Light Regulation of Gibberellin Biosynthesis in Pea Is Mediated through the COP1/HY5 Pathway*†

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Light regulation of gibberellin (GA) biosynthesis occurs in several species, but the signaling pathway through which this occurs has not been clearly established. We have isolated a new pea (Pisum sativum) mutant, long1, with a light-dependent elongated phenotype that is particularly pronounced in the epicotyl and first internode. The long1 mutation impairs signaling from phytochrome and cryptochrome photoreceptors and interacts genetically with a mutation in LIP1, the pea ortholog of Arabidopsis thaliana COP1. Mutant long1 seedlings show a dramatic impairment in the light regulation of active GA levels and the expression of several GA biosynthetic genes, most notably the GA catabolism gene GA2ox2. The long1 mutant carries a nonsense mutation in a gene orthologous to the ASTRAY gene from Lotus japonicus, a divergent ortholog of the Arabidopsis bZIP transcription factor gene HY5. Our results show that LONG1 has a central role in mediating the effects of light on GA biosynthesis in pea and demonstrate the importance of this regulation for appropriate photomorphogenic development. By contrast, LONG1 has no effect on GA responsiveness, implying that interactions between LONG1 and GA signaling are not a significant component of the molecular framework for light–GA interactions in pea.

INTRODUCTION

Light has profound effects on plant growth and development, and there is widespread interest in understanding the molecular basis of these effects. One general mechanism by which light acts is the regulation of plant hormone production (Symons and Reid, 2003), and changes in hormone levels occur in several different light responses. Examples include changes in gibberellin (GA) and abscisic acid levels during light-regulated seed germination (Oh et al., 2006; Seo et al., 2006) and changes in auxin levels in response to simulated shade (Tao et al., 2008).

In deetiolating seedlings, changes in expression of hormone biosynthetic genes in response to light or specific photoreceptor activity have been identified in several transcriptional profiling studies in Arabidopsis thaliana (Ma et al., 2001; Tepperman et al., 2001; Folta et al., 2003), and this is generally understood to imply that changes in actual hormone levels also occur during, and contribute to, the process of deetiolation. However, the clearest example of light-regulated hormone biosynthesis during deetiolation comes from pea (Pisum sativum), where transfer of etiolated pea seedlings to light induces a rapid drop in levels of the active GA (GA4), to <10% of dark levels within 4 h (Ait-Ali et al., 1999; Gil and García-Martínez, 2000; O’Neill et al., 2000; Symons and Reid, 2003). This drop is associated with changes in transcript levels of GA biosynthesis genes and depends on the activity of the phyA and cry1 photoreceptors (Reid et al., 2002; Foo et al., 2006). A similar but somewhat less dramatic drop in active GA (GA4) content has recently been shown to occur in Arabidopsis (Zhao et al., 2007; Symons et al., 2008) and is also temporally correlated with changes in expression of GA biosynthesis genes (Zhao et al., 2007; Alabadi et al., 2008).

Despite the apparent importance of these changes for the inhibition of elongation in deetiolating seedlings, relatively little is known about how they are achieved. One of the earliest molecular responses to light is the transcriptional induction or repression of a small group of genes encoding transcription factors, including the PIF family of bHLH proteins, the bZIP protein HY5, and the myb protein CCA1 (Tepperman et al., 2001, 2004). Transcriptional profiling shows that these genes in turn regulate the expression of a much broader range of genes, including a significant number involved in hormone biosynthesis or signaling. Among these, auxin signaling genes are particularly prominent, but genes for ethylene, cytokinin, and GA biosynthesis also feature (e.g., Monte et al., 2004; Sibout et al., 2006; Lee et al., 2007). These observations suggest that light effects on hormone synthesis and signaling depend on these master regulators. Several recent reports have identified specific interactions between light and hormone signaling pathways (Khanna et al., 2007; Alabadi et al., 2008; Chen et al., 2008; de Lucas et al., 2008; Feng et al., 2008), but relatively few studies have addressed the mechanisms by which hormone biosynthesis is regulated.

One of the main insights into light regulation of GA biosynthesis to date has come from studies of germinating Arabidopsis seeds by Oh et al. (2006), who showed that induction of GA biosynthesis by light is achieved through degradation of the bHLH transcription factor PIF1/PIL5, a transcriptional repressor of GA biosynthetic genes. As PIF proteins are bound to and targeted for degradation by activated phytochromes (Castille et al., 2007),
this represents a relatively direct mechanism in which light activates GA biosynthesis through repression of a repressor. In deetiolating seedlings, however, light acts to repress rather than activate GA biosynthesis (Symons et al., 2008), and the mechanism underlying this effect is still unclear.

The Arabidopsis HYS protein has an important role in light-regulated development. Mutants for HYS were first isolated on the basis of a long-hypocotyl phenotype under several different monochromatic light conditions and were subsequently shown to impair a range of light responses in shoot and root (Koornneef et al., 1980; Oyama et al., 1997). More recently, HYS has also been implicated in the light regulation of hormone responses, based on findings that HYS and the related protein HYH regulate numerous genes involved or implicated in signaling from plant hormones, including auxin, cytokinin, and abscisic acid (Holm et al., 2002; Cluis et al., 2004; Sibout et al., 2006; Chen et al., 2008). Several studies have also reported the reciprocal regulation of HYS by plant hormone action, including the regulation of HYS protein by cytokinin (Vandenbussche et al., 2007) and by members of the DELLA family of GA signaling proteins (Alabadı et al., 2008).

In this article, we report on the isolation and functional characterization of the pea LONG1 gene. This gene is a representative of a group of divergent legume HYS orthologs previously characterized from soybean (Glycine max), fava bean (Vicia faba), and Lotus japonicus (Cheong et al., 1998; Nishimura et al., 2002b). We used a presumed null long1 mutant containing a premature stop codon to show that LONG1 has roles in deetiolation, flowering, and root system development and that it interacts genetically with LIP1, the pea ortholog of Arabidopsis COP1 (Sullivan and Gray, 2000). We also examined the possibility that elongation of the long1 mutant results from elevated production of GAs. Our results show that LONG1 has a major role in mediating the light regulation of GA biosynthesis that occurs in deetiolating seedlings and thus provide a new insight into the mechanisms by which light and GAs interact during deetiolation.

RESULTS

Genetic Analysis of long1, a New Elongated Pea Mutant

In screens of ethyl methanesulfonate–mutagenized pea seedlings of wild-type cv Torsdag under white light, we isolated a new, recessive mutant with an extremely elongated epicotyl and early internodes (Figures 1A and 1B). This mutant was not allelic with other elongated mutants and apparently defined a novel locus, which we designated LONG1. In various crosses, we observed tight linkage between LONG1 and the ST locus and weaker linkage of LONG1 with other group III classical markers B and DNE. This indicated a position near the LA gene (Weeden et al., 1998), recently shown to encode a GA-signaling DELLA protein (Weston et al., 2008), and we therefore considered the possibility that long1 and la might be allelic. However, the presence of several recombinants in a cross segregating for long1 and la excluded this possibility and suggested a LA–LONG1 distance of ~4 centimorgans.

Figure 1. Shoot Phenotypes of long1, a New Elongated Pea Mutant.

(A), (B), and (E) Phenotypes of elongated mutant seedlings under glasshouse conditions. Appearance of representative seedlings (A), internode lengths (B), and stem chlorophyll (chl) content (D). (C) and (E) Photoperiod response of wild-type and long1 mutant plants for node of flower initiation (E) and stem length between nodes 1 and 3 (C). All plants received an 8-h photoperiod of natural daylight either with (LD) or without (SD) a 16-h extension with low-irradiance cool-white fluorescent light. Values represent mean ± SE for n = 8 plants except for (D), where n = 4.

Shoot Phenotype of the long1 Mutant

The pronounced effect of long1 on the length of the first two internodes is most similar to that of the constitutive GA-response double DELLA mutant la cry-s (Potts et al., 1985; Weston et al., 2008) and the GA-overproducing sln mutant, which has a mutation in the GA catabolism gene GA2ox1 (Reid et al., 1992; Lester et al., 1999) (Figures 1A and 1B). By contrast, the phyB mutant, although equivalently elongated over later internodes, has only a weak effect on elongation of early internodes (Figures 1A and
1B). All four mutants also had reduced chlorophyll content in internodes 1 and 2 (Figure 1D) but differed in their relative effects in an internode-specific manner. In internode 1, the effect of long1 was much stronger (80% reduction compared with the wild type) than any of the other three mutants (30 to 50% reduction). However, in internode 2, both long1 and phyB had stronger effects (54 and 68% reduction, respectively) than the GA-related mutants la cry (23% reduction) and sln (27% reduction). Thus, long1 seedlings have a characteristic phenotype distinguished from these other elongated mutants by strong effects on both elongation and chlorophyll content in the first internode, regardless of whether chlorophyll content is expressed relative to fresh weight (Figure 1D) or per internode (3.9 ± 0.3 μg in wild type versus 2.5 ± 0.3 μg in long1). These observations suggested that LONG1 might act on both light signaling and GA synthesis/response in early seedling development.

In Arabidopsis, increased elongation also results from mutations affecting the circadian clock, such as elf3 (Zagotta et al., 1996) and elf4 (Doyle et al., 2002), but this is photoperiod dependent and associated with defects in photoperiodic flowering. However, the effect of long1 on elongation was similar in both long and short photoperiods (Figure 1C), and long1 had no effect on photoperiodic flowering (Figure 1E), suggesting that long1 was unlikely to have a defect in the circadian clock or the photoperiod response mechanism.

**LONG1 Participates in Signaling from Multiple Photoreceptors**

long1 seedlings grown in complete darkness have an etiolated appearance similar to the wild type, with elongated epicotyl and internodes, a normal apical hook, and strong suppression of leaf development (Figures 2A and 3C). The elongated phenotype of long1 seedlings grown under white light (W) is therefore light dependent and different from that of the GA-related la cry and sln mutants despite the similar internode length profile (Figure 1B) (Reid, 1988). Mutant long1 seedlings were also much longer than the wild type under monochromatic blue (B) or far-red (FR) light and slightly longer under red (R) (Figure 2A), suggesting that LONG1 affects signaling from multiple photoreceptors.

In pea seedlings, phyA and phyB both contribute to deetiolation under R and act together with cry1 under B (Platten et al., 2005). To examine which specific photoreceptor signals were impaired by long1, we generated long1 phyA and long1 phyB double mutants. Figure 2B shows that the small effect of long1 under R is retained and even slightly enhanced in the phyA and phyB backgrounds. Because the phyA phyB double mutant is insensitive to R (Weller et al., 2001), this shows that long1 affects both phyA and phyB signaling under R. It also shows that phytochrome signaling under R is not completely dependent on LONG1 because both the phyA long1 and phyB long1 double mutants are more responsive to R than the phyA phyB double mutant. Under B, the phyA long1 double mutant was less responsive than any of the three photoreceptor double mutants (Figure 2B), and as the phyA phyB cry1 triple mutant is essentially insensitive to B (Platten et al., 2005), this implies that long1 affects signaling from all three photoreceptors in blue light.

**Figure 2.** LONG1 Functions in Phytochrome and Cryptochrome Signaling.

(A) Internode elongation of wild-type and long1 seedlings grown from sowing in darkness (D) or under continuous irradiation with far-red (FR), red (R), or blue (B) light (15 μmol m⁻² s⁻¹) or white light (100 μmol m⁻² s⁻¹). (B) Internode elongation and leaflet area of long1 mutant seedlings in different photoreceptor-deficient genetic backgrounds under continuous red (R) or blue (B) light (15 μmol m⁻² s⁻¹). Values represent mean ± SE for n = 8 to 10 plants.

**The long1 Mutation Is Epistatic to lip1**

The light-dependent nature and lack of spectral specificity of the long1 elongated phenotype are similar to the phototyptic characteristics of mutants for Arabidopsis genes HY5, HFR1, and STH2 genes, which all encode transcription factors whose stability is regulated through interaction with COP1 ubiquitin ligase (Osterlund et al., 2000; Kim et al., 2002; Datta et al., 2007). A direct molecular interaction between HY5 and COP1 was initially suggested by allele-specific epistatic relationships between hy5 and cop1 mutants (Ang and Deng, 1994). More recently, both hfr1 and sth2 mutants have been shown to partially overcome the effects of cop1 (Kim et al., 2002; Datta et al., 2007). We therefore tested the genetic interaction of long1 with lip1, a
loss-of-function mutant of the pea COP1 ortholog (Sullivan and Gray, 2000), which when grown in W has a dark-green, dwarf phenotype opposite to that of long1 (Frances et al., 1992). In seedlings grown under continuous W, long1 was almost completely epistatic to lip1 (Figures 3A and 3B) and also strongly suppressed the lip1 phenotype in dark-grown seedlings, although long1 itself had little effect in darkness (Figures 3C and 3D). This suppression was almost complete for early stem elongation, which was similar in long1 and long1 lip1 double mutants, but only partial for leaf expansion, which in the long1 lip1 double mutant was intermediate between long1 and lip1 single mutants (Figure 3D).

**LONG1 Belongs to a Group of Divergent Legume Orthologs of Arabidopsis HY5**

In view of the physiological similarities between LONG1 and COP1-interacting transcription factors HY5, HYH, STH2, and HFR1, we searched for legume sequence information that might help narrow the range of candidate genes. Close legume homologs of HFR1 were not identified, and a Medicago truncatula STH2 ortholog (AC183777_9/TC101468) was excluded as a candidate by its location on chromosome 1 (syntenic with pea linkage group II). Several HY5-like legume genes are known, including VFBZIPZF from V. faba, STF1 from soybean, and BZF/ASTRAY from L. japonicus (Cheong et al., 1998; Nishimura et al., 2002b), and a Medicago EST contig (TC123156) also belongs to this group. As a map position was not available for this sequence, we isolated a cDNA covering the entire predicted coding sequence of the corresponding gene from pea and mapped this gene to the middle of linkage group III near the position previously determined for LONG1. Sequencing results from the long1 mutant identified a G-to-A substitution in exon 3, causing a nonsense mutation of the codon specifying Trp-124 (TGG) to a stop codon (TGA) (Figure 4B), which cosegregated with the long1 phenotype, strongly supporting the conclusion that LONG1 is the pea ortholog of Lotus ASTRAY. An alignment of LONG1 and related proteins is shown in Supplemental Figure 1 online.

As previously reported for STF1 and ASTRAY (Cheong et al., 1998; Nishimura et al., 2002b), the C-terminal bZIP domain of LONG1 is highly similar to Arabidopsis HY5 and clusters with the other legume genes in a distinct HY5 clade (Figure 4A). However, the 189–amino acid N-terminal region encoded by the first four exons of LONG1 contains a Zn-finger domain and an acidic domain not present in Arabidopsis HY5, HYH, or HY5 homologs from other species (Nishimura et al., 2002b). This region is similar to the N-terminal region of cellulose synthase A subunits and is most similar to Arabidopsis CES1 (At4g32410). Intron/exon boundaries are well conserved and suggest that the legume genes may represent a fusion of the first three exons of CES1 to the last three exons of HY5 (Figure 4B). As the long1 mutation would eliminate the entire HY5-homologous region (Figure 4B),

**Figure 3. The long1 Mutation Is Epistatic to lip1.**

(A) and (B) Interaction of long1 and lip1 in control of development in plants grown under continuous white light. (A) Appearance of representative seedlings. (B) Stem length between nodes 1 and 3 (n = 8 to 10) and chlorophyll content of internode 1 (n = 4 plants). Bars represent SE. (C) and (D) Interaction of long1 and lip1 in control of development in plants grown in continuous darkness. (C) Appearance of representative seedlings. (D) Stem length between nodes 1 and 3, and leaflet area (n = 8 to 10). Bars represent SE.
been assessed on agar plates with root systems developing in a light-dependent root phenotype, we grew pea seedlings on inclined agar plates. As observed for plants grown in soil, there was little difference in the root systems of wild-type and long1 seedlings grown in complete darkness (data not shown). However, when grown under continuous white light, wild-type seedlings showed decreased elongation and increased thickness of both primary and lateral roots and pronounced chlorophyll accumulation in the primary root (see Supplemental Figure 2 online). By contrast, the root systems of long1 mutants grown in the light were very similar to those of dark-grown plants, showing that long1 impairs the response of pea roots to light. Other traits affected by hy5 and astray mutations, such as the timing of emergence or number of lateral roots, were not apparently influenced by long1.

**LONG1 Mediates the Rapid Effects of Light on GA Economy**

Transfer of etiolated pea seedlings to light is rapidly followed by a dramatic decrease in the content of the active gibberellin GA1 (O’Neill et al., 2000; Symons and Reid, 2003), and we next tested whether LONG1 was also required for this response. Figure 5A shows that when 7-d-old wild-type seedlings were transferred to continuous W for 4 h, the GA1 content of the apical portion (including the apical bud and 20 mm of expanding internode) dropped by more than 95%, consistent with the recent report of Symons et al., (2008). In equivalent long1 mutant seedlings, however, this did not occur (Figure 5A). The 4-h light treatment was also much less effective for inhibition of internode elongation in long1 seedlings than in the wild type (Figure 5B). Light transfer also caused a 50% drop in GA19 and GA20 content and a 2-fold increase in GA20 content in the wild type within 4 h (Figure 5A), and these changes were also largely blocked by the long1 mutation. By contrast, IAA levels were similar in wild-type and long1 seedlings in darkness and after light exposure (Figure 5C).

In parallel with GA measurements, we also monitored transcript levels of shoot-expressed GA biosynthesis genes GA3ox1 (LE), GA2ox1 (SLN), and GA2ox2. GA3ox genes catalyze the conversion of inactive GA20 to the active form GA1, whereas the GA20ox genes convert GA19 to the inactive product GA29 (Figure 5A). GA2ox1 but not GA2ox2 also has the ability to convert GA20 to another inactive product GA29 (Lester et al., 1999). Figure 5D shows that the clearest effect of light was seen for GA2ox2. In expanding shoot tissue from wild-type seedlings, GA2ox2 expression increased 9-fold after light treatment, but only 2.4-fold in long1 seedlings, despite similar dark expression levels, suggesting that the increased GA1 content of light-exposed long1 seedlings mainly resulted from a reduction in GA2ox2-dependent catabolism. In comparison, expression levels of other genes showed relatively minor changes in response to light or LONG1 action (Figure 5D). For example, the long1 mutant showed a small (40%) decrease in GA3ox1 expression and a small increase (2.4-fold) in GA2ox1 expression, which would oppose the effects of the strong decrease in GA2ox2 expression and would tend to increase rather than decrease the amount of GA1 after transfer. These changes are more consistent with those expected as part of feedback regulation in response to the increased GA1 level (Yamaguchi, 2008). Consistent with this interpretation, the double DELLA mutant la cry had similar effects to long1 on GA3ox1 and GA2ox1 expression, but in contrast with long1, had

**LONG1 Has Light-Dependent Effects on Root System Development**

In addition to its effects on photomorphogenesis, the hy5 mutant also affects the root system, developing longer and more numerous lateral roots and an increased root angle (Oyama et al., 1997; Cluis et al., 2004; Sibout et al., 2006). The astray mutant in *L. japonicus* has similar effects on lateral root elongation and angle, enhanced primary root elongation, and precocious initiation of nodules (Nishimura et al., 2002a, 2002b). We therefore examined root phenotypes of the long1 mutant. In seedlings grown in pots, the wild type and long1 developed very similar root systems with respect to primary root length and the length, number, and angle of lateral roots (see Supplemental Figure 2 online). This growth system approximates natural conditions in which the root system is underground and not exposed to light. By contrast, root phenotypes of hy5 and astray have been assessed on agar plates with root systems developing in the light. To test whether long1 seedlings might show a light-dependent root phenotype, we grew pea seedlings on inclined agar plates. As observed for plants grown in soil, there was little difference in the root systems of wild-type and long1 seedlings grown in complete darkness (data not shown). However, when grown under continuous white light, wild-type seedlings showed decreased elongation and increased thickness of both primary and lateral roots and pronounced chlorophyll accumulation in the primary root (see Supplemental Figure 2 online). By contrast, the root systems of long1 mutants grown in the light were very similar to those of dark-grown plants, showing that long1 impairs the response of pea roots to light. Other traits affected by hy5 and astray mutations, such as the timing of emergence or number of lateral roots, were not apparently influenced by long1.

![Figure 4](https://example.com/image4.png)

**Figure 4.** LONG1 is a Divergent Ortholog of Arabidopsis HY5.

(A) Phylogenetic analysis of HY5-related genes. Deduced amino acid sequences were aligned and HY5-homologous regions (amino acids 77 to 151 in AtHY5) were used to construct a neighbor-joining tree, shown with a root between HY5 and HYH clades. Bootstrap values were determined from 1000 replications and given above each branch as a percentage. The alignment is shown in Supplemental Figure 1 online.

(B) Structure of the LONG1 gene and comparison with related Arabidopsis genes HY5 and CESA1. Boxes represent exons, and shaded regions within boxes represent coding sequence. The site of the long1-1 mutation is indicated.

the long1 mutant thus appears likely to be null for HY5-like function. Other HY5-related sequences present in soybean (CX517746) and *Medicago* (AC146793_14) seem to represent more conventional orthologs of Arabidopsis HYH (Figure 4A).
increased rather than decreased expression of GA2ox2 (see Supplemental Figure 3 online).

**LONG1 and LIP1 Interact in the Regulation of GA Biosynthesis during Deetiolation**

The clear epistasis of long1 over lip1 in the control of stem elongation prompted us to examine whether lip1 might also affect GA1 content. Apical stem portions from 7-d-old dark-grown lip1 seedlings contained 3- to 4-fold less GA1 than the wild type (Figure 5E), and this was associated with a 4-fold increase in transcript level of GA2ox2 and a doubling in expression level of GA2ox1 relative to the wild type (see Supplemental Figure 4 online). Nevertheless, GA1 content in lip1 was still strongly responsive to light, dropping to a very low level after 4 h, similar to the wild type. Expression of GA2ox and GA3ox genes was also similarly regulated by light in the wild type and lip1, with a strong induction of GA2ox2, a moderate induction of GA2ox1, and a moderate repression of GA3ox1 (see Supplemental Figure 4 online). The effect of 4 h of light on elongation was also proportionately similar in the wild type and lip1 (50 and 46% inhibition, respectively) (Figure 5F). Consistent with the epistasis of long1 over lip1 in the control of elongation (Figures 3 and 5F), lip1 did not affect GA1 content or GA gene expression in the long1 genetic background (Figure 5E; see Supplemental Figure 4 online), showing that its effects in both dark- and light-exposed seedlings are largely dependent on LONG1.

**LONG1 Also Regulates GA Production in Deetiolated Seedlings**

The long1 mutant clearly impairs short-term regulation of GA biosynthesis and inhibition of elongation. However, from the single time point examined, we could not distinguish whether
long1 mutant blocked or merely delayed the downregulation of GA$_4$ production. We therefore examined the effect of long1 over a longer period following light transfer. In wild-type apical stem segments, GA$_4$ content was again strongly repressed by 4 h after transfer and maintained at this low level for at least 12 h (Figure 6A). From 24 h after transfer, the GA$_4$ level slowly increased and by 72 h reached ~20% of the dark control level. By contrast, downregulation of GA$_4$ production did occur in long1, but this was slower and much weaker than in the wild type, reaching a minimum 20% of the dark level 8 h after transfer. After this point, GA$_4$ levels in long1 rapidly increased, reaching ~2.5 times the dark level by 48 h, before returning to dark levels by 72 h (Figure 6A). The GA$_4$ content in long1 was therefore >20-fold higher than in the wild type by 4 h, and this difference was maintained until at least 48 h after transfer.

In this time course, GA2ox1, GA2ox2, and GA3ox1 transcripts showed distinct temporal patterns of accumulation and were all affected by long1 (Figure 6B). GA2ox2 was the most strongly light-regulated in wild-type seedlings, reaching a peak of expression 40-fold higher than the dark level from 4 to 12 h after transfer, before gradually returning to the dark level by 72 h. In long1, it reached a maximum only 3-fold higher than the dark control. The level of GA3ox1 transcript showed a small (50%) drop by 4 h after transfer before rising to 2-fold higher than the dark level by 12 h and returning to dark level by 48 h. In long1, the initial drop was also evident, but the subsequent recovery and induction was much weaker, such that the expression level did not exceed the dark control at any point. GA2ox1 expression in the wild type was induced more slowly than GA2ox2, reaching a maximum at 12 h and subsequently maintained at a level ~8 to 10-fold above dark levels until 72 h. In long1, the initial induction was retained, but from 12 h onwards, GA2ox1 transcript levels dropped to near dark levels at 48 h.

Internode length measurements of mature plants showed that long1 and lip1 continue to function in control of elongation throughout development and that, as in seedlings, long1 remained largely epistatic to lip1 (see Supplemental Figure 5A online). We also measured GA$_4$ content in apical shoot tissue of 30-d-old plants, which contained expanding tissue from internodes 9, 10, and 11. Supplemental Figure 5B online shows that long1 and lip1 also affect GA$_4$ content in this tissue, with a significant (P = 0.008) 2-fold increase in long1 and a 75% decrease in lip1. Once again, long1 overrode the effect of lip1 on GA$_4$ content, with the double mutant containing 3-fold higher levels than in the wild type (P = 0.032) (see Supplemental Figure 5A online). However, in contrast with seedlings, these differences were not correlated with expression of GA biosynthesis genes (see Supplemental Figure 5C online).

**Interactions between GA and Light Signaling during Deetiolation**

Several recent reports in Arabidopsis have identified interactions between light- and GA-signaling components. For example, DELLA proteins were recently shown to bind to and interfere with the transcriptional activation activity of the PIF3 and PIF4 transcription factors (de Lucas et al., 2008; Feng et al., 2008), while other studies have reported light effects on DELLA transcript levels in seeds (Oh et al., 2006) and deetiolating seedlings (López-Juez et al., 2008). To examine whether crosstalk at the transcriptional level between light and GA signaling might occur in pea, we used long1, lip1, and la cry mutants to examine the regulatory interactions of the corresponding genes. As shown in Figure 7A and Supplemental Figure 4 online, neither light exposure, long1, or lip1 had a significant effect on transcript levels of LA and CRY. LONG1 expression in wild-type seedlings showed a 4-fold induction by 4 h (Figures 7A and 7B), which was sustained for at least 48 h (Figure 7B), but there was no significant effect of the lip1 mutation on LONG1 expression in either the dark (P = 0.26) or 4 h after transfer (see Supplemental Figure 4 online). LONG1 expression was significantly lower in the la cry mutant after 4 h light (Figure 7B; 20% decrease, P = 0.016), but the small size of this change suggests that the GA pathway does not interact substantially with LONG1 function through transcriptional control.

Another recent study has shown that DELLA proteins also influence elongation by promoting the stability of the HY5 protein (Alabadi et al., 2008). We reasoned that if the GA signaling pathway in pea seedlings acts through LONG1, then long1 should affect responsiveness to GA. However, we found no difference in responsiveness of light-grown wild-type and long1 plants to applied GA$_3$ after depletion of endogenous GA$_4$ by a saturating dose of the GA biosynthesis inhibitor paclobutrazol (Figure 7C). There was also no significant effect of the la and cry mutations on elongation in a long1 background (Figure 7D; P = 0.097). This indicates that loss of LONG1 does not significantly impair GA signaling in the light and shows that the large difference in elongation of untreated wild-type and long1 plants is mainly due to the large difference in GA content rather than increased activation of GA signaling. We also examined how the loss of LONG1 function might influence the development of GA-limited seedlings grown in darkness. Figure 7E shows that wild-type and long1 seedlings have a near-identical dose–response relationship for the effect of paclobutrazol on elongation, suggesting that LONG1 also has no clear role in mediating the effects of DELLA proteins in darkness.

**DISCUSSION**

There is a growing consensus that the regulation of active GA levels is an important part of the mechanism by which light controls stem elongation. Effects of light on levels of bioactive GA were first reported in lettuce (Lactuca sativa) (Toyomasu et al., 1992) and have been firmly established for GA$_4$ in pea (Ait-Ali et al., 1999; Gil and Garcia-Martinez, 2000; O’Neill et al., 2000). Similar changes have also been inferred to occur in Arabidopsis from measurements of GA biosynthesis gene expression (Achard et al., 2007; Alabadi et al., 2008), and this has recently been confirmed by direct measurements of GA$_4$ (Zhao et al., 2007; Symons et al., 2008). In this study, we show that the pea LONG1 gene is a divergent ortholog of the Arabidopsis bZIP transcription factor HY5 and is necessary for effects of light on GA biosynthesis during deetiolation. This result provides a new insight into the deetiolation mechanism and the interaction between light and GA signaling.
LONG1 Functions Similarly to *Arabidopsis* HY5 in Control of Photomorphogenesis

Like the divergent HY5 orthologs previously identified in other legume species, LONG1 is distinguished from HY5 by the presence of an additional N-terminal domain with close similarity to the N-terminal RING-type Zn-finger domain of the cellulose synthase A subunit (Nishimura et al., 2002b; Song et al., 2008). Despite this structural difference, however, LONG1 and HY5 appear to have largely similar functions in photomorphogenesis. Similar to HY5, LONG1 is necessary for deetiolation under R, B, and FR light, it acts downstream of phyA, phyB, and cry1 photoreceptors, and it interacts genetically with LIP1, the pea ortholog of *Arabidopsis* COP1, throughout development. This provides strong evidence that HY5 function and its mechanisms of regulation may be widely conserved across flowering plants, extending the conclusions of more limited functional analyses of HY5 orthologs in other species. RNA interference knockdown of a conventional HY5 ortholog in tomato (*Solanum lycopersicum*) resulted in increased hypocotyl elongation and reduced chlorophyll content in leaves and pericarp (Liu et al., 2004). A mutant for the *L. japonicus* LONG1 ortholog ASTRAY shows increased hypocotyl elongation and reduced chlorophyll and anthocyanin content (Nishimura et al., 2002a). Expression of the soybean ortholog STF1 in transgenic *Arabidopsis* complemented the hy5 mutant phenotype with respect to these three traits (Song et al., 2008). In addition, STF1 and HY5 have a similar DNA binding repertoire (Song et al., 2008). Although more detailed comparisons of the legume genes with *Arabidopsis* HY5 are needed, there is little evidence so far that the additional N-terminal domain of the legume HY5-like genes has any additional role.

Although LONG1 is clearly essential for full expression of photomorphogenic responses, residual light responses in long1 indicate that other factors can mediate partial light responsiveness when LONG1 is absent. In *Arabidopsis*, both HYH and STH2 contribute to the residual light response in the hy5 mutant (Holm et al., 2002; Datta et al., 2007), and it is possible that pea orthologs may function in a similar manner. The fact that the residual light response of the long1 mutant is enhanced by the lip1 mutation does suggest that these LONG1-independent responses are nevertheless regulated by LIP1 (Figure 8A).

LONG1 and Light Regulation of GA Biosynthesis

Previous studies in pea have identified two phases of GA regulation during deetiolation: an initial rapid drop in GA1 content followed by a gradual recovery to dark levels (Ait-Ali et al., 1999; Gil and García-Martínez, 2000; O’Neill et al., 2000; Reid et al., 2002; Symons and Reid, 2003). The results presented here showed that the long1 mutant cannot downregulate GA1 production in response to light during this initial phase. Also, the fact that long1 seedlings exhibit normal sensitivity to exogenous GA shows that
the increased elongation of the long1 mutant during seedling growth is largely due to this elevated GA content. The main target of LONG1-dependent light regulation appears to be GA2ox2, consistent with the conclusions of Reid et al. (2002), although smaller effects on other genes may also contribute. Induction of Arabidopsis GA2ox genes by light has also recently been reported (Achard et al., 2007; Zhao et al., 2007; Alabadi et al., 2008), and Arabidopsis GA2ox1 was also found to be HY5-regulated in transcript profiling studies (Sibout et al., 2006; Lee et al., 2007). These findings suggest that Arabidopsis HY5 may play a similar role in light regulation of the GA pathway, although this has yet to be directly tested.

Previous studies in pea have shown that high GA levels are necessary to maintain the etiolated phenotype of dark-grown seedlings and that GA acts to promote internode elongation and to repress leaflet expansion and expression of RbcS genes (Alabadi et al., 2004). Epistasis of long1 over lip1 in control of deetiolation (Figure 3) and effects of lip1 on GA1 content (Figure 5) and GA gene expression (see Supplemental Figure 4 online) show that LIP1 is necessary for maintenance of high GA1 levels in dark-grown seedlings in a LONG1-dependent manner. This may partially reflect LIP1 regulation of LONG1 transcription, but these effects are weak compared with the strong effects on GA2ox2 expression (see Supplemental Figure 4 online). This suggests that LIP1 repression of LONG1 action most likely occurs through a different mechanism that, by analogy with Arabidopsis, may involve LIP1 control of LONG1 protein stability (Osterlund et al., 2000). With respect to GA1 levels, the effect of lip1 in dark-grown seedlings was much smaller than the effect of 4 h light on wild-type seedlings even though the effect on elongation was greater, suggesting that the lower level of GA1 in dark-grown lip1 seedlings may not be sufficient to explain the short internode phenotype. A GA-independent effect of LIP1 is also revealed in light-exposed seedlings, where lip1 is shorter than the wild type despite both genotypes showing a similar depletion of GA1 to trace levels (Figure 5). However, the interaction with long1 shows that this GA-independent effect of lip1 must nevertheless act through LONG1 (Figure 8A). It is also interesting to note that light exposure had proportionately similar effects on elongation in both wild-type and lip1 seedlings but a much smaller effect in
the lip1 long1 double mutant, highlighting a potentially LIP1-independent effect of LONG1 (Figure 8A).

One explanation for a GA-independent regulation of elongation through LONG1 and LIP1 could involve changes in levels of, or response to, other hormones, such as auxin. Changes in the level of auxins themselves are unlikely, as IAA content in expanding stem tissue from long1 seedlings was not significantly different from the wild type after 4 h of light exposure (Figure 6C), and in Arabidopsis, the hy5 mutation has no obvious effect on auxin content (Cluis et al., 2004). However, hy5 mutants do show several auxin-related phenotypes and the misregulation of numerous auxin-related genes (Oyama et al., 1997; Cluis et al., 2004; Sibout et al., 2006), suggesting that HY5 may influence auxin signaling rather than levels. If auxin signaling was regulated in a similar manner by the LONG1/LIP1 pathway in pea, we might expect auxin-dependent elongation to be increased in long1 in the light and decreased in lip1 in the dark. This might also help explain the apparent differences in tissue sensitivity to endogenous GAs between light- and dark-grown plants (Reid, 1988).

**LONG1 and Homeostatic Control of GA Biosynthesis**

The longer deetiolation time course in Figure 6 shows that GA1 levels in long1 mutant are not completely unresponsive to light but undergo a weak transient downregulation, accompanied by a residual inhibition of elongation, indicating that other genes act together with LONG1 to regulate GA levels and elongation. The time course also showed that LONG1 has persistent effects on the GA pathway for at least 3 d after transfer and thus acts well into the recovery phase described above. The molecular basis for this recovery is not clear but is likely to involve homeostatic autoregulation of GA production. This has been noted in several systems (Yamaguchi, 2008) and would tend to increase GA3ox1 expression and reduce GA2ox expression in response to the initial GA1 depletion. All three of the genes examined here show feedback control during deetiolation (see Supplemental Figure 3 online; Reid et al., 2002), but in wild-type seedlings only GA3ox1 showed a clear reversal in sign from an initial repression to a subsequent induction (Reid et al., 2002), suggesting GA autoregulation during deetiolation may be mainly achieved through GA3ox1.

Interestingly, long1 had little effect on the initial light-dependent repression of GA3ox1, but the subsequent induction was strongly impaired in the long1 mutant, an effect most simply interpreted as a consequence of the elevated GA1 content in long1 feeding back to maintain low GA3ox1 expression. By contrast, from 24 h onwards, expression of both GA2ox genes is lower in long1 than in the wild type despite dramatically elevated GA1 content, suggesting that LONG1 has a role in maintenance of GA catabolism throughout the time period examined but also that without LONG1, feed-forward upregulation of these genes in response to high GA1 level cannot proceed. This raises the possibility that LONG1 may be necessary for both light and GA1 effects on GA2ox2 expression. Studies in Arabidopsis may provide some precedent for this scenario. Arabidopsis HY5 does not contain a transcriptional activation domain (Ang et al., 1998), and DNA binding by HY5 alone is neither light regulated nor sufficient to confer light-dependent transcriptional regulation, suggesting that the transcriptional regulation activity of HY5 is likely to depend on other coregulators, such as the putative transcriptional coregulator STH2 (Datta et al., 2007). It is therefore conceivable that the effect on GA production of factors such as light and GA itself might be integrated at the promoters of GA metabolism genes through different transcription factors acting together with HY5/LONG1.

**LONG1 and GA Signaling**

Recent discussions of light and GA in Arabidopsis have focused mainly on interaction between signaling pathways. The HY5, PIF, and GA signaling pathways initially emerged as independent pathways for light control of elongation but are now believed to

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**Figure 8.** Interactions between Light and GA Pathways.

(A) Physiologically and/or genetically distinct responses to light in pea identified in this study. Operators specify the direction but not the molecular nature of the interaction.

(B) Model for interactions between light and GA pathways in dark- and light-grown seedlings. This diagram summarizes interactions identified from studies in Arabidopsis and pea. Genes and operators shown in black are active under the indicated light conditions; those shown in gray are inactive. The new interaction described in this study is shown as a dashed line.

(C) Model for interactions between light and GA pathways in Arabidopsis seeds. Genes and operators shown in black are active; those shown in gray are inactive. Arrows represent activation; lines with flat ends represent inhibition.
interact in several different ways (Figure 8B) (Alabadi et al., 2008; de Lucas et al., 2008; Feng et al., 2008). One interaction occurs between the DELLAs and members of the PIF family, PIF3 and PIF4. PIF3 and PIF4 proteins are abundant in darkness and necessary for skotomorphogenic development. After transfer to light, they are destabilized through interaction with PHYB, and their transcriptional activation activity is blocked through physical interactions with the DELLA proteins (de Lucas et al., 2008; Feng et al., 2008). A second interaction involves COP1-dependent maintenance of low HY5 protein levels in the dark by GA signaling (Alabadi et al., 2008). In both mechanisms, a GA signaling component (DELLA) is proposed to regulate activity of a light-signaling component (HY5 or PIF). However, it is important to note that both mechanisms also invoke a primary effect of light on GA content since the DELLA protein level is presumed to be determined as a result of prior light regulation of GA levels (Alabadi et al., 2008; de Lucas et al., 2008; Feng et al., 2008).

The identification of LONG1 as a key gene through which light regulates GA level thus places it at an earlier step than either of these mechanisms and stands in contrast with the emphasis on Arabidopsis HY5 as a target rather than a regulator of GA signaling. However, as mentioned above, it does seem likely that HY5 also participates in regulation of GA levels during deetiolation in Arabidopsis. On the other hand, the fact that LONG1 acts in light regulation of GA biosynthesis does not exclude the possibility that the response to these light-dependent GA changes may occur through DELLA effects on PIF and LONG1 activity, as proposed in Arabidopsis. A comparison of transcript profiles in Arabidopsis hy5, pif3/4, and GA pathway mutants may also help distinguish the extent to which light acts through HY5 and PIF-dependent mechanisms as opposed to direct DELLA-dependent transcriptional regulation. Interestingly, if DELLA-dependent stabilization of HY5 and HY5 regulation of GA biosynthesis are found to both occur in the same species, this would mean that after the initial HY5-dependent drop in GA level, two opposing DELLA-dependent mechanisms would potentially act during deetiolation to influence GA levels; one being the feedback upregulation of GA biosynthesis and the other an indirect repression through increased HY5 stability (Figure 8B).

An Expanding Molecular Framework for Light–GA Interactions

The role for LONG1 in GA biosynthesis not only adds another link in the network of interactions controlling stem elongation, it also provides a interesting contrast to the mechanism through which light regulates the GA pathway in germinating seeds (Figure 8C). In Arabidopsis seeds, light acting through phyA or phyB induces de novo GA biosynthesis through activation of GA2ox and repression of GA2ox genes (Oh et al., 2006). The PIF family gene PIL5 (PIF1) is a phyB-dependent negative regulator of germination that plays a central role in this modulating these effects. PIL5 was also found to bind the promoters and activate transcription of the DELLA genes GA4 and RGA, providing an alternative means by which light could derepress DELLA-dependent inhibition of germination. In contrast with this direct regulation of DELLA genes, PIL5 regulation of GA metabolism genes is apparently not direct because binding of PIL5 to promoters of these genes was not detected in specific chro-

matin immunoprecipitation analyses (Oh et al., 2007), and the existence of an unknown intermediate has been proposed. A possible role for HY5 in this system has not been tested, but may warrant examination, given the positive regulation of germination by light through HY5 and the abscisic acid signaling component ABF5 (Chen et al., 2008). Moreover, light regulation of GA levels in seeds may depend in part on prior light regulation of abscisic acid synthesis (Seo et al., 2006), and under some conditions light clearly regulates GA levels in a PIL5-independent manner (Oh et al., 2007). These observations raise the possibility that HY5 could also contribute to photoregulation of GA biosynthesis in seeds.

METHODS

Plant Material, Mutagenesis, Measurements, and Growth Conditions

The pea (Pisum sativum) mutant lines long1-1, phyA-1, and phyB-5 were derived from ethyl methane sulfonate mutagenesis of cv Torsdag [WT (TOR)] as previously described (Weller et al., 1997). Unless otherwise specified, plants were grown in growth cabinets at 20°C or in the glasshouse using previously described growth media light sources and conditions (Hecht et al., 2007). The la cry-s double mutant was derived from the second backcross of Hobart line 197 (LE la-1 cry-s) into cv Torsdag. The original lip1 mutant (Frances et al., 1992) was backcrossed three times into the cultivar Torsdag background before use. The SLN (L309+) and sln near-isolines were derived by single plant selection from a cross between line NSB6074 (Reid et al., 1992) and cv Torsdag. Unless otherwise indicated, internode length was measured as the distance between nodes 1 and 3 in 2-week-old seedlings, and leaflet area was estimated as the product of the length and width of a single leaflet from the first true foliage leaf (leaf 3). Chlorophyll content was determined as previously described (Hiscox and Israelstam, 1979).

Genetic Analysis of long1 and Phylogenetic Analysis of LONG1

Allelism tests were performed by crossing the long1 mutant to other elongated mutants phyB and sln and observing wild-type seedling elongation phenotypes in the F1 and F2 generations. The la monogenic mutation has no phenotype in an otherwise wild-type background, and potential allelism of long1 and la was therefore assessed in the F2, F3, and F4 progeny of a cross between long1 and the la cry double mutant. Briefly, F3 families segregating for all three mutations were genotyped for la and cry mutations using molecular markers (Weston et al., 2008), and recombinants were identified as elongated plants that that were heterozygous for the la mutation (implying a long1 long1 LA la genotype and the contribution of a recombinant long1 la gamete) or as plants with a wild-type phenotype that were homozygous LA LA (implying the presence of at least one wild-type LONG1 allele and recombinant LONG1 LA gamete). The genetic distance between LONG1 and LA was estimated from this segregation data using JOINMAP software (van Ooijen, 2006). Amino acid sequences of proteins related to LONG1 were aligned using ClustalX (Thompson et al., 1997). Distance and parsimony-based methods were used for phylogenetic analyses in PAUP*4.0b10 (http://paup.csit.fsu.edu/) using the alignment shown in Supplemental Figure 1 online.

Sequence Isolation, Mapping, and Molecular Markers

Partial sequence of a pea gene homologous to Lotus japonicus ASTRAY was isolated by PCR using genomic DNA and cDNA from 2-week-old tissue with degenerate primers designed from legume sequences (L. japonicus AB002677, Vicia faba X97904, Medicago truncatula TC103975,
and Glycine max L28003) by the CODEHOP strategy (Rose et al., 1998) as described previously (Hecht et al., 2005). A full-length cDNA sequence for LONG1 was obtained by 5’ and 3’ rapid amplification of cDNA ends PCR performed using the BD SMART RACE cDNA amplification kit (BD Bioscience Clontech), PCR fragments were cloned in pGEM-T (Promega) and sequenced at the Australian Genome Research Facility (Brisbane, Australia). A single nucleotide polymorphism in intron 4 of LONG1 between lines J281 and J399 was converted to a cleaved amplified polymorphic sequence (CAPS) marker (Haeli site in J281) and used to map the gene in a J281 × J399 recombinant inbred line population (Hall et al., 1997). The longf1-1 point mutation was converted into a derived CAPS marker, introducing a diagnostic Ncol site. Molecular markers for detection of the phyA-1, phyB-5, la-1, and cry-s mutations have been described previously (Platten et al., 2005; Weston et al., 2008). Details of all primers are provided in Supplemental Table 1 online.

Hormone Quantification and Application

IAA and GAs were extracted and quantified as described by Jones et al. (2005) and Jager et al. (2005), respectively, with the following changes. Samples were methylated in a 1:7.5 mixture of methanol and 0.2 M trimethylsilyldiazomethane (Sigma-Aldrich) in diethyl ether at room temperature for 30 min and then (after drying) either partitioned against diethyl ether as before (Jones et al., 2005) or transferred in diethyl ether at room temperature for 30 min and then (after drying) either partitioned against diethyl ether as before (Jones et al., 2005) or transferred in diethyl ether (200 μL) to a clean vial prior to trimethylsilylation. For gas chromatography-selected ion monitoring analysis of GA1, a BPX60 column (SGE) was sequenced at the Australian Genome Research Facility (Brisbane, Australia). A single nucleotide polymorphism in intron 4 of LONG1 between lines J281 and J399 was converted to a cleaved amplified polymorphic sequence (CAPS) marker (Haeli site in J281) and used to map the gene in a J281 × J399 recombinant inbred line population (Hall et al., 1997). The longf1-1 point mutation was converted into a derived CAPS marker, introducing a diagnostic Ncol site. Molecular markers for detection of the phyA-1, phyB-5, la-1, and cry-s mutations have been described previously (Platten et al., 2005; Weston et al., 2008). Details of all primers are provided in Supplemental Table 1 online.

Gene Expression Studies

Harvested tissue consisted of 20 mm of young stem immediately below the apical bud. Samples were immediately frozen in liquid nitrogen and total RNA extracted using the Promega SV total RNA isolation system (Promega) with an on-column DNase treatment. RNA concentrations were determined using Ribogreen RNA quantification reagent (Molecular Probes) in a Picofluor fluorometer (Turner Biosystems). Reverse transcription was performed in 20 μL with 1 μg of total RNA using the ImPromII reverse transcriptase (Promega) according to the manufacturer’s instructions. RT-negative (no enzyme) control was performed for each sample to monitor for genomic DNA contamination. Real-time PCR were performed as described previously (Hecht et al., 2007). Details of primers are presented in Supplemental Table 1 online. Transcript levels were normalized to an ACTIN reference gene using nonequal efficiencies (Pfaffl, 2001). All data shown represent the mean ± s.e of three biological replicates, with each consisting of pooled material from three plants.

Accession Numbers

Genomic and cDNA sequences are deposited in GenBank under the provisional accession numbers bankit 1141280 (LONG1 genomic) and bankit 1141295 (LONG1 cDNA). GenBank accession numbers for other sequences used are V. Lumin BZIPZF (CA66478), L. japonicus BZF/ASTRAY (BAC20318), G. m. STF1 (AAC05017) and bZP69 (AB34671), Populus trichocarpa HYS (Genes4954.0.1, X1330000127_2_83275_89109), HYSb (estExt.Genesew1.x.1.C.1.LG_V10000127 protein 717128) and HYH (grail3.0102003601 protein 657788), Arabidopsis thaliana HYS (NP_568246, At5g11260) and HYH (NP.850604, At3g17609), M. truncata HYH (ABE88841), Arabidopsis CES1 (NM_119393, At4g3241), and P. sativum ACTIN (X66849).

Supplemental Data

The following materials are available in the online version of this article.

Supplemental Figure 1. Sequence Alignment of LONG1 and Related Proteins.

Supplemental Figure 2. Light-Dependent Effects of long1 in Roots.

Supplemental Figure 3. Effect of the Constitutive Activation of GA Signaling on Expression of GA Metabolism Genes.

Supplemental Figure 4. Interaction of LONG1 and LIP1 in Regulation of GA Metabolism and Signaling Genes in Deetiolating Seedlings.

Supplemental Figure 5. Interactions of LONG1 and LIP1 in the Control of Internode Length, GA Levels, and the Expression of GA Metabolism Genes in Mature Plants.

Supplemental Table 1. Primers.

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Light Regulation of Gibberellin Biosynthesis in Pea Is Mediated through the COP1/HY5 Pathway
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