ANADOLU ÜNİVERSİTESİ BİLİM VE TEKNOLOJİ DERGİSİ
ANADOLU UNIVERSITY JOURNAL OF SCIENCE AND TECHNOLOGY
Cilt/Vol.: 5 - Sayı/No: 1 : 1-7 (2004)

DERLEME/REWIEW

VEGETATIVE STORAGE PROTEINS IN PLANTS

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ABSTRACT

Vegetative storage proteins were originally identified as leaf proteins that accumulated in depodded plants. In leaves, the vegetative storage proteins are mainly localized in the vacuoles of bundle sheath cells. Based on the developmental pattern of accumulation of the vegetative storage proteins, their localization, and accumulation in response to removal of reproductive organs and blocking leaf phloem export, it has been suggested that these proteins serve as vegetative sinks for temporary storage of carbon and nitrogen. In addition, they are thought to have important nutritional roles during plant development and stress adaptation. The availability and reutilization of vegetative storage proteins as nitrogen resources are crucial in survival and competitive ability of plants. Several vegetative storage proteins have also been shown to have enzymatic effect. Vegetative storage proteins are rapidly synthesized or degraded according to the need for nutrients by other plant tissues during plant growth.

In this review, general information on vegetative storage proteins, factors affecting their gene expression and accumulation, and their possible functions are given.

Anahtar Kelimeler: Vegetative storage proteins, Methyl jasmonate.

BİTKİLERDEKİ VEJETATİF DEPO PROTEİNLERİ

ÖZ

Vejetatif depo proteinleri ilk olarak tohum kapsüllerini döken bitkilerde biriken yaprak proteinleri olarak tanımlandı. Bu proteinler yapraklardaki demet kını hücrelerinin vakuollerinde yer almıştır. Vejetatif depo proteinlerinin gelişme sırasındaki birikim şekli, yerleşimleri, üreme organlarının uzaklaştırılması ve yaprakta floem iletiminin engellenmesine cevap olarak birikimi dikkate alındığ ında bu proteinlerin karbon ve azotun geçici depolanmasında vejetatif havuzlar olarak görev yaptıkları ileri sürülmüştür. Ayrıca, bu proteinlerin bitki gelişimi ve strese uyum sırasında önemli besinsel rollere sahip olduğ u düşünülmektedir. Vejetatif depo proteinlerinin azot kaynakları olarak mevcut bulunması ve yeniden kullanımı bitkilerin hayatta kalmalarında ve rekabetle ilgili yeteneklerinde önemlidir. Bazı vejetatif depo proteinlerinin enzimatik etkiye de sahip oldukları gösterilmiştir. Vejetatif depo proteinleri, bitkinin büyümesi sırasında, diğ er bitki dokularının besin gereksinimine göre hızla sentezlenir ya da yıkılırlar.

Bu derlemede, vejetatif depo proteinleri, bu proteinlerin gen ifadesi ve birikimini etkileyen faktörler ve bu proteinlerin olası fonksiyonları üzerine genel bilgi verilmiştir.

Key Words: Vejetatif depo proteinleri, Metil jasmonat.

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Geliş: 30 Aralık 2002 ; **Düzeltme:** 21 Ağustos 2003 ; **Kabul:** 8 Aralık 2003.

1. WHAT IS VEGETATIVE STORAGE PROTEIN?

Plants accumulate nutrient elements and assimilate them into a wide variety of compounds necessary for their growth and development. These elements are often found limited in the environments in which plants live and therefore, they must be rationed among the many metabolic processes requiring them. When plentiful, however, nutrients can be stored for later use at a time when the assimilation capacity may be inadequate. Starch, proteins and lipids are classic examples of stored reserves.

Plants store proteins in embryos and vegetative cells to provide carbon, nitrogen, and sulfur resources for subsequent growth and development (Herman and Larkins, 1999). The storage and mobilization cycles of amino acids that compose these proteins are critical to the life cycle of plants. For instance, during seed and pollen germination, storage proteins are catabolized and provide building materials for rapid growth (Derbyshire et al., 1976). Similarly, in vegetative cells these proteins provide the building materials for seed and fruit set during reproductive growth and for rapid expansion of vegetative structures after period of dormancy. The annual storage of nitrogen in tree bark during the fall, and its subsequent mobilization for re-growth in the spring is another example (Titus and Kang, 1982).

Storage reserves not only provide nutrients for future needs, but they can also conserve resources by recovering nutrients that would be lost in tissues senescence (Staswick, 1994). The redistribution of nutrients from mature organs to actively growing tissues is therefore an important strategy for the efficient utilization of potentially limiting resources. This review focuses on specific proteins that function as storage reserves in the vegetative parts of plants.

Vegetative storage proteins, VSPs, were first described by Wittenbach (1983) as two glycosylated polypeptides in soybean (Glycine max.) leaves. Because of their abundance in all vegetative tissues, they have been called vegetative storage proteins. VSPs form one of the storage proteins found also in several other plant species including Calystegia sepium (Van Damme et al., 2001), hybrid poplars (Populus trichocarpa Torr. & Gray X Populus deltoids Bartr. Ex Marsh. and Populus nigra Muench X Populus maximowiczii A. Henry), (Lawrence et al., 1997, 2001; Beardmore et al., 2000), Brassica napus L. (Rossato et al., 2002), Arabidopsis thaliana (Benedetti et al., 1995; Berger et al., 1995; Mira et al., 2002), Trifolium repens L. (Goulas et al., 2001) and Lolium perenne (Louahlia et al., 1999).

Since it is the first discovered VSP, soybean VSP has been studied in more detail. The soybean VSP has two subunits, VSPα and VSPβ. These are 80 % identical in amino acid sequence (Staswick, 1989a, 1990; Mason et al., 1988) and exist as homodimers (α,β) and heterodimers (α/β) (Staswick, 1988). Based on cDNA sequences, the predicted protein molecular masses are 25.1 (α) and 25.3 kDa (β), and based on chemical analysis, the mature proteins contain approximately 3% carbohydrate (Spilatro and Anderson, 1989). The VSPs have been reported to migrate on SDS-PAGE gels with apparent molecular masses of 25-28 kDa for VSPα and 27-31 kDa for VSPβ (Wittenbach, 1982; Franceschi and Giaquinta, 1983a; Bozarth et al., 1987). Molecular analyses indicated that the VSPs are encoded by a small multigene family of at least three members (Rapp et al., 1990). In soybean, the genes vsp A and vsp B encode the subunits VSPα and VSPβ, respectively.

The vegetative storage proteins are distinct from seed and most other plant storage proteins because they accumulate transiently, and are synthesized and degraded within a single life cycle (Staswick, 1994). In addition, the VSPs may be synthesized and degraded simultaneously in organs that differ in their stage of development (Staswick, 1990). In soybean seedlings, VSPs and its mRNAs accumulate in apical tissues, including stems, cotyledons, and young leaves (Mason et al., 1993). In more mature plants, the VSPs and their mRNAs accumulate in developing leaves, stems, pods, and flowers but only to low levels in roots, mature seeds, and mature leaves (Staswick, 1989a; Mason and Mullet, 1990). This pattern of expression is consistent with the role of the VSP as vegetative sink for temporary storage of carbon and nitrogen in growing regions of the shoot (Mason et al., 1992).

VSPs start to accumulate prior to the beginning of seed development, and can account for up to 15% of the total soluble protein in the leaves at the time of flowering. When the pods and seeds begin to develop, VSP levels decrease. They are subsequently broken down and the resulting amino acids or their metabolites are presumably exported to developing seeds via the phloem transport system to support seed protein synthesis. As seed maturation nears completion, VSPs begin to accumulate again in the vegetative tissues (Rapp et al., 1990). But expression of the VSP genes is not restricted to the vegetative phase, because VSPs are present in flowers and seed pods (Staswick, 1989b).

VSP synthesis occurs on the rough endoplasmic reticulum and synthesized proteins appeared to be stored in vacuoles by a Golgi-mediated process (Staswick, 1988; Klauer and Franceschi, 1997). Franceschi and co- workers (1983) determined that the vegetative storage proteins are localized in vacuoles of the bundle sheath and paraveinal mesophyll cells of leaves. It was also shown that these proteins also accu-

mulate in epidermal cells at some stages of development (Staswick, 1990). The paraveinal mesophyll cells are hypothesized to act as an intermediary for temporary storage and mobilization of nutrients among photosynthetic source tissues, the vasculature of the plant, and the reproductive sink organs, the developing pods, or regions of organogenesis during vegetative growth (Franceschi and Giaquinta, 1983ab; Everard et al., 1990ab; Tranbarger et al., 1991).

2. WHAT CAUSE VSP GENE EXPRESSION AND VSP ACCUMULATION?

Expression of the VSP genes is complex and varies with respect to organ and cell type, developmental stage, and in response to several stimuli such as source/sink status, phloem blockage, nitrogen availability, wounding, water deficit, light, jasmonic acid and its methyl ester, MeJA, phosphate and sucrose (Staswick, 1994). In soybean plants, Mason and Mullet (1990) observed that VSP mRNA levels increased in wounded tissues; and they hypothesized that wounding increases the synthesis of JA/MeJA, which in turn stimulates the accumulation of VSP mRNAs. The spatial regulation of VSP mRNAs and VSP proteins were also studied to test whether VSP accumulation is part of the systemic response of Arabidopsis to wounding (Berger et al., 2002). They observed a dramatic increase of VSP mRNA as well as VSP protein levels in plants challenged with diamondback moth larvae or Egyptian cotton worms. Subsequently, they suggested that VSPs are part of the local plant response to herbivore attack. In order to obtain further information on VSP regulation, they also analyzed a fusion of a soybean vspB promoter fragment to the β-glucuronidase gene in transgenic Arabidopsis plants. The vspB promoter responded to both jasmonate and herbivor treatments implying that in both soybean and Arabidopsis species similar signals regulate VSP gene expression.

In addition to these factors, soluble sugars also appear important for VSP gene regulation. Sucrose, fructose, and glucose interact synergistically with MeJA to induce VSP genes in soybean leaves and in suspension cell cultures (Mason and Mullet, 1990) and in Arabidopsis leaves (Berger et al., 1995).

In Arabidopsis, two cDNAs encoding VSP genes (VSP1 and VSP2) were identified (Utsugi et al., 1998). Unlike soybean in which VSPs accumulate at high levels in leaves, Arabidopsis VSP mRNAs were abundant in flowers. The expression patterns of VSP1 and VSP2 were examined using transgenic Arabidopsis plants carrying a promoter from VSP1 and VSP2 fused to a bacterial β-glucuronidase (GUS) reporter gene. The promoter from VSP1 expressed in gynoecia, especially in styles, the basal and distal ends of ovaries and in siliques, whereas promoter from VSP2 expressed in vegetative shoots, petioles, peduncles, and receptacles of floral organs. These results suggest that in Arabidopsis, expression of VSP1 and VSP2 may be developmentally regulated.

VSP gene expression in leaves, stems, and seed pods is closely related to whether these organs are currently a sink for nitrogen or a source of mobilized nitrogen for other organs (Staswick, 1989ab; Staswick, 1997). For example, immature leaves and pods of soybean are net N-importers and contain elevated levels of VSP. As they mature, these organs become a source of nitrogen, which is then exported to new sinks, such as young leaves, apices, or seeds. The influence of plant sinks on leaf VSP gene expression has also been demonstrated by manipulating the size of the sinks. Removal of developing pods from soybean plants, or petiole girdling to block phloem transport from leaves, cause the accumulation of the VSP and their mRNAs (Staswick, 1989b; Wittenbach, 1982; Louahlia, 1999).

Another condition that increases VSP gene expression is drought stress (Mason et al., 1988). Bozarth et al. (1987) first reported that VSP-α accumulated in cell wall fractions in soybean seedlings exposed to water deficit. In white clover (Trifolium repens L.), VSP accumulation increased as a response to exposure to low temperature (Boachart et al., 1998; Goulas et al., 2001).

Expression of the VSP genes is also induced rapidly in whole plants, leaves, and in suspension cell cultures by MeJA (Staswick et al., 1991; Berger et al., 1995; Beardmore et al., 2000; Rossato et al., 2002). Jasmonate is widely distributed in plants, including soybean, and the concentrations that have been found are comparable with other plant growth regulators (Meyer et al., 1984). Furthermore, developmental changes in VSP gene expression correlate with general changes in jasmonate levels in plants. Highest levels of both are generally found in young plant organs and a direct relationship between them was demonstrated in soybean hypocotyls (Mason et al., 1992). The cell-specific pattern of VSP gene expression in leaves can be abolished by exogenous MeJA, which causes high-level expression in all cell types, rather than in just the paraveinal mesophyll and bundle sheath cells (Huang et al., 1991). This could indicate that although all cells are competent to express VSP, expression is normally limited to those tissues having higher concentration of jasmonate, or greater sensitivity to endogenous jasmonate. However, this hypothesis requires further testing.

Recently, Mira et al. (2002) isolated two copper-

induced mRNAs encoding a vegetative storage protein (VSP2) from copper-treated Arabidopsis thaliana plants. Their study on the expression pattern of VSP2 also showed that under natural senescence and various conditions causing oxidative stress, such as ozone exposure, paraquat and H_2O_2 treatments cause an increase in VSP2 accumulation.

3. POSSIBLE FUNCTIONS OF VSPs

Protein storage is quite common in plants, occurring in a variety of organs and for different purposes. Some provide nutrients for rapid growth after a period of dormancy, whereas others, such as the soybean VSPs, play a more transient role during a single growing season. VSPs play a key role during the mobilization of amino acids from germinating seeds to developing stems and leaves and from mature leaves to developing reproductive structures (Mason and Mullet, 1990). Although both wounding and water deficit induce the soybean VSP genes, there is no indication that the VSPα and VSPβ are directly involved in plant defense, as are the wound-inducible proteinase inhibitors of the Solanaceae (Ryan, 1992). It is not clear whether VSPα and β ameliorate the effects of water deficit. However, under stress condition the VSP genes may be responding to a decrease in the strength of plant sinks, because of stress-induced slowing of plant growth.

Several VSPs have been shown to exhibit enzymatic activity. For example, patatin, a vegetative storage protein in potato, is lipid amyl hydrolase (Andrews et al., 1988). Also DeWald et al. (1992) showed that purified soybean VSP homodimers (VSPα and VSPβ) and heterodimers (VSPα/β) have acid phosphatase activity. The stimulation of vsp expression by sucrose, glucose, or fructose and inhibition when plants are grown on limiting nitrogen (Staswick et al., 1991; Mason et al., 1992) indicate that if VSP phosphatase activity is important it most likely facilitates the uptake, storage, and assimilation of carbon/nitrogen in apical growing zones.

During normal seed pod development, the VSPs are rapidly degraded, possibly to enhance amino acid pool available for the critical early stages of seed pod and seed growth (Wittenbach, 1983; Franceschi and Giaquinta 1983a-b). A role in the early nutrition of developing seeds may be the major function of the VSPs since they accumulate in the leaves even under low nitrogen availability (deVeau et al., 1990) and in developing leaves, where the demand for nitrogen for cell division and growth must be very high (Klauer et al., 1991). In this way, the VSPs can be predicted as an important determinant of seed protein quantity and quality.

In agriculture, proteins stored in seeds and vegetative tissues account for much of the protein consumed directly as food by humans and livestock. In order to study the potential of producing high levels of VSPs for the nutritional improvement of forage crops, recently, expression of soybean VSPα, a high-lysine protein, was achieved in transgenic tobacco (Guenoune et al., 1999). The VSPα was correctly processed and accumulated in the vacuoles of this plant. This study suggested that VSPs could be used as a protein source for improving the nutritional quality of crop plants, particularly cereal forage and grains, which contain limiting levels of lysine.

In conclusion, apart from their role in nitrogen storage, little is known about the functions of VSPs. Detailed functional analyses of these proteins are necessary in order to better understand their relationship to physiological processes. By eliminating expressions of VSP genes in transgenic plants, how these genes play role in plant development could be tested. In addition, identification and characterization of VSPs from different plant species will increase our understanding on the role of VSPs (as nitrogen reserves) in stress tolerance and may lead to innovative approaches for improving forage persistence and productivity.

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