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A single chromosome addition from *Thinopyrum elongatum* confers a polycarpic, perennial habit to annual wheat

Doug Lammer[1], Xiwen Cai[2], Matthew Arterburn[1], Jeron Chatelain[1], Timothy Murray[3] and Stephen Jones[1],*

[1] *Department of Crop and Soil Sciences, Washington State University, Pullman, Washington 99164–6420, USA*

[2] *Department of Plant Sciences, North Dakota State University, Fargo, ND 58105–5051, USA*

[3] *Department of Plant Pathology, Washington State University, Pullman, Washington 99164–6420, USA*

Abstract

Annual wheat displays monocarpic senescence, but amphiploids between wheat and its wild perennial relatives in the genus *Thinopyrum* generally display a polycarpic, perennial growth habit. In order to determine the chromosomal basis of this phenomenon, life-history characteristics were examined using Chinese Spring wheat and a complete *Thinopyrum elongatum* (2n=2x=14) chromosome addition series in a Chinese Spring background. Both monosomic and disomic additions and substitutions of *Th. elongatum* chromosome 4E conferred a polycarpic life history to annual Chinese Spring wheat. Disomic addition lines were found to be perennial under field conditions. This is the first report of a single alien chromosome conferring a polycarpic growth habit to a monocarpic species. Chromosome 4E altered the timing of tiller initiation, such that two growth phases could be clearly identified, the first phase being indistinguishable from the growth of euploid Chinese Spring, followed by a second phase of tiller initiation after the sexual cycle of the first phase tillers was complete (post-sexual cycle regrowth).

Introduction

Angiosperms exhibit wide variation in life history that reflect different combinations of two major traits: monocarpic versus polycarpic growth, and annual versus perennial. Shifts in life history appear to have taken place frequently and rapidly in angiosperm evolution, since many genera of plants contain both annual and perennial species. Further, annual and perennial forms can exist as ecotypes of the same species (e.g. the wild rice *Oryza rufipogon*) (Khush, 1997). Within some genera, cladistic and systematic data have suggested that an annual monocarpic form was the ancestral state, whereas in other taxa, a polycarpic perennial form is the likely progenitor (Bena *et al.*, 1998). This observation has led to the suggestion that shifts between monocarpic and polycarpic strategies can be realized in evolution through relatively minor shifts in developmental processes without the need for dramatic genetic innovation (Thomas *et al.*, 2000). Within the grass tribe Triticeae, it is generally accepted that the ancestral grass was a polycarpic perennial, and that the monocarpic annual habit is a derived trait (Chapman, 1996). Modern cultivars of domesticated Triticeae grains such as wheat (*Triticum aestivum* and *Triticum durum*), rye (*Secale cereale*), and barley (*Hordeum vulgare*), exhibit an extreme form of an annual monocarpic habit, characterized by a co-ordinate cessation of tiller production, the abortion of vegetative tillers, and the highly synchronous senescence of the remaining reproductive tillers during seed ripening. Undomesticated 'annual' Triticeae grasses exhibit a range of tillering and senescence patterns, including species with an indeterminate growth habit, in which older tillers have flowered and senesced while new tillers are still being produced from the crown (T Murray and X Li, unpublished data). Consistent with the idea that monocarpic annualism is a derived trait in the Triticeae, direct hybrids between wheat and its wild perennial relatives, as well as many

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genetically stable amphiploids and partial amphiploids derived from these hybrids exhibit a perennial, polycarpic life history. Plant breeders have exploited this fact in attempts to develop perennial grain crops (Cai *et al.*, 2001; Scheinost *et al.*, 2001; reviewed in Cox *et al.*, 2002; Wagoner, 1990). The amphiploid line AgCS ($2n=8x=56$) (Dvorak and Knott, 1974) is a polycarpic perennial octaploid that combines the A, B, and D genomes of hexaploid wheat (*Triticum aestivum*) with the E genome of the perennial *Thinopyrum elongatum* (Dewey) (synonyms *Lophopyrum elongatum, Agropyron elongatum*). Although the chromosome addition stocks used in this study have been extensively studied for abiotic and biotic stress resistances carried, they have not previously been examined with regard to life history.

Perennial habit is a highly complex suite of traits, encompassing such requirements as the ability to enter a dormant period to avoid environmental stresses, usually cold or drought, the ability to preserve viable meristems through adverse environmental conditions, and appropriate phenology for a given environment. Most of these traits are quantitative in nature, but this report describes a trait from the perennial AgCS amphiploid that has some of the features of a relatively simple genetic trait: the ability to preserve viable axillary meristems past the period of grain ripening, and then to initiate a second period of tiller outgrowth. This trait is termed post-sexual cycle regrowth, or PSCR.

Materials and methods

Genetic stocks

AgCS ($2n=8x=56$), an amphiploid between Chinese Spring Wheat (CS) ($2n=6x=42$) and *Thinopyrum elongatum* ($2n=2x=14$), and each of the single disomic *Th. elongatum* additions and substitutions used in this study were obtained from Dr J Dvorak, University of California at Davis. The chromosome constitution was confirmed using acetocarmine-stained squashes of root tips from young seedlings and/or acetocarmine-stained squashes of metaphase microsporocytes (Cai *et al.*, 1996).

Growth conditions

Greenhouses were maintained at 21/16 °C day/night temperature on a 14 h photoperiod. Plants were grown in a commercial potting mix supplemented with a commercial 20:20:20 fertilizer and were watered using an automated watering system. Controlled environment chambers used the same potting mixture and temperature and daylight regime, but were hand-watered. Field-grown plants were sown into moisture on 2 May 2000, and grown without supplemental water. Fully ripened tillers were hand-harvested using a sickle in September 2000. Ammonium nitrate fertilizer was applied to the field by broadcasting in October 2000.

Morphometric analysis

The chromosome number in four plants containing disomic 4E additions (CS+4E), two plants containing ditelosomic 4EL additions (CS+4EL), and one CS line were confirmed cytologically and selected as parents. These parental plants were self-pollinated. Seventy-five CS+4E progeny, 20 CS, and 20 CS+4EL progeny

were used in the morphometric analysis. In order to confirm the transmission of alien chromosome additions in these progeny, the chromosomal constitution of 43 of the 75 CS+4E progeny plants used in this study were determined either by cytological observation of mitotic cells in seedling roots, or meiotic cells in microsporocytes. Thirty-four out of 43 plants maintained the disomic 4E constitution of the parent while the remaining nine plants were found to be monosomic for the 4E addition. No plants were observed to have lost the alien chromosome completely. Tiller height and number were measured at 145 days after sowing (DAS), when all tillers of the CS control had completed senescence. Soil moisture was maintained past senescence, and plants were assessed for regrowth tissue again at 171 DAS. Regrowth tillers were scored after reaching a length of 3 cm.

Results

F_1 hybrids between wheat and its perennial relatives are polycarpic. In order to understand the chromosomal basis of this phenomenon, the amphiploid line AgCS ($2n=8x=56$; AABBDDEE), which combines the genomes of common wheat ($2n=6x=42$; AABBDD) and the diploid perennial wheat relative *Th. elongatum* ($2n=2x=14$; EE) were used. A series of disomic chromosome addition lines derived from AgCS ($2n=42+2$) were also analysed (Dvorak and Knott, 1974). Evaluation of the phenotypes of CS, AgCS, and all seven disomic CS-*Th. elongatum* addition lines indicated that only AgCS and the disomic CS-*Th. elongatum* addition line 4E (CS+4E) exhibited regrowth from the crown following senescence of the main stem and tillers (the PSCR trait) (Fig. 1). These regrowth tillers eventually flowered and set seed, exhibiting a polycarpic growth habit. CS and the other six disomic CS-*Th. elongatum* addition

Fig. 1. Chromosome 4E of *Thinopyrum elongatum* confers a post-sexual cycle regrowth phenotype on 'Chinese Spring' wheat. Wheat plants were grown from seed in the same greenhouse, and photographed after the completion of seed set. (A) Chinese Spring wheat (CS); (B) AgCS, an amphiploid containing the CS genome and the *Th. elongatum* genome; (C) a disomic CS addition line containing the *Th. elongatum* chromosome 4E (CS+4E); and (D), a CS a ditelosomic CS addition line containing the long arm of *Th. elongatum* chromosome 4E (CS+4EL). CS and CS+4EL have undergone whole plant senescence following seed set, while AgCs and CS+4E have initiated a second round of vegetative growth following seed set.

lines senesced after the sexual cycle was completed and did not regrow. In addition, the disomic CS-*Th. elongatum* substitution line 4E/4D, in which *Th. elongatum* 4E is substituted for wheat chromosomes 4D, exhibited PSCR (results not shown). This result indicates that chromosome 4E of *Th. elongatum* contains a gene or genes that act to initiate PSCR in an annual wheat background.

To determine which arm of *Th. elongatum* chromosome 4E carries the genes conditioning PSCR, the ditelosomic CS-*Th. elongatum* addition line 4EL (long arm of chromosome 4E) was evaluated for PSCR. The ditelosomic CS-*Th. elongatum* addition line 4ES (short arm of chromosome 4E) was not included in the evaluation because it has not been isolated. The addition line 4EL exhibited the same monocarpic growth habit as CS (Fig. 1). This result suggests that the short arm of *Th. elongatum* chromosome 4E carries a gene or genes necessary for initiating PSCR. The long arm of *Th. elongatum* chromosome 4E might also carry genes required for PSCR, but, if so, these are incapable of initiating regrowth in the absence of loci on 4ES.

In order to characterize the PSCR phenomenon more fully, height, tiller number at senescence, and the timing and extent of senescence in greenhouse-grown plants of the monocarpic lines CS, and CS+4EL, and the polycarpic line CS+4E (Table 1) were compared. No significant differences were observed in the number of senesced tillers between the three lines. No significant differences were observed in the height of senesced tillers between CS and CS+4E. New tillers were observed growing from the crown of 26 out of 75 plants derived from the disomic 4E addition lines, but were never observed in the CS or CS+4EL lines. In 23 out of these 26 plants exhibiting PSCR, the tillers present in the CS+4E population fell into two clear classes, one group representing a first stage of growth in which senescence was complete, and a second group of much younger tillers consisting of several vegetative leaves, produced by a second phase of tiller initiation. Only three of the 148 regrowth tillers observed in this experiment could not unambiguously be assigned to the first versus the regrowth phase of tiller initiation because the tiller had flowered, like those associated with the first phase of growth, but had not senesced. This interpretation, that 4E conditions a second, temporally distinct phase of development, was strengthened by the observation that a further six plants in the CS+4E population, which did not show any regrowth at 145 DAS, produced observable regrowth tissue at 171 DAS, long past the time when the primary tillers had senesced. The number of regrowth tillers visible at 145 DAS varied from one to 18 (mean=4.6 regrowth tillers/plant). Regrowth was initiated from the axils of the first leaf of second order tillers in the crown in 140 out of 148 cases, and from higher nodes of second order tillers in the remaining eight cases (Fig. 2). Plants known to be disomic 4E additions through cytological analysis displayed a higher frequency of regrowth than plants known to be monosomic for 4E (15 out of 34 versus two of nine).

In order to determine if the relatively poor penetrance of the PSCR trait in the above experiment could be modified by environmental conditions, 20 seeds of CS and 20 seeds of CS+4E from the above population were sown in a controlled environment chamber. In this experiment, penetrance was greatly improved, with 19/20 of the CS+4E population exhibiting PSCR, compared with 0/20 of the CS control.

The behaviour of CS and CS+4E was compared under field conditions in eastern Washington State, USA, to see if the polycarpic phenotype would convert the annual spring wheat CS into a perennial. The lines were planted in two parallel rows in early May 2000. No obvious differences in the lines were observed during the first growing season until the completion of senescence following grain filling, at which time several small vegetative regrowth tillers could be observed on most CS+4E plants prior to the onset of frost in September 2000. Senesced tillers were carefully removed from both lines to avoid seed drop. After a mild winter, vigorous vegetative growth was observed originating in the CS+4E stubble, but was absent in the CS stubble in spring 2001. CS+4E plants set seed and ripened in August 2001 (Fig. 3), but did not regrow in spring 2002, possibly due to winter kill. The 4E addition is therefore capable of converting the annual wheat line CS into a weak polycarpic perennial, at least in favourable environments.

Table 1. *Morphometric analysis*

Comparison of average primary tiller number, average tiller height, fraction of population exhibiting PSCR, and average number of regrowth tillers in: euploid Chinese Spring (CS); Chinese Spring carrying chromosome additions of *Thinopyrum elongatum* chromosome 4E (CS+4E) (2*n*=42″+2″ or 42″+1′); and Chinese Spring carrying ditelosomic additions of the long arm of *Thinopyrum elongatum* chromosome 4E (CS+4EL). Primary tiller number was determined by counting the number of senesced tillers at 148 DAS in 20 CS plants, 20 CS+4EL plants, and in 26 CS+4E plants exhibiting regrowth. Primary tiller height was determined at 148 dps, when all the CS population had completely senesced, by measuring the height of all tillers on 10 CS plants (*n*=163), and 10 CS+4E plants exhibiting regrowth (*n*=162). The average number of regrowth tillers/plant was determined by counting the number of green, vegetative tillers that had achieved a length of approximately 3 cm on 26 CS+4E plants, 148 DAS. Three tillers in the CS+4E population could not be assigned to primary tiller versus the regrowth tiller category, since they had flowered at the time of observation, but had not ripened. (ND=not determined.)

Genotype	Primary tiller number	Primary tiller height	Number of plants showing PSCR	Regrowth tillers/plant
CS	16.3 (sd=2.45)	120 cm (sd=15.07 cm)	0/20	0
CS+4E	16.62 (sd=3.41)	126.2 cm (sd=11.5 cm)	32/75	4.65 (range 1–18)
CS+4EL	16.5 (sd=2.68)	ND	0/20	0

Fig. 2. Position of regrowth tillers in CS+4E plants. In the majority of cases, regrowth initiated from the crown, at the axil of basil leaves of second order tillers (narrow arrow). Occassionally (4/148 regrowth tillers examined) regrowth initiated from the node of higher leaves (broad arrow).

Fig. 3. Addition of chromosome 4E can confer a perennial growth habit to wheat under favourable environmental conditions. Seeds of CS (left stubble) and a CS+4E disomic addition line (plants on left) were sown in spring, 2000. Because of a favourable winter, the CS+4E line initiated PSCR and was able to produce a second crop of seed during the summer of 2001 when the picture was taken.

The assignment of homoeology groups in the *Th. elongatum* chromosome addition series used in this study was initially made by assessing the ability of each chromosome to complement gametophytic and sporophytic phenotypes associated with wheat disomic deletion lines (Dvorak, 1980). To confirm that the PSCR trait was indeed conditioned by a Triticeae homoeology group 4 chromosome, the PSCR addition stocks were examined using STS and SSR-EST molecular markers previously mapped to the group 4 chromosomes of barley and wheat. In barley, homoeology group 4 has been subdivided into a series of 13 bins based on the position of deletion break points for the purposes of physical genetic mapping

(http://barleygenomics.wsu.edu). Unique alleles of the following loci were observed in the disomic addition and substitution stocks capable of conditioning PSCR: *MWG634* (barley group 4 bin 1, short arm telomere); *LOXA* (barley group 4 bin 3); *WG464* (barley group 4 bin 6, centromeric region); *HIR* (barley group 4 bin 10); *BMY1* (barley group 4 bin 13, long arm telomere). In addition, unique alleles of *RPS1* and the proline transporter, which lie within the region delineated by barley group 4 bins 6 through 9, have been detected. These results support the initial assignment of the foreign *Th. elongatum* chromosome in these lines to Triticeae homoeology group 4, and further suggest that no large translocations involving homoeology group 4 occurred during speciation in *Thinopyrum elongatum,* relative to the consensus Triticeae homoeology groups.

Discussion

Amphiploids and partial amphiploids between wheat and its wild perennial relatives in the genus *Thinopyrum* often display a polycarpic perennial growth habit. In an attempt to understand the chromosomal basis of perennial polycarpic growth in the perennial amphiploid AgCS, seven disomic addition lines of wheat were examined for traits contributing to perennial life history. These additions encompass the complete genomic complement of the diploid perennial *Th. elongatum* (2n=2x=14). The addition of a single alien chromosome, 4E, was sufficient to confer a polycarpic growth habit on the annual wheat cultivar Chinese Spring, and to produce a weak perennial phenotype under favourable environmental conditions. The inability of a disomic telocentric addition of the long arm of chromosome 4E (4EL) to condition PSCR suggests that a gene or genes on the short arm of 4E are required for PSCR. Screening is currently taking place for stable deletions of the long arm of 4E, which will allow it to be determined if the short arm is both necessary and sufficient to condition PSCR when present in a ditelosomic state. The regrowth conditioned by 4E exhibits variable penetrance depending on environmental conditions. Vigorous and uniform regrowth has been observed in the parental amphiploid line AgCS under all environments observed, whereas regrowth in CS+4E has been observed to vary from 43% to 95% of the population in greenhouse conditions. Loci present on other chromosomes within the *Th. elongatum* genome are therefore likely to enhance the regrowth phenotype, although these are incapable of initiating PSCR in the absence of 4E. Agronomically useful perennial wheat–*Thinopyrum* amphiploids and partial amphiploids may therefore be expected to possess at least one pair of homoeology group 4 chromosomes from the perennial parent.

To begin to understand the developmental mechanisms underlying PSCR, tiller number was compared between Chinese Spring, CS+4E, and CS+4EL at the time of

senescence. During vegetative growth, annual wheat produces a main shoot and a variable number of tillers, depending on the genotype of the plant and the environment. Only the main shoot and a few early-formed tillers are likely to complete development and form seeds. In annual wheat, tillers are produced from axillary meristems at regular intervals up to the time of floral transition (spikelet initiation) in the primary tiller. At this time, new outgrowth of lateral meristems is halted. Concurrent with the elongation of the main stem at the time of the emergence of the spike, later-formed vegetative tillers that have not yet undergone floral initiation undergo senescence (Rawson, 1971; Jewiss, 1972; Darwinkel, 1978; Kirby and Appleyard, 1987; Simmons *et al.*, 1982; Fraser *et al.*, 1982; Simmons, 1987, Davidson and Chevalier, 1990). Nutrient mobilization from these senescent tillers may make a modest contribution to those tillers that have undergone floral transition (Chafai-Elaloui and Simmons, 1988). Reproductive tillers that have undergone floral transition at the time of main stem elongation complete development, and senescence in these tillers is tightly co-ordinated with grain maturation. It was first observed that the pattern and timing of senescence of the main stem and reproductive tillers during seed set is not noticeably altered in the addition lines. This suggests that the regrowth phenomenon conditioned by 4E is not caused by the alteration of some very general feature of the senescence syndrome. Second, the number of tillers that reach reproductive maturity before the onset of PSCR is not significantly different between CS and CS+4E. The regrowth mechanism conditioned by 4E seems, therefore, to act at the level of maintaining axillary meristems during senescence that usually occurs in this tissue at the time of spike emergence in the main stem. The fact that there is no difference between tiller numbers in CS and CS+4E, also suggests that 4E does not affect senescence of vegetative tillers that also normally occurs at the time of spike emergence on the main stem. Any mechanism that blocks senescence of these tillers would be expected either to increase the number of tillers reaching maturity, and/or the presence of a large number of unripe tillers. Only three tillers were observed that could not unambiguously be assigned to a first or second stage of growth at 148 DAS.

The fact that only three tillers in the CS+4E population could not unambiguously be assigned to either the regrowth or primary growth phases, suggests that 4E conditions a temporally unique phase of tiller development within the plant. No such variation in tiller maturity occurred in the CS control population. The PSCR phenomenon described here therefore differs from other genetic effects on tiller number described in grasses. Mutants affecting tiller number in grasses are implicated in pathways affecting axillary meristem initiation (*MONOCULM 1* in rice) (Li *et al.*, 2003) and outgrowth (*teosinte branched 1*; *Teopod 1 Teopod 2* in maize and *OsTB1* in rice) (Hubbard *et al.*, 2002; Bassiri *et al.*, 1992; Dudley and Poethig, 1993;

Takada *et al.*, 2003). Certain alleles of each of these genes act to increase significantly the number of tillers present at reproductive maturity, an effect often interpreted as decreased apical dominance. Increased tiller number in these mutant maize and rice lines is also associated with dwarfism, an effect not observed in CS+4E lines.

Recently, QTL loci associated with rhizome production have been described in syntenous regions of the *Sorghum propinquum* and *Oryza longistaminata* genome (Paterson *et al.*, 1995; Hu *et al.*, 2003). These regions are associated with rhizomatous growth in hybrids between these two perennial species, and annual sorghum and rice, respectively. The perennial habit in *Th. elongatum* is caespitose, as opposed to rhizomatous, with regrowth occurring through the production of morphologically unmodified tillers from axillary meristems in the crown. Because perennialism is achieved via different developmental mechanisms in these cases, it is unclear whether the regrowth pathways conditioned by 4E and those leading to rhizome production have any common genetic and developmental mechanisms. It was noted that one major and one minor QTL for rhizome production shared between *S. propinquum and O. longistaminata*, map to rice group 3 (Hu *et al.*, 2003), in a region that has synteny with Triticeae group 4 chromosomes. Determining whether orthologous genes might be involved in rhizomatous perennialism and caespitose perennialism will require finer mapping resolution, and NEM mutagenesis and deletion mapping strategies are currently being employed to this end.

Acknowledgements

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