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panicle phytomer 1 mutations affect the panicle architecture of rice

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Abstract We have characterized three *panicle phytomer 1* (*pap1*) mutations from the phytomer viewpoint. In *pap1* mutants, rachis phytomers were strongly affected involving a severe reduction of rachis internode length and an increase in the number of rachis internodes (number of phytomers), resulting in a large number of primary branches. In addition, bracts were frequently over-developed. By contrast, *pap1* differently affected primary branch phytomers resulting in a reduction in both the number and length of internodes. Spikelets were also modified. Rudimentary and empty glumes were frequently elongated. Floral organs were mostly normal. However, a double mutation between *pap1* and *fon1* markedly increased the number of floral organs compared with the single *fon1* mutation, suggesting that *PAP1* has a distinct role in the differentiation of floral organs. The functions of *PAP1* on panicle architecture are: (1) the negative regulation of the number of phytomers on the rachis but a positive regulation of the number on primary branches, (2) an elongation of internodes, and (3) the negative regulation of bract development.

Key words Rice · *panicle phytomer 1* · Mutation · Panicle · Phytomer

Introduction

The diversity of flower and inflorescence architecture has long been of interest to many botanists Weberling (1965, 1989) classified angiosperm inflorescence types according to taxonomic groups, and suggested that the inflorescence is composed of similar structural units, with a minor change in the unit, or in the alignment of the units, causing a large modification of inflorescence shape.

The plant body consists of reiterative structural units called metamers or phytomers. Although the metameric or phytomeric concept of the plant body is still controversial (Rutishauser and Sattler 1985; van Groenendael 1985), the interpretation of plant architecture based on the metamer (phytomer) concept would be particularly valuable for a new understanding of mutant phenotypes. Schultz and Haughn (1991) classified the body plan of *Arabidopsis* into four types of metamers: type 1 is the rosette showing short internodes and under-development of the lateral buds; type 2 is the later part of the vegetative phase having bracts and elongated internodes; type 3 is the flower-bearing inflorescence; and type 4 is the flower showing determinate development. They also characterized several developmental mutations for modifying metameric structure.

In monocots, Bossinger et al. (1992) introduced the concept of phytomeric units for characterizing plant organization and suggested that many barley mutations can be interpreted as modifying such units. Although few studies on plant development have been made incorporating the phytomer concept, many mutations affecting inflorescence architecture are supposed to be associated with the deletion of phytomers or with the developmental fate of each phytomeric component.

In rice, since panicle size and the number of caryopses set on the panicle have been important agronomical traits, many mutants affecting panicle (inflorescence) development have been reported (Kinoshita and Takahashi 1991; Murai and Iizawa 1994). For example, *Dn-1* and *lax* affect spikelet density in an opposite manner. An examination of several

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dense-panicle mutants indicates that dense-panicle phenotypes can be caused by different mechanisms such as the reduction of branch length and an increase in the number of branches and caryopses (Futsuhara et al. 1979). A *lax* panicle shows a unique phenotype: normal differentiation of the terminal spikelet on each primary rachis branch and the severe suppression of secondary rachis branches and lateral spikelets, although the number of primary rachis branches is not affected. This phenotype is caused by the degeneration or under-development of the axillary meristem on primary rachis branches, and indicates the existence of two kinds of phytomers on the rachis and on the primary branch, which are differently regulated. Although Matsuba (1991) conducted a detailed phenomenological analysis of the panicle branching system in rice, the genetic programs directing panicle architecture are largely unknown.

In the present study we characterize *pap1* mutations which modify the number of phytomers and the development of phytomeric components, and show that altered panicle architecture can be deduced from the change in phytomeric units.

Materials and methods

Three recessive mutants showing similar phenotypes of panicle architecture were isolated from the M_2 population of rice (*Oryza sativa* L.) mutagenized with MNU (N-methyl-N-nitrosourea). The M_2 seeds were kindly provided by Dr. H. Satoh, Kyushu University. The allelism test revealed that these three mutations are allelic. They were designated as *pap1-1* (*panicle phytomer1-1*), *pap1-2* and *pap1-3*; *pap1-1* and *pap1-2* were derived from cv Taichung 65 and *pap1-3* from cv Kinmaze.

For scanning electron microscopy (SEM), young panicles and caryopses were pre-fixed with 2.5% glutaraldehyde in 0.1 M sodium phosphate buffer (pH 7.2) overnight at 4°C. After rinsing twice with 0.1 M phosphate buffer (pH 7.2), they were fixed with 1% osmium tetroxide in the same buffer for about 4 h at room temperature until their surfaces became brown. After rinsing twice with the same buffer, the fixed samples were dehydrated in a graded ethanol series from 30% to 100% at room temperature, substituted by 3-methyl-butyl-acetate, and critical-point-dried. Under a dissecting microscope, samples were mounted on cover glasses with double sticky tape and sputter-coated with silver. The specimens were viewed with a scanning electron microscope (Hitachi S-4000) at an accelerating voltage of 10 kV.

For plastic sectioning, caryopses were fixed in FAA (formaldehyde : acetic acid : 50% ethanol = 1 : 1 : 18) for about 1 h, dehydrated in a graded ethanol series, and embedded in Technovit 7100. Samples were sectioned at 3 μm and stained with Toluidine blue. The lengths of empty and rudimentary glumes and of internodes on the rachis and primary rachis branches were measured under a dissecting microscope.

For elucidating allelic interaction, the three mutants were crossed with one another and the phenotypes of the trans-heterozygotes were examined. Furthermore, *pap1-2* was crossed with *fon1*, in which the number of floral organs was increased (Nagasawa et al. 1996), to analyze the genic interaction between *PAP1* and *FON1*.

Results

Rachis of *pap1* mutants

In *pap1* mutations, the development of vegetative shoots was not affected, and defects were observed only in the panicles (Table 1, Fig. 1). A remarkable difference was detected in the rachis length between wild-type and two *pap1* mutants, *pap1-2* and *pap1-3*, whereas there was no significant difference between *pap1-1* and wild-type. Compared with the wild-type, *pap1-2* and *pap1-3* mutants showed a 17.0% and a 20.1% truncation of rachis length, respectively. The number of rachis internodes in *pap1-1*, *pap1-2* and *pap1-3* was increased to 141.7%, 172.2% and 183.3% of the wild- type, respectively. Consequently, the mean internode length in the rachis of *pap1-2* and *pap1-3* was reduced to about half that of the wild-type. In *pap1-1*, although rachis length was comparable to the wild-type, the internode length was reduced to 75% of that of the wild-type. Moreover, *pap1-2* and *pap1-3* had more primary rachis branches than the wild-type, whereas *pap1-1* did not affect its number.

In addition, bracts were frequently developed in *pap1* mutants at the basal nodes of the panicle which degenerate at the early developmental stage in the wild-type (Fig. 2). Several primary rachis branches frequently degenerated in the basal region of the rachis in *pap1-2* and *pap1-3*. In *pap1-1*, under-developed primary rachis branches were observed depending on growth conditions.

The above results indicate that the *pap1* mutation primarily modifies the phytomeric panicle structure, i.e. the number of internodes (phytomers) is increased, leaves (bracts) are over-developed, internodes are truncated, and axillary buds (primary branches) frequently degenerate in the basal region.

Table 1 Panicle phenotypes of wild-type and *pap1-1*, *pap1-2* and *pap1-3* mutants

Material	No. of panicles examined	No. of caryopses	Rachis length (cm)	No. of rachis internodes	Rachis internode length (cm)	No. of primary rachis branches
Wild-type	10	132.0 ± 7.4	15.40 ± 0.79	7.20 ± 0.37	2.02 ± 0.09	13.52 ± 0.52
pap1-1	10	106.4 ± 10.1*	14.93 ± 0.61	10.20 ± 0.20**	1.54 ± 0.05*	12.71 ± 0.52
pap1-2	10	79.7 ± 3.3**	12.79 ± 1.40**	12.40 ± 0.68**	1.02 ± 0.03**	16.57 ± 1.04**
pap1-3	10	55.3 ± 3.3**	12.30 ± 0.55**	13.20 ± 1.02**	0.95 ± 0.04**	17.00 ± 0.76**

*,** Significantly different from the wild-type at 5% and 1% levels, respectively

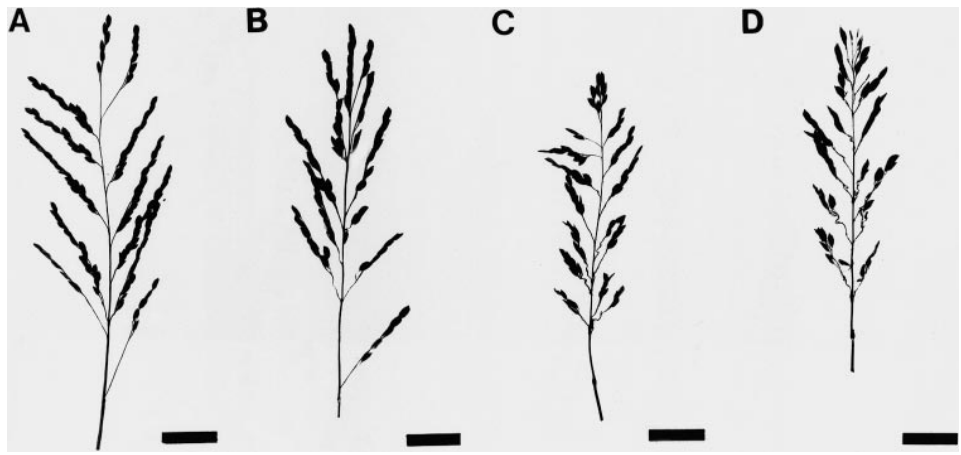

Fig. 1A–D Phenotypes of *pap1* panicles. **A** wild-type with 12 primary branches. **B** *pap1-1* with 12 primary branches. **C** *pap1-2* with 16 primary branches. **D** *pap1-3* with 16 primary branches. Bar = 3 cm

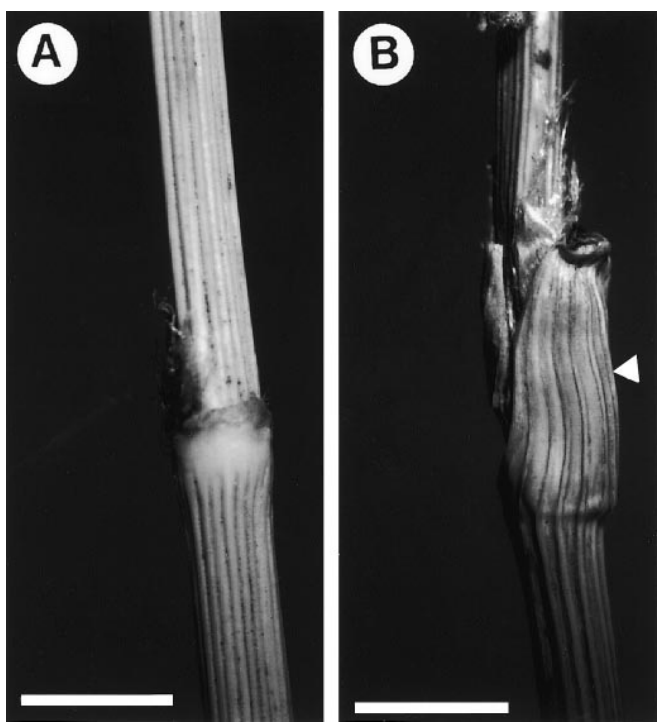

Fig. 2A, B Abnormal bract on *pap1* rachis. **A** wild-type; bract is degenerated. **B** *pap1-2*; bract (*arrowhead*) is highly elongated. Bar = 2 mm

Rachis branches of *pap1* mutants

As in the rachis phytomers, abnormalities were also observed in the phytomers on primary rachis branches (Table 2). *pap1-2* and *pap1-3* mutants showed a significant reduction in the length of primary rachis branches like that of the rachis (Table 2). In addition, secondary and tertiary rachis branches were almost absent, and spikelets frequently degenerated in the basal region of the primary rachis branches. The internode length of the primary rachis branches was significantly reduced in *pap1-2* and *pap1-3*, although that in *pap1-1* was equivalent to the wild-type. The number of phytomers (internodes) on primary rachis branch was significantly reduced in *pap1-2* and *pap1-3*, but not in *pap1-1*. Bracts remained degenerated, as in the wild-type.

As shown above, phytomers of primary rachis branches were also affected by the *pap1* mutation. Modifications of the rachis branch phytomers were partly similar to those of the rachis itself, involving short internodes and the degeneration of axillary buds (secondary branches and spikelets). However, different responses to the *pap1* mutation between the rachis and primary branches were detected in the number of phytomers and bract development. The number of phytomers was increased on the rachis, but reduced on the primary rachis branches. Bracts were overdeveloped on the rachis, but not on the primary branches.

Although the phenotypic variation was slight from generation to generation, *pap1-2* and *pap1-3* consistently showed more extreme panicle phenotypes than *pap1-1*. These results indicate that the panicle phytomer is altered by *pap1* mutations since abnormal development was observed in all phytomer components: internode, bract and axillary bud.

Spikelets of *pap1* mutants

Spikelets of the mutants also exhibited various morphological abnormalities (Table 3, Fig. 3). Rudimentary and empty glumes were frequently elongated in *pap1-2* and *pap1-3* (Fig. 3 C, E), but not in *pap1-1*. In the wild-type, both the rudimentary and the empty glumes on the adaxial side are longer than those on the abaxial side. This tendency was conserved in all three *pap1* mutants. Rudimentary and empty glumes on the adaxial side of the strongest allele, *pap1-3*, were highly elongated (Fig. 3 E). Plastic sections of highly elongated empty glumes revealed that they had three vascular bundles, in contrast to only one in the wild-type

Table 2 Phenotypes of primary rachis branches in *pap1* mutants

Material	No. of panicles examined	Length (mm)	No. of internodes	Internode length (mm)
Wild-type	10	49.1 ± 0.02	8.40 ± 0.32	5.95 ± 0.32
pap1-1	10	47.4 ± 0.02	8.00 ± 0.27	5.86 ± 0.30
pap1-2	10	26.7 ± 0.02**	7.30 ± 0.42*	3.45 ± 0.19**
pap1-3	10	20.5 ± 0.00**	5.90 ± 0.40**	3.42 ± 0.21**

*,** Significantly different from the wild-type at 5% and 1% levels, respectively

Table 3 Length (mm) of rudimentary and empty glumes in *pap1* mutants

Mutant	No. of spikelets examined	Adaxial side		Abaxial side	
		Rudimentary glume	Empty glume	Rudimentary glume	Empty glume
Wild-type	50	0.36 ± 0.01	2.53 ± 0.04	0.26 ± 0.01	2.45 ± 0.05
pap1-1	50	0.38 ± 0.01	2.57 ± 0.05	0.27 ± 0.04	2.46 ± 0.04
pap1-2	50	1.19 ± 0.04**	3.77 ± 0.20**	0.96 ± 0.04**	3.31 ± 0.11**
pap1-3	50	2.75 ± 0.29**	5.23 ± 0.23**	1.60 ± 0.21**	4.30 ± 0.12**

** Significantly different from the wild-type at the 1% level

(data not shown). Also, elongated rudimentary glumes had additional vascular bundles. The surface structure of the highly elongated empty glume suggested that this malformed glume resembled the palea or lemma (Fig. 3 H). An additional rudimentary glume was observed in about 5% of *pap1-2* and *pap1-3* spikelets. In addition, caryopses with no empty glume were observed at a low frequency. Some spikelets showed positional alterations of glumes. Although rudimentary and empty glumes were not elongated in *pap1-1*, about 33% of caryopses were malformed (Fig. 3 B). Rarely, in *pap1-2* and *pap1-3* caryopses, the internode between two rudimentary glumes was elongated (Fig. 3 D). Briefly, *pap1* mutations affect the morphology of empty and rudimentary glume phytomers. Similar to panicle phenotype, *pap1-2* and *pap1-3* showed stronger phenotypes on glumes than did *pap1-1*.

In addition, *pap1* slightly affected the number of floral organs. In about 4% of caryopses, the number of lodicules or stamens was reduced. These results suggest that *PAP1* may function in the development of empty and rudimentary glumes, and regulate the glume phytomer, i.e. the length and number of empty and rudimentary glumes. Since the phytomeric abnormality in the floral organs was not so severe as that in the inflorescence or glumes, it is unclear whether or not *PAP1* has a major role in floral organ development.

Analysis of trans-heterozygotes among *pap1* alleles

To elucidate the allelic interaction among *pap1-1*, *pap1-2* and *pap1-3,* the phenotypes of trans-heterozygotes were examined. Three trans-heterozygotes, *pap1-1*/*pap1-2*, *pap1-1*/*pap1-3* and *pap1-2*/*pap1-3,* showed similar panicle phenotypes (Table 4). Panicles of *pap1-1*/*pap1-2* were comparable to *pap1-2* in rachis length and rachis internode length and intermediate between *pap1-1* and *pap1-2* in the number of primary rachis branches and the number of rachis internodes. The *pap1-1*/*pap1-3* panicles were intermediate between the *pap1-1* and *pap1-3* panicles in many characters. The *pap1-2*/*pap1-3* panicles did not exhibit any fixed tendency, probably due to the small difference between *pap1-2* and *pap1-3* mutants. These results suggest that the panicle phenotype of the trans-heterozygote would be determined by the amount of *PAP1* activity.

An elongation of rudimentary and empty glumes was observed in all three trans-heterozygotes, although *pap1-1* did not show the elongation (Table 5). The glume phenotypes in trans-heterozygotes showed a different tendency from that of the panicle. *pap1-1*/*pap1-2* and *pap1-1*/*pap1-3* showed glumes similar to *pap1-2* and *pap1-3*, respectively. This indicates that *pap1-2* and *pap1-3* are dominant over *pap1-1* for glume length. The phenotypes of *pap1-2*/*pap1-3* glumes were intermediate between the parental mutants.

Analysis of the double mutant between *pap1-2* and *fon1*

The abnormalities of *pap1* mutants were manifested mainly on the phytomers of the rachis, the primary rachis branch, and rudimentary and empty glumes, and only slightly in flowers. To clarify the role of *PAP1* in floral organ development, we selected a double mutant between *pap1-2* and *fon1* which showed an increased number of floral organs but no change in panicle shape. The panicle shape of the double mutant was identical to that of *pap1-2*. The number of floral organs was

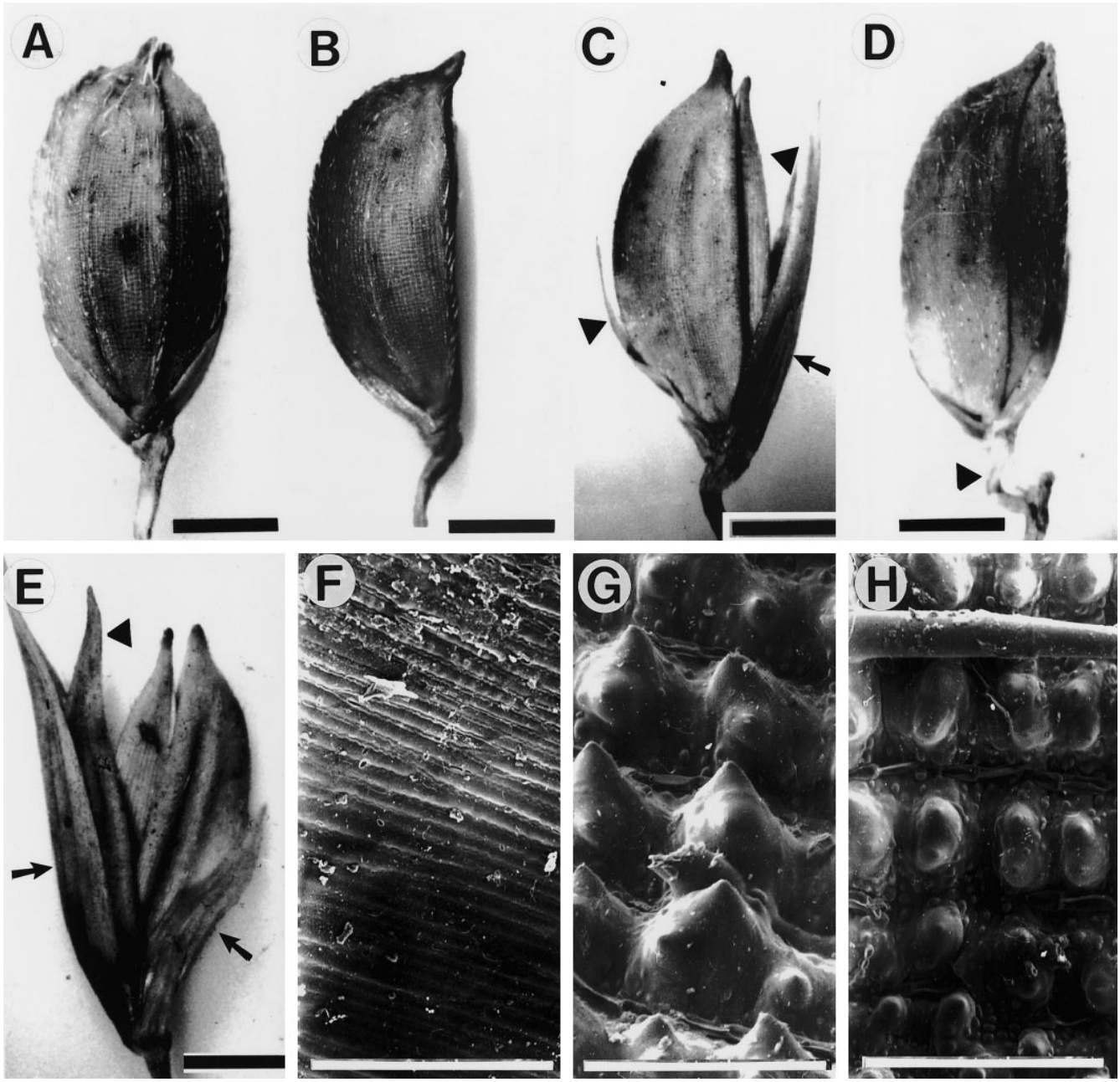

Fig. 3A–H Caryopses of *pap1* mutants. **A** wild-type. **B** *pap1-1* caryopsis showing depressed palea. **C** *pap1-2* caryopsis with elongated rudimentary (*arrow*) and empty (*arrowhead*) glumes. **D** *pap1-2* caryopsis showing elongated internode (*arrowhead*) between two rudimentary glumes. **E** *pap1-3* caryopsis with elongated rudimentary (*arrow*) and empty (*arrowhead*) glumes. **F** Surface of wild-type empty glume. **G** Surface of wild-type lemma. **H** Surface of elongated empty glume in *pap1-2*. Bar = 2 mm in A–E and 0.1 mm in F–H

much larger in the double mutant than in the *fon1* single mutant (Fig. 4, Table 6). This indicates that in the flower the *fon1* phenotype is enhanced in a *pap1-2* background, suggesting a synergic interaction between *PAP1* and *FON1*. Accordingly, *PAP1* plays an important role not only in the construction of panicle architecture through the regulation of phytomeric structure, but also in determining the number of floral organs through positive regulation of *FON1* expression. However, it is unknown whether the increase in the number of floral organs is due to the increase of floral phytomers or to the increase of the number of primordia in a whorl.

Discussion

The regulatory mechanism of phytomers is important to understand plant form and development. In the

Table 4 Panicle phenotypes of *pap1* trans-heterozygotes

Genotype	No. of panicles exmined	No. of caryopsis	Rachis length (cm)	No. of rachis internodes	Rachis internode length (cm)	No. of primary branches
pap1-1/pap1-2	10	61.73 ± 2.22	12.55 ± 0.51	11.00 ± 0.71	1.14 ± 0.05	14.82 ± 0.78
pap1-1/pap1-3	10	62.13 ± 3.00	13.44 ± 0.47	11.14 ± 0.68	1.21 ± 0.41	15.38 ± 0.60
pap1-2/pap1-3	10	65.89 ± 4.03	12.30 ± 0.42	11.14 ± 0.72	1.10 ± 0.14	15.00 ± 0.58

Table 5 Length (mm) of rudimentary and empty glumes in *pap1* trans-hetrozygotes

Mutant	No. of spikelets examined	Adaxial side		Abaxial side	
		Rudimentary glume	Empty glume	Rudimentary glume	Empty glume
pap1-1/pap1-2	50	1.56 ± 0.10	3.68 ± 0.09	1.03 ± 0.05	3.54 ± 0.09
pap1-1/pap1-3	50	2.24 ± 0.30	4.66 ± 0.16	1.33 ± 0.12	4.21 ± 0.13
pap1-2/pap1-3	50	1.72 ± 0.12	4.21 ± 0.16	1.24 ± 0.05	3.92 ± 0.10

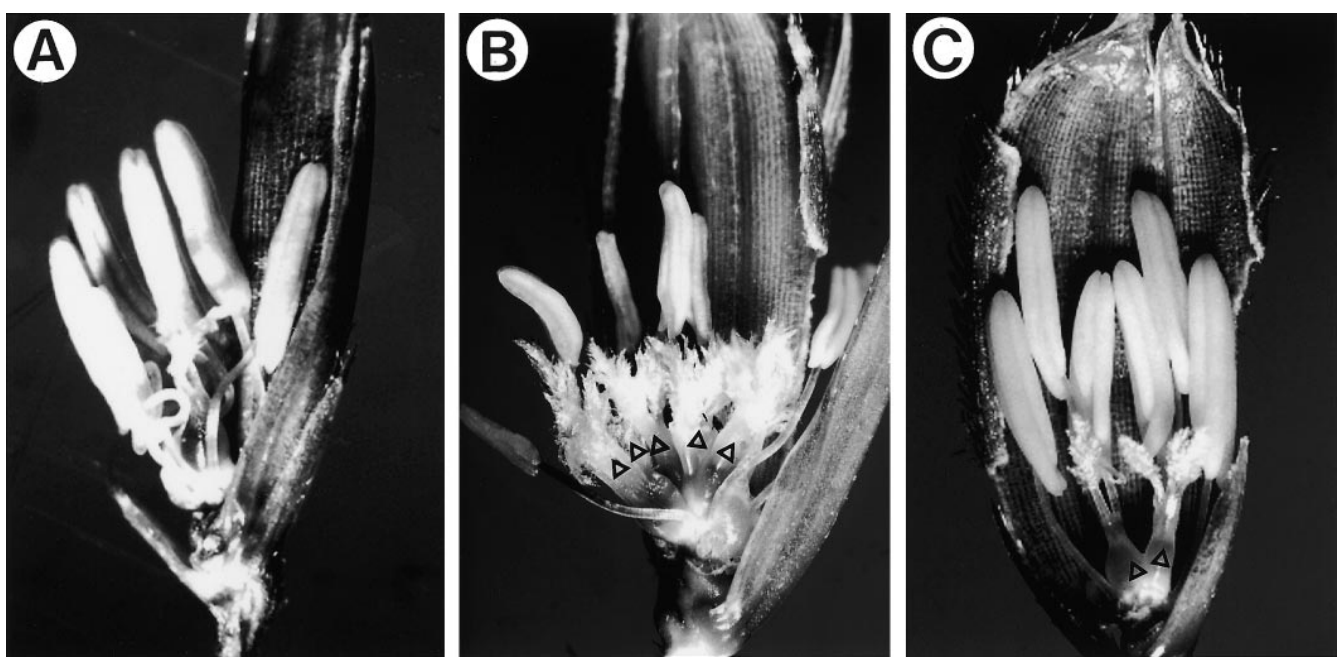

Fig. 4A–C Floral organs in the *pap1 fon1* double mutant. **A** *pap1-2*; the number of floral organs is normal. **B** *pap1-2 fon1* double mutant; pistils (*arrowheads*) are increased to five. **C** *fon1*; two pistils (*arrowheads*) are seen

present study, we analyzed *pap1* mutations from the viewpoint of phytomeric panicle structure, and revealed that the abnormal panicle shape in *pap1* was derived from a modification of the phytomeric structure.

The rachis phytomer is composed of the rachis internode, a bract that degenerates in the early developmental phase, and the primary rachis branch. The phytomer of the primary rachis branch is similarly considered to comprise the internode, a bract, and a secondary rachis branch or lateral spikelet. The observations on *pap1* mutants suggest that the functions of *PAP1* in panicle architecture are: (1) to negatively regulate the number of phytomers on the rachis but positively regulate that on the primary branches, (2) to promote the elongation of internodes, and (3) to negatively regulate bract development. It is obvious that *PAP1* regulates the whole phytomer in a coordinate fashion, and not just one component of the panicle phytomer.

Rudimentary and empty glumes are also considered to be phytomer components and are characterized by their short internodes and the lack of axillary buds. In

Table 6 Frequency (%) of floral organ number in *pap1-2*, *fon1* and in the *pap1-2 fon1* double mutant

Mutant	Lodicule				Stamen				Pistil					
	1	2	3	4	5	6	7	8	1	2	3	4	5	6
Wild-type		100				100			100					
pap1-2	3.8	96.2			4.2	95.8			100					
fon1		90.5	9.5		2.5	70.3	27.2		53.4	39.7	6.9			
pap1-2 fon1	0.7	85.0	5.1	9.2	1.5	61.8	33.8	2.9	40.0	27.2	22.8	6.8	2.5	0.7

pap1, the rudimentary and empty glumes, which are homologous to leaves from the viewpoint of phytomers, are highly elongated. Accordingly, *PAP1* has an important role in regulating the length of rudimentary and empty glumes. Some highly elongated empty glumes may be homoeotically changed to a lemma or a palea. The surface observation of lemma and empty glumes may support this idea. However, the panicle phenotype of *pap1* is difficult to explain based on homoeotic mutations. The empty glume, if elongated, may resemble a lemma or palea, since empty glumes of rice are supposed to be homologous to the lemma in origin.

Although a single *pap1* mutation does not largely affect the number of floral organs, a double mutation, *pap1 fon1*, causes a large increase in organ number. This indicates that *PAP1* shares a redundancy with other genes, such as *FON1*, in the regulation of floral organ number. Since *FON1* would not be involved in panicle development, *PAP1* is considered to have two functions, on panicle architecture and on floral organ number. A redundancy of developmental genes is implicated in animals (Cooke et al. 1997). Recent studies also showed the occurrence of genetic redundancy in plant development (Bowman et al. 1993; Aida et al. 1997). A developmental gene may thus be involved in a character other than that in which a phenotypic modification is recognized.

A dominant mutation, *Ur-1*, which shows phenotypes partially similar to *pap1*, has been identified (Nagao et al. 1958; Murai and Iizawa 1994). Both *pap1* and *Ur-1* increase the number of primary rachis branches. However, functional differences are detectable between *pap1* and *Ur-1*. Thus, *pap1* and *Ur-1* affect the number of spikelets in opposite directions. In addition, the lengths of rachis and primary branches are reduced in *pap1*, but not affected in *Ur-1*. Thus *PAP1* may have an important role in panicle development distinct from that of *Ur-1*, although their functions are partially redundant. It is considered that the rice panicle is constructed through complicated interactions, synergic or antagonistic, of many genes associated with panicle phytomers.

Although many genetical studies have been associated with grass panicles, almost no studies have been carried out from the phytomer viewpoint. Recently, truncation and homogenization have been suggested to occur during the evolution of panicles in *Paspalum* (Camara-Hernandez and Rua 1991; Rua 1996). Phytomeric analysis is thus indispensable not only for characterizing each gene function but also for evolutionary studies on the Poaceae.

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