Proc. Natl. Acad. Sci. USA
Vol. 92, pp. 6127–6131, June 1995
Agricultural Sciences

The weediness of wild plants: Molecular analysis of genes influencing dispersal and persistence of johnsongrass, *Sorghum halepense* (L.) Pers

(Poaceae/rhizomes/genome mapping/biotechnology risk assessment/plant growth regulation)

ANDREW H. PATERSON*†, KEITH F. SCHERTZ*‡, YANN-RONG LIN*, SIN-CHIEH LIU*, AND YUEH-LONG CHANG*

*Department of Soil and Crop Sciences, Texas A&M University, and ‡U.S. Department of Agriculture, College Station, TX 77843-2474

Communicated by Perry L. Adkisson, Texas A&M University, College Station, TX, March 22, 1995

ABSTRACT **Many major weeds rely upon vegetative dispersal by rhizomes and seed dispersal by "shattering" of the mature inflorescence. We report molecular analysis of these traits in a cross between cultivated and wild species of *Sorghum* that are the probable progenitors of the major weed "johnsongrass." By restriction fragment length polymorphism mapping, variation in the number of rhizomes producing above-ground shoots was associated with three quantitative trait loci (QTLs). Variation in regrowth (ratooning) after overwintering was associated with QTLs accounting for additional rhizomatous growth and with QTLs influencing tillering. Vegetative buds that become rhizomes are similar to those that become tillers—one QTL appears to influence the number of such vegetative buds available, and additional independent genes determine whether individual buds differentiate into tillers or rhizomes. DNA markers described herein facilitate cloning of genes associated with weediness, comparative study of rhizomatousness in other Poaceae, and assessment of gene flow between cultivated and weedy sorghums—a risk that constrains improvement of sorghum through biotechnology. Cloning of "weediness" genes may create opportunities for plant growth regulation, in suppressing propagation of weeds and enhancing productivity of major forage, turf, and "ratoon" crops.**

Weeds cause a host of problems in agriculture, competing with crops for light, water, and nutrients, providing a reservoir for insects and diseases, and contaminating seedlots.

Vegetative dispersal by rhizomes (underground stems) and seed dispersal by disarticulation of the mature inflorescence ("shattering") cause perennial monocots such as "johnsongrass" [*Sorghum halepense* (L.) Pers, 2N = 2X = 40] to rank among the world's most noxious weeds (1). The importance of rhizomes to weed persistence is reflected in the facts that under poor conditions, nutrients are allocated to rhizomes even at the expense of seeds (2) and that rhizomes are largely unaffected by the senescence processes that autolyze other vegetative organs (3).

Johnsongrass may have been introduced into the United States intentionally as a prospective forage and/or unintentionally as a contaminant of seedlots. The rapid spread of johnsongrass is attributed to commercial sale, seedlot contamination, Civil War cavalry movements, post-Civil War planting, flooding, and leakage from railroad boxcars. The term johnsongrass supplanted some 40 epithets and is first documented in an 1874 letter referring to Colonel William Johnson, an Alabaman who sowed it on his farm (4). The first federal appropriation for weed research, in 1900, targetted johnsongrass (5). Reductions in yield of up to 45% in monocots such as sugarcane (6) and dicots such as soybean (7) are caused by johnsongrass. Modern herbicides control johnsongrass at a cost of $12–20 per acre (1 acre = 4047 m^2); however, none can kill johnsongrass without damaging closely related sorghum [*Sorghum bicolor* (L.) Moench., 2N = 2X = 20], grown on 8–14 million acres in the southern plains of the United States (M. Chandler, personal communication).

Rhizomes are the primary morphological feature that distinguish johnsongrass from sorghum (8). Both rhizomatousness and geographic distribution suggest that johnsongrass is an interspecific hybrid descendant of *S. bicolor* and *Sorghum propinquum* (Kunth.) Hitchc. (2N = 2X = 20), a rhizomatous native of southeast Asia, Indonesia, and the Philippines (9). The center of diversity for *S. bicolor* is in Africa, while that of *S. halepense* is in Asia, supporting the proposal that *S. propinquum* contributed to *S. halepense* (8). A related weed, *Sorghum almum* ("Columbus grass," 2N = 4X = 40), is also widespread (9).

Weeds that are closely related to major crops pose special risks. Sorghum can be transformed with exogenous genes (10), such as those for herbicide resistance. Across 8–14 million acres of sorghum, sympatric with naturalized johnsongrass, even a tiny level of interspecific gene flow might permit such herbicide resistance (for example) to enter the gene pool of johnsongrass. This risk is minimized by the exemplary level of responsibility shown by researchers and careful monitoring by federal agencies. Nonetheless, the risk of gene flow from sorghum to johnsongrass (11) precludes realization of many potential economies through sorghum biotechnology.

Crops that are closely related to major weeds facilitate study of the molecular basis of "weediness." Because of its dual importance as a crop and a weed, we have investigated the genus *Sorghum*. Genes studied herein appear responsible for much of the weediness of johnsongrass, and our results lay the groundwork for cloning these genes. This may afford opportunities for growth regulation of major weeds and of pasture and turf grasses essential to agro-ecosystems.

MATERIALS AND METHODS

Genetic Stocks. Backcross 1 (BC_1) and F_2 populations from an artificial cross between *S. bicolor* BTx623 and *S. propinquum* (unnamed accession) were made by conventional means. On April 30, 1992, 370 F_2 and 378 BC_1 seedlings were transplanted to the field near College Station, TX. On April 18–20, 1994, 50–150 seedlings per family of 48 F_3-selfed families derived from F_2 individuals (see below) were transplanted to an adjacent field.

Phenotype Analysis. For BC_1 and F_2 plants, tiller number was counted on June 10, 1994, immediately prior to flowering.

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "*advertisement*" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

Abbreviations: QTL, quantitative trait locus; LAR, $\log_{10}$ of rhizome number estimated from above-ground rhizome-derived shoots; LSR, $\log_{10}$ of subterranean rhizome score; LG, linkage group; BC, backcross; lod, logarithm of odds ratio.

†To whom reprint requests should be addressed.

Spikelet disarticulation was assessed at seed maturity. Above-ground rhizome-derived shoots were counted on November 28, 1994—in cases of uncertainty whether a shoot was derived from a rhizome, we dug down until reaching (or not finding) the rhizome. The minimum number of different rhizomes producing the observed shoots was estimated from spatial arrangement of the shoots (i.e., a linear series suggested a single rhizome). The maximum distance of rhizome shoots from the center of the crown was measured (in cm). After frost on November 27–28, 1992, plants were mowed at 10 cm above ground level. In March, April, and May 1993, regrowth was rated on a scale of 0 (none) to 10 (extensive), independently by K.F.S. and A.H.P., and ratings were averaged. Plants were then killed with glyphosate, each stump was excavated, and the soil was gently removed. Subterranean rhizome growth was rated on a scale of 0 (none) to 6 (extensive rhizomes) independently by K.F.S. and A.H.P., and ratings were averaged. For each of the 3488 F_3 plants, the number of rhizomes producing above-ground shoots was estimated and then averaged across F_3 families.

Genetic Analysis. All F_2 individuals were assayed at 78 restriction fragment length polymorphism loci spaced at 10- to 15-centimorgan intervals throughout the genome, by using published techniques (12). Quantitative trait locus (QTL) mapping used MAPMAKER-QTL and a significance threshold of logarithm of odds (lod) 2.5 (13). Analysis of variance, F_3/F_2 regressions, and phenotypic correlations used SAS (14). Predicted phenotypes based on QTL mapping were determined as described (15). Most measures of rhizomatousness are "counts" and follow a Poisson distribution—$\log(n+1)$ transformation was applied to reduce dependence between mean and variance (16). The only exception was "rhizome distance," which was normally distributed. Although tillering was also "count" data, it showed a near-normal distribution with no correlation between mean and variance and, thus, was analyzed directly.

RESULTS

Genome Composition of Johnsongrass. Eleven *S. bicolor* accessions representing most cultivated and wild races of this species, the only two accessions of *S. propinquum* available, and six *S. halepense* and four *S. almum* accessions of diverse geographic origin were characterized with 39 mapped nuclear DNA probes (12). On average, individual accessions showed only 1.19 restriction fragments, thus most novel fragments represented allelic variants (Table 1).

About 94% (117 of 125) of restriction fragment length polymorphism alleles found in *S. halepense* and 93% (88 of 95) of alleles found in *S. almum* can be accounted for by *S. bicolor* and *S. propinquum* (collectively). Only 9 alleles were found in *S. halepense* and/or *S. almum* but not in either *S. bicolor* or *S. propinquum*. Among 125 alleles found in *S. halepense*, 49 (39.2%) were shared with *S. bicolor* but were absent from *S. propinquum*, and 30 (24%) were shared with *S. propinquum* but were absent from *S. bicolor*. *S. bicolor* and *S. propinquum* alleles accounted for equal proportions of the allelic repertoire of *S. almum*.

QTLs That Influence Rhizomatousness. Three measures of rhizomatousness were evaluated for F_2 plants, including the $\log(n+1)$ of the number of rhizomes producing above-ground shoots (LAR), the distance between the center of the crown and the most distal rhizome-derived shoot, and the $\log(n+1)$ of subterranean rhizomatousness (rhizome score; LSR) measured after overwintering. All *S. propinquum* plants were highly rhizomatous, and *S. bicolor* plants were nonrhizomatous.

Three distinct regions of linkage group (LG) C accounted for 21.8% of phenotypic variance in LAR (including all significant QTLs), and 14% of variance in LSR (including two of eight significant QTLs; Fig. 1 and Table 2). The interval *pSB300a–pSB088* accounted for the largest portion of variation in LAR and significant variation in LSR and was the only interval associated with rhizome-derived shoots, although this association was slightly below the significance threshold. The interval *pSB195–SHO68* accounted for significant variation in LAR, and the largest portion of variation in LSR. The interval *pSB102–pSB158* accounted for significant variation in both LAR and LSR, but the effect on LAR was confounded with the interval *pSB643b–pSB041*, and the effect on LSR was confounded with *pSB195–SHO68* (Table 2). Gene action of the LAR QTL in the interval *pSB195–SHO68* was largely dominant, while the other two were largely additive.

Table 1. Allele composition of *S. halepense* and *S. almum*

Restriction fragment	*S. b.*	*S. p.*	*S. h.*	*S. a.*
Average no. per indiv.	1.19	1.19	1.50	1.92
Total no. per species	98	81	125	95
S. b. specific no.	57 (58)	—	49 (39)	25 (26)
S. p. specific no.	—	40 (49)	30 (24)	25 (26)
No. common to *S. b.* and *S. p.*	41 (42)	41 (51)	38 (30)	38 (40)
S. h. specific no.	—	—	2 (2)	—
S. a. specific no.	—	—	—	1 (1)
No. common to *S. h.* and *S. a.*	—	—	6 (5)	6 (6)

S. bicolor (*S. b.*) included cultivated races bicolor ("Atlas"), durra ("B35"), caudatum ("El Mota"), kafir ("Segalone," BTx623), guinea (IS3620C), and feterita ("Ajabsido") and wild races aethiopicum (IS14564), verticilliflorum (IS14505), arundinaceum (IS18826), and virgatum (IS18809). *S. propinquum* (*S. p.*) included PI302191 and an unnamed accession (from K.F.S.). *S. halepense* (*S. h.*) included PI209217 (South Africa), 271615 (India), 302162 (Australia), 539065 (Kazakhstan), 539066 (USSR), and a local sample. *S. almum* (*S. a.*) included PI173315 (Chile), 202410 (Argentina), 208702 (Algeria), and 302110 (New Zealand). Numbers in parentheses are percentage of total number of restriction fragments per species.

The extent of subterranean rhizomes (LSR) was influenced by additional QTLs on LGs B, D, F, G, H, and I (Fig. 1 and Table 2). These accounted for an additional 31% of the variance in the extent of below-ground rhizomes, beyond the 14% accounted for by the two LG-C QTLs. The *S. propinquum* allele increased rhizomatousness in all cases except LG D, where the *S. propinquum* homozygote showed a marginally significant (lod 3.09) reduction in rhizomatousness. Gene action for four of the eight QTLs was additive, two were dominant, one was recessive, and one was "overdominant," with the heterozygous genotypes showing greater rhizomatousness than either parental homozygote.

Corroboration of Genetic Mapping by Progeny Testing. The predictive value of the mapped QTLs was assessed by evaluating 3488 F_3 plants, including 50–150 plants from each of the 48 F_3-selfed families derived from F_2 individuals spanning the range of phenotypes observed. Narrow-sense heritability (22) was 0.34 ± 0.06 (mean ± SEM).

QTLs associated with F_2 LAR, as well as additional QTLs associated only with F_2 LSR, were each predictive of F_3 family LAR. Predicted values for F_2 LAR were calculated (15) based on (*i*) the repertoire and phenotypic effects of LAR QTLs mapped in the F_2 generation, (*ii*) the repertoire and phenotypic effects of LSR QTLs mapped in the F_2 generation, (*iii*) LSR effects of the LG-C QTLs in the F_2 generation, and (*iv*) LSR effects of QTLs not on LG C in the F_2 generation. Observed F_2 plant LAR accounted for 41% of variance in observed F_3 family LAR. The F_2-predicted value based on LAR QTLs (all on LG C; see Table 2 and Fig. 1) accounted for 17% of variance in F_3 family means ($P = 0.004$), confirming the influence of these loci on the trait. The F_2-predicted value based on the eight LSR QTLs accounted for 44% of variance in F_3 family LAR, virtually the same as did F_2-observed phenotype. This suggests that the eight LSR QTLs may be a

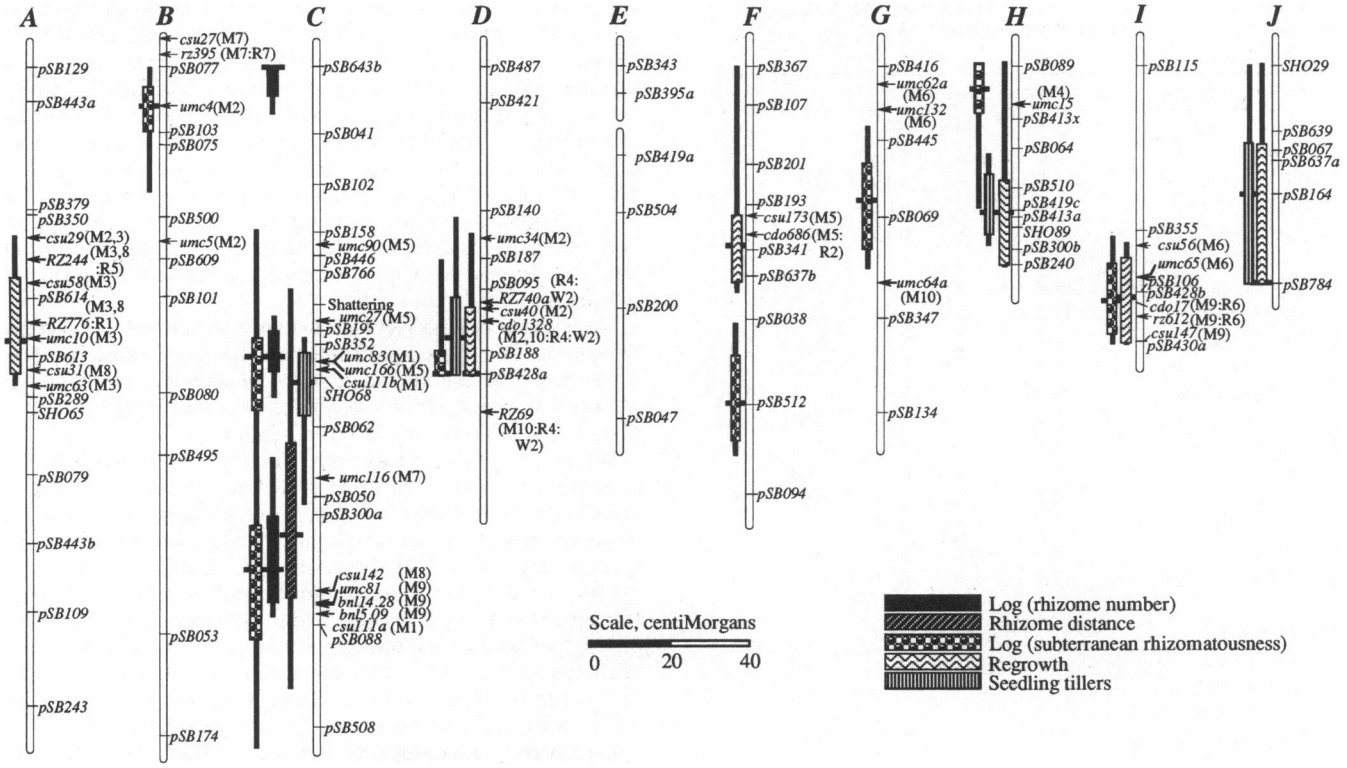

FIG. 1. QTLs affecting rhizomatousness and tillering of sorghum. The 10 LGs of sorghum are denoted A–J (12). DNA markers indicated by lines crossing a LG were used in QTL mapping; those indicated by arrows were mapped on a subset of 56 progeny (12), and locations were inferred relative to flanking markers. Chromosomal locations of selected markers in maize (M) (17, 18), rice (R) (18, 19), and wheat (W) (20) are indicated. Maximum-likelihood locations (arrowhead) and 1-lod (box) and 2-lod (whiskers) likelihood intervals for each QTL are to the left of appropriate linkage groups. The pattern within the 1-lod likelihood interval indicates trait.

nearly complete set of the genes accounting for variation in rhizomatousness in this population.

LSR was probably a more comprehensive measure of rhizomatousness than LAR, rather than an independent measure of a population of rhizomes that fail to produce shoots. The six QTLs associated with LSR (but not LAR) of F_2 plants were predictive of LAR in F_3 progenies. F_2 predicted phenotype based on LSR for the LG-C QTLs accounted for ≈22% of phenotypic variance ($\alpha < 0.001$), while F_2 predicted phenotype based on LSR effects of the remaining six QTLs accounted for ≈23% of variance in LAR of F_3 progenies ($\alpha < 0.0009$). Extensive replication of the F_3 test afforded greater precision than measurement of individual F_2 plants, for determining the genetic potential for LAR.

QTLs That Influence Tillering. Four QTLs, located on LGs C, D, H, and J, accounted for 23.7% of phenotypic variation in the number of tillers 8 weeks after seeding (prior to flowering). At each locus, the *S. propinquum* allele increased tillering. Gene action for two loci (LG C and LG H) was largely dominant, one (LG J) was largely additive, and one (LG D) was largely recessive.

The LG-C tillering QTL, in the interval *pSB195–pSB062*, corresponded very closely to one of the three QTLs affecting both LAR and LSR, with largely overlapping 1-lod likelihood intervals and maximum-likelihood peaks ≈7 centimorgans apart.

Regrowth After Overwintering Is Associated with Both Rhizomatousness and Tillering. Among the 370 F_2 progeny, 341 (92.2%) survived winter in the test environment (30′ N latitude). Air temperatures sufficient to kill exposed rhizomes (23) occurred only on November 27 (−4°C) and 28 (−3°C), 1992, and March 14, 1993 (−3°C). Winterkill *per se* in the F_2 was too infrequent to map genes associated with it. However, survival (perenniality) was clearly enhanced by *S. propinquum* chromatin—as only 175 (46.3%) BC_1 progenies grown simultaneously with the F_2 showed spring regrowth. All *S. propinquum* plants showed spring regrowth scores of 9 (maximum), while no *S. bicolor* plants survived. Rhizomatous plants had a higher rate of survival than nonrhizomatous plants (Table 3).

Six QTLs, mapping to LGs A, D, F, H, I, and J (Fig. 1), accounted for 29.9% of phenotypic variation in regrowth ("ratooning") among the 341 surviving F_2 progeny. For all except the LG-D QTL (see below), the *S. propinquum* allele increased regrowth. Gene action of four QTLs (LGs A, F, H, and I) was largely dominant, one was largely additive (LG J), and one (LG D) was recessive.

Regrowth was positively correlated with all measures of rhizomatousness, most closely with LSR ($r = 0.55$; $\alpha < 0.0001$). QTLs affecting regrowth on LGs F and I corresponded to regions that showed tentative effects on LSR but were confounded with effects of genetically linked regions (Table 2). Regrowth was also positively correlated with extent of tillering ($r = 0.23$; $\alpha < 0.0001$); QTLs affecting tiller number corresponded closely to QTLs affecting regrowth on LGs H and J.

LG-D QTLs for regrowth, tillering, and LSR correspond closely to the sorghum photoperiodic (short day) flowering locus (Y.-R.L., K.F.S., and A.H.P., unpublished data). Plants carrying the *S. propinquum* allele flowered in October and November, while *S. bicolor* homozygotes flowered in June and July. This was the only region in which the *S. propinquum* allele was associated with reduced LSR and regrowth. These effects may be pleiotropic or physiological consequences of short-day flowering.

Disarticulation (Shattering) of the Sorghum Inflorescence Is Due to a Single Genetic Locus. Disarticulation was scored as positive or negative and mapped to LG C between markers *pSB766* and *pSB195* (Fig. 1). If this score reflected extraneous variation, its insertion into the genetic map would greatly inflate the length of this interval (because phenotypic variation would incorrectly be attributed to recombination between the

Table 2. Biometrical parameters of QTLs affecting rhizomatousness, tillering, and regrowth in *S. bicolor* × *S. propinquum*

Trait/LG:Interval	% variance	lod	a	d	Mode
LAR: Full model	21.8	13.4	—	—	—
C: *pSB643b–pSB041*	7.8	4.7	0.09	−0.04	AR
C: *pSB102–pSB158**	6.7	4.6	0.10	0.0	A
C: *pSB195–SHO68*	9.6	5.9	0.04	0.11	DA
C: *pSB300a–pSB088*	12.6	6.7	0.13	−0.06	AR
LSR: LG-C model	14.0	9.6	—	—	—
Non-LG-C model	31.2	22.0	—	—	—
B: *pSB077–pSB103*	4.3	2.7	−0.03	0.13	ADR
C: *pSB102–pSB158**	5.8	3.9	0.08	0.06	D
C: *pSB195–SHO68*	9.5	5.3	0.08	0.11	DA
C: *pSB300a–pSB088**	5.1	3.8	0.10	−0.02	A
D: *pSB188–pSB428*	5.6	3.1	−0.10	0.11	R
F: *pSB193–pSB341**	5.7	4.0	0.09	0.08	D
F: *pSB038–pSB512*	6.2	4.6	0.11	0.01	A
G: *pSB445–pSB069*	5.4	3.0	0.05	0.12	D
H: *pSB089–pSB413*	7.3	4.6	0.12	0.01	A
I: *pSB106–pSB430a*	5.6	4.0	0.11	0.0	A
RD: Distance traveled from crown by most distal rhizome					
C: *pSB300–pSB088*	12.3	2.4	4.08	−0.57	AR
Tillers: Full model	23.7	19.6	—	—	—
C: *pSB195–pSB062*	4.9	3.6	0.18	1.3	DA
D: *pSB095–pSB428*	9.0	6.3	1.36	−0.76	RA
H: *pSB510–pSB300b*	7.2	5.4	1.14	0.98	D
J: *pSB067–pSB784*	6.7	5.5	1.15	0.41	AD
Regrowth: Full model	29.9	24.4	—	—	—
A: *pSB614–pSB613*	6.7	4.6	0.49	0.61	D
D: *pSB095–pSB428*	3.7	2.7	−0.20	0.57	R
F: *pSB193–pSB341*	8.0	6.4	0.49	0.62	D
F: *pSB038–pSB512**	5.9	3.9	0.57	−0.04	A
H: *pSB510–pSB300b*	4.6	3.1	0.39	0.52	D
I: *pSB106–pSB430a*	4.2	3.4	0.39	0.42	D
J: *pSB067–pSB784*	4.8	3.0	0.51	0.15	AD

a, additive effect; d, dominance deviation; RD, rhizome-derived shoot. Gene action [in order of decreasing likelihood (15)]: A, additive; D, dominant; R, recessive.

*Effects of these intervals were partly confounded with adjacent intervals on the same chromosomes (as described in refs. 13 and 21) and, thus, were not deemed to contain independent QTLs. They appear for reference to other traits that show significance.

locus and flanking DNA markers). However, insertion of the shattering locus added only 1 centimorgan to the interval length, indicating a maximum of 0.5% error in scoring the phenotype (since one error would be treated by MAPMAKER as two recombination events flanking the locus).

DISCUSSION

Genes for Weediness of *S. halepense* Are Probably Derived from *S. propinquum*. The repertoire of restriction fragment length polymorphism alleles found in johnsongrass supports the classical inference (8, 9) that it is a polyploid hybrid of *S. bicolor* × *S. propinquum*—and implies that the genes imparting rhizomatousness to johnsongrass are derived from *S. propinquum*. Interspecific origin leaves only 6% of johnsongrass alleles unaccounted for, while a proposed intraspecific origin (24) fails to account for at least 24% of johnsongrass alleles. The 2 accessions of *S. propinquum* examined were remarkably diverse, harboring almost as many alleles as the 11 accessions of *S. bicolor*. This diversity may account for findings (25) that four *S. halepense* isozyme alleles were absent in (only) one *S. propinquum* accession studied.

Table 3. Relationship of winterkill to rhizomatousness

Overwintering	BC_1	F_2
% total that survived	46	92
% rhizomatous plants that survived	81	98
% total that died	54	8
% rhizomatous plants that died	19	2

Assessment of Risks Associated with Release of Transgenic Sorghums. The allele repertoire of *S. halepense* showed somewhat closer correspondence to *S. bicolor* than *S. propinquum*. In contrast, the *S. almum* accessions showed equal contributions from *S. bicolor* and *S. propinquum*.

While many factors may contribute to such a bias in allele composition (cf. ref. 26), one disturbing possibility is introgression from *S. bicolor* to *S. halepense*, perhaps by association of the weed with cultivated sorghum. Hybrids between the two species can occur (11); however, the contribution of such hybrids to the johnsongrass gene pool remains unknown. Introgression from *S. bicolor* would be consistent with morphology of nonoverwintering populations of *S. halepense* at its northerly extreme (27). In view of the possible consequences of "transgene flow" from sorghum to johnsongrass (see Introduction), this topic warrants further investigation.

Regrowth (Ratooning) Is Related to Both Tillering and Rhizomatousness. Regrowth in our environment (30′ N latitude) was correlated with subterranean rhizomatousness—but was not clearly related to above-ground "rhizome shoots" in the seedling year. Several factors may account for this result. Prior work (23) showed that overwintering was less dependent on the presence of rhizomes than on rhizome depth—a factor not assessed in our study. Some subterranean rhizomes may not produce above-ground shoots, may not initiate elongation until after overwintering, or may simply serve as a carbohydrate repository (3).

Persistence may be partly due to new tillering from the original crown. Among the six QTLs affecting regrowth, three coincided closely with tillering QTLs on LGs D, H, and J. Tillering in *S. bicolor* has previously been attributed to a single genetic locus (28). Mapping of four tillering QTLs in the *S. bicolor* × *S. propinquum* cross suggests that we have accessed alleles that were absent from (or undetected in) *S. bicolor*.

Comparative Locations of Weediness Genes in Divergent Poaceae Taxa. Heterologous DNA probes reveal the chromosomal locations in maize, rice, and wheat that correspond to the mapped sorghum QTLs (Fig. 1). Further, the chromosomes of sorghum and sugarcane correspond closely (S.-C.L. and A.H.P., unpublished data) affording additional inference. Rhizomatousness, tillering, and regrowth are of interest in many Poaceae—"ratoon cropping" is practiced in sorghum, sugarcane, and rice (28–30), and the latter two are cross-compatible with rhizomatous species. Productivity of turf and pasture grasses is enhanced by rhizomatousness and tillering. Since diverse Poaceae share a common gene order over large chromosomal segments (cf. ref. 12), the map positions of weediness genes in *Sorghum* may help to predict the location of corresponding genes in other species.

Abundance and Differentiation of Rhizomes and Tillers. One mapped QTL, on LG C, may influence the abundance of axillary buds available to form tillers or rhizomes, while additional QTLs are involved in the commitment of a particular bud to one developmental path or the other. Both basal tillers and rhizomes develop from axillary buds at the lowermost nodes of the erect leafy shoot of the plant, with basipetally increasing the tendency to develop into rhizomes (31). In the region near *pSB195–pSB062*, the *S. propinquum* allele

increases the number of tillers and rhizomes, each with similar gene action ("DA"; see Fig. 1 and Table 2). The remaining six QTLs affecting rhizomatousness (LAR or LSR: LG B, C, F, G, H, and I) do not correspond to QTLs affecting tillering.

Cloning of Genes Influencing Rhizomatousness, Toward Control of Rhizomatous Weeds. Cloning of genes responsible for rhizomatousness would provide a point of entry into developmental pathways that might be regulated by endogenous (genetic) or exogenous (chemical) means. While johnsongrass can be chemically controlled in crop fields, new infestations quickly occur from roadside or other nearby populations. Nonspecific eradication of such populations, along with companion grasses, could cause massive erosion. Down-regulation of rhizome production might afford integrated management strategies to selectively impede the spread of johnsongrass, while leaving companion populations intact to ensure erosion control. Closely linked DNA markers described herein, a detailed genetic map (12), and megabase DNA libraries (32) provide the tools essential to map-based cloning.

An alternate approach to isolating genes associated with rhizome development may be derived from the suggestion (above) that rhizome initials have been recently committed to a genetically programmed fate different from that of tiller initials. By using techniques (33, 34) to isolate genes expressed in incipient rhizomes but not incipient tillers, candidate genes likely to be associated with rhizomatousness might be obtained. Those which map near QTLs influencing rhizomatousness can be subjected to more detailed analysis to determine whether they account for phenotypic variation in rhizomatousness.

Enhancement of Rhizomatousness in Forage and Turf Grasses. The infamy of Colonel Johnson notwithstanding, rhizomes are an important asset to turf and forage grasses that cover vast land areas. The importance of forage in livestock diets, and turf for aesthetic and sporting purposes, is widely recognized. Further, grasses are important in erosion control—failure to recognize this was a partial cause of the "Dust-Bowl" epochs that have periodically crippled United States agriculture. Genes responsible for rhizome development and tillering in *Sorghum* may at least partly account for these traits in other grasses, in which up-regulation of rhizomatousness might improve agricultural productivity. *Sorghum* provides a facile model for detailed investigation of genes controlling rhizomatousness, a trait important to productivity, quality, and protection of agro-ecosystems.

We thank B. Burson, M. Chandler, T. Cothren, M. Engelke, J. Giovannoni, M. Hussey, and J. Irvine for comments and E. Coe, J. Gardiner, S. McCouch, M. Sorrells, and S. Tanksley for DNA probes. Aspects of this work were funded by the U.S. Department of Agriculture (USDA) Plant Genome Research Program, Pioneer Hibred International, USDA–Agricultural Research Service, and Texas Agricultural Experiment Station.

1. Holm, L. G., Plucknett, D. L., Pancho, J. V. & Herberger, J. P. (1977) *The World's Worst Weeds: Distribution and Biology* (University Press of Hawaii, Honolulu), pp. 54–61.
2. Benech Arnold, R. L., Fenner, M. & Edwards, P. J. (1992) *Oecologia* **92,** 138–144.
3. Oyer, E. B., Gries, G. A. & Rogers, B. J. (1959) *Weeds* **7,** 13–19.
4. McWhorter, C. G. (1971) *Weed Sci.* **5,** 496–500.
5. Anonymous (1900) *House Bill 121*, 56th Congress, first session (GPO, Washington, DC).
6. Millhollen, R. W. (1970) *Weed Sci.* **18,** 333–336.
7. McWhorter, C. G. & Hartwig, E. E. (1972) *Weed. Sci.* **20,** 56–59.
8. Celarier, R. P. (1958) *Bull Torrey Bot. Club* **85,** 49–62.
9. Doggett, H. (1976) in *Evolution of Crop Plants*, ed. Simmonds, N. W. (Longman, Essex, U.K.), pp. 112–117.
10. Casas, A. M., Konowicz, A. K., Zehr, U. B., Tomes, D. T., Axtell, J. D., Butler, L. G., Bressan, R. A. & Hasegawa, P. M. (1993) *Proc. Natl. Acad. Sci. USA* **90,** 11212–11216.
11. Hadley, H. H. (1958) *Agron. J.* **50,** 278–282.
12. Chittenden, L. M., Schertz, K. F., Lin, Y.-R., Wing, R. A. & Paterson, A. H. (1994) *Theor. Appl. Genet.* **87,** 925–933.
13. Lander, E. S. & Botstein, D. (1989) *Genetics* **121,** 185–199.
14. SAS Institute (1989) *SAS/STAT User's Guide*, (SAS Institute, Cary, NC), Version 6, 4th Ed.
15. Paterson, A. H., Damon, S., Hewitt, J. D., Zamir, D., Rabinowitch, H. D., Lincoln, S. E., Lander, E. S. & Tanksley, S. D. (1991) *Genetics* **127,** 181–197.
16. Snedecor, G. W. & Cochran, W. G. (1980) *Statistical Methods* (Iowa State Univ. Press, Ames), pp. 287–292.
17. Coe, E. H. & Neuffer, M. G. (1993) in *Genetic Maps*, ed. O'Brien, S. J. (Cold Spring Harbor Lab. Press, Plainview, NY), pp. 6.157–6.189.
18. Ahn, S. & Tanksley, S. D. (1993) *Proc. Natl. Acad. Sci. USA* **90,** 7980–7984.
19. Causse, M., Fulton, T. M., Cho, Y.-G., Ahn, S. N., Chunwongse, J., Wu, K., Xiao, J., Yu, Z., Ronald, P. C., Harrington, S. C., Second, G., McCouch, S. & Tanksley, S. D. (1994) *Genetics* **138,** 1251–1274.
20. Ahn, S., Anderson, J. A., Sorrells, M. E. & Tanksley, S. D. (1993) *Mol. Gen. Genet.* **241,** 483–490.
21. Paterson, A. H., Lander, E. S., Hewitt, J. D., Peterson, S., Lincoln, S. E. & Tanksley, S. D. (1988) *Nature (London)* **335,** 721–726.
22. Falconer, D. S. (1981) *Introduction to Quantitative Genetics* (Longman, Essex, U.K.), 2nd Ed., pp. 134–169.
23. Warwick, S. I., Phillips, D. & Andrews, C. (1986) *Weed Res.* **26,** 381–387.
24. Bhatti, A. G., Endrizzi, J. & Reeves, R. G. (1960) *J. Hered.* **51,** 106–110.
25. Morden, C. W., Doebley, J. & Schertz, K. F. (1990) *Theor. Appl. Genet.* **80,** 296–304.
26. Harlan, J. R. & deWet, J. M. J. (1975) *Bot. Rev.* **41,** 361–390.
27. Warwick, S. I., Thompson, B. K. & Black, L. D. (1984) *Can. J. Bot.* **62,** 1781–1790.
28. Duncan, R. R., Miller, F. R. & Bockholt, A. J. (1980) *Can. J. Plant Sci.* **60,** 473–478.
29. Simmonds, N. W. (1976) in *Evolution of Crop Plants*, ed. Simmonds, N. W. (Longman, Essex, U.K.), pp. 105–108.
30. Chang, T. T. (1976) in *Evolution of Crop Plants*, ed. Simmonds, N. W. (Longman, Essex, U.K.), pp. 98–104.
31. Gizmawy, I., Kigel, J., Koller, D. & Ofir, M. (1985) *Ann. Bot.* **55,** 343–350.
32. Woo, S. S., Jiang, J., Gill, B. S., Paterson, A. H. & Wing, R. A. (1994) *Nucleic Acids Res.* **22,** 4922–4931.
33. Lee, S. W., Tomasetto, C. & Sager, R. (1991) *Proc. Natl. Acad. Sci. USA* **88,** 2825–2829.
34. Liang, P. & Pardee, A. B. (1992) *Science* **257,** 967–970.