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The Barley Phytomer

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• *Background and Aims* Morphological mutants have been useful in elucidating the phytomeric structure of plants. Recently described mutants have shed new light on the ontogeny (development of plant structures) and the phytomeric system of barley (*Hordeum vulgare*). Since the current model for barley phytomers was not adequate to explain the nature of some mutants, a new model is proposed.

• *Methods* New phytomer mutants were detected by visual assessment of mutant families in the Optic barley mutation grid population. This was done at various growth stages using laboratory, glasshouse and field screens. Simple explanations were adopted to account for aberrant phytomer phenotypes and a thesis for a new phytomer model was developed.

• *Key Results and Conclusions* A barley phytomer model is presented, in which the origins of vegetative and generative structures can be explained by a single repeating phytomer unit. Organs on the barley plant are divided into two classes, single or paired, depending on their origin. Paired structures are often fused together to create specific organs. The model can be applied to wheat (*Triticum aestivum*) and related grasses.

Key words: Barley, *Hordeum vulgare*, phytomer, floral structure, mutants.

INTRODUCTION

The concept that organisms are composed of repeated building blocks containing fixed regions of cell division and origins of differentiation can be traced back to Bateson (1894). In higher plants the repeated unit is referred to as a phytomer and the most basic form is the 'stem and leaf' model proposed by Rutishauser and Sattler (1985). The phytomer unit contains a specific spatial arrangement of meristematic regions that give rise to an ordered development of organs. Different organs, e.g. floral structures, can arise by variation, but the phytomer structure provides a degree of rigidity and predictability to the morphological development of the plant. The phytomer is therefore of fundamental importance in plant development and systematics (evolution, speciation and taxonomy) as well as pure and applied aspects of botany.

Barley (*Hordeum vulgare*) was chosen by Bossinger *et al.* (1992) to develop the phytomer concept in higher plants because it has a relatively simple, two-rowed (distichous) arrangement of leaves and spikelets produced on opposite and alternating sides of vegetative stems and floral axes, respectively (for morphology and anatomy, see Reid, 1985). Barley also has an advantage in that several developmental mutants were available for study from which Bossinger *et al.* (1992) developed an elaborate phytomeric system for the vegetative and generative structures. Two phytomer types were proposed: type 1, which are produced in series (one on top of the other), and type 2, which is produced as a branch in axillary buds. Various combinations of these provided the architectural

structures of the barley stem, tillers (stem branching), rachis, rachilla and floret (Fig. 1). The phytomeric structure of barley given in the model of Bossinger *et al.* (1992) has a number of weaknesses: embryo structure is not considered, suppression of phytomer regions is not clearly explained and the origins of floral units and reproductive organs are not explained (connections between these structures are undefined black boxes, Fig. 1). Phenotyping of new induced mutant families (B. P. Forster *et al.*, unpubl. res.) has provided additional and novel morphological mutants that shed new light on the structure of the barley phytomer and stimulated a review of previous ontogeny studies.

The nodal structure of barley (and other grasses) is critical with respect to grass architecture as all other structures are derived from it. Nodes are structures that link phytomer units together to form axes for vegetative and reproductive structures, as outlined by Bossinger *et al.* (1992) (Fig. 1). The node is composed of two segments or half nodes. Internodes of the stem (culm), rachis and rachilla phytomers are connected together by a half node at each end. Buds and root initials arise from the half node at the base of the phytomer, the upper half of the node. The half node at the top of the phytomer, the lower half node, gives rise to a single side arm. The nodal concept brings together contributions from two phytomers, thus the developing components of one phytomer are protected by the sheath produced by the phytomer below it. This concept is also important in the inflorescence where internode elongation of the rachis and rachilla is restricted and floral organs arise from branching phytomers.

Taxonomically, barley belongs to the section *Hordeum* of the genus *Hordeum*, which forms part of the tribe Triticeae of the grass family Poaceae. The Triticeae is composed of
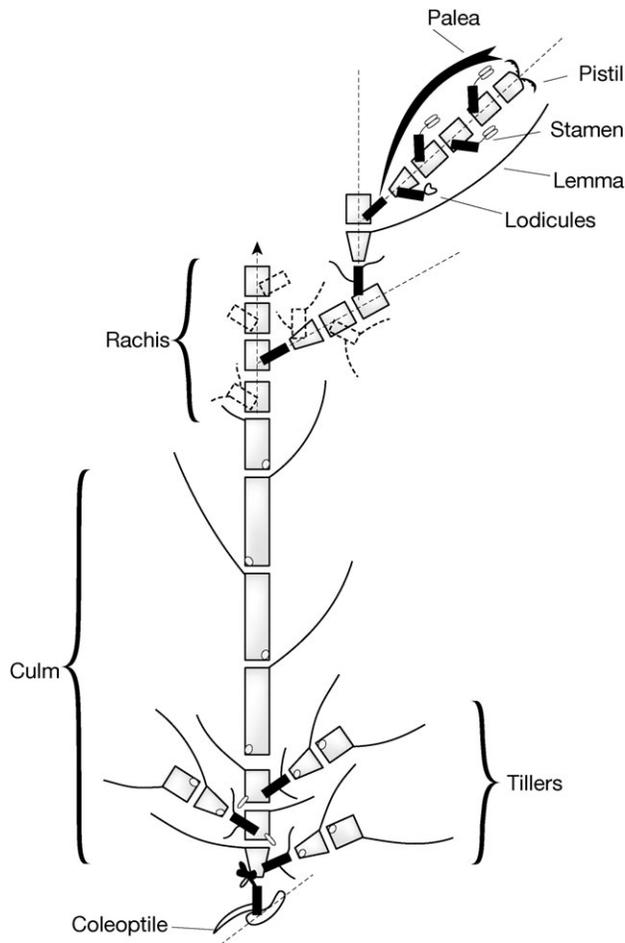
Fig. 1. The phytomeric structure of barley, re-drawn from Bossinger *et al.*, 1992.

Fig. 2. The basic barley phytomer.

Fused paired bracts

A morphological mutant of the palea was amongst the first of a set of new unfused organ mutants that brought into question the earlier phytomeric model of Bossinger *et al.* (1992). In barley, the palea is a bifid structure (von Bothmer and Jacobsen, 1985) which, along with the lemma, protects floral parts (Fig. 3B) and, after pollination, the caryopsis (one-seeded fruit) develops. A split palea mutant was detected in the Optic mutant population (Fig. 3B). Our explanation for a split palea is that the normal palea in barley represents two paired structures that are fused together at a common edge. The normal fusion mechanism was dysfunctional in the mutant. This assumption is supported by the fact that the normal palea has two keels and the awned palea (*adp1*) mutant possesses two awns (see Table 1 for references to all quoted phytomer mutants of barley). Also, split and divided paleas are well known in other members of the Triticeae and are botanical descriptors of species such as *Triticum timopheevi* and

over 350 species. In addition to barley, the Triticeae is home to other important small grain cereals, bread and durum wheats (*Triticum* spp.), rye (*Secale cereale*) and the wheat/rye hybrid crop, triticale (×*Triticosecale*), as well as several forage grass species (von Bothmer, 1992; von Bothmer *et al.*, 1995). The phytomer model developed for barley has implications for these related species and other monocots.

THE THESIS

The development of a modified phytomer model has been progressive and based on recent novel morphological mutants induced and detected in the barley 'Optic' (Caldwell *et al.*, 2004; B. P. Forster *et al.*, unpubl. res., see also http://germinate.scri.sari.ac.uk/barley/mutants/) as well as mutants described in the Barley Genetics Stocks Database (http://ace.untamo.net). As a guide, the simplest explanation for each new phytomer mutant detected was adopted. Patterns in organ development became apparent from which the revised phytomer structures were deduced (Fig. 2).
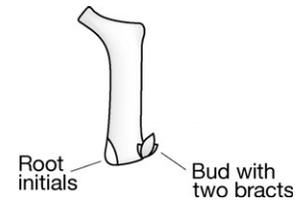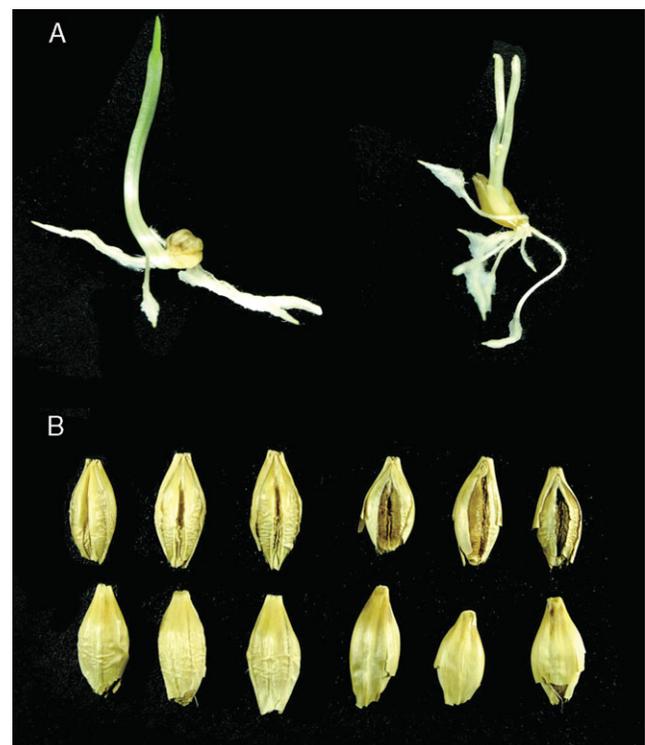

Fig. 3. Split organ phytomer mutants in barley: (A) split coleoptile (right, wild type to left): (B) split palea (abaxial and adaxial surfaces of the caryopsis, mutant to right, wild type to left).

TABLE 1. *Mutants of barley that alter phytomer development*

Gene symbol	Gene or locus name/description	Type specimen (where available)
abr1	Accordion basal rachis internode 1	BGS 472
acr1	Accordion rachis 1	BGS 097 and others
adp1	Awned palea 1	BGS 593
als1	Absent lower laterals 1	BGS 101
ant4	*Anthocyanin-deficient 4*	BGS 595
ari	*Breviaristatum*/short awn	BGS 132 and others
ari-e.156	*Breviaristatum-e.156*/short awn	BGS 328
asp1	Aborted spike	BGS 649
blf1	Broad leaf 1	BGS 326
bra	*Bracteatum*/leafy bracts on rachis	BGS 586, 619
brc1	Branched 1/branched spike	BGS 613
brh	Brachytic/dwarf	BGS 001 and others
brh13	Brachytic 13	BGS 656
brh16	Brachytic 16	BGS 044
btr	Non-brittle rachis	BGS 115 and others
cal	*Calcaroides*/hooded lemma	BGS 146 and others
com1.a	*Compositum*/branched spikelets	BGS 473 and others
crl1	Curly laterals 1/curled awns on lateral spikelets	BGS 325
cud	Curly dwarf/leaves short and twisted	BGS 229, 324
cul	Uniculm	BGS 253 and others
cur	Curly/all plant parts appear twisted	BGS 262 and others
dsp	Dense spike/reduced rachis internode length	BGS 009 and others
dub1	Double seeds 1	BGS 661
Dwf2	Dominant dwarf 2/insensitive to gibberellic acid	BGS 542
eam	*Early maturity/photoperiod responses*	BGS 065 and others
eli-a	*Eligulum-a*/liguleless	BGS 623
eog1	Elongated outer glume 1	BGS 057
ert	*Erectoides*/short rachis internodes	BGS 028 and others
flo	Extra floret	BGS 074, 182, 327
fol	*Angustifolium*/organs reduced in size	BGS 073, 548
gig	*Gigas*/culm and other organs greater in size	BGS 463, 612
glo	*Globosum*/short spikelets, round grain	BGS 168 and others
gra1	*Granum 1*/numerous tillers with thin leaves	BGS 131
hcm1	Short culm 1	BGS 077
int	*Intermedium spike*/extra spikelets	BGS 320 and others
int-c	*Intermedium spike-c*/six-rowed spike modifier	BGS 178
int-h	*Intermedium spike-h*	BGS 544
int-i	*Intermedium spike-i*	BGS 545
int-m	*Intermedium spike-m*	BGS 547
Kap1	Hooded lemma 1/deformed floret on lemma	BGS 152
lax	*Laxatum*/lax spike	BGS 475 and others
lax-a	*Laxatum-a*	BGS 474
lbi	Long basal rachis internode	BGS 308 and others
lel1	Leafy lemma 1	BGS 235
Lfb1	Leafy bract 1/leafy collar	BGS 343
lfs	Leaf-less/variable leaf blade development	
Lga1	Long glume awn 1	BGS 549
lig1	Liguleless 1	BGS 060
lin1	Lesser internode number 1	BGS 099
Lin2	Lesser internode number 2	BGS 636
lks	Short awn	BGS 010 and 172
Lks1	Awn-less 1	BGS 075
lnt1	Low number of tillers	BGS 118

Continued

TABLE 1. *Continued*

Gene symbol	Gene or locus name/description	Type specimen (where available)
mac3	*Maculosus*/necrotic fleck plus a broad leaf	
min	Semi-minute dwarf	BGS 160, 161
mnd	Many-noded dwarf	BGS 633 and others
mov1	Multi-ovary 1	BGS 043
mov2	Multi-ovary 2	BGS 147
msg	Male sterile genetic	BGS 357 and others
mul1	Multiflorus 1/supernumerary florets = *vrs4*	BGS 124
mul2	Multiflorus 2/rachilla florets formed	BGS 251
nld1	Narrow leaf dwarf 1/also degenerate auricles	BGS 323
ops	Opposite spikelets/variable rachis internodes	BGS 624 and others
ovl	Ovary-less	BGS 176, 646
pyr	*Pyramidatum*/pyramide spike shape	
raw	Smooth awn	BGS 312 and others
rtt1	Rattail spike	BGS 051
sbk1	Subjacent hood 1/*Calcaroides*	BGS 062
sci	*Scirpoides*/narrow leafed dwarf	BGS 525 and others
scl	*Scirpoides leaf*/narrow folded leaf blade	BGS 526 and others
sdw	Semi-dwarf	BGS 518 and others
sdw2	Semi-dwarf 2	BGS 133
seg8	Shrunken endosperm 8	BGS 455
sid1	Single elongated internode dwarf 1	BGS 180
Sil1	Subcrown internode length 1	BGS 228
sld	Slender dwarf	BGS 126 and others
sls1	Small lateral spikelet 1	BGS 227
snb1	Subnodal bract/additional bract on spikelet 1	BGS 026
srh1	Short rachilla hair 1	BGS 321
tfl	Thick filament	
trd1	Third outer glume 1/additional bract on spikelet	BGS 202
trp1	Triple awned lemma 1	BGS 061
tst	Tip sterile	BGS 636, 647
ubs4	Unbranched style 4	BGS 011
uzu1	Semi-brachytic/shortened organs	BGS 102
viv	*Viviparoides*/plantlets on the spike	BGS 627 and others
vrs1.a	Six-rowed spike 1	BGS 006 and others
vrs3	Six-rowed spike 3	BGS 315
vrs4	Six-rowed spike 4 = Multiflorus 1	BGS 124
Vrs1.t	*Deficiens 1*/extremely reduced lateral spikelet	BGS 067
wnd1	Winding dwarf 1/coiled peduncle	BGS 023
Zeo	Zeocriton, short culms, dense spike	BGS 082 and others

These mutants are described in greater detail in the Barley Genetics Stocks AceDB Database (http:/ace.untamo.net), in *Barley Genetics Newsletter* Vol. 35 and by personal communication. Gene nomenclature is based on rules given at the 9th International Barley Genetics Symposium (2004).

T. diccocoides (Peterson, 1965). The palea was therefore considered to have a similar origin as other paired structures of the barley plant, e.g. coleoptile, outer glumes, lodicules, styles, etc. (Tables 2 and 3).

A second split organ mutant observed in seedlings of the Optic mutant population was a split coleoptile (Fig. 3A). The coleoptile is a sheath that protects the terminal bud of the embryo (plumule); it grows out as a tube which protects the shoot during germination. The coleoptile has two mid-ribs and two vascular bundles opposite each other

TABLE 2. *Single and paired organs of barley*

Single organs	Paired organs
Plumule	Coleoptile
Leaf sheath	Prophyll
Leaf blade	Auricles
Ligule	Outer glumes
Lemma	Palea
Awn	Lodicules
Anther	Style/stigma
Pistil	Integuments
Ovule	Lateral lobes of the endosperm
Nucellus	
Central lobe of the endosperm	

(Arber, 1934) and is thought to originate from two fused structures (Bossinger *et al.*, 1992). This conclusion is supported by the finding of a split coleoptile mutant, which is assumed to be dysfunctional in the fusing process. The *uzu1* semi-dwarf mutant produces two notches at the tip of the coleoptile and may represent a partial split of the coleoptile into two parts. The coleoptile is also regarded as having a structure similar to that of the prophyll (Jacques-Felix, 1957; Guignard, 1962; Gould and Shaw, 1983). The prophyll is the organ that protects the developing axillary shoots (tillers); however, to date no split prophyll mutant has been reported.

It became apparent that vegetative organs could be classed as either paired (fused or unfused) or as single structures (Table 2). Furthermore, paired organs were always associated with a single-structured organ, e.g. coleoptile (paired) and the first seedling leaf (single); auricles (paired) and leaf blade (single), prophyll (paired) and the first tiller leaf (single) (Figs 4–7).

Paired bracts in reproductive structure

The paired-single-paired-single sequence was also apparent in generative structures, thus the spikelet is subtended by a pair of outer glumes with a single lemma inside followed by a palea (fused pair), etc. (Fig. 8). The logical extension of the $2 + 1$ series of spikelet organs is: palea (paired), then the first stamen (single), followed by lodicules (paired), the second stamen (single), followed by an unknown paired structure, the third stamen and finally the pistil complex (Fig. 8). A missing piece in the series is a paired structure following the second anther. The mature barley floret shows no obvious twin structure at this point.

TABLE 3. *Organs classed by phytomeric origin*

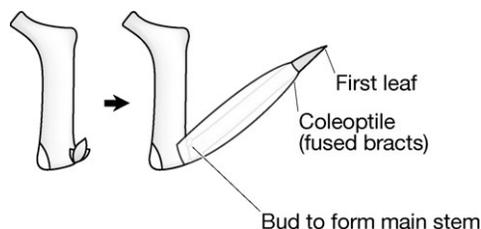| Paired basal buds	Side arm	Phytomer on side arm
Coleoptile	Leaf sheath	Leaf blade
Prophyll	Collar	Awn
Outer glumes	Lemma	Stigma
Palea	Stamen anther	
Lodicules	Carpel	
Stigma/styles		
Auricles		
Styles		

FIG. 4. Phytomeric structure of the first leaf.

However, several grass species are known to possess two pairs of lodicules, a dorsal and an anterior pair, with the dorsal pair being absent in some species (Guedes and Dupuy, 1976; Dahlgren *et al.*, 1985). It is therefore reasonable to assume that formation of the second pair of lodicules is suppressed in barley (see below for further discussion on abortive paired structures during transitional phases).

Phytomer models

The branch or type-2 phytomer model was developed by Bossinger *et al.* (1992) to take into account the $2 + 1$ association of leaf-like organs in buds. It is the modification of the 'stem and leaf' type-1 phytomer proposed by Bossinger *et al.* (1992). In the original model (type 1) contiguous phytomer units are added on top of each other by the activity of the apical meristem. This one-dimensional activity is responsible for the build-up of vegetative stem units, and, after transition to generative growth, to those of the rachis. The leaf sheath is placed at the side and top of the phytomer and is attached to the upper half node. The next type-1 phytomer is orientated $180°$ to protect the bud initials and expose the root initials. New type-1 phytomer units can also be added onto the branch or
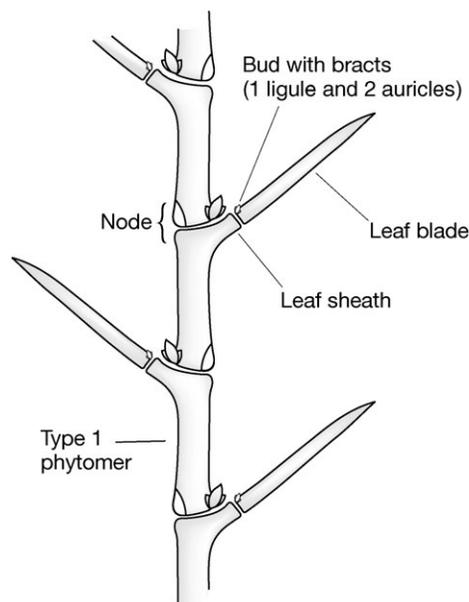

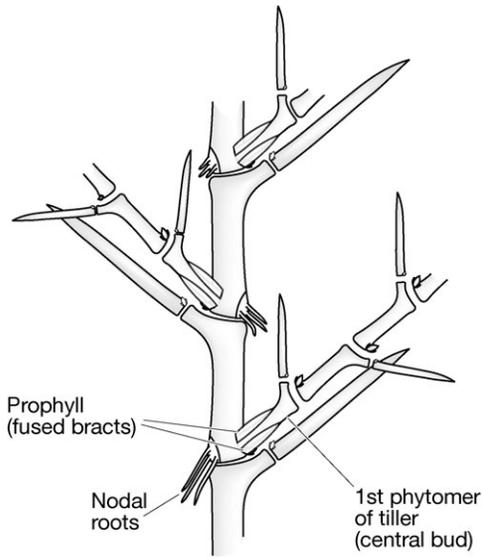FIG. 5. Phytomeric structure of the culm.

FIG. 6. Phytomeric structure of tiller production.

FIG. 8. Phytomeric structure of the spikelet.

type-2 phytomer. A key difference in the model proposed here is that all structures can be derived from one phytomer design. Some structures may be simple (e.g. bracts) whereas others require specific combinations of phytomers produced by branching, series and side arm development.

Bud numbers and positions

Normally one axillary bud (with a pair of bracts) forms at the base of the phytomer; it is likely that the development of other buds is suppressed in stems. The exception in barley is that three buds generally develop on the rachis phytomers and produce three spikelets at each rachis
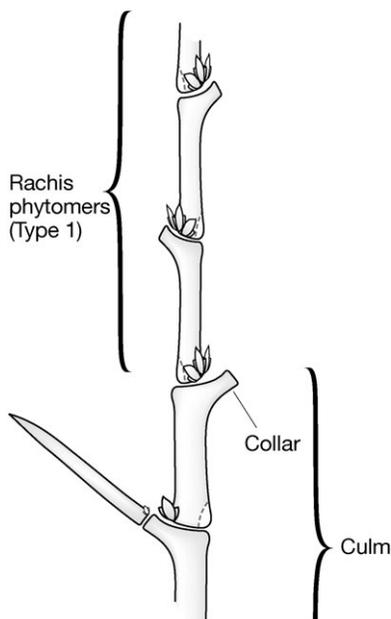

FIG. 7. Phytomeric structure of the transition from culm to rachis.
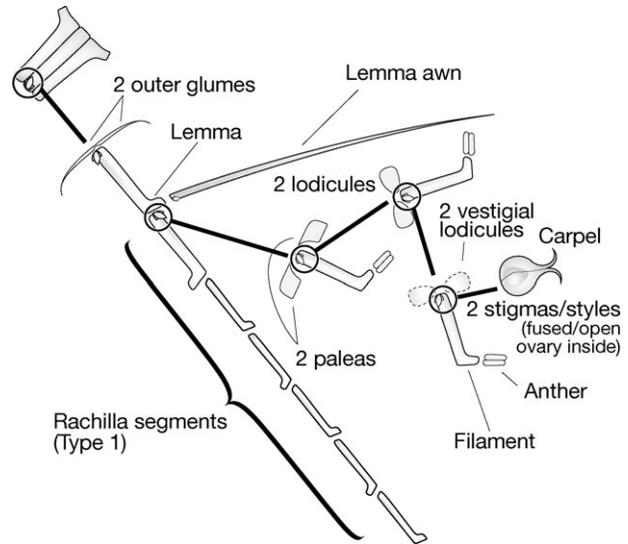
internode. The number of floral buds is partially unrestricted, however, in multiflorous mutants such as *mul1* or *vrs4*. Two additional adventitious buds develop in pairs near the base and on opposite sides of the previous adventitious bud, giving a bud number series of 1, 3, 7, and possibly 15. Further proliferation of floral buds produces the rattail-like spike (*rtt*) mutants. In addition, a single adventitious floral bud (spikelet) occasionally can arise below the central bud (spikelet) in the case of the extra floret (*flo*) mutants. Lateral spikelets can have a short pedicel in some *intermedium* and six-rowed spike mutants (*int-c*, *vrs3* and *vrs4*). Seminal root number has not been studied in detail, but it is likely that these are also produced in the same $(2^n - 1)$ series as adventitious buds.

Figure 5 shows the phytomeric composition of a barley culm (stem) and leaf development. In the model, the leaf sheath develops from a broad meristematic region on the upper half node of the phytomer. The meristematic region at the tip of the sheath forms a bud which develops into a phytomer at the tip of the sheath, which produces the leaf blade and two auricles and the leaf blade in a $2 + 1$ association. The leaf blade forms on top of the side arm of the phytomer below. The ligule may represent an aborted segment of the phytomer that is below the blade attachment point.

Bud development

Tillering proceeds by an axillary bud developing into the first phytomer of the side shoot. The growing point of the bud is protected by the prophyll (a fused organ produced by two lateral bracts of the phytomer). Root buds are assumed to be present at the base of the phytomer opposite the bud position, but they are only active in stem sections near the base of the plant (Fig. 2). The number of buds that develop into tillers can be restricted by environmental and genetic factors. The uniculm 2 (*cul2*) mutant has only a primary tiller. Low tiller number (*lnt1* or *int-l*) mutants

produce only two to four well-formed tillers. Other *cul* mutants produce a primary tiller plus several weak secondary tillers. Besides drastically reduced tillering, the *cul*, *als1* and *lnt1* mutants cause spike malformations. Excess tillering is observed in multi-noded dwarf (*mnd*), *granum* (*gra1*) and leaf-less (*lfs*) mutants.

Internode and leaf elongation

Elongation of internodes can occur in the sub-crown region, the culm and reproductive structures such as the rachis, rachilla, etc. A number of genes control stem growth or plant height producing either tall (*gig* and *ant4*) or semi-dwarf (*ari*, *brh*, *dwf*, *ert*, *hcm*, *lzd*, *mnd*, *sdw*, *sid*, *sld*, *uzu* and *Zeo*) mutants. The rachis internodes can be lengthened in accordion rachis (*acr*) and *laxatum* (la*x*) mutants or shortened (*ari*, *brh*, *ert*, *dsp*, *pyr* and *Zeo* mutants). The opposite spikelet (*ops*) mutants have irregular rachis internode lengths. The length of the sheath, leaf blade, awns and coleoptiles can be altered by a number of the same genes. Some *ari* and *lks* mutants only have shortened awns. Elongation of the sub-crown internode is suppressed by the *Sil1* gene in some winter barley cultivars. Elongation of internodes is suppressed in numerous barley organs and the presence of phytomers can be deduced only by development of buds or branches.

The width of leaf blades and related organs such as the lemma is also under genetic control. Wide-leafed phenotypes include six-rowed barley and some mutants (*blf1*, *gig2* and *mac3*) while narrow-leafed phenotypes include mutants of the *blf2*, *gra1*, *mnd*, *nld*, *sci* and *sci* series. Excessive twisting of leaves and other organs is caused by curly (*cur*) and curly dwarf (*cud*) mutants. The winding dwarf (*wnd1*) mutant appears to only affect coiling of the peduncle.

Transition to reproductive structures

Spike development is preceded by the final culm phytomer unit (called the peduncle) in which the leaf is reduced to a collar (Fig. 7). A number of photoperiod response or early maturity (*eam*, *mat* and *ppd*) genes determine the timing of this transition. Physical transition to the collar and spike is delayed in the many-noded dwarf (*mnd*) mutants and nearly stopped in some tillers of the *viviparoides* (*viv*) mutants, which remain vegetative. The collar is a leaf-like structure in the leafy bract (*Lfb1*) and semidwarf 2 (*sdw2*) mutants. The leaf-like structure can persist for several rachis nodes in the third outer glume (*trd1*) and *bracteatum* (*bra*) mutants. An extreme example of transition failure is the aborted spike (*asp1*) mutant in which spike formation partially or completely fails.

The rachis (spike axis) like the vegetative stem is composed of a single file of phytomers and produces spikelets in a strict distichous fashion, but with a much reduced internode length. Elongation of the first rachis internode is not adequately suppressed in the long basal internode (*lbi*) mutants and in some *intermedium* (*int-h* and *int-i*) mutants. In the accordion basal rachis internode (*abr1*) mutant, several basal rachis internodes are elongated and

secondary or tertiary vegetative branches may form at the lower rachis nodes. The number of fertile rachis nodes on the rachis can be reduced by lesser internode number (*lin*) and tip sterile (*tst*) mutants.

Spikelet development

A diagnostic feature of the *Hordeum* genus is the possession of three one-flowered spikelets at each rachis node (von Bothmer *et al.*, 1995). Since alternating triplets appear opposite each other in two ranks, six files of spikelets can be observed. Rachis phytomers therefore have three buds at their base, which develop into three separate spikelets. If the three spikelets at each rachis internode are fertile the plant is identified as a six-rowed barley. In two-rowed forms only the central spikelet of the triplet is fertile. Positioning of extra spikelets is considered above.

The outer glumes are the first visible structure of the spikelet, but do not necessarily define a spikelet, as supernumerary and branched spikes can form in the case of some many-noded dwarf (*mnd*) mutants and the branched spike (*brc1*) mutant, respectively. Bonnett (1966) provides a detailed description of the development of supernumerary spikelets. A series of mutants can cause fasciation at the tip of the spike (*ari-e.156*, *brh13*, *brh16*, *int-i* and *int-m*) and *com1.a* caused fasciations at the base. Fasciations of the floret (wide lemma trait) results in the formation of double- (*dub1*) and triple-kernel (flower) mutants.

From the lower half node of each rachis node, side branches can develop into spikelets, each having a rachilla axis made up of phytomers in series. Flowering in barley is determinate with the production of a single floret per spikelet. The main axis of the spikelet continues to develop, forming a vestigial rachilla with greatly reduced internode lengths (Fig. 8). In the multiflorous 2 (*mul2*) mutant, the rachilla of lateral spikelets develops a small lemma-like structure, which can develop into a floret and set a seed in some six-rowed cultivars. Spike-like branches arise from the rachilla in the branched inflorescence rachilla (*com*) mutants. Several sterile basal rachis nodes are observed in some accordion rachis (*acr*) and *laxatum* (*lax*) mutants and in the absent lower laterals (*als1*) and the slender (*sln1*) mutants.

Floral components

The floret is composed of a series of organs derived from branch phytomers linked to two other phytomers (Fig. 8). In the $2 + 1$ sequence of the model, the two outer glumes are followed by an awned lemma. A fused palea (paired structure) develops from the pair of bracts of a bud phytomer above the lemma and is protected by the lemma. The palea has the same reverse orientation of the bracts that form the prophyll. The second phytomer of the bud produces a stamen on its side arm; its internode elongates to produce a filament on top of which an anther is formed. The palea and associated stamen is another $2 + 1$ organ series. Continuing this repeating pattern, the bud of the second phytomer of the palea branch develops into a pair of lodicules (bracts) followed by the second stamen. The

third stamen is associated with a pair of vestigial lodicules. Finally the pistil complex is formed (Fig. 8).

Mutants that can cause a conversion of floral parts into other floral components are common in barley. The outer glumes can range in size from normal to lemma-like as determined by alleles of the elongated outer glume (*eog*) locus. The lodicules of the multi-ovary 1 (*mov1*) mutant become somewhat leafy or sepal-like. Conversion of the lodicules into anthers occurs in the *laxatum-a* (*lax-a*) mutants, but the extra anthers are deficient in having two rather than four microsporangia (Bossinger *et al.*, 1992), their incomplete development being symptomatic of their aberrant origins. In the multi-ovary (*mov*) mutants, stamens are partially or completely converted into pistils. Failure of a functional ovary to develop occurs in ovary-less (*ovl*) mutants, while anther development fails in many male-sterile genetic (*msg*) mutants. Reversion of the floral structures to plantlets occurs in the *viviparoides* (*viv*) mutants. The Optic population contained sterile mutants where the palea–lemma association was repeated numerous times and other floral organs were not present (G. Simpson, pers. comm., recorded in http://germinate.scri.sari.ac.uk/barley/mutants/).

Differentiation of pistil structures

Assuming the repeated pattern of the spikelet continues, the next set of $2 + 1$ structures should be the styles and the ovule. Based on drawings of the vascular structure of the wheat ovary by Batygina (see Lersten, 1987), a pair of styles arise below the ovule, i.e. formed from paired bracts. The next repeated structural combination is the integuments that surround the nucellus. The $2 + 1$ association can be extended further to the three lobes of the endosperm. In the shrunken endosperm genetic 8 (*seg8*) mutant, only the central lobe fails to enlarge and results in the formation of very thin kernels with a distinct dorsal crease in the caryopsis (Felker *et al.*, 1985).

Phytomers in awns and leaves

According to our model the lemma-awn is a distinct phytomeric unit (Fig. 8). Several mutants can be expressed at the lemma/lemma-awn junction. For example, in the hooded lemma (*Kap1*) mutant floral-like structures are produced at the tip of the lemma instead of an awn (Bonnett, 1966). The gene causing this is similar to the *Knotted 1* mutant in maize (Müller *et al.*, 1995). The leafy lemma (*lel1*) mutant converts the lemma and lemma-awn into a leaf-like structure that is divided into distinct sheath and blade segments. Positioning of the meristematic region is lower on the lemma in the subjacent hood (*sbk1*) or *calcaroides* (*cal*) mutants. Bonnett (1966) published a detailed morphological description of the hood produced by the *Kap1* mutant and showed that the tip of the lemma of the normal floret serves as the lemma of the accessory spikelet (Bonnett, 1966). There are therefore phytomeric similarities between leaf (sheath and blade) and lemma structures (lemma and lemma-awn). Morphological similarities between the lemma-awn and the leaf blade include the

possession of multiple veins. Awn growth is prevented at the awn-less (*Lks1*) mutant, while the leaf-less (*lfs*) mutants partially prevent leaf blade development. The placement of the auricles is variable in some uniculm (*cul*) mutants while development of awn branches is variable in the triple-awned lemma (*trp1*) mutant. The base of the lemma-awn is malformed in the curly lateral (*crl1*) and is easily broken in a number of barley cultivars and in *ari-k* mutants.

Multifloreted spikelets

A spikelet of an indeterminate flowering mutant is shown in Fig. 9. In this mutant, two or more florets are produced within a spikelet, the alternating florets face each other and the multi-floreted structure is contained within a pair of glumes. The phytomeric structure of this mutant spikelet is similar to that of wheat and can be created simply by the production of fertile (rather than infertile) rachilla phytomers (Fig. 10). This mutant is of major significance because it not only has the floral structure of another genus, but challenges the taxonomic distinction of the *Hordeum* genus, which is characterized by having one-flowered spikelets.

Nodal structure

Barley mutants also can alter the fusion of nodal segments and this suggests that the node is not simply half nodes attached to each other. The phytomer model assumes that half nodes are cemented together and their separation does not occur. This is not the case in wild barley where disarticulation at the rachis nodes occurs. The brittle rachis mutants (*btr*) prevent shattering of the spike. Disarticulation in two-rowed barley cultivars occurs at the base of the spikelet. The nodal structure, therefore, may be complex. Some support for this concept comes from *eligulum-a* (*eli-a*) mutants where the ligule develops poorly and the stem breaks easily at the junction of the two half nodes.

FIG. 9. Indeterminate floral mutant of barley (right) compared with a single floreted spikelet of wild-type barley (left).
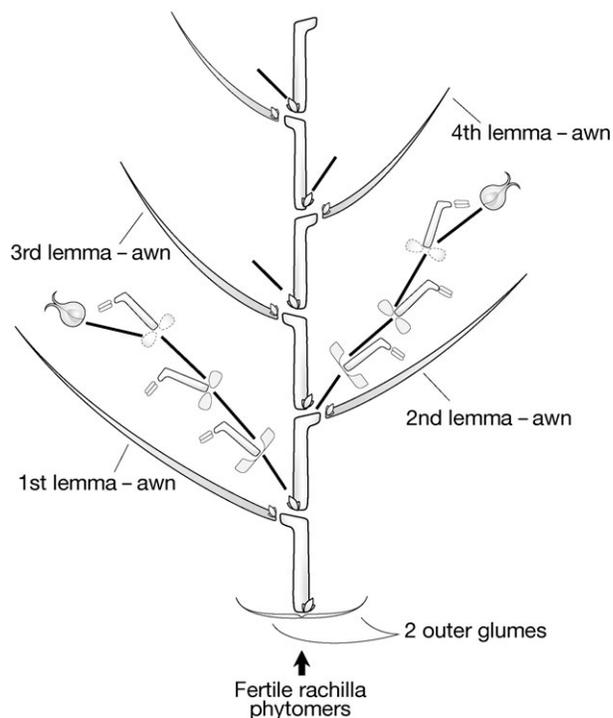
FIG. 10. Phytomeric structure of wheat spikelet.

FEATURES OF THE MODEL, FURTHER ASSUMPTIONS AND CONSEQUENCES

Similarities to the model of Bossinger et al.

As in the model of Bossinger *et al.* (1992), phytomer units in structures such as the culm, rachis and rachilla are added in single file with a 180° orientation between contiguous phytomers. Tillers and roots emerge from buds arising from the lower regions of the phytomer in half nodes near the base of the plant. These phytomers have relatively short internode lengths and are close to the soil surface. Buds of the elongated internodes that make up the culm are normally suppressed. The rachis is a continuation of the shoot with reduced internode lengths. No leaves or roots are produced on the rachis. Each rachis section produces one or more spikelets from the upper half of each node (Fig. 1).

Differences from the model of Bossinger et al.

The main difference with the previous model is that one phytomer unit can explain the entire architecture of the plant. The phytomer can arise in series from an apical meristem or as a branch (meristematic side bud) or from the top of a side arm. Key elements in the new model are (*a*) the activity and suppression of various regions of the phytomer, and (*b*) their associations with linked phytomers. Paired bracts, for example, arise during branching and are essentially dead-end organs, whereas floral structures are associated with three phytomers expressing different activities. The importance of branching, especially in floral structures, is underestimated by Bossinger *et al.* (1992) and, as a

consequence, there is some disagreement in the origins of some organs.

The 2 + 1 organ series

The model divides the organs of the barley plant into paired and single structures arising from either bracts or buds, respectively. All paired structures have a common origin, as outgrowths (possibly modified bracts) at the base of the phytomer unit. Single structures arise as side arms of the phytomer from the lower half of a node. From this, structures can be classed as having paired or single origins (Tables 2 and 3). The relatedness of these structures can then be investigated. Support for this model comes from other phytomer mutants (Table 1). For example, the lemma is in the single origin category and is turned into a leaf-like structure in the leafy lemma (*lel1*) mutant. The junction between the lemma and awn is similar to the sheath–blade juncture because it can be converted into an organ with multiple parts, as in the hooded (*Kap1*) mutant. The model also predicts that buds at the end of side arms produce leaf blades and lemma-awns and stigmas. Smooth awn (*raw*) mutants cause reduced awn barbing and stigma hair numbers on these modified leaf blades. The unbranched style (*ubs4*) mutants reduce both awn length and stigma length.

Bud suppression during transitional developmental phases

Various transitional/end phases can be identified during developmental stages of a plant's life cycle. In barley and other grasses, these include germination, crown formation and tillering, spike development, fertilization and grain growth and caryopsis maturation. Bud suppression and cessation of organ growth appear to occur during and at the end of these phases. For example, stem elongation is often associated with the suppression and cessation of root development and lateral bud development. Leaf numbers are limited by spike development. The basal bud and bracts of the first rachilla phytomer are suppressed during floret development. The lack of a second pair of lodicules in the barley floret may be a consequence of a transition from the production of male to female reproductive organs. Determinate flowering is also brought about by a suppression of bud activity in producing floret structures from rachilla phytomers once the first floret is formed. In the model presented, axillary buds fail to develop in branch phytomers of vegetative organs such as the tiller and rachilla, which is in marked contrast to floral structures where phytomer branching is the basis of floral structures. It is likely that bud dominance and suppression are also effective during embryo development, germination and establishment of the first culm phytomer.

Phytomer units of the culm carry leaf phytomers, but leaves are missing on the rachis and rachilla. In this respect, the lemma can be considered as a modified leaf. Leaf-like structures can be produced from the lower half of the rachis node at which spikelets are attached, in such mutants as *bracteatum* (*bra*) and third outer glume (*trd1*)

(Table 1) in the precise location at which a leaf unit would be expected if it was present.

Developmental associations can be inferred from mutants that have similar effects on related structures. For example, the smooth awn (*raw*) mutants reduce the number and size of barbs on the lemma-awn, but also reduce the number of hairs on the stigma (as a result *raw* mutants are often associated with reduced female fertility). Branching and shortening of the rachilla hairs is caused by the short rachilla hair (*srh1*) mutant, but the rachis margin and the outer glumes also have shortened hairs. The unbranched style (*ubs4*) mutants reduce both stigma length and awn length. Conversely, mutants that affect plant height, awn length, dense and lax spike, grain shape, leaf width and coiling of plant parts often show pleiotropic effects on phytomers in other parts of the plant.

Taxonomic problems and evolutionary aspects

Morphological and anatomical descriptors are traditional tools used to distinguish all levels of taxonomy in the plant kingdom, and these are inextricably linked to phytomer activity. For example, morphological and anatomical descriptors are used to divide the *Hordeum* genus into four sections, *Hordeum*, *Anisolepis*, *Critesion* and *Stenostachys*; the section *Anisolepis* is characterized as lacking auricles, which can be accounted for by phytomer bract suppression. The identification of a barley mutant with fertile multiple florets is a taxonomic *non sequitur* as *Hordeum*, by definition, is a genus with a one-floreted spikelet. Indeterminate/determinate floret production is a result of bud growth regulation in rachilla phytomers. Clearly, genus and species borders can be transgressed by mutation. The ability to produce mutants that transgress long-established taxonomic boundaries emphasizes the relatedness between species and genera, especially since differences which may be caused by single genes. A benefit is that the barley phytomer model can be applied to other related species, such as wheat, to study phytomer evolutionary differences. The barley model is easily adapted to produce the wheat spikelet architecture by assuming indeterminacy of the rachilla. Species variation can be of interest to plant breeders as it may be possible to manipulate one species to attain a trait present in another, thus the development of indeterminate flowering in barley may have the potential to increase barley yields to levels of wheat. Subtleties in phytomer orientation/angle may also give rise to morphological differences between species.

Applications

The structure of phytomers is of basic interest to botany and has the potential to elucidate the evolutionary development of organs, species and genera. The patterns of organ development are determined by the positioning and switching on and off the development of phytomeric units, and the suppression of various phytomeric components can be studied in a more predictive manner.

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