Isolation from Lima Bean Lectin of a Peptide Containing a Cysteine Residue Essential for Carbohydrate Binding Activity*

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The location and amino acid sequence surrounding a cysteine residue required for carbohydrate binding in the lima bean lectin (LBL) was determined. Following selective conversion of the sulfhydryl group to its S-cyano derivative, LBL was cleaved at the essential cysteine residue to give two fragments, estimated by sodium dodecyl sulfate-polyacrylamide gel electrophoresis in two buffer systems to have molecular masses of 16.5–19 kDa and 10.5–11 kDa. The larger fragment, which contained the glycosyl moiety of the lectin, was shown by sequence analysis to contain the NH₂-terminal sequence of LBL. The smaller COOH-terminal fragment was found to contain the cysteine residue involved in the intersubunit disulfide bond of LBL.

Digestion of LBL with pepsin and trypsin yielded four peptides containing the essential cysteine. Sequencing of the three major peptides gave a single consensus sequence, Val-Glu-Phe-Asp-Thr-Cys-His-Asn-Leu-Asp−, for the primary sequence surrounding the cysteine.

The peptide sequence and site of cyanylation cleavage were used to predict alignment of the LBL peptide with the primary sequence of concanavalin A. Maximum homology was found with a sequence in concanavalin A beginning at valine 7. Implications of this alignment to the function of the cysteine in carbohydrate and metal ion binding of LBL, and for conservation of carbohydrate binding site residues in legume lectins are discussed.

LBL1 specifically binds glycoconjugates containing terminal nonreducing α-D-GalNAc residues (1–3). In addition, sites were identified which bind Ca" and Mn" (3–5) and a variety of nonpolar ligands (6). Occupation of the divergent cation sites is required for carbohydrate binding (3, 4). LBL subunits contain two cysteine residues, one of which forms an intersubunit disulfide bond (7). The carbohydrate binding activity of LBL was shown to be sensitive to modification of the single free cysteine sulfhydryl group present on each subunit of the lectin (7, 8). Modification by several cysteine-specific reagents, including dithiobis-(2-nitrobenzoic acid) Nbs, N-ethylmaleimide, mercurials, and Cu²⁺, inactivated the lectin (8). Furthermore, the modification and inactivation of LBL by Nbs, and N-ethylmaleimide was inhibited in the presence of β-GalNAc but not β-GlcNAc (8). These findings established that this cysteine is required for carbohydrate binding and suggested that it may be located in the carbohydrate binding site.

In the accompanying paper (9), we have used a kinetic assay to further examine the reactivity of this thiol, its interaction with carbohydrate and its participation in metal ion binding in LBL. These studies confirmed the earlier work of Gould and Scheinberg (8) and established that one sulfhydryl group on each subunit is required for and protected by carbohydrate binding. This is intriguing in light of the stoichiometry of carbohydrate binding as measured by equilibrium dialysis using [¹⁴C]methyl-α-D-GalNAc. Bessler and Goldstein (10) found two binding sites/tetramer of component III, which is equivalent to one sugar binding site for two subunits. To account for this behavior, a sugar binding site may be situated between 2 subunits in close proximity to a sulfhydryl group from each subunit, or sugars may bind with negative cooperativity so that binding to one subunit induces a conformation change blocking the second site on a subunit pair and concomitantly masking the second sulfhydryl. Alternatively, equilibrium dialysis may yield an incorrect stoichiometry due to the low affinity of binding. In the latter case, 4 mol of GalNAc may bind to component III with one sugar protecting each sulfhydryl group. However, Pardolfino and Magnuson (5) also reported apparent half-of-sites metal ion binding to LBL, which is consistent with the observed sugar binding stoichiometry of one site/two subunits.

In order to gain further insight into the role of the sulfhydryl groups in carbohydrate binding to LBL, we determined the position and alignment of the essential and disulfide cysteines. In the present paper, we report the localization of these cysteines and the isolation and primary sequence of a peptide containing the cysteine required for carbohydrate binding. The homology between this peptide and other known lectin sequences was also examined.

EXPERIMENTAL PROCEDURES

Materials

Lima bean lectin was prepared from green lima beans (Phaseolus lunatus, Thorogreen or Sieva varieties) by affinity chromatography on Synsorb A (11). All buffers were degassed and saturated with nitrogen and maintained under a nitrogen atmosphere. Lectin prepared by this method contained 1.06 ± 0.03–SH group/subunit as determined by titration with Ellman’s reagent (12) and was stable to prolonged storage at 4 °C. Iodo[¹⁴C]acetamide and [¹⁴C]KCN were...
obtained from ICN (Irvine, CA). 2-Nitro-5-thiocyanatobenzoic acid was prepared as described by Degani and Patchornik (13). Mercapto acid (Affi-Gel 501) was purchased from Bio-Rad. Trypsin (L-1-toxylamido-2-phenethyl chloromethyl ketone-treated) and pepsin were obtained from Worthington. HPLC solvents were obtained from Burdick and Jackson Laboratories, Inc. (Muskegon, MI).

**Methods**

**Chemical Modification of LBL.**—Modification with iodoaceta-

dem was done in 0.1 M NH$_4$HCO$_3$, pH 8.2. Native lectin or lectin reduced with 3 eq of dithiothreitol for 24 h under N$_2$ was treated with 1.5 eq of iodo[14C]acetamide (relative to total thiol) for 4 h at room temperature in the dark. Excess reagents were removed by dialysis. Incorporation of label was determined by scintillation counting in ACS (Amerham). Lectin concentration was determined by absorbance at 280 nm using $\varepsilon_{280}$ = 12.3 (7).

Preparation of CN-LBL was done using the indirect method of Vanaman and Stark (14). The free sulfhydryl of LBL was converted to the thionitrobenzoate disulfide by reaction with excess Nbs$_2$ and isolated by gel filtration on Sephadex G-50 in sodium phosphate (pH 7.0, 1/2 = 0.1) containing 1 mm EDTA. Following adjustment to pH 8.9, the LBL mixture was prepared by reaction with 0.01 M KCN for 16 h at room temperature. The reaction mixture was dialyzed against 0.1 M acetic acid and the CN-LBL recovered by lyophilization.

CN-LBL was cleaved at the modified cysteine by incubation in 0.1 M Tris acetate, pH 9.0, containing 0.5% SDS for 48 h at 37°C. The LBL fragments were separated by preparative SDS-polyacrylamide gel electrophoresis on 12% acrylamide gels (15) and electrophoretically eluted (16) into dialysis tubing (Spectra Por 2000 molecular weight cutoff, Pierce Chemical Co.). Following dialysis into water, the fragments were recovered by precipitation with 8 volumes of acetone in the presence of 0.01 M HCl.

**Isolation of Cysteine-containing Peptides.**—Lyophilized salt-free LBL (40 mg) was dissolved at 30 mg/ml in 88% formic acid. The denatured lectin was diluted to 1 mg/ml in 1 mm HCl containing 0.05 mg/ml of pepsin and digested with stirring for 30 min. The reaction mixture was brought to pH 6.6 by addition of 2 M NH$_4$NOH and applied to a column (0.7 x 5.5 cm) of mercuarial agarose. Unbound peptides were eluted successively with 0.1 M ammonium acetate, pH 6, 2 M guanidine HCl in 0.1 M ammonium acetate, and 0.1 M ammonium acetate, pH 6. Bound peptides were eluted with 50 mm 8-mercaptoethanol in the same buffer and recovered by lyophilization. The peptides were dissolved in 0.1 M NH$_4$HCO$_3$, reduced with 1 eq of dithiothreitol, and alkylated with [14C]iodoaceta-

tone (25).

**Sequence and Amino Acid Analysis.**—End group analysis of pu-

Amino acid analyses were done by HPLC analysis of phenylthio-

carbamoyl amino acids (20). Tryptophan was determined spectropho-

**Electrophoresis.**—Analytical SDS-gel electrophoresis was done in 12 and 15% acrylamide gels using either a Tris glycine (15) or a sodium phosphate, pH 7.2, buffer system containing 6 mm urea (22).

Gels were stained for protein with Coomassie brilliant blue R-250 and for carbohydrate using the thymol-sulfuric acid stain (23). Radioactivity in gel slices was determined as described in Ref. 24. In the presence of 8 mm urea was performed as described previously (11).

**Oxidation.**—Activity of LBL was determined by hemagglutina-

tion of human Type A1 red blood cells (3). Activity was also deter-

**RESULTS**

Our strategy for determining the position and sequence surrounding the essential cysteine of LBL was first to locate the position of the cysteine on the LBL sequence and then to determine the amino acid sequence surrounding the cysteine. Incubation of polypeptides containing S-cyano derivatives of cysteine at alkaline pH often results in specific cleavage of the polypeptide on the amino side of the modified cysteines (25). By determining the size of the resulting fragments and location of aminothiolodine derivatives of cysteine, the approximative position of the cysteine in the original polypeptide may be assigned. To determine the amino acid sequence surrounding the cysteine, the lectin was subjected to proteolytic digestion to give fragments with a free NH$_2$-terminus containing the essential cysteine.

In order to distinguish the cysteines required for carbohydrate binding and the disulfide cysteines, methods were developed for selective modification of the two thiols on each subunit. The failure of iodoaceta-

tone to react with LBL was reported previously (8). Iodo[14C]acetamide was used to confirm this finding and to establish conditions for labeling. Native LBL did not react with iodoaceta-

tone (0.001 mol/mo1 of subunits incorporated). Following reduction of the lectin with dithiothreitol, however, treatment with iodo[14C]acetamide resulted in incorporation of 0.9 mol/mo1 of subunit. Specific labeling of cysteine was verified by determining the radioactivity associated with dansyl-carboxymethylcysteine following hydrolysis, reaction with dansyl chloride, and separation on polyamide thin layer sheets. Determination of radioactivity in the three subunit forms of LBL (11) following separation by isoelectric focusing in 8 m urea indicated identical incorporation of label into the three subunits. The modified lectin still contained 1 -SH/subunit by Nbs2 assay which was protected by D-GalNAc. The lectin was also completely active as a hemagglutinin. From these data, it was concluded that the disulfide cysteine was specifically labeled whereas the essential cysteine in both dithiothreitol-reduced and native LBL was unreactive towards iodoaceta-

With the disulfide cysteine specifically labeled and protected, we next attempted to cyanate the essential cysteine. Initial experiments using 2-nitro-5-thiocyanatobenzoic acid were unsuccessful. Treatment with 1 mm reagent at pH 7.0 gave no release of thionitrobenzoate as monitored by absorbance at 412 nm. Some reverse reaction with the reagent to release CN$^-$ may occur (26), although the lectin was still active after the above reaction. The indirect method of Van-

Several conditions were examined for cleavage of S-cyano-

**Optimum cleavage was obtained using a 48-h incubation period at pH 9 in the presence of 0.5% SDS. SDS-gel electropho-

Several conditions were examined for cleavage of S-cyano-

**Lectin Activity.**—Activity of LBL was determined by hemagglutina-

**Cysteine-containing Peptide from Lima Bean Lectin.**
radioactivity in fragments resulting from cleavage of [14C]cyano-LBL demonstrated exclusive labeling of the 10.5-kDa fragment (Fig. 2A). During cleavage, the labeled carbon on S-cyano-cysteinyl residues is retained in the new NH2-terminal residue. Therefore, the 10.5-kDa fragment is the carboxyl-terminal fragment of LBL and the 19-kDa fragment is the NH2-terminal fragment of LBL. To confirm this assignment, the two polypeptides were isolated by preparative SDS-gel electrophoresis (Fig. 1, lanes b and c). The 10.5-kDa fragment was blocked to Edman degradation (25) but the 19-kDa fragment would be expected to contain the same NH2-terminal sequence as the intact lectin. Ten cycles of manual Edman degradation gave the same sequence for the 19-kDa fragment as determined previously for the three subunit forms of LBL (11).

S-cyano-LBL labeled with iodo[14C]acetamide in the disulfide cysteine was then used to determine the location of the disulfide cysteine. Labeling was found exclusively in the 10.5-kDa fragment (Fig. 2B), indicating that the disulfide cysteine is located in the COOH-terminal region of the lectin. Staining of the fragments resolved on an SDS gel for carbohydrate indicated that only the NH2-terminal fragment contained carbohydrate (Fig. 2C). The 19-kDa fragment was also selectively retained when a mixture of fragments was chromatographed on concanavalin A-Sepharose in 0.05% SDS. The bound fragment was eluted using 0.1 M methyl-α-D-mannoside. These results indicated that the glycosyl moiety is located on the NH2-terminal portion of LBL.

Pepsin-generated fragments of LBL containing the essential cysteine residue were isolated on a mercurial agarose column at low pH to minimize disulfide interchange. The isolated peptides were alkylated with iodo[14C]acetamide and analyzed by reversed phase HPLC, giving a broad multiplet eluting at 45-55% CH3CN. On SDS-gel electrophoresis, a single band of apparent molecular weight 4300 was seen. Several peaks were isolated by HPLC using a shallow gra-
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dient. Dansyl end group analyses of these peptides gave multiple NH₂-terminal residues. The peptide mixture was therefore redigested with trypsin. HPLC now gave well resolved peaks, four of which contained ¹⁴C label (Fig. 3). The three major labeled peptides, denoted a, b, and c in Fig. 3, were isolated and subjected to manual Edman degradation (Tables I–III). Amino acid compositions of the three peptides (Table IV) indicated that sequencing terminated before reaching the carboxyl end of all three peptides. Low yields of tryptophan were released on cycle 9 of peptide b and cycle 11 of peptide c. Thus, tryptophan was tentatively assigned at this position. The three peptides can be aligned to give the following consensus sequence from which the three peptides could be derived by staggered pepsin cleavage at the NH₂-terminus and having a unique trypsin cleavage site following the COOH-terminal lysine: Val-Glu-Phe-Asp-Thr-Cys-His-Asn-Leu-Asp-Trp-(Asx, Pro)-Lys.

Pepsin digests were also conducted using the three isolated subunit forms of LBL prepared by isoelectric focusing in 8 M urea (11). Sulfhydryl-containing peptides were purified on mercurial agarose and analyzed by HPLC. Identical elution profiles were obtained for all three subunits, indicating that there are probably no differences in primary sequence of the three subunits in the vicinity of the essential cysteine.

Homology between the LBL sequence surrounding the essential cysteine and other lectin sequences was examined by a computer program using two PAM matrices to test all possible alignments, including amino acid insertions and deletions (27, 28). Comparing the first 10 residues of the LBL peptide, which sequenced with high yields, with the primary sequence of ConA (29) gave one significant alignment of Val 119 of favin (4.0 standard deviations) and a secondary alignment with Val 7 of ConA (4.1 standard deviations from mean alignment score). Comparison with the primary sequence of favin (30, 31) gave the best alignment with Val 119 of favin (4.0 standard deviations) and a secondary alignment with Ile 165 (3.4 standard deviations).

**DISCUSSION**

Assignment of the relative positions for the essential and disulfide cysteinyl residues and the glycosyl moiety of LBL, based on cleavage of S-cyano-LBL, are summarized schematically in Fig. 4. A disulfide-linked dimer of two 31-kDa subunits is depicted. Only the position of the essential cysteine is known relative to the NH₂ and COOH termini of LBL. The glycosyl moiety (CHO) and disulfide cysteine have been assigned to the 19 and 10.5-kDa fragments, respectively; but their relative positions within the respective fragments is unknown. Attempts to locate the disulfide cysteine by cleaving LBL cyanlated at this residue were unsuccessful.²

Previous investigators noted NH₂-terminal sequence homology among many legume lectins, including LBL (11, 32). In lectins composed of two chains, e.g. favin and the lectins from lentil and pea, the region of homology is located at the

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**Table I**

| Cycle | Residue | Yield a nmol |
|-------|---------|-------------|
| 1     | Asp     | 0.41        |
| 2     | Thr     | 0.13        |
| 3     | Cys     | 0.27        |
| 4     | His     | 0.16        |
| 5     | Asn     | 0.11        |
| 6     | Leu     | 0.13        |
| 7     | Asp     | 0.07        |

* Determined by scintillation counting.

**Table II**

| Cycle | Residue | Yield a nmol |
|-------|---------|-------------|
| 1     | Phe     | 0.82        |
| 2     | Asp     | 0.79        |
| 3     | Thr     | 0.24        |
| 4     | Cys     | 1.27        |
| 5     | His     | 0.47        |
| 6     | Asn     | 0.38        |
| 7     | Leu     | 0.23        |
| 8     | Asp     | 0.17        |
| 9     | Trp     | 0.11 (0.05 D) |
| 10    | (Asp)   | 0.06        |

* Yields and identities for amino acids other than the identified amino acid residue are indicated in parentheses.

* Determined by scintillation counting.

**Table III**

| Cycle | Residue | Yield a nmol |
|-------|---------|-------------|
| 1     | Val     | 0.86        |
| 2     | Glu     | 1.06        |
| 3     | Phe     | 0.63        |
| 4     | Asp     | 1.33        |
| 5     | Thr     | 0.11        |
| 6     | Cys     | 1.31        |
| 7     | His     | 0.39        |
| 8     | Asn     | 0.31 (0.14 H) |
| 9     | Leu     | 0.20 (0.06 N) |
| 10    | Asp     | 0.16 (0.06 L) |
| 11    | Trp     | 0.08 (0.04 D) |

* See Footnote a, Table II.

* Determined by scintillation counting.

**Table IV**

| Amino acid | Peptide |
|------------|---------|
|            | a       | b       | c       |
| Asx        | 4.4 (4)* | 3.6 (4) | 3.7 (4) |
| Glu        | 1.2 (1)  |         |         |
| Cm-Cys     | 1.0 (1)  | 1.0 (1) | 1.0 (1) |
| His        | 1.2 (1)  | 1.0 (1) | 1.1 (1) |
| Gly        | 1.1 (1)  | 1.0 (1) | 1.1 (1) |
| Thr        | 1.4 (1)  | 1.1 (1) | 1.1 (1) |
| Pro        |         |         |         |
| Ala        |         |         |         |
| Val        |         |         |         |
| Leu        | 1.4 (1)  | 1.0 (1) | 1.0 (1) |
| Lys        | 1.0 (1)  | 0.9 (1) | 1.1 (1) |
| Phe        | 0.8 (1)  | 1.0 (1) |         |
| Trp b      | ND b     |         |         |
| Total      | 10-11    | 12      | 14      |

* Numbers in parentheses are nearest integer values.

b Determined spectrophotometrically.

b Not determined.

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² D. D. Roberts, and I. J. Goldstein, unpublished observations.
NH₂ terminus of the β-chain (30, 33). The amino acid sequence of concanavalin A is circularly permuted relative to that of other legume lectins (30). Homology with other lectins was observed when the NH₂ terminus of these lectins were aligned with residues 120–123 of ConA (30). Determination of complete amino acid sequences for ConA, favin, and lentil lectin demonstrated that regions of homology extended throughout the lectin sequences. Since the three-dimensional structure of ConA is also known and some of the residues involved in carbohydrate binding tentatively identified (34–36), we were interested in determining whether the essential cysteine of LBL could be aligned with regions of ConA thought to function in carbohydrate binding. The position of the essential cysteine is now known relative to the NH₂ and COOH terminus of LBL. Therefore, the approximate position on the ConA sequence corresponding to the cysteine of LBL was aligned with residues 120–123 of ConA (30). Determination of the specific interactions between the essential cysteine and carbohydrate or metal ligands of LBL will require crystallographic analysis of the lectin. The present work provides strong indirect evidence, however, for localization of the cysteine residue between the carbohydrate and metal binding sites of LBL. Inactivation of LBL following cyanylation, which adds only two atoms to the sulfhydryl group, also strengthens the argument for an intimate role of the cysteine sulfhydryl group in carbohydrate binding.

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FIG. 5. Homology between the cysteine peptide of LBL and aligned sequences of ConA, favin, and lentil lectin.
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