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RESEARCH PAPER

Parallel origins of photoperiod adaptation following dual domestications of common bean

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Abstract

Common bean (*Phaseolus vulgaris* L.) is an important grain legume domesticated independently in Mexico and Andean South America approximately 8000 years ago. Wild forms are obligate short-day plants, and relaxation of photoperiod sensitivity was important for expansion to higher latitudes and subsequent global spread. To better understand the nature and origin of this key adaptation, we examined its genetic control in progeny of a wide cross between a wild accession and a photoperiod-insensitive cultivar. We found that photoperiod sensitivity is under oligogenic control, and confirm a major effect of the *Ppd* locus on chromosome 1. The red/far-red photoreceptor gene *PHYTOCHROME A3 (PHYA3)* was identified as a strong positional candidate for *Ppd*, and sequencing revealed distinct deleterious *PHYA3* mutations in photoperiod-insensitive Andean and Mesoamerican accessions. These results reveal the independent origins of photoperiod insensitivity within the two major common bean gene pools and demonstrate the conserved importance of *PHYA* genes in photoperiod adaptation of short-day legume species.

Keywords: Common bean, florigen, flowering, *Phaseolus*, photoperiod, phytochrome.

Introduction

Common bean (*Phaseolus vulgaris* L.) is a major legume crop that is widely grown around the world as a dry grain and fresh vegetable. It is arguably the most important grain legume for human consumption globally, and throughout large parts of the developing world it is a staple food providing essential protein and nutrients and a significant proportion of complex carbohydrates. The recent sequencing of the common bean genome is beginning to provide new insights into its diversity and origins, and is opening new avenues for crop improvement.

Most recent data suggest that wild *P. vulgaris* originated in Mesoamerica and subsequently spread to Andean South America, giving rise to two distinct wild gene pools by approximately 100 000 years ago (Schmutz *et al.*, 2014; Rendón-Anaya *et al.*, 2017). The substantially lower genetic diversity in Andean relative to Mesoamerican wild germplasm is consistent with the occurrence of a narrow bottleneck, potentially imposed by refugial survival during the last glacial maximum (Bitocchi *et al.*, 2013; Schmutz *et al.*, 2014; Rendón-Anaya *et al.*, 2017). Common bean was independently domesticated from the Mesoamerican and Andean gene pools around 8000 years ago (Gepts *et al.*, 1986; Kwak and Gepts, 2009) and, as in many crop species, key initial steps in domestication of common bean are

likely to have been a reduction in seed dispersal and dormancy (Gepts and Debouck, 1991). Two other developmental features have clearly been important during domestication and early expansion, and are the outcome of selection for adaptation to cultivated environments: these are the acquisition of a determinate growth habit and a reduction in photoperiod sensitivity (Smartt, 1990; Gepts, 2014). Wild bean typically has an indeterminate climbing habit and, similar to many other species originating at low latitudes, a strong short-day requirement for flowering. The existence of numerous landraces with these traits indicates that they were not an impediment for domestication (White and Laing, 1989). However, it is clear that adjustment of photoperiod sensitivity through relaxation of the short-day requirement has been valuable in the selection of varieties for diverse environmental conditions, particularly at higher latitudes, while the determinate growth habit confers significant advantages for plant support, yield synchrony, and harvest efficiency that may have permitted the intensification of cultivation (Gepts and Debouck, 1991; Acosta-Gallegos *et al.*, 1996; Gepts, 2004).

Despite the importance of these adaptive traits, understanding of their genetic basis and evolution has so far been limited. Genetic analyses have defined several loci controlling pod dehiscence and seed dormancy (Koinange *et al.*, 1996; Gioia *et al.*, 2013; Di Vittori *et al.*, 2017) but the underlying genes have yet to be discovered, and only shoot determinacy has been characterized to the molecular level. The determinate growth habit is primarily conditioned by recessive alleles at a single major locus, *Fin* (Norton, 1915), which was recently shown to be an ortholog of the Arabidopsis gene *TERMINAL FLOWER 1* (*TFL*) referred to as *TFL1y* (Repinski *et al.*, 2012). The presence of distinct *TFL1y* mutations in Mesoamerican and Andean germplasm groups and little evidence for introgression support the conclusion that shoot determinacy arose independently through *TFL1y* loss of function in these two gene pools (Kwak *et al.*, 2012).

The genetic and environmental control of flowering in common bean has been of persistent interest. It has long been observed that certain varieties of common bean are insensitive to photoperiod, and a survey by White and Laing (1989) showed three broad categories of photoperiod response in a global bean germplasm collection—insensitive, sensitive, and highly sensitive—which were present in roughly equal proportions. Common bean varieties belonging to these categories are cultivated in different conditions around the world (Beebe, 2012), and photoperiod-insensitive varieties exist in both Andean and Mesoamerican gene pools (White *et al.*, 1992). In addition, temperature has an important relationship with photoperiod sensitivity in common bean, with varieties from cooler locations (e.g. Colombia) being more photoperiod sensitive than those from warmer sites (e.g. Venezuela) at similar latitudes (White *et al.*, 1996). The consensus view from several older classical genetic studies and more recent quantitative trait loci (QTL) analyses is that at least two loci are likely to contribute to this variation. Complete photoperiod insensitivity in certain material is conferred by recessive alleles at a major locus on chromosome 1, termed *Photoperiod* (*Ppd*; Wallace *et al.*, 1993), and crosses between photoperiod insensitive Mesoamerican and Andean lines indicate that *ppd* alleles are likely to be present in both gene pools (Kornegay *et al.*, 1993). As well as *Ppd*, at least one additional locus has been suggested to influence flowering time in a photoperiod- and temperature-dependent manner in several different contexts (Leyna *et al.*, 1982; Kornegay *et al.*, 1993; White *et al.*, 1996; Gu *et al.*, 1998), but these studies have not been reconciled using common material or environments.

In this study we carried out a detailed genetic analysis of flowering time in a wide cross between a Mesoamerican wild accession and an Andean domesticated accession of common bean with contrasting photoperiod sensitivity. Our results clarify the genetic control of this trait, identify a compelling candidate for the *Ppd* locus, and provide molecular evidence to support the independent evolution of photoperiod insensitivity in the two major germplasm groups.

Materials and methods

Plant material and growth conditions

To enable detailed genetic analysis of flowering time in common bean, we generated an F_2 population from a cross between the Mesoamerican wild accession G12873 and cv. Midas, a determinate, photoperiod-insensitive Andean accession previously shown to carry recessive alleles at the *Fin* and *Ppd* loci (Koinange *et al.*, 1996). This population (n=198) was grown under long-day (LD) conditions in a temperature-limited glasshouse in Hobart, Australia, under an 18 h photoperiod consisting of a natural day extended before dawn and after dusk with ~50 µmol m^{-2} s^{-1} light provided by sodium vapour lamps. Flowering time was recorded as the number of days from sowing to the appearance of the first open flower. Progeny were subsequently grown under either the same conditions or 12 h short-day (SD) conditions in an automated phytotron, where they were transferred from day conditions in the glasshouse to night compartments. Where necessary, plants grown in LD conditions were transferred to SD conditions after flowering or on termination of the experiment, to promote flowering and strong pod development.

Near-isogenic lines (NILs) for *Ppd* were developed from progeny of a single recombinant *Fin/Fin Ppd/ppd* F_2 individual that did not flower in LD conditions, by marker-assisted selection of *Ppd* heterozygotes in subsequent generations and visual selection for phenotypic uniformity. Lines segregating *Fin* in a *Ppd* or *ppd* background or *Ppd* in a *fin* background were similarly selected from appropriate recombinants in the F_3 and subsequent generations.

The photoperiod responsiveness of a wider selection of wild and domesticated common bean accessions was assessed in greenhouse trials at Pontevedra, Spain (latitude 42° 24′ 17.99″ N, longitude 8° 38′ 38.2″ W, altitude 40 m above sea level), according to a complete randomized block design with three replications under natural SD (<12 h light, 20–25 °C night–day regime, relative humidity 70–90%) and LD (>12 h light, 20–35 °C night–day regime, relative humidity 50–70%) conditions over 2 years. Each accession was planted in one row, with plant and row spacing of 0.8 m. Crop management was in accordance with local practices.

Mapping, sequencing, and expression analysis

Genes of interest were identified by BLASTp searches on the *P. vulgaris* genome v2.1 in Phytozome (https://phytozome.jgi.doe.gov) using sequences from other legumes and from Arabidopsis as queries. Intron-spanning fragments of selected genes were generated by PCR and sequenced to identify suitable polymorphisms for genotyping. Details of these markers, including their methods of detection, are provided in Supplementary Table S1 at *JXB* online. Genetic maps were constructed using JoinMap4 (Van Ooijen, 2006; Kyazma BV, The Netherlands). PCR from genomic DNA was used to amplify the full-length *PHYA3* gene in

eight overlapping fragments ranging in size from 795 to 1291 bp using primers indicated in Supplementary Table S1. PCR products from diverse accessions were sequenced by conventional Sanger technology using BigDye® Terminator v3.1 chemistry and the Applied Biosystems™ 3500 Series Genetic Analyzer.

Sequence analysis and alignments were performed using Geneious software (https://www.geneious.com). The median-joining haplotype network shown in Fig. 3 was constructed using PopArt (http://popart.otago.ac.nz; Leigh and Bryant, 2015). For the expression experiments shown in Fig. 4, F_5 *Ppd* NILs were grown under the LD or SD conditions described above for Hobart, and comparable leaf material was harvested for RNA isolation 2 and 4 weeks after sowing. RNA extraction, reverse transcription, and real-time PCR analysis were performed as previously described by Liew *et al.* (2009), using primers listed in Supplementary Table S1.

Physiological experiments

Grafting was performed using the apical shoot of 2-week-old seedlings excised at the first (epicotyl) or second internode, and wedge-grafted into the stem of 3-week-old stock plants excised at the third or fourth internode (i.e. above the second or third leaf). Any leaves on the scion that were larger than 10 mm in length were also excised at the time of grafting. Graft junctions were secured with a small ring of silicone tubing and plants were maintained in elevated humidity for the first few days until the grafts were established. Seedling photomorphogenesis was assessed by growing plants for 12 days from sowing under continuous far-red light provided by the 735 nM channel of Heliospectra RX30 lighting units (https://www.heliospectra.com) and filtered through 700 nm cut-off plexiglass. Leaf movements were quantified using ImageJ (https://imagej.nih.gov/ij/) from images obtained with a Brinno TLC200 time-lapse camera (https://brinno.com).

Results

Several interacting loci affect flowering and determinacy in progeny of a wide cross

Under extended natural LD conditions in the greenhouse, the wild parental accession G12873 did not flower for over 140 days, whereas the domesticated parental accession, cv. Midas, flowered at around 35 days after sowing. Fig. 1 shows that the F_2 progeny grown under the same conditions segregated a number of different phenotypes with respect to flowering and determinacy. One group of F_2 individuals (early; n=62) flowered as early as the Midas parent (32–38 days after sowing), whereas two other less well-defined groups flowered in the range 58–80 days (intermediate; n=45) and 87–134 days (late; n=54) after sowing (Fig. 1A). A fourth group (NF; n=37) did not flower before termination of the experiment at 140 days after sowing. This segregation pattern suggests the presence of at least two loci, at which recessive alleles conferring early flowering are contributed by the cv. Midas parent. The proportion of individuals in the early class (62/198; 31%) did not differ significantly from 25% (P=0.55), confirming that this early-flowering phenotype is conferred by a recessive allele at a single locus. This result also shows that this recessive variant is epistatic to other genetic variation for flowering time segregating in the cross.

The majority of the early-flowering F_2 segregants (46/62) were also clearly determinate in habit, consistent with the presence of recessive alleles at the *Fin* locus. However, this

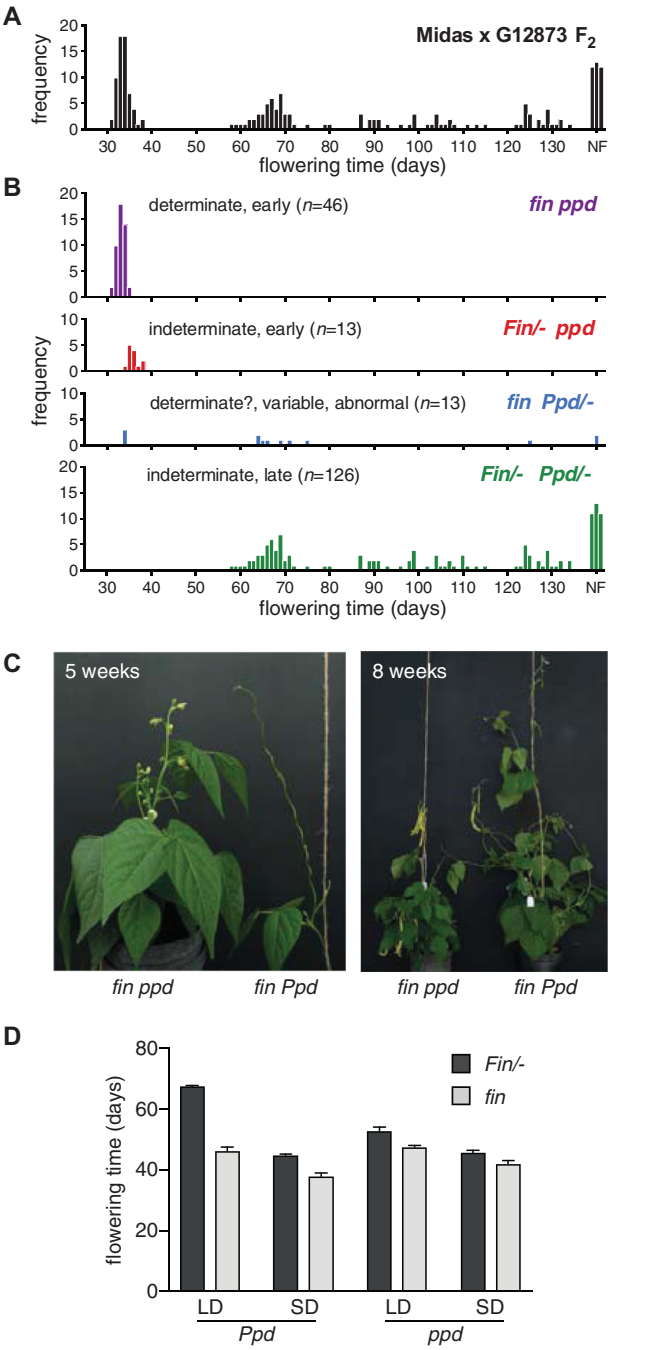

Fig. 1. Genetic analysis of flowering time and determinacy in a wide cross of common bean (*Phaseolus vulgaris* L.). (A) Distribution of flowering time in an F_2 progeny of a cross between the Mesoamerican wild accession G12873 (indeterminate, photoperiod sensitive) and the Andean cultivar Midas (determinate, photoperiod insensitive) grown under 18 h long-day (LD) conditions. The wild parent G12873 and a proportion of F_2 individuals remained vegetative until termination of the experiment 140 days after sowing (non-flowering; NF), whereas cv. Midas flowered between 30 and 35 days after sowing. (B) Data replotted from (A) showing individual distributions of flowering time in the genotypic classes representing different allelic combinations at *Fin* and *Ppd* loci. (C) Images illustrating representative effects of *Ppd* on growth habit in a determinate (*fin*) background under LD conditions, at 5 weeks (left panel) and 8 weeks (right panel) after sowing. In the left panel, only the apical internodes of the *fin Ppd* plant are shown for clarity. (D) Genetic interaction of *Fin* and *ppd* in the control of flowering time under LD (18 h) and SD (12 h) conditions.

early-flowering class also included a small number of individuals (n=13) with an indeterminate growth habit (Fig. 1B). This number is substantially fewer than would be expected in an independent digenic segregation, and points to relatively close linkage between a major locus controlling flowering time and *Fin*, consistent with this being the *Ppd* locus described and mapped by Koinange *et al.* (1996). A small difference in mean days to flowering between the indeterminate (35.9±0.3) and determinate (33.1±0.1) segregants in this class (P<0.001) is consistent with previous reports that, in addition to effects on determinacy, *Fin* also inhibits the transition to flowering (e.g. González *et al.*, 2016; Bhakta *et al.*, 2017).

Interaction of Fin *and* Ppd

Among the intermediate-, later-, and non-flowering segregants (n=136) presumed to carry the dominant *Ppd* allele, the majority (n=117) showed a normal indeterminate phenotype (Fig. 1B), with vigorous growth from the main shoot apex, and flowers (if initiated) opening several nodes behind the apex. Across the population as a whole, we also observed a number of individuals with an unusual growth phenotype, which, although variable in expression, had several consistent features. In these individuals, the shoot apex gradually grew weaker and lost vigor, leaves failed to expand, and the twining of the main stem often intensified into a conspicuous tight coil. Some individuals failed to initiate flowers, while others produced flowers that did not develop; a small number (n=3) initiated flowering relatively early, developed inflorescences that were near normal in structure, and produced one or two open flowers, but showed several abnormalities including flower abortion, failure of pod set, and weak pod growth (Fig. 1C). However, after transfer to SD conditions, these plants showed a more normal growth pattern and in most cases produced mature pods and viable seeds, indicating a strong photoperiod dependence of the phenotype. The proportion of these individuals in the population (n=13/198) was identical to that of the *ppd Fin* class, suggesting that they might represent the *Ppd fin* recombinant class, with the severity of the abnormal phenotypes likely influenced by segregation at additional loci. Genotyping of these individuals with a marker for the *Fin/TFL1y* gene confirmed that they were all homozygous for the Midas allele. As expected, all clearly determinate individuals were also homozygous for the Midas *fin/TFL1y* allele.

This interaction was confirmed in F_3 progeny segregating for *Ppd* in a *fin* background, and for *Fin* in a *Ppd* background, where it became clear that the unusual stem structures observed in the *Ppd fin* F_2 segregants were essentially abnormal terminating secondary inflorescences. In *ppd fin* segregants, the main axes of lateral and terminal secondary inflorescences were typically distinct in structure from the normal vegetative stem, with thicker, shorter internodes and the absence of any twining tendency. In *Ppd fin* segregants, however, secondary inflorescences retained features of indeterminate stems, with elongated internodes and partial retention of the twining tendency (Fig. 1C). Analysis of F_3 progeny also confirmed the effect of *fin* on flowering time, and revealed that this effect could be relatively large in certain photoperiod-sensitive *Ppd* genetic backgrounds (Fig. 1D).

Mapping identifies the phytochrome A gene PHYA3 *as a strong candidate for* Ppd

The *Fin* locus was previously identified as the *TFL1y* gene (Kwak *et al.*, 2012), which now specifies its precise location on chromosome 1 at 45.56 Mb in v2.1 of the *P. vulgaris* genome (Phvul001G189200). To locate *Ppd* on the physical map, we scanned this genomic region and identified several genes potentially related to control of flowering time and photoperiod responsiveness. We previously observed that this region is syntenic with the region of soybean chromosome 19 containing the *Dt1* determinacy locus (Glyma19g194300) and *E3* maturity locus (Glyma19g224200) (Weller and Ortega, 2015). *E3* is a *PHYTOCHROME A* (*PHYA*) homolog (*PHYA3*) and recessive alleles confer early flowering under LD conditions (Cober *et al.*, 1996; Watanabe *et al.*, 2009), implicating the bean *E3/PHYA3* ortholog (Phvul.001G221100) as a strong candidate for *Ppd*. In the same general region of chromosome 1, we also identified orthologs of the circadian clock gene *ELF4* (Phvul.001G242900), which is known to affect photoperiod responsiveness in the LD plants pea and Arabidopsis (Doyle *et al.*, 2002; Liew *et al.*, 2009), and *EID1* (Phvul.001G207000), which has been reported to affect light signaling through PHYA in Arabidopsis (Dieterle *et al.*, 2001) and to influence circadian rhythms in tomato (Müller *et al.*, 2016). Markers for these three genes and for *TFL1y/Fin* were scored in the F_2 population, yielding a genetic map consistent with their physical locations (Fig. 2A). Cosegregation of markers with flowering time revealed several clear recombinations with *EID1* and *ELF4* that excluded these genes as candidates for *Ppd* and identified *PHYA3* as the candidate most closely linked to the early-flowering phenotype (Fig. 2A).

Three individuals scored as early flowering were heterozygous for the *PHYA3* marker and initially appeared to be possible recombinants between *PHYA3* and *Ppd*. However, these individuals showed defects in shoot growth, inflorescence structure, and flower/pod development typical of the *fin Ppd*/- recombinant class, despite initially producing one or two open flowers. We considered that the early flowering of these three plants most likely reflected an impenetrance of the *Ppd*/- late-flowering phenotype, potentially due to the influence of other loci. Excluding these three individuals, there was no evidence of recombination between *Ppd* and *PHYA3*. In total, codominant marker scores identified 40 recombinations between *Fin/TFL1y* and *PHYA3*, corresponding to a recombination frequency of 20.2% and a Kosambi map distance of 21.4 cM.

On the basis of these genotyping results, we selected non-flowering F_2 individuals homozygous for the wild-type *Fin* allele and heterozygous for the *PHYA3* marker. These plants were induced to flower and produce seed by transfer to SD conditions. Analysis of their F_3 progeny under LD conditions showed that, as expected, some families segregated only non-flowering and early-flowering plants, whereas others segregated an additional intermediate-/late-flowering class (Fig. 2B). In contrast, F_3 families derived from non-flowering F_2 plants homozygous for the G12873 *PHYA3* allele were either uniformly non-flowering or segregated individuals with an intermediate flowering phenotype (60–80 days). These results

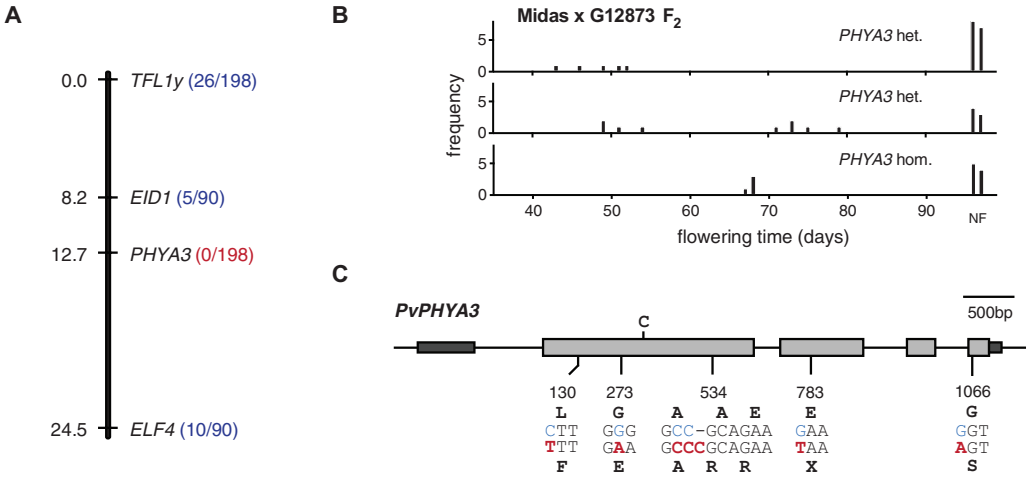

Fig. 2. Mapping of the *Ppd* locus and evaluation of the *PHYA3* gene as candidate for *Ppd*. (A) Genetic map for the *Fin-Ppd* region of chromosome 1 showing the position of candidate genes for *Ppd* relative to *Fin/TFL1y*. Numbers on the left represent map distance in cM; numbers the on right represent the number of recombinants with the *Ppd* locus relative to the total number of individuals genotyped, for each marker. (B) Distribution of flowering time in F_3 families derived from non-flowering segregants (either heterozygous or homozygous for the G12873 allele of *PHYA3* as indicated) in the G12873 × Midas F_2. Representative families are shown to illustrate the individual effects of segregation at *Ppd* and a second locus conferring intermediate flowering time. (C) Diagram of the *PHYA3* gene showing details of significant polymorphisms identified in different early-flowering accessions.

support the conclusion that in addition to *Ppd,* cv. Midas differs from G12873 in at least one other major locus influencing photoperiod sensitivity, and the effects of this locus are hypostatic to the *ppd* allele.

Photoperiod-insensitive early flowering is associated with mutations in PHYA3

In view of the proximity of the *Ppd* locus and the *PHYA3* gene, and the fact that the soybean *PHYA3* ortholog functions in photoperiod sensitivity, we sequenced the *PHYA3* gene from G12873 and Midas. We identified 12 single nucleotide polymorphisms (SNPs) between these genotypes across the complete coding sequence, including 10 synonymous substitutions, one non-synonymous substitution (Q890H), and the insertion of a single cytosine in codon 534 of exon 1 (Supplementary Table S3, Fig. 2C). This insertion predicts truncation of the PHYA3 protein and loss of the C-terminal histidine kinase regulatory domain essential for phytochrome function (Rockwell *et al.*, 2006), similar to phyA null mutants in Arabidopsis and pea (Dehesh *et al.*, 1993; Weller *et al.*, 2004). The amino acid at position 890 is located in a region of relatively low conservation between the PAS and histidine kinase domains and shows variability across angiosperm PHYA sequences that includes the presence of both Q and H residues (Rockwell *et al.*, 2006). It therefore seems that the insertion/frameshift is more likely to impair PHYA3 function, and as such provides the more plausible basis for the *ppd* early-flowering phenotype.

To examine whether this mutation might be present in other early-flowering accessions, and to gain a broader view on *PHYA3* sequence diversity, we sequenced the *PHYA3* gene from a diverse selection of 52 other wild and domesticated accessions representing both Mesoamerican and Andean germplasm groups (Supplementary Table S2). As shown in Supplementary Table S3, these analyses identified 61 polymorphic sites across the *PHYA3* coding sequence, and defined 23 haplotypes. Results of phylogenetic analysis (Fig. 3) showed that these haplotypes fell into three distinct groups corresponding to Mesoamerican wild (MW), Mesoamerican domesticated (MD), and Andean identity. Whereas individual Andean wild (AW) haplotypes were distinguished from Andean domesticated (AD) haplotypes by at most two SNPs across the entire coding sequence (including introns), MW and MD haplotypes overall differed at 22 SNPs and one 3 bp indel, of which 9 SNPs were uniquely present in MW accessions and the remaining 14 differences were common to the MW and Andean lines. Eleven SNPs were shared between MW and MD lines (Supplementary Table S3).

The Midas haplotype (haplotype 20) was shared with four other accessions that, like cv. Midas, were all early-flowering with a type I determinate growth habit. We also found that five early-flowering Mesoamerican accessions, including Jamapa and ICA Pijao, carried a nonsense mutation in exon 2 of *PHYA3* that, like the Midas insertion, would be expected to truncate and seriously impair the function of the PHYA3 protein (Fig. 2C). Across the other accessions, we identified nine non-synonymous substitutions. Three other photoperiod-insensitive determinate Andean accessions (haplotypes 17–19) shared a missense mutation in exon 1 (G273E) with potential functional significance. Residue G273 is located in the N-terminal chromophore-binding P3/GAF domain, and is perfectly conserved across 122 plant, fungal, and prokaryote phytochromes (Rockwell *et al.*, 2006; Supplementary Fig. S1). These accessions also carried a substitution of another exon 1 residue conserved across all PHYA-type phytochromes (L130F; Supplementary Fig. S1), and this polymorphism was shared with another insensitive accession, PHA1666. Another group of photoperiod-insensitive Andean accessions (haplotypes 21–23) carried a conservative substitution of a residue (G1066), which, despite being highly conserved in general across phyA and phyB-type phytochromes (Supplementary Fig. S1), shows

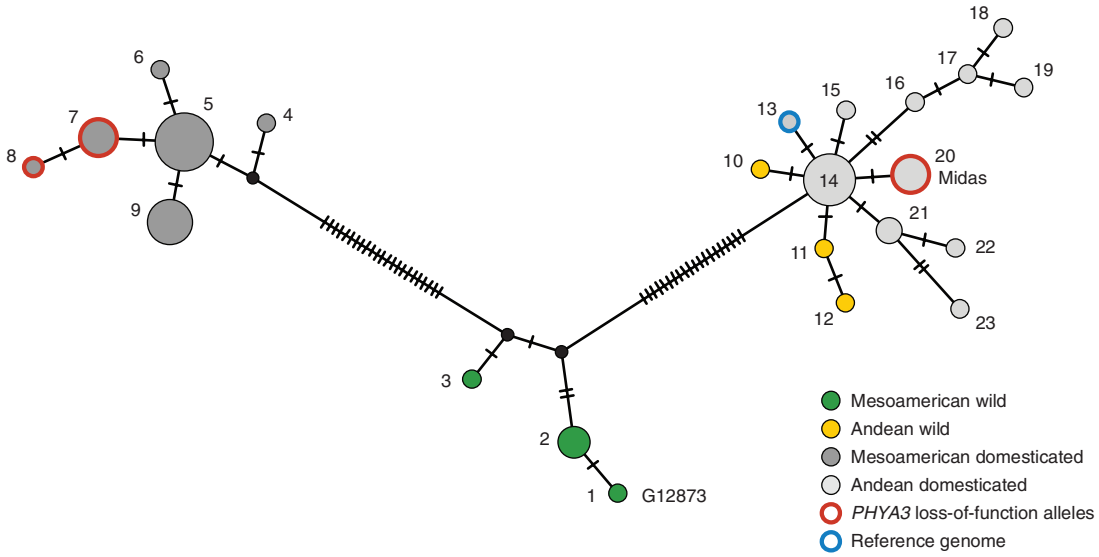

Fig. 3. Median-joining network illustrating the relationships among 23 *PHYA3* haplotypes identified in a selection of 54 diverse wild and domesticated accessions from both major germplasm groups of common bean. Predicted loss-of-function mutations in haplotypes 7 and 8 (nonsense mutation in codon 783) and in haplotype 20 (1 bp insertion/frameshift at codon 534) are indicated by red outlines.

the same substitution in soybean GmPHYA3, arguing against a major effect on PHYA3 function. In addition, we identified two early-flowering Mesoamerican accessions (PHA0078 and PHA0686) that carried only synonymous changes in *PHYA3* relative to wild accessions and shared the same haplotype (5) as other photoperiod-sensitive domesticated accessions. We crossed these lines to cv. Midas or PHA1875 (both haplotype 20) to examine the potential allelism with the *ppd* mutation, and found that the F_1 progeny were very early-flowering under LD conditions, similar to both parents. This result suggests that PHA0078 and PHA0686 might carry loss-of-function *PHYA3* alleles resulting from mutation outside the *PHYA3* gene.

Early flowering of the ppd *genotype is associated with elevated expression of several* FT *genes*

PHYA has a well-established role in control of flowering in several species, including Arabidopsis, pea, and soybean (Valverde *et al.*, 2004; Weller *et al.*, 2004; Liu *et al.*, 2008; Watanabe *et al.*, 2009). Similar to many other genes influencing flowering time, the effects of *PHYA* are mediated at least in part by changes in the level of expression of genes in the *FT* family encoding mobile florigen proteins (Kong *et al.*, 2010). To confirm the existence of a similar mechanism of action for *Ppd*, we identified *FT* genes in the common bean genome and compared their expression in the *Ppd* and *ppd* genotypes. As shown in Supplementary Fig. S2, common bean has five *FT* genes that belong to the three major clades of the *FT* family previously identified by Hecht *et al.* (2011) and Nelson *et al.* (2017), with the single genes *FTa1*, *FTa3*, *FTb1*, *FTb2*, and *FTc* corresponding to five of the six pairs of *FT* homeologs described in soybean (Kong *et al.*, 2010; Wu *et al.*, 2017). As in soybean and other legumes, the *FTa1/FTc* and *FTb1/b3* genes are arranged in tandem. However, there was no evidence in the *P. vulgaris* v2.1 reference genome for the tandem duplication of the *FTa3* gene, unlike in soybean, where tandem duplications are present in the corresponding regions of chromosome 16 (*FT2a/FT2b*) and chromosome 2 (*FT2c/FT2d*) (Kong *et al.*, 2010; Wu *et al.*, 2017). In soybean, the *FTb* clade gene *FT4* has acquired a repressive role suggested to derive from amino acid changes in an external loop that is critical for *FT* signaling (Zhai *et al.*, 2014), whereas its homeolog *FT1b* has a conventional sequence in this region, which is shared by the bean ortholog *FTb3*. None of the bean *FT* genes show any conspicuous differences from their legume orthologs in conserved regions, suggesting that all these genes are likely to promote flowering (Supplementary Fig. S3).

In order to examine the specific physiological effect of *ppd* on *FT* gene expression, we selected a pair of NILs from F_3 families (described above) that segregated only at *Ppd* but not at *Fin* or the putative second flowering locus. The results in Fig. 4A show that two of the five bean *FT* genes (*FTa3* and *FTc*) were expressed at a significantly higher level in leaf tissue of 4-week-old *ppd* plants than in equivalent *Ppd* plants, under both LD and SD conditions. This is similar to soybean, where the respective homologs, *FT2a* and *FT5a*, are thought to be the main photoperiod-regulated *FT* genes, are induced by SD, and show derepressed expression in *e3* and *e4* mutants (Kong *et al.*, 2010) (Fig. 4A). There was some indication that the expression of two other genes, *FTb1* and *FTa1*, might also be elevated in the *ppd* genotype, but no statistically significant differences were observed. The fifth gene, *FTb3*, was expressed at a similar level in both genotypes regardless of photoperiod.

We also compared the ability of *Ppd* and *ppd* leafy stocks to stimulate flowering of wild G12873 under LD conditions (Fig. 4B–D), and found that *ppd*, but not *Ppd*, stocks were effective, causing the initiation of flowers at approximately 11 nodes on the main shoot (from 8.9±0.3 to 18.7±1.0 nodes above the graft) before reversion of axillary structures to vegetative buds. However, in most cases, the initiated flowers showed arrested growth at a very early stage (Fig. 4E), suggesting that a stronger florigen source would be required to sustain full flower

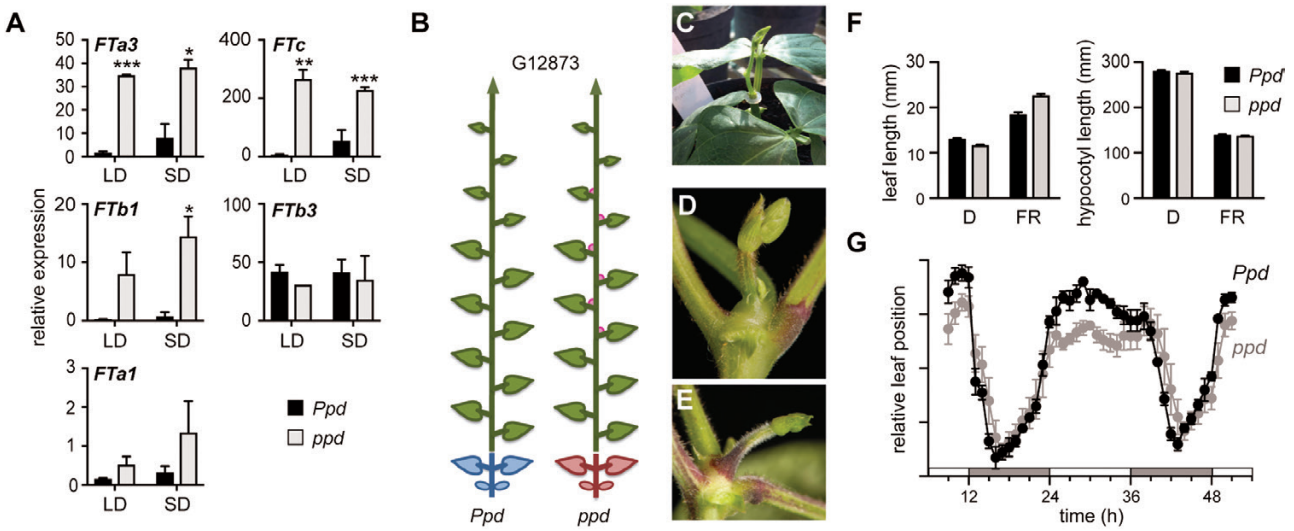

Fig. 4. Physiological effects of *Ppd*. (A) The *ppd* allele is associated with increased expression of several *FT* genes. Transcript levels were determined in expanded leaf tissue harvested at 4 h after dawn from 4-week-old plants of *Ppd* and *ppd* near-isogenic lines (NILs) grown under either long-day (LD) or short-day (SD) conditions. Each sample consisted of pooled material from two plants, and each data point represents mean ±SE for n=3. Statistically significant differences in mean expression between *ppd* and *Ppd* lines are indicated: *P=0.05, **P=0.01, ***P=0.001. (B–E) Graft-transmissible effects of *ppd* on the initiation of flowering under LD conditions. (B) Diagram illustrating the experimental comparison. Scions of G12873 were grafted to leafy stocks of *Ppd* and *ppd* NILs using wedge-type I-grafts (C) and maintained in LD conditions. Scions grafted to *Ppd* stocks remained vegetative (D), whereas those grafted to *ppd* stocks showed transient initiation of flowering (E) for 10–12 nodes on the main stem. (F) The *ppd* allele does not impair seedling responses to far-red light. Length of leaflet from the first primary leaf (left panel) and hypocotyl length (right panel) in 12-day-old seedlings of *Ppd* and *ppd* NILs grown from sowing in complete darkness or under 10 μmolm^{-2}s^{-1} continuous far-red light. (G) The *ppd* allele does not affect circadian rhythms of leaf movement under continuous white light. Seedlings of *Ppd* and *ppd* NILs were grown for 10 days from sowing under a 12 h photoperiod (150 μmolm^{-2}s^{-1}) at 23 °C before transfer to continuous light (50 μmolm^{-2}s^{-1}) at zeitgeber time 0. Data represent mean ±SE for n=3.

development or that additional factors local to the developing bud might also be needed.

PPD *has no apparent effect on photomorphogenesis or circadian rhythms*

In addition to effects on flowering, phyA photoreceptors have a well-established role in the control of seedling photomorphogenesis, where they exclusively control the inhibition of stem elongation and promotion of leaf expansion under continuous far-red light, and share control with other photoreceptors under red and blue light (Weller *et al.*, 2001a, b; Franklin and Quail, 2010). However, a comparison of seedling de-etiolation in the *Ppd*/*ppd* NILs revealed no clear difference in hypocotyl elongation or leaf expansion (Fig. 4F). In soybean, loss of *E4*/*PHYA2* gene function significantly impairs de-etiolation under far-red light, but a strong *e3* mutant had no effect, even in an *e4* background, suggesting the possible subfunctionalization of these proteins with respect to flowering control and photomorphogenesis (Liu *et al.*, 2008). A second *PHYA* gene orthologous to the soybean *PHYA1*/*PHYA2* (*E4*) homeolog pair is present in common bean (*PvPHYA1*) and other phaseoloid legumes, and it is possible that a similar subfunctionalization has occurred in these species. Comparison of PHYA sequences to identify possible signatures of this subfunctionalization revealed unique substitutions of two highly conserved residues adjacent to the chromophore attachment site (C330) common to phaseoloid PHYA3 orthologs (A327P and S341I in PvPHYA3), relative to paralogous PHYA1 sequences and a wide range of other PHY sequences (Supplementary Fig. S1).

The importance of the circadian clock for photoperiod responsiveness is also well established. In Arabidopsis and several other species, important components of the photoperiod response mechanism are directly or indirectly regulated by the clock, and many clock mutants have altered photoperiod sensitivity (Bendix *et al.*, 2015). In Arabidopsis, the PHYA photoreceptor has two roles—one downstream of the clock controlling the stability of the key *FT* activator CO (Valverde *et al.*, 2004), and another in which it participates in entrainment of the clock by light (Millar, 2003). We therefore examined whether the effects of *Ppd* on photoperiod response might be associated in some way with effects on clock function. To test this, we compared the rhythmic leaf movement of *Ppd* and *ppd* NILs following transfer to continuous light after a 12 h entraining photoperiod. However, as shown in Fig. 4G, we found no evidence of any difference between *Ppd* and *ppd* NILs, with both genotypes anticipating dawn in a similar manner, suggesting that the effect of *Ppd* on flowering is unlikely to derive from a primary effect on the circadian clock.

Discussion

In common bean, as in many crops, understanding the effects of photoperiod on flowering and reproductive growth is critical to efficient breeding and targeting of germplasm to different environments. Here, we present evidence that the *Ppd* gene, a major determinant of photoperiod sensitivity and broad adaptation in common bean, encodes a phytochrome A photoreceptor, PHYA3. The *PHYA3* gene is tightly linked to *Ppd* (Fig. 2A), and

a clearly deleterious *PHYA3* sequence variant is associated with early flowering and photoperiod insensitivity in several accessions of Andean origin, while a second distinct deleterious allele is present in certain early-flowering Mesoamerican accessions (Figs 2C and 3; Supplementary Table S2). These results support the earlier case made for the potential importance of *PHYA3* as a *Ppd* candidate based on synteny with soybean (Weller and Ortega, 2015), and its association with flowering time in a diversity panel of Andean material (Kamfwa *et al.*, 2015).

Structure–function relationships are particularly well understood for the phytochromes owing to their prominence in early molecular genetic analyses. Evidence from mutant and transgenic studies in several species indicates that a C-terminally truncated molecule lacking the histidine kinase related domain has no biological activity (Rockwell *et al.*, 2006), establishing a strong case that the frameshift and nonsense mutations identified here are likely to seriously impair *PvPHYA3* function. This case is further strengthened by comparison with soybean, where mutations in the single functional ortholog *E3* (*GmPHYA3*) also confer adaptively significant early flowering and reduced photoperiod sensitivity (Watanabe *et al.*, 2009). In addition, the naturally occurring *e3* allele carries a large deletion spanning exon 4, while an induced mutant *e3* allele has sustained a deletion and frameshift in the second half of exon 1 very similar in effect to the Midas allele of *PvPHYA3* (Watanabe *et al.*, 2009).

Our preliminary survey of diversity in the *PvPHYA3* gene revealed three distinct groups of haplotypes corresponding to MW, MD, and Andean material (Fig. 3), broadly consistent with groupings evident in multiple-marker analyses (e.g. Kwak and Gepts, 2009; Rossi *et al.*, 2009). The similarity of AW and AD accessions (Fig. 3) was consistent with previous observations of a strong predomestication bottleneck in the Andean lineage and three-fold weaker reduction in diversity associated with domestication in the Andean germplasm relative to the Mesoamerican germplasm (Bitocchi *et al.*, 2013). However, the apparent strong divergence of the MD material from the four MW accessions included in our study may be a consequence of the fact that we did not systematically sample the diversity present in the Mesoamerican wild gene pool, and may not have included material from the subgroup of Mexican wild germplasm most closely related to the MD group.

The majority of genetic studies featuring the *Ppd* locus have focused on photoperiod insensitivity in lines of Andean origin, notably Redkloud (Wallace *et al.*, 1993) and Midas (Koinange *et al.*, 1996). However, photoperiod insensitivity is common in both Andean and Mesoamerican gene pools (White and Laing, 1989), and Kornegay *et al.* (1993) described a clear case of non-complementation in crosses between Redkloud and an insensitive Mesoamerican accession, pointing to the relevance of *Ppd* in Mesoamerican material. Our results clearly demonstrate the origins of the Midas and Jamapa variants within distinct Andean and Mesoamerican *PHYA3* haplotype groups (Fig. 3), and hence support the conclusion that the *Ppd*-dependent photoperiod-insensitive habit has arisen independently in the two major bean gene pools.

Given the relatively small number of accessions included in our survey, it is unlikely that we have captured all of the functionally significant variation in the *Ppd* gene. While the occurrence of these two haplotypes in multiple accessions suggests that they could be responsible for a significant proportion of the photoperiod insensitivity within the common bean germplasm, we did identify three other cases that might represent additional functional variants. The most convincing of these is the substitution of a highly conserved glycine by glutamate in the P3/GAF chromophore-binding domain, but a role for two other substitutions (L130F in the P2/PAS domain and G1066S towards the C-terminus of the P4/PHY domain) cannot be discounted (Fig. 2; Supplementary Table S2, Supplementary Fig. S1). More detailed genetic analyses will clearly be needed to clarify the relationship between *PHYA3* sequence variation and flowering time in these accessions, and more widely in global bean germplasm.

Extensive characterization of photoperiod responsiveness in a large collection of domesticated bean germplasm by White and Laing (1989) identified three major phenotypic groups—day-neutral, intermediate, and strongly responsive—a distribution interpreted to indicate genetic control by a simple two-gene model. This interpretation was supported by the genetic analysis of Kornegay *et al.* (1993) and by our data, which indicate recessive epistasis of *Ppd* over a second locus conferring an intermediate response (Figs 1 and 2). Intermediate response types occur in both Mesoamerican and Andean material, but it is currently unclear whether they share the same genetic basis. QTL and association analyses have suggested the existence of multiple loci influencing flowering time and reproductive duration in addition to *Ppd*; these loci are distributed across 8 of the 11 common bean chromosomes (Koinange *et al.*, 1996; Gu *et al.*, 1998; Tar'an *et al.*, 2002; Beattie *et al.*, 2003; Blair *et al.*, 2006; Pérez-Vega *et al.*, 2010; Moghaddam *et al.*, 2016; Bhakta *et al.*, 2017), but there is currently no clear consensus on their relative importance or relevance in the two domesticated gene pools.

Interpretation of QTL effects in the region of *Ppd* itself is complicated by the relatively close location of the *Fin* locus. While the proximity of these loci has often been noted, their relationship and potential interaction has not been directly addressed, although several authors (e.g. Koinange *et al.*, 1996; Bhakta *et al.*, 2017) have alluded to distinct QTLs for flowering time over the *Fin* and *Ppd* loci. *Fin* is one of three common bean orthologs of Arabidopsis *TFL1* (Repinski *et al.*, 2012), a gene that, in addition to controlling meristem determinacy, also controls flowering time, and *tfl1* mutants are both determinate and early-flowering (Shannon and Meeks-Wagner, 1991). We were able to examine *fin* effects independently of *ppd* and show that *fin* is indeed able to promote flowering in its own right. This effect is relatively small under conditions where flowering is early, such as under SD conditions or in the presence of *ppd*, but can be substantial under longer photoperiods in a photoperiod-sensitive background (Fig. 1D). This observation may provide an explanation for reports of flowering time QTLs in the *Fin*/*Ppd* region of chromosome 1 even in populations not segregating for *Ppd* (e.g. González *et al.*, 2016; Bhakta *et al.*, 2017). *TFL1* genes in some plant systems are targets of flowering time pathways (Strasser *et al.*, 2009; Iwata *et al.*, 2012; Rantanen *et al.*, 2015; Serrano-Mislata *et al.*, 2016)

and it is possible that in bean *Ppd* (and other flowering time genes) could in part influence growth habit through regulation of *Fin*. However, the fact that photoperiod and *Ppd* action can modify shoot and inflorescence growth, flower opening, and pod set in *fin* genotypes also suggests the importance of other genes that may act in parallel with *Fin* to regulate determinacy and reproductive development.

The dual domestication events in common bean present a relatively rare opportunity to examine parallel evolution of key adaptive traits. Our results extend those of Kwak *et al.* (2012) on determinacy to show that a second major adaptation, photoperiod insensitivity, has also been achieved in the two bean gene pools through different modifications of the same gene. This may indicate an underlying genetic architecture in which loss of *TFL1y* and *PHYA3* function provide optimal solutions. In the case of determinacy, this is not particularly surprising, since the role of *TFL1* genes is central and widely conserved (Wickland and Hanzawa, 2015). However, although the involvement of phytochromes in responses to photoperiod is also well established, phyA generally has a relatively minor role that is largely restricted to far-red-rich light, shared with cryptochromes and subsidiary to phyB-type phytochromes (Takano *et al.*, 2005). In legumes, however, phyA appears to be more centrally important for responses to photoperiod, because in both pea and soybean, *phyA* mutants have major effects on flowering. In soybean, photoperiod sensitivity is progressively reduced by mutations in *GmE3/PHYA3* and its paralog *E4* (Cober *et al.*, 1996; Jiang *et al.*, 2014). This prominence of *E3* and *E4* is reflected in their strong repressive effect on the expression of *FT* genes (Xia *et al.*, 2012; Lu *et al.*, 2017), a feature also shared by *Ppd* (Fig. 4).

In its Mesoamerican center of domestication, bean was likely to have been grown together with maize (Zizumbo-Villarreal and Colunga-García Marin, 2010), and it has been suggested that in such a scenario the early selective pressure on determinacy may have been lower than in the Andean center, where domestication probably occurred without maize (Kwak *et al.*, 2012). This suggests that the timing of these innovations may have been different in the two gene pools, an idea that should now be possible to test by examining the relationship between sequence diversity at *TFL1y* and at *PHYA3*.

Conservation in the genetic basis for flowering time adaptation is increasingly well documented, with examples including the role of *PRR37* in cereals (Murphy *et al.*, 2011; Fjellheim *et al.*, 2014) and the *FLC* gene in brassicas (Ridge *et al.*, 2015; Irwin *et al.*, 2016; Bouché *et al.*, 2017). We previously described the recruitment of orthologous genes for photoperiod adaptation in long-day legumes, where mutations in orthologs of the circadian-clock-related *ELF3* gene confer early flowering and reduced photoperiod sensitivity in pea, lentil, and chickpea (Weller *et al.*, 2012; Ridge *et al.*, 2017). Our characterization of the bean *Ppd* locus provides the first evidence for a similar conservation of adaptive mechanisms in the short-day legumes, and suggests that *PHYA* genes might also be important in other species in this group. Knowledge on conserved gene functions in other legumes should also help in future studies of adaptation in common bean, whose diploid nature, small genome, and well-characterized genetic diversity make it an attractive system for functional studies in domestication and crop evolution.

Supplementary data

Supplementary data are available at *JXB* online.

Table S1. Primer details.

Table S2. Details of *Phaseolus vulgaris* accessions used for analysis of *PHYA3* diversity.

Table S3. Details of *PvPHYA3* haplotypes.

Fig. S1. Phytochrome protein alignments.

Fig. S2. Maximum-likelihood tree illustrating relatedness of legume PEBP-family proteins.

Fig. S3. Alignment of legume PEBP amino acid sequences.

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