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A review of the role of lectins in animal gametes and embryo development

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Abstract

Lectins are carbohydrate binding proteins found in most of the plants and in some animals. Sperm glycocalyx modifications are known to occur during capacitation and the acrosome reaction. These changes are very important for gamete recognition and fertilization in mammals but are not fully understood. Moreover, studies on lectin treatment of oocytes have yielded inconsistent effects on fertilization rates, suggesting a complex interplay of mechanisms. Beyond fertilization, the mitogenic properties of lectins are associated with germinal vesicle breakdown and cumulus cell expansion, indicating their involvement in oocyte maturation. Lectins have been also implicated in modulating cell adhesion, cell surface remodeling, and signaling pathways during early embryonic cleavage stages, influencing successful preimplantation embryo development. This article discusses the roof lectins in sperm, oocyte and embryo biology.

Keywords: Embryogenesis, Lectin, Oocyte, Reproductive, Sperm, Spermatozoa.

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Contents

Contribution of this paper to the literature
In the past years, a review study on the effect of lectins on animal reproduction had not been conducted. The purpose of this study was to review the studies that have been conducted on the effect of lectins on the reproductive system in one article. This study reviews the effect of lectins on the male and female reproductive systems, which has not been done so far.

1. Introduction

Lectins are carbohydrate binding proteins present in most of the plants and in some animals [1]. The term 'Lectins' is derived from the Latin 'Legree', meaning to pick or select. Unlike antigens, lectins do not stimulate the immune system; however, they have the innate ability to bind in a manner analogous to antibodies [1]. These lectins selectively bind to carbohydrate moieties of glycoproteins that are present on the surface of most animal cells. Structurally, these lectins have a diverse class of proteins, which have the ability to bind carbohydrates with considerable specificity [2]. Numerous studies have explored the in vivo and in vitro effects of lectins. In vitro, they have been shown to affect lymphocyte mitogenesis, exhibiting both stimulating and inhibitory effects, particularly in lymphocytes from the Gastrointestinal Tract (GIT). They possess the ability to aggregate immunoglobulin's, to trigger the alternative complement pathway, to inhibit fungal growth and also to induce histamine release from basophilic and mast cells. Lectins are relatively resistant to both heat (withstanding over 30 min at 70°C) and digestion. Moreover, some of the lectins are highly resistant to gastric acid and proteolytic enzymes [3].

1.1. Structure of Lectins

According to Goldstein, et al. [4] lectins primarily consist of carbohydrate-binding proteins or glycoproteins of nonimmune origin, which bind cells, precipitate glycoconjugates, or sometimes both. The specific ability of lectins to bind with the cell surface mainly depends on the presence of monosaccharides or simple oligosaccharides, which, when present, inhibit the lectin-associated reaction [4]. In some cases, carbohydrate-associated enzymes with multiple combining sites may agglutinate or precipitate glycoconjugates and thus may be classified as lectins [5].

Some lectins are structurally differentiated such as:

1. Erythrine C lectins.
2. Concanavalin C lectins.
3. Ulex europaeus lectins.
4. C type lectins.

The binding of lectins is reversible and noncovalent, involving either simple or complex carbohydrate conjugates, whether free in solution or on cell surfaces. Surfaces containing glycoconjugates act solely as lectin receptors. The specificity of lectins generally relies on the hapten inhibition test, in which various sugars are tested for their ability to inhibit hemagglutination of erythrocytes. All lectin molecules possess two or more carbohydrate-binding sites, essential for their capacity to agglutinate cells or to interact with complex carbohydrates. Some lectins can accommodate up to five or more sugar residues at their combining sites. Multibranched oligosaccharides typically exhibit stronger lectin binding reactivities than linear ones due to cooperative binding effects of lectin and carbohydrate complexes. Some lectins have dual or multiple affinities for different disaccharides. Interactions between these molecules are hydrophobic, and electrostatic forces are rarely involved. Lectins are purified from crude aqueous buffer or saline extracts of various tissues using standard protein chemistry methods, including ammonium sulfate or ethanol precipitation, and affinity chromatography [6].

1.2. Biological Role

The biological role of lectins is speculative. Lectins may be involved in sugar transport or carbohydrate storage. Some lectins may be associated with the binding of symbiotic rhizobia to form root nodules. Due to their crucial role in adhesion and agglutination, lectins have been considered important in both symbiotic and pathogenic interactions between some microorganisms and hosts. Microbial lectins may play an important role in adhesion to surfaces colonized by the microorganisms. For example, tomato lectins bind to mucosal cells and resist denaturation by acids and proteolytic enzymes [7]. There are several studies which have established lectins as specific agglutinins for blood groups of erythrocytes. Due to their multifaceted biological properties, lectins were later developed by cell biologists as probes to investigate cell surface structures and functions. Some lectins have been used to fractionate animal cells, including B and T lymphocytes, and to demonstrate changes in cell surface architecture following virus or parasite infection [8]. Lectins have been used as carriers for the delivery of chemotherapeutic agents. They are significant reagents for investigating cell surface receptors in bacteria, protozoa, and higher organisms. The interactions of plant lectins with microorganisms have been applied for typing bacteria, fungi, and protozoa. Lectins serve an important role in the characterization of bacterial cell components and in the identification of bacteriophage receptors. Many bacteria contain surface-associated lectins that enable these microorganisms to adhere to surfaces. One of the major advantages of applying lectins in microbiology is that cellular or surface receptor sites can be partially characterized by hapten inhibition [9].

1.3. Advantages of Lectins

- Stability.
- Activity in small concentration.
- Commercial availability of many lectins.
- Ability to probe subtle surface structural differences between various isolates [10].

1.4. Disadvantages of Lectins

In humans, lectins have been reported to cause damage, including mass food poisoning from uncooked kidney beans and it also causes hemolytic anemia and jaundice from Mexican fava beans. Lectins may cause acute gastrointestinal symptoms including nausea and vomiting. They bind to the luminal surface of absorptive

erythrocytes in the small intestines. This will cause severe damages to the microvilli of the intestine, thus disrupting the digestion and absorption [11, 12]. Lectins can also promote the growth of harmful bacteria in the gut. Lectins also disrupt proteins and carbohydrate malabsorption. In protein malabsorption, gut lectins bind to erythrocytes, causes inflammation which blocks the production of enterokinase, a protein enzyme. In case of carbohydrate malabsorption, it reduces intestinal glucose uptake by 50%. Wheat germ agglutinin and other lectins can even bind to insulin receptors on cells, disrupting glucose metabolism. Grains will have high content of lectins, which may cause inflammatory bowel and celiac diseases in humans [11, 12].

1.5. The Role of Lectin on Primary Sperm Attachment

Sperm glycocalyx modifications, known to occur during capacitation and the acrosome reaction, are critical for gamete recognition and fertilization in mammals but are not fully understood [13]. During the process of sperm-egg interactions, at least three separate events involving cell surface recognition occur: (1) the interaction between sperm and egg components (e.g., egg jelly or glycoprotein coat) before the acrosome reaction; (2) the attachment of sperm to the egg envelope surface after the acrosome reaction; and (3) the fusion of sperm and egg plasma membranes [14]. Secondary attachment examinations have been conducted across various species of invertebrates, including the adhesion of either the sperm acrosome process or acrosome granule contents to the egg vitelline layer or chorion [15-18]. In sea urchins, the acrosome reaction is induced when spermatozoa initially contact the egg jelly coat, triggered by a sulfated fucose component [19].

The investigation by Rosati and De Santis [20] focused on the attachment process and revealed that binding sites for concanavalin A (Con A) and asparagus pea lectin (APL) are present on both the egg chorion and sperm surfaces [20]. Moreover, competition experiments involving monosaccharides have suggested that fucose may be implicated in gamete attachment [21, 22]. Lectins, proteins with high saccharide-binding specificities, have become popular membrane probes [22]. They have been employed in studies to identify the presence of sugars on gamete surfaces. It has been demonstrated that both spermatozoa and the egg chorion of Ciona have binding sites for fluorescein-conjugated Con A and APL [20]. Despite a decrease in fertilization following lectin treatment of eggs, the outcomes were inconsistent. Huang, et al. [23] found that FITC-conjugated and gold-labeled WGA attached to the chorion of the ascidian, Phallusia mammillata, and hindered fertilization Huang, et al. [23]. In Limulus, FITC-APL and FITC-Con A adhered to the envelope surface of the egg; however, only APL reduced sperm attachment. There was no indication of FITC-GPL binding except on the egg cortex, and GPL did not impede sperm attachment.

1.6. Lectin Receptors Changes During Spermatozoon Epididymal Maturation and Capacitation

Sperm glycocalyx composition in mammals has been extensively studied by various authors Bearer and Friend [24]; Schröter, et al. [25]; Tecle and Gagneux [26] and Töpfer-Petersen [27]. Similarly, studies suggest that the distribution of lectin receptors changes during spermatozoon epididymal maturation, capacitation, and the acrosome reaction in mammals [22, 28, 29]. According to other researchers, lectins may prove useful in selecting spermatozoon subpopulations with the highest fertilizing capacity [30-32] highlighting the importance of understanding how the glycocalyx varies in other biologically or commercially valuable species. The knowledge of molecular changes undergone by spermatozoa during in vitro capacitation could facilitate the selection of spermatozoa subpopulations with the highest fertilizing potential for use in artificial insemination processes. This would also promote genetic exchange and increase genetic variability, helping to maintain group stability, avoid animal transport, or reduce the number of breeding males needed in a single facility [13].

Sperm receptors comprised of sugars are also present on egg membranes of brown algae, Fucus serratus [33] and the ascidian, Ciona intestinalis [21]. Isolated Fucus egg membranes have shown to compete with whole eggs for spermatozoa, thereby lowering the percentage of eggs fertilized [33]. The Lewis-a antigen, a type of carbohydrate antigen that belongs to the Lewis blood group system, was found attached to viable sperm with intact acrosomes. However, when sperm were fixed, having their acrosomes removed through freezing and thawing, no binding was observed. Furthermore, enzymatic removal of fucose from the epithelium led to a significant decrease in binding [34]. In the case of hamster sperm, it appears that a lectin on the sperm can identify a carbohydrate structure containing sialic acid. Colloidal gold-labeled fetuin (a biochemical reagent used in microscopy and binding assays to visualize interactions involving carbohydrate-binding molecules) was observed binding to the heads of fresh epididymal hamster sperm, but did not bind to the apical regions of the heads of sperm incubated under capacitating conditions until they were hyperactivated [35]. The hyperactivated or capacitated hamster sperm failed to adhere to the epithelium upon introduction into the oviduct [36]. This suggests that a lectin present on the sperm surface undergoes a loss or modification during capacitation, enabling the sperm to detach from the epithelium.

The glycosylated chains present on the membrane play a crucial role in gamete recognition, adhesion, and fertilization in mammals. Changes in the plasma membrane during in vitro capacitation and the acrosome reaction (AR), such as the removal or appearance of specific proteins or glycoproteins, have been investigated using lectins that selectively bind to carbohydrate residues [13]. Different lectins, each tagged with distinct fluorochromes, have been utilized to investigate the expression, distribution, and alteration of membrane glycoconjugates. Studies involving flow cytometry and electron microscopy in human sperm have demonstrated alterations in lectin binding patterns throughout the capacitation process and the AR [37]. For instance, in humans, Concanavalin A (Con-A) binds to the anterior head region of capacitated sperm, but following the induction of the AR, this lectin binds to the equatorial region and the internal acrosome membrane. Notably, Con-A exhibited weak binding to the head membrane and midpiece of fresh boar spermatozoa. An elevation in mannose residues was noted in the acrosomal region of capacitated sperm, with the labeling becoming especially pronounced at the acrosomal border following the acrosome reaction. Consequently, these findings illuminate the glycosylation patterns of boar spermatozoa [13].

Alterations in the distribution of lectin binding sites during capacitation and the acrosome reaction have been documented in various mammalian species, although there are conflicting findings. While Lee and Ahuja [38] reported no significant changes in distribution patterns in mouse sperm, other researchers have observed alterations in the distribution of plasma membrane glycoproteins during capacitation in boar spermatozoa [39]. Additionally, Vázquez, et al. [40] identified a notable decrease in lectin binding (Con-A) in capacitated and acrosome-reacted boar

spermatozoa [40]. Furthermore, the distribution of N-acetylglucosamine, sialic acid, mannose, and fucose residues in the boar sperm glycocalyx undergoes changes during capacitation and the acrosome reaction [13].

1.8. The Role of Lectin Receptors Sites in the Zona Pellucida of Follicular and Ovulated Oocytes

The mammalian oocyte is surrounded by a transparent, extracellular coat called the zona pellucida (ZP) [41]. This extracellular matrix plays a crucial role during fertilization [42-44]. The ZP restricts interspecies fertilization, is involved in the induction of the acrosome reaction in bound sperm, and assists in establishing the block to polyspermy after fertilization. In a wide variety of species studied, the ZP is composed of only a few glycoproteins. It has been suggested that carbohydrate determinants of the ZP glycoproteins are crucial in sperm-egg interaction [45, 46]. The most studied species in this respect is the mouse, where it has been shown that the ZP consists of three glycoproteins, namely ZP1, ZP2, and ZP3, each of which has a unique polypeptide chain and oligosaccharides [47]. It was demonstrated that sperm-egg interaction in the mouse is controlled by O-linked oligosaccharides of the ZP glycoprotein, serving as sperm binding sites and the polypeptide chain as an inducer for the acrosome reaction [48, 49]. In that respect, specific sugar residues of ZP O-linked oligosaccharides, e.g., α-galactosyl (Gal) residues, were shown to play a role in sperm binding activity [50]. It may be assumed that the ability of specific sugar residues to function as sperm receptors largely depends on their spatial distribution and availability on the ZP surface before and after fertilization, and on their species-specific biochemical nature. Therefore, there is an increasing demand to expand our ability to localize and characterize specific sugar residues in the ZP at the ultrastructural level and to correlate their distribution with maturational changes and fertilization.

Lectins, sugar-binding proteins or glycoproteins of non-immune origin, which agglutinate cells and/or precipitate glycoconjugates having saccharides of appropriate complementarity [4] have been used extensively in numerous studies to inhibit sperm-egg adhesion [51-55]. Lectins have previously been used for the characterization of ZP at the electron microscopic (EM) levels [56-58]. It was shown by FITC-labeled lectins that mouse ZP contains receptors to several lectins, particularly those that bind to Gal, N-acetylgalactosaminyl (GalNAc), and N-acetylglucosaminyl (GlcNAc) residues [58]. EM analysis of lectin binding sites in the ZP of several mammalian species [57] revealed a high density of specific lectin receptors, including RCA-I and WGA, at the outer regions of the ZP, whereas Con A receptors were sparsely distributed throughout the entire thickness of the ZP. Shalgi, et al. [59] demonstrated that in ovulated oocytes, most sugar residues were homogeneously distributed throughout the entire depth of the ZP or located mainly in its inner portion, whereas in follicular oocytes, at all developmental stages, the sugar residues were mainly located at the outer regions of the ZP, adjacent to the cumulus cells [59]. The results clearly reflect a change in both the content and distribution of sugar residues in the ZP following ovulation, which may have significance in fertilization. Previous studies have indicated that after hormonal stimulation for ovulation, the zona pellucida exhibits a progressive enhancement in its permeability to sperm [59-62]. Other studies reported that new antigens originating from the oviduct epithelium are found on the ZP after ovulation [56, 63-67].

1.9. The Effect of Lectin on the Physiology of Oocyte Maturation

The developmental potential of oocytes matured in vitro is often reduced compared to those matured in vivo [68]. To enhance the bubaline oocyte maturation rate, it is essential to modify a suitable oocyte maturation medium with various supplements. In vitro matured oocytes are commonly used for the production of IVF or cloned calves. Complete maturation of oocytes is critical for the developmental competence of embryos [69]. Although in vitro maturation is achievable, it is associated with a loss of developmental competence, which is linked to the absence of specific proteins in oocytes cultured to metaphase II in vitro [70]. The production of embryos in the laboratory involves three major steps: oocyte maturation, fertilization, and embryo culture. Sirard, et al. [71] characterized five levels of oocyte developmental competence, including the ability to resume meiosis, to cleave upon fertilization, to develop into blastocysts, to induce pregnancy, and to generate healthy offspring. Cytoplasmic changes accompanying oocyte growth include mRNA transcription, protein translation, and post-translational modifications [72, 73]. Oocytes are complex cells containing many organelles and molecules, each of which must be in the appropriate state for the egg to be competent to sustain subsequent embryo development [74]. Despite at least 80% of bovine oocytes collected from antral follicles undergoing spontaneous nuclear maturation in culture [75] gonadotropins are often added to maturation media to induce cytoplasmic maturation, cumulus expansion, and to improve embryonic development. Follicle-stimulating hormone (FSH) induces expansion of cumulus oocyte complexes in vitro [76] enhancing bovine fertilization and regulating the cleavage rate, growth, and reproductive processes of the mammalian body [77]. Luteinizing hormone (LH) controls the length and sequence of the female menstrual cycle, including ovulation and ovarian production of both estrogen and progesterone [78]. Additionally, it has been reported that serum is required for hormonally induced cumulus expansion of COCs, although the percentage may be as low as 0.01–5% [76]. In most cases, supraphysiological hormone concentrations are added to in vitro maturation (IVM) media, and it is not clear if these high concentrations are strictly required [79]. Recently, recombinant gonadotropins have become commercially available; these are very pure sources of hormone that can allow the individual roles of FSH and LH to be investigated without the hormone cross-contamination of pituitary, serum, or urinary preparations. General mitogens, specifically lectins, can stimulate the maturation of isolated mouse cumulus oocyte complexes (COCs) [80]. Lectins are carbohydrate-binding proteins or glycoproteins of nonimmune origin that have profound effects on a variety of cultured cells, including agglutination and mitogenesis [8]. They serve many different biological functions in animals, from the regulation of cell adhesion to glycoprotein synthesis and the control of protein levels in the blood. The mitogenicity of lectins is strongly associated with the stimulation of germinal vesicle breakdown (GVB) as well as cumulus expansion. Funsho Fagbohun and Downs [81] reported that the dosage of lectin concentration and maturation rate of the COCs are directly proportional to each other. Studies demonstrated that lectin doses enhance both oocyte maturation and the regulation of gene expression in oocytes. The processes of meiotic maturation and the acquisition of developmental competence determine the ability of the oocyte to undergo successful fertilization, cleavage, and embryonic development. These important steps depend upon various factors that lead to proper nuclear and cytoplasmic maturation [82]. Oocyte meiotic maturation is a complex process involving germinal vesicle breakdown, chromosome condensation and segregation, formation of the metaphase plate, completion of meiosis I, extrusion of the first polar body (PB), and arrest at metaphase II [83]. It

is well known that oocyte developmental potential is a reflection of proper cytoplasmic maturation. Even though most bovine oocytes resume meiosis and progress to metaphase II following IVM [84] cytoplasmic in vitro maturation is generally compromised, leading to lower rates of development compared to in vivo matured oocytes.

Lectins have been used as probes for determining the presence and physiological role of carbohydrates on cell surfaces [57, 85, 86]. Binding of lectins to the plasma membrane and investing layers of mouse, hamster, rat, amphibian, ascidian, and sea urchin eggs has been documented. Treatment of oocytes or sperm of some species with lectins has been shown to negatively affect fertilization, implicating oligosaccharides as important participants in gamete-gamete interaction [87-90]. Furthermore, treatment of mature oocytes with lectins has been reported to stimulate activation, as manifested in the cortical granule reaction [88, 91, 92]. Of particular interest to the present study is the finding reported many years ago by Shida, et al. [93] that the lectin phytohemagglutinin stimulated GVB in starfish oocytes. Although this are needs further research, variety of important physiological processes in germ cells could potentially be mediated by surface glycoconjugates [93]. In line with this, it will be important to identify the glycoconjugates and receptors responsible for the actions of lectins on the cumulus cell-enclosed oocyte and to determine if they are related or identical to receptors for other stimulatory ligands such as growth factors and gonadotropins. The primary objective of these studies is to comprehend the mechanisms through which the oocyte-cumulus cell complex is prompted to initiate maturation. While lectins cannot be considered physiological inducers of cumulus expansion and oocyte maturation, they nevertheless can serve as useful tools in elucidating the mechanism(s) involved.

1.10. The Effect of Lectin on the Physiology of Embryogenesis

By influencing cell adhesion, guiding cell-cell communication, modulating intracellular signals, and affecting morphogenetic movements, lectins contribute in shaping the physiological and morphological landscape of the developing embryo. Francoise Poirier, et al. [94] provided the first evidence that soluble lectins may play a role in mammalian development as early as implantation. The significance of soluble lectins during early embryogenesis has been demonstrated in two other species as well [94]. In Xenopus embryos, a soluble lectin with a relative molecular mass of 43 × 10^3 is first detected in fertilized eggs and later secreted into the extracellular matrix during gastrulation [95, 96]. In contrast, in chick embryos, two similarly sized lactose-binding proteins (one being L14) are detected in some migrating cells during gastrulation [97-99]. These findings suggest that interactions between lectins and associated glycoconjugates may play a crucial role in the dynamic changes of the extracellular environment during embryogenesis in these species. Francoise Poirier, et al. [94] found that the expression of L14 lectin is tightly regulated during several stages of embryogenesis. The striking regulation of its synthesis at the time of implantation strongly suggests that this carbohydrate-binding protein may play a key role in the attachment of the hatched blastocyst to the uterine epithelium [94].

As another example, Wang, et al. [100] demonstrated the differential impacts of lectins (wheat germ agglutinin (WGA), soybean agglutinin (SBA), and peanut agglutinin (PNA)) from three commonly used plant protein sources (wheat, soybean, and peanut meals) on embryonic development and liver cells of zebrafish. Supported by cell signaling and metabolic analyses, their study showed that both WGA and SBA caused apoptosis, while PNA stimulated cell proliferation in contrast. This study cautions against the general consideration of plant lectins as toxic without discrimination. Therefore, further characterization of the distinct functions of individual lectins could be valuable for both nutrition and other potential applications [100].

2. Conclusions

Throughout this exploration of lectin's roles in reproductive processes reproductive processes involving the sperm, egg, and embryo, significant insights have emerged regarding their function in mammalian fertilization and oocyte maturation. Modifications to the sperm glycocalyx, which occur during capacitation and the acrosome reaction, are pivotal for gamete recognition and successful fertilization, yet the intricacies of these modifications are not fully elucidated. This article has highlighted the potential of lectins to serve as a proxy in assessing the fertilizing capacity of sperm, reflecting their binding affinity to specific glycosylated regions on the sperm surface. Moreover, lectins have proven instrumental in inducing oocyte maturation and cumulus expansion within mouse oocyte-cumulus cell complexes. This induction points to lectins' ability to stimulate specific signal transduction or metabolic pathways that are crucial for both mitogenesis and the comprehensive maturation of the oocyte-cumulus cell complex. Such findings underscore the dual functionality of lectins, suggesting that they can significantly enhance our understanding of, and capabilities in, reproductive biology. By leveraging lectins to manipulate and study reproductive processes, we gain a deeper understanding of cellular interactions and developmental mechanisms essential for successful fertilization and embryo development. This comprehensive approach not only clarifies the biological functions of lectins but also highlights their potential therapeutic applications in addressing fertility issues and optimizing in vitro fertilization techniques.

Abbreviations

MAP: mitogen activated protein; GIT: Gastro Intestine Tract; Con A: concanavalin A; APL: asparagus pea lectin; ZP: zona pellucida; Gal: a-galactosyl; EM: electron microscopic; GalNAc: Gal, N-acetylgalactosaminyl; GlcNAc: Nacetylglucosaminyl; FSH: Follicle stimulating hormone; LH: Luteinizing hormone; IVM: in vitro maturation; COCs: cumulus oocyte complexes; GVB: germinal vesicle breakdown; MAP: mitogen activated protein kinase; WGA: wheat germ agglutinin; SBA: soybean agglutinin; PNA: peanut agglutinin; AR: acrosome reaction; mRNA: messenger RNA; FITC: Fluorescein isothiocyanate; RCA-I: Ricinus Communis Agglutinin I; PHA-M: Phytohemagglutinin M.

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