishment (e.g., Schaal 1980).

Much information on population distribution is masked by looking at means only, especially for such highly variable populations as our BC₀. Warwick et al. (1984) found that nonoverwintering populations of *S. halepense* were more homogeneous than overwintering types. This was similar to our result for BC₀ relative to the other sorghum generations.

Our work to develop a perennial grain sorghum depends on the lack of a strict trade-off between high seed yield and overwintering ability. Reekie and Bazzaz (1987a, 1987b) reported an inflorescence biomass of *Agropyron repens* ranging from 0 to 10% of total biomass. Inclusion of reproductive support structures increased RA to 20–40%. In one of the six genotypes they examined RE was negative in several treatments, suggesting that there was an increased supply of photosynthate as a result of reproduction.

Proportion of reproductive biomass allocated to seeds varies widely. Lloyd (1988) reported seed and fruit allocation ranging from 34 to 83% (to >90% in females of dioecious species) of total reproductive biomass. In our study, seed allocation as a percentage of reproductive mass ranged from 46.8% in BC₀ to over 70% in the other three populations.

Reproduction versus total biomass

In some perennial species, RA increases with plant size (Piñero et al. 1982; Oyama and Dirzo 1988; Schat et al. 1989). In other species, however, RA is constant across plant sizes (Ackerly and Jasiensky 1990). In either case, most variation in reproductive output is due to variation in plant mass. Reproductive allocation is only one component of fecundity, however, and to link allocation and reproductive output it must be considered in relation to plant size.

In each of the sorghum generations, both reproduction and seed mass were positively correlated with plant size. Thus, depending on the generation, anywhere from 42 to 74% of the variation in seed yield was attributable to plant size, indicating that seed yield is a linear function of plant size for these plants. Reproductive allocation, however, was inversely related to stem biomass in both BC₁ and BC₂ generations, suggesting a potential for selection to improve RA without appreciable loss of biomass. Our results were similar to those of other studies showing a simple linear relationship between plant size and reproductive output (Samson and Werk 1986; Hartnett 1990; Thompson et al. 1991; Piper 1992).

Variation in RA is oftentimes less than variation in biomass, such that reproductive mass is strongly correlated with plant size. Here, this was consistently true, with CV for RA ranging from 35.6% (in *S. bicolor*) to 45.1% (in BC₀) but CV for total biomass ranging from 58.1% (in BC₁) to 76.1% (in BC₂).

Seed versus rhizome production

Production of rhizomes is the sole means by which Johnson-grass and sorghum hybrids can remain perennial in temperate latitudes. Therefore, a major concern in developing an overwintering grain sorghum is the feasibility of combining good agronomic quality (high seed yield, shatter resistance, large seeds, compact inflorescences, stalk strength) with the ability to persist year to year. Thus, it is promising that there was no apparent trade-off between allocation to rhizome versus allocation to seed within any of the hybrid generations. Independence of rhizome expression from undesirable traits would allow the combination of overwintering ability with crop-like characteristics. It is imperative in the breeding effort that a perennial sorghum hybrid not retain the aggressive weedy attributes of *S. halepense*.

The hope for the project lies with the hybrids that produced large amounts of rhizomes. It is encouraging that a few individuals of the BC₁ and BC₂ generations expressed rhizomes. Unfortunately, we do not know the minimum mass of rhizome that will enable a plant to overwinter. Moreover, this critical mass is likely to vary with environment, year, and location. Because of the need for destructive sampling of plants in this study, we were unable to measure overwintering ability in plants of known rhizome mass. Another study of this BC₀ generation, however, showed that 57% of plants overwintered and that likelihood of overwintering is directly related to rhizome production (P.A. Kulakow, unpublished).

It is worth noting that the extrapolated mean seed yield of even the BC₀ generation was 62% of the 1980–1992 average dryland grain sorghum yield for Saline County. The importance of perennial hybrid sorghum in addressing the issue of high seed yield in herbaceous perennials is clear in demonstrating the possibility for such plants, grown with few inputs, to yield similarly to annual grains. It remains to be discovered

whether high yield in overwintering lines can be sustained over several growing seasons.

The various theories proposed to explain resource allocation patterns assume that vegetative and reproductive processes compete for a common pool of resources and that an increase in one activity necessarily results in a proportional decrease in the other activity. Several studies, however, have failed to demonstrate such a cost of reproduction. For example, Pitelka et al. (1985) found that rhizome growth was not reduced by flowering in *Clintonia borealis*, although flowering in that species is plant size dependent. Similarly, in a study of *Agropyron repens* by Reekie and Bazzaz (1987b), reproduction failed to reduce growth and even enhanced growth in some cases where resources were most favorable. Jackson (1990) detected no differences in growth between high and low seed yielding forms of *Tripsacum dactyloides*. These results suggest that, in some perennial species at least, increased reproductive output may not always be associated with a significant decline in future growth or reproductive success (see also Piper 1992).

Minerals may be as important a measure of reproductive allocation as biomass as it is likely that allocation of a mineral to one organ will come at the expense of its allocation to another. Patterns of mineral allocation may not reflect patterns of carbohydrate allocation (e.g., Pate et al. 1991). Benech Arnold et al. (1992) found that allocation of most macronutrients changed with biomass allocation to seeds of both *S. bicolor* and *S. halepense*, but not to *S. halepense* rhizomes.

There are several reasons why one should not automatically assume a trade-off between growth and reproduction. For example, extra resources may be taken up or produced prior to or during reproduction for the sole purpose of reproduction, green flowers and fruits can contribute photosynthate to their own development, or reproduction and vegetative growth may be limited by different resources altogether (Tuomi et al. 1983; Willson 1983; Watson 1984). Overall, growth seemed the best predictor of sizable rhizome production in our sorghum hybrids. One or more of these mechanisms may explain why we found no negative correlations between reproduction and rhizome production within the BC₀ generation.

Prognosis

This work stands apart from other work on resource allocation in two important ways. First, the populations we studied were highly variable genetically. Although it was useful to compare means of the BC₀, BC₁, and BC₂ populations, variation within generations was probably just as important, especially as the BC₁ and BC₂ generations did not produce appreciable amounts of rhizomes. Hence, much of the interesting results on patterns of rhizome production were imbedded within the BC₀ generation. An apparent paradox that has characterized this work is that there is no obvious trade-off between perennation and seed yield within generations based on correlations, but perennation has been lost except in a portion of the BC₀ plants. The second distinguishing feature of this work is the practical objective of combining the perennial habit and high seed yield. We are addressing both how much seed yield is enough and how much rhizome production will allow overwintering; we expect that there are ideal ratios among plant parts that must be achieved. If hybrids have higher total biomass than grain sorghum, as occurred here, then lower allocation percentages could be tolerated.

TABLE 5. A comparison of a perennial sorghum ideotype with the parent and hybrid to meet the goals of high seed yield and overwintering ability

Parent	
<i>S. halepense</i> to rhizomes (%)	30–40*
<i>S. bicolor</i> to seed (%)	30–40*
Hybrid	
Rhizome mass needed for overwintering (g)	80†
Desirable seed yield (g)	100
Mass attained by hybrids (g)	500–600‡
Ideotype	
Plant mass (g)	500
Seed mass (g)	100
Rhizome mass (g)	80

*Benech Arnold et al. (1992).

†P.A. Kulakow (unpublished).

‡Present study.

Benech Arnold et al. (1992) found that total biomass of *S. halepense* is higher than for *S. bicolor*. If one subtracts rhizome mass the difference between the two is much less. Their results, coupled with the results of our study, suggest that perennation may be achieved partly through increased biomass. Our empirical results, combined with published results of others, led us to explore whether a perennial grain sorghum is theoretically feasible (Table 5). Thirty to 40% of total biomass is devoted to reproduction in *S. bicolor* or to rhizomes in *S. halepense* (Benech Arnold et al. 1992). Perhaps total energy devoted to these two functions would be shared in hybrids. We considered the total biomass achievable in hybrids, sufficient seed production ($100 \text{ g} \cdot \text{plant}^{-1} = 440 \text{ g} \cdot \text{m}^{-2}$ at a density of $4.4 \text{ plants} \cdot \text{m}^{-2}$), and rhizome mass needed to assure overwintering for a perennial sorghum ideotype (Table 5). The model suggests that a high-yielding perennial is a realistic selection goal.

Warwick et al. (1984) found that both overwintering and annual type *S. halepense* produce rhizomes but in much different patterns. There may be a simple switch between these two physiological patterns or a continuous range of expression that is subject to strong selection that resulted in the two contrasting types. Our situation is similar in that many of our hybrid individuals produced rhizomes but in insufficient quantity to be perennial. Such plants have already lost this physiological switch that allocates a significant portion of biomass to rhizomes. The plants to focus on are the exceptional BC₀ individuals that have not completely lost this modulation of rhizome production within the sufficient range, the "overwintering type" hybrids.

The idea, that as one breeds to increase seed yield in a perennial species energy devoted to overwintering structures will decrease, appears to be an oversimplification and it may be possible to achieve relatively high seed yields in some perennials. Once stable high seed yield has been selected, a logical next step in perennial grain research is to examine ways of maintaining sufficient yields via intercropping and field management.

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- Ackerly, D.D., and Jasiensky, M. 1990. Size-dependent variation of gender in high density stands of the monoecious annual, *Ambrosia artemisiifolia* (Asteraceae). *Oecologia*, **82**: 474–477.
- Alex, J.F., McLaren, R.D., and Hamill, A.S. 1979. Occurrence and winter survival of Johnson grass (*Sorghum halepense*) in Ontario. *Can. J. Plant Sci.* **59**: 1173–1176.
- Bazzaz, F.A., and Ackerly, D.D. 1992. Reproductive allocation and reproductive effort in plants. In *Seeds: the ecology of regeneration*. Edited by M. Fenner. C.A.B. International, Wallingford, Oxford. pp. 1–26.
- Bazzaz, F.A., Chiarello, N.R., Coley, P.D., and Pitelka, L.F. 1987. Allocation of resources to reproduction and defense. *BioScience*, **37**: 58–67.
- Benech Arnold, R.L., Fenner, M., and Edwards, P.J. 1992. Mineral allocation to reproduction in *Sorghum bicolor* and *Sorghum halepense* in relation to parental nutrient supply. *Oecologia*, **92**: 138–144.
- Doggett, H. 1988. *Sorghum*. 2nd ed. Longman Scientific and Technical, Essex, England.
- Hancock, J.F., and Pritts, M.P. 1987. Does reproductive effort vary across different life forms and seral environments? A review of the literature. *Bull. Torrey Bot. Club*, **114**: 53–59.
- Hartnett, D.C. 1990. Size-dependent allocation to sexual and vegetative reproduction in four clonal composites. *Oecologia*, **84**: 254–259.
- Horvitz, C.C., and Schemske, D.W. 1988. Demographic cost of reproduction in a neotropical herb: an experimental field study. *Ecology*, **69**: 1741–1749.
- Horowitz, M. 1973. Spatial growth of *Sorghum halepense* (L.) Pers. *Weed Res.* **13**: 200–208.
- Jackson, L.L. 1990. Life history consequences of greater seed production in a perennial grass, *Tripsacum dactyloides*: a comparison of high and low seed-yielding genotypes. Ph.D. thesis, Cornell University, Ithaca, N.Y.
- Jones, T.B. 1991. Evaluation of five germplasm groups for overwintering ability and agronomic characteristics in sorghum crosses: *Sorghum bicolor* (L.) Moench × *Sorghum halepense* (L.) Pers. *Land Inst. Res. Rep.* **8**: 12–18.
- Kansas State Board of Agriculture. 1980–1992. Kansas farm facts. United States Department of Agriculture, Topeka, Kansas.
- Law, R. 1979. The cost of reproduction in annual meadow grass. *Am. Nat.* **113**: 3–16.
- Lloyd, D.G. 1988. Benefits and costs of biparental and uniparental reproduction in plants. In *The evolution of sex*. Edited by R.E. Michod and B.R. Levin. Sinauer Associates, Sunderland, Mass. pp. 233–252.
- McWhorter, C.G. 1971. Introduction and spread of johnsongrass in the United States. *Weed Sci.* **19**: 496–500.
- Oyama, K., and Dirzo, R. 1988. Biomass allocation in the dioecious tropical palm *Chamaedorea tepejilote* and its life history consequences. *Plant Species Biol.* **3**: 27–33.
- Pate, J.S., True, K.C., and Kuo, J. 1991. Partitioning of dry matter and mineral nutrients during a reproductive cycle of the mistletoe *Amyema linophyllum* (Fenzl) Tieghem parasitizing *Casuarina ogesa* Miq. *J. Exp. Bot.* **42**: 427–440.
- Piñero, D., Sarukhán, J., and Alberdi, P. 1982. The costs of reproduction in a tropical palm, *Astrocaryum mexicanum*. *J. Ecol.* **70**: 473–481.
- Piper, J.K. 1989. Light, flowering, and fruiting within patches of *Smilacina racemosa* and *Smilacina stellata* (Liliaceae). *Bull. Torrey Bot. Club*, **166**: 247–257.
- Piper, J.K. 1992. Size structure and seed yield over 4 years in an experimental *Cassia marilandica* (Leguminosae) population. *Can. J. Bot.* **70**: 1324–1330.
- Pitelka, L.F., Hansen, S.B., and Ashmun, J.W. 1985. Population biology of *Clintonia borealis*. I. Ramet and patch dynamics. *J. Ecol.* **73**: 169–183.
- Reekie, E.G., and Bazzaz, F.A. 1987a. Reproductive effort in plants. 1. Carbon allocation to reproduction. *Am. Nat.* **129**: 876–896.
- Reekie, E.G., and Bazzaz, F.A. 1987b. Reproductive effort in plants. 3. Effect of reproduction on vegetative activity. *Am. Nat.* **129**: 907–919.
- Samson, D.A., and Werk, K.S. 1986. Size-dependent effects in the analysis of reproductive effort in plants. *Am. Nat.* **127**: 667–680.
- Schaal, B.A. 1980. Reproductive capacity and seed size in *Lupinus texensis*. *Am. J. Bot.* **67**: 703–709.
- Schat, H., Ouborg, J., and DeWit, R. 1989. Life history and plant architecture: size-dependent reproductive allocation in annual and biennial *Centaureium* species. *Acta Bot. Neerl.* **38**: 183–201.
- Sohn, J.J., and Policansky, D. 1977. The costs of reproduction in the mayapple *Podophyllum peltatum* (Berberidaceae). *Ecology*, **58**: 1366–1374.
- Soule, J.D., and Piper, J.K. 1992. *Farming in nature's image*. Island Press, Washington, D.C.
- Thompson, B.K., Weiner, J., and Warwick, S.I. 1991. Size-dependent reproductive output in agricultural weeds. *Can. J. Bot.* **69**: 442–446.
- Tuomi, J., Hakala, T., and Haukioja, E. 1983. Alternative concepts of reproductive effort, costs of reproduction and selection in life history evolution. *Am. Zool.* **23**: 25–34.
- Wagoner, P. 1990. Perennial grain development: past efforts and potential for the future. *Crit. Rev. Plant Sci.* **9**: 381–409.
- Warwick, S.I., and Black, L.D. 1983. The biology of Canadian weeds. 61. *Sorghum halepense* (L.) Pers. *Can. J. Plant Sci.* **63**: 997–1014.
- Warwick, S.I., Thompson, B.K., and Black, L.D. 1984. Population variation in *Sorghum halepense*, Johnson grass, at the northern limits of its range. *Can. J. Bot.* **62**: 1781–1790.
- Warwick, S.I., Phillips, D., and Andrews, C. 1986. Rhizome depth: the critical factor in winter survival of *Sorghum halepense* (L.) Pers. (Johnson grass). *Weed Res.* **26**: 381–387.
- Watson, M.A. 1984. Developmental constraints on population growth and patterns of resource allocation in a clonal plant. *Am. Nat.* **123**: 411–426.
- Weiner, J. 1988. The influence of competition on plant reproduction. In *Plant reproductive ecology*. Edited by J. Lovett Doust and L. Lovett Doust. Oxford University Press, New York. pp. 228–245.
- Willson, M.F. 1983. *Plant reproductive ecology*. John Wiley & Sons, New York.
- Wolfe, L.M. 1983. The effect of plant size on reproductive characteristics in *Erythronium americanum* (Liliaceae). *Can. J. Bot.* **61**: 3489–3493.