Lectins in the United States diet: a survey of lectins in commonly consumed foods and a review of the literature[1, 2]

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ABSTRACT Plant lectins or phytohemagglutinins possess potent in vivo biological activities. Some, primarily of the family Leguminosae, have been shown to have deleterious nutritional effects. Little information exists, however, regarding the prevalence of lectins or the specific foods that contain lectins in the United States diet. In the present study the edible parts of 29 of 88 foods tested, including common salad ingredients, fresh fruits, roasted nuts, and processed cereals were found to possess significant lectin-like activity as assessed by hemagglutination and bacterial agglutination assays. Based on this survey and a review of the literature we conclude that dietary exposure to plant lectins is widespread. The spectrum of nutritional consequences of such exposure remains to be determined. *Am. J. Clin. Nutr.* 33: 2338–2345, 1980.

Plant lectins, otherwise known as phytohemagglutinins or hemagglutinins, have been shown to possess a remarkable array of biological activities. In vitro they have been shown to effect lymphocyte mitogenesis (both stimulating (1) and inhibiting (2), with the lymphocytes of the gastrointestinal tract being the most susceptible (3)), to possess the ability to aggregate immunoglobulins (4), to trigger the alternate complement pathway (5), to inhibit fungal growth (1), and to induce histamine release from basophils and mast cells (6). Their in vivo effects have been shown to be equally as impressive. Given orally some lectins can interact with the mucosa of the gastrointestinal tract (7–12), to cause acute gastrointestinal symptoms (12), failure to thrive (7–11), and even death (7–11) in experimental animals. Administered parenterally they can alter host resistance to infection (13–15) or to tumor challenge (16). Under certain circumstances they may be highly allergenic (17, 18). As the knowledge of their biological potency has expanded, so too has speculation regarding their dietary role in a variety of pathological conditions ranging from dental caries (19–21) to inflammatory bowel (22) and celiac disease (23). Considering the vast and varied biological activities that lectins can effect it is surprising that there exists a paucity of studies related to the nutritional consequences of dietary lectins. The reasons for the experimental gap are obscure but may, in part, be due to a lack of awareness within the medical community of which foods in our diet contain lectin activity and the extent of exposure.

A handful of investigators (7–11) led by Jaffe (8) and Liener (7) have, over the last 20 years, established a definitive relationship between the poor nutritive value of raw bean (legume) diet and its content of phytoagglutinin. To our knowledge, no representatives of any plant family other than the Leguminosae have been studied for their nutritive action with the possible exception of the castor bean lectin of the family Euphorbiacae (7, 8). Yet lectins are not exclusively found in legumes but are widely distributed throughout the plant kingdom (24).

To help fill these gaps we embarked upon a study specifically designed to identify *lectins in the edible parts of commonly consumed foodstuffs.* The results of a survey of foods purchased from local retail markets in the greater metropolitan New York area are reported here. Included also is a detailed review

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of previously reported lectin activity in edible plants.

Materials and methods

Preparation of extracts

Foods were purchased from local retail fruit and vegetable markets and supermarkets in the greater metropolitan New York area. Portions (100 mg) of the *edible parts* of each food were placed in a Waring blendor. Saline (100 ml) was added and the contents were homogenized for 1 to 3 min. The resulting suspension was filtered through cheese cloth and the filtrate was then centrifuged. The pH of the clear supernatant was checked and if found to be less than pH 5 was raised to pH 5 to 7 with dilute NaOH.

Hemagglutination and hemagglutination inhibition assays

Outdated human blood of types A, B, and O obtained from the University Hospital Blood Bank was used in all of these assays. Some extracts were also tested for reactivity toward rabbit erythrocytes obtained fresh by venipuncture. Both untreated and enzyme treated cells were employed. The latter were prepared by incubating for 15 min at 37 C, one volume of a 1% crude ficin (Nutritional Biochemicals) solution in 0.9% saline or a 1% papain (Cal-Biochem) solution (0.01 M sodium phosphate and 0.9% sodium chloride) with four volumes of a 6% suspension of three times saline washed erythrocytes. Treated cells were washed four times with saline. Neuraminidase treatment of cells was accomplished by incubating 50 units/ml of neuraminidase (Boehringer Mannheim) with a 4% suspension of erythrocytes for 60 min at 37 C followed by four washes in 0.9% NaCl.

Hemagglutination titrations were performed by a slight modification of the method previously described (25). Briefly, two drop aliquots of doubly diluted extract were mixed with two drops of a 4% suspension of erythrocytes on hemagglutination slides. The slides were rotated on a TekTator variable speed rotating platform at 100 rpm for 30 min. Assays were read macroscopically on a scale of 0 (no agglutination) to 4+ (all cells agglutinated into a single large clump).

Inhibition assays with specific sugars were performed by incubating the extract at the last dilution previously demonstrated to give 4+ agglutination with the indicator cells in the presence of doubling dilutions of a 1% solution of sugar for 30 min at 25 C on a rotary shaker. Test erythrocytes were then added and hemagglutination was assessed as described above. Sugar inhibition was determined to have occurred if the degree of agglutination was significantly less (e.g., a change from a 4 + to a 2 + or less reaction) than a control (no sugar) run simultaneously.

The following sugars were tested for their inhibitory activity: D-glucose, D-galactose, D-mannose, D-fucose, N-acetyl-D-glucosamine, N-acetyl-D-galactosamine, N-acetyl-D-mannosamine, chitobiose, cellobiose, lactose, and fructose.

Bacterial agglutination

Streptococcus mutans strains were a gift of Dr. Gerald D. Shockman, Department of Microbiology, Temple University, Philadelphia, Pa. *Streptococcus sanguis* strains were a gift of Dr. Burtan Rosan, Department of Microbiology, Center for Oral Health Research, University of Pennsylvania, Philadelphia, Pa. *Actinomyces viscosus* was a gift of Dr. Jerry J. Pollock, Department of Oral Biology and Pathology, State University of New York at Stony Brook. *Actinomyces neuslendi* was a gift of Dr. Vincent Iacono, Department of Oral Biology and Pathology, State University of New York at Stony Brook. *Staphylococcus aureus,* Kerwin no. 73, was a gift of Dr. Jeanette Winter of this Department. These bacteria were chosen because of their representation in normal, pathological or opportunistic flora of the oro-pharynx, their association with disease states (e.g., dental caries, periodontal disease, pharyngitis, endocarditis, and enterocolitis) and the likelihood of exposure to lectins during mastication.

S. mutans and *S. sanguis* were maintained on brain heart infusion (Difco) slants and grown for agglutination assays in a defined liquid medium (26). The other organisms were maintained on brain heart infusion slants and were grown overnight in brain heart infusion liquid media for agglutination assays. All organisms were sedimented and washed three times with normal saline and resuspended to an A_{580} of 1.200 in 0.005 M ammonium acetate, 0.05 M sodium chloride buffer, pH 6.8. Agglutination assays were performed on hemagglutination slides. Two-fold serial dilutions of a 1 mg/ml solution of purified lectins were made in the buffer used for bacterial suspension, and 2 drops were added to each well followed by 2 drops of the bacterial suspension. Controls consisted of wells containing the bacterial suspension to which no lectin was added or to which a sugar inhibitor of lectin activity was added.

Plates were placed in a high humidity chamber and rotated on a variable speed rotating platform at 100 rpm. Agglutination was observed at 0, 15, 60, and 120 min under a dissecting microscope.

The degree of agglutination or clumping was assessed by comparing a control (no lectin or extract) to that containing the lectin or extract. Agglutination was scored semiquantitatively on a scale of 0 (no change from controls) to 2+ (very markedly more agglutinated than controls). Each assay was performed in triplicate and agglutination was determined to have occurred only if all three determinations were in agreement. To eliminate observed bias the assays were read by one or the other of the authors without knowledge of which wells contained an extract or lectin.

Results

The ability to agglutinate human erythrocytes or representatives of human indigenous microflora was detected in 29 of 88 food items tested (see **Table 1**). Many of the foods contained substantial amounts of agglutinating activity as extracts could be diluted several-fold and still produce agglutination. It should be pointed out that great variation in agglutinating activity was observed in the same food item purchased from different stores or

TABLE 1
Survey of the agglutinating[a] activity in the edible parts of various foodstuffs

Name	Latin name	Sugar inhibitor[b]	Comment
Vegetables			
Tomato	*Lycopersicon esculentum*	Chitobiose	Purified (2), agglutinates bacteria (*A. viscosus* and *S. aureus.*)
Potato	*Solanum tuberosum*	Chitobiose	Purified (28)
String bean	*Phaseolus vulgaris*	N-acetyl-D-galactosamine[c]	Reactivity best toward type A cells. Reacts with *S. Mutans.*
Carrot	*Daucus carota*		Does not agglutinate human erythrocytes. Selectively agglutinates *S. mutans*[d] (29)
Zucchini	*Cucurbita pepo*	N-acetyl-D-glucosamine	Reactivity best toward ficin treated cells. Purified from stem exudate (30).
Green peas	*Pisum sativum*	α-D-methylmannoside D-glucose	Purified (31), reacts with *A. neuslundi, A. viscosus, S. mutans*[d]
Soybean sprouts	*Glycine Max*	N-acetyl-D-glucosamine	Purified from bean (32). Reacts slightly better with type A cells.
Mung bean sprouts	*Phaseolus mungo*	D-galactose	Purified from bean (33). Does not react with human cells but with rabbit erythrocytes.
Lentil sprouts	*Lens esculenta*	α-D-methylmannoside and D-glucose	Purified from bean (34).
Fruits			
Canteloupe	*Cucumis melo cantalupensis*	Chitobiose	Reactivity only toward papain treated erythrocytes. Agglutinates *S. mutans.*
Grapes	*Vitus vinifera*	NT[e]	Very high activity in the seeds.
Cherries	*Prunus avium bigarreaus*	NT[e]	Better activity toward nonenzyme treated erythrocytes.
Pomegranate	*Punica granatum*	Chitobiose	Very strong reactivity, best toward B cells.
Raspeberries	*Rubus idaeus*	[c]	Reactivity mainly in seeds. Fruit produces lysis. Reacts only with ficin treated erythrocytes.
Blackberries	*Rubus fruticosus*	[c]	Reactivity only toward nonenzyme treated O and A cells.
Cereals			
Wheat germ	*Tritium vulgaris*	N-acetyl-D-glucosamine, sialic acid	Purified (35). Reacts with salivary glycoproteins (21) and streptococci of groups A and C (36).
Corn flakes[f]		[c]	Made from corn.[g] Reacts best with A cells. Agglutinates *S. mutans.*
Wheaties[h]		[c]	Weakly reactive.
Product 19[f]		[c]	Made from corn, oats, rice, wheat flour.[g] Reacts best with A cells.
Rice Krispies		NT[e]	Made from rice.[g] Weak reactivity for rabbit cells. Does not react with human cells.
All Bran[f]		[c]	Made from wheat.[g] Agglutinates *S. mutans.*
Shredded wheat[f]		[c]	Made from wheat.[g] Agglutinates *S. mutans.*
Special K[f]		[c]	Made from rice and wheat germ.[g] Strong reactivity. Agglutinates *S. mutans.*
Raisin Bran[f]		NT[e]	Made from raisins and wheat germ.[g] Strongly reactive.
Total		NT[e]	Weak reactivity for A cells.

TABLE 1 (*continued*)

Name	Latin name	Sugar inhibitor[a]	Comment
Spices			
Garlic	*Allium sativum*	NT[e]	Weak reactivity only toward papain treated erythrocytes.
Marjorum	*Labiaceae origanum*	[c]	Reactivity only toward papain treated cells.
Allspice	*Pimenta officialis*	[c]	Reactivity only toward papain treated cells.
Other			
Peanuts (dry roasted)	*Arachis hypogea*	D-galactose	Purified (37). Reactivity only toward neuraminidase treated cells.
Mushrooms	*Agaricus bisporus*	N-acetyl-D-galactosamine	Purified (38). Reactivity best toward A cells. Moderate activity in snow white mushrooms.

[a] Unless otherwise stated all lectins listed in Table 1 agglutinated human erythrocytes of A, B, and O blood types. [b] As determined in the present study. [c] Activity not inhibited by battery of simple sugars (see "Methods"). [d] M.S. Nachbar, unpublished observation. [e] Not tested. [f] Product of Kellogg Company, Battlecreek, Mich. [g] According to information on the package supplied by manufacturer. [h] Product of General Mills, Minneapolis, Minn.

from the same store on different days. Sometimes a food that possessed substantial activity on one day was found to have little or even no activity on another day. Varietal differences were also observed, a phenomenon originally described by Kruppe (27). In addition, foods found not to contain activity the first time were not retested and in some assays agglutination may have been obscured by lytic substances or natural inhibitors present in the foods and, finally, all cell extracts were not tested for agglutination of bacteria. For all of these reasons it seems quite probable that an even higher percentage of food would have been found to contain agglutinating activity if tested more frequently or under more optimum conditions.

Discussion

The survey of the edible portions of fresh and processed foods reported here found lectin activity in about 30% of the food stuffs tested, including such common foods as salad ingredients, fruits, spices, dry cereals, and roasted nuts (Table 1). Moreover, a review of the literature (**Table 2**) uncovered 53 additional edible plants in which phytohemagglutinins have been identified. While, in most cases, the significance of the latter is somewhat obscured since the nonedible parts of the plant were tested, nevertheless, it is quite apparent that exposure to dietary lectins is a frequent and widespread event.

Although both cooking and the normal digestive processes might be expected to blunt or abrogate dietary lectin activity, this need not necessarily be the case. Liener (7) has pointed out that dry heat may not completely destroy lectin activity. This phenomenon is clearly illustrated in the finding of hemagglutinating activity in the processed wheatgerm, peanuts, and dry cereals that we tested (Table 1). Similar findings for wheat germ have been presented by Brady et al. (61). In addition, several of the lectins have been found to be resistant to proteolytic digestion e.g., wheat germ agglutinin (61), tomato lectin (2), navy bean lectin (10)) and, when looked for, have been recovered intact in stool (7, 10, 61). It can be concluded that at least some lectins in foodstuffs will survive one or both degradative processes to interact with cells, secretions, and microflora of the digestive tract resulting in, as yet unknown, functional consequences.

Given the significant exposure of the populace to dietary lectins and the unusual breadth of biological activities potentially affected, it is obvious that future investigations of their nutritional effects will have to encompass a wider spectrum of functional parameters than heretofore tested. It is hoped that the information provided by our survey will assist investigators in various disciplines interested in this intriguing area.

TABLE 2
Literature survey of lectin activity[a] in other edible plants[b]

Name	Latin name	Reference source	Comment
Vegetables			
Rhubarb	*Rheum rhapontium*	(39)	Reactivity only toward bromelin treated cells.
Sweet potato	*Ipomea batatas*	(40)	Does not react with human cells. Reacts with rabbit cells. Enzyme treated cells not tested. Reacts with spores of *Ceratocystis fimbirata.*
Asparagus	*Asparagus officinalis*	(39)	
Chicory (endive)	*Cichorium intybus*	(24)	
Swiss chard	*Beta vulgaris*	(24)	
Rutabaga	*Brassica napobrassica*	(39)	
Turnip or beet	*Brassica campestris rapa*	(39)	Reactivity only toward bromelin treated cells
Radish	*Raphanus sativus*	(24)	
Cucumber	*Cucurbita sativus*	(41)	Activity in stem exudate and in seeds.
Sweet peppers	*Capsicum annum*	(27)	
Celery	*Apium graveolens*	(39)	
Parsley	*Petrosecinum hortense* or sativum	(24)	
Rice	*Oryza sativa*	(42)	Purified (42). Specificity for N-acetyl-D-glucosamine. Lectin only in embryo (43).
Corn	*Zea mays*	(44)	Purified (44). Does not react with human erythrocytes. Reacts with Erwinia species.
Barley	*Hordeolum sativum vulgare*	(27)	Specificity for (43) N-acetyl-D-glucosamine. Lectin only in embryo (43).
Okra	*Abelmoschus esculentus*	(39)	Reacts with bromelin treated cells only.
Pumpkin	*Cucurbita maxima*	(45)	Purified (45). Specificity unknown.
Jack bean	*Canavalia ensiformis*	(46)	Oral toxicity. Purified (46). specificity for α-methyl-mannoside or α-methyl glucoside.
Horse gram	*Dolichos bifloris*	(47)	Oral toxicity (11). Purified (48). Specificity for type A cells (48).
Field bean	*Dolichos lablab*	(27)	Oral toxicity (11). Also reacts well with rabbit erythrocytes. May have specificity for A and B cells (62).
Lima bean	*Phaseolus lunatus*	(63)	Oral toxicity (1). Purified (49). Specificity for A cells ($A_1 > A_2$) (63).
Kidney bean	*Phaseolus vulgaris*	(11)	Oral toxicity (11). Purified (50). Also reacts well with rabbit, guinea pig and sheep erythrocytes.
Navy bean	*P. vulgaris*	(11)	Oral toxicity (9, 10). Purified (52).
Pinto bean	*P. vulgaris*	(51)	Oral toxicity (11).
Wax bean	*P. vulgaris*	(51)	Purified (53)
Processor bean	*P. vulgaris*	(10)	Oral toxicity (10). Purified (64). Also reacts well with rabbit cells (64).
Tora bean	*P. vulgaris*	(54)	Purified (54). Specificity for N-acetyl-D-galactosamine (54).
Kintoki bean	*Phaseolus vulgaris*	(55)	Purified (55).
Castor bean	*Ricinus communis*	(24)	Oral toxicity (8). Purified (56). Specificity for D-galactose (56).
Sweet pea	*Lathyrus odoratus*	(27)	Purified (57). Reacts strongly with rabbit erythrocytes.
Fava bean	*Vicia faba*	(27)	Purified (58). Also reacts well with rabbit and guinea pig erythrocytes.
Cow peas (black eyed)	*Vigna unguiculata*	(59)	Purified (59). Specificity for D-galactose, D-glucose, D-mannose and amino sugars (59).
Fruits			
Apples	*Malus* species	(27)	
Quince	*Cydonia oblonja* or *vulgaris*	(27)	
Watermelon	*Citrullus vulgaris*	(24)	

TABLE 2 (*continued*)

Name	Latin name	Reference source	Comment
Grapefruit	*Citrus medica*	(27)	
Lemon	*Citrus aurantium*	(27)	
Orange	*Citrus aurantium*	(27)	
Banana	*Musa paradisiac*	(27)	
Papaya	*Carica papaya*	(24)	
Strawberries	*Fragaria vesca*	(27)	
Currants	*Ribes rubrum*	(27)	
Plum	*Prunus americana*	(27)	
Spices			
Nutmeg	*Myristica fragrans*	(27)	
Peppermint	*Menta piperita*	(27)	
Other			
Coffee	*Coffee arabica*	(27)	
Cocoa	*Theobroma cacao*	(24)	Reacts best with cells of combined B and H activity (24)
Coconut	*Cocus nucifera*	(24)	
Walnut	*Juglans regia*	(27)	
Hazelnut	*Corylus avellania* or *maxima*	(27)	
Carraway seeds	*Carum carvi*	(27)	
Sesame seeds	*Sesamum indicum*	(60)	Purified (60). Specific for D-galactose (60).
Sunflower seeds	*Helianthus annus*	(24)	Anti-O specificity (24)

[a] Unless otherwise stated the activity manifested was toward human erythrocytes of A, B, and O blood types. [b] Unless otherwise stated the part of the plant tested was the seed.

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