2.2 Source-sink relationships during storage root formation

Whether a storage root continues to enlarge also depends on whether a strong sink has actually been established. Leaves serve as the main carbon source. Carbon fixed through photosynthesis is first converted into transportable compounds such as sucrose and is then translocated through the phloem to belowground organs. Fan et al. (2021) noted that once storage roots develop a strong capacity for assimilate unloading and starch synthesis, they can continuously attract and utilize these assimilates. In other words, high photosynthetic activity in the leaves is only the first step. If carbon remains in the stems and leaves rather than being transferred belowground, storage-root growth will still be limited.

Using isotope tracing to compare high- and low-yielding genotypes, Jiang et al. (2024) found that the high-starch-yielding genotype H283 fixed approximately 8.19%-26.07% more ^{13}C, whereas the amount of ^{13}C transported into the storage roots was approximately 282.73%-1,017.01% greater. The difference in carbon allocation to storage roots was therefore much larger than the difference in carbon fixation itself. This result is particularly informative because it suggests that yield differences are not caused simply by leaves producing more assimilates, but also by how efficiently those assimilates are transported into the storage roots. Regulatory factors such as IbPMA1 and IbbHLH49 are thought to participate in this coordination between source activity and sink strength.

2.3 Hormonal regulation of storage root development

Hormonal regulation cannot be described simply in terms of "promotion" or "inhibition." An appropriate auxin level supports root primordium development and cambial activity, but excessive auxin is not necessarily beneficial. In plants overexpressing IbNF-YA1, storage-root yield decreased by 29.15%-40.22%. When its target gene *IbYUCCA4* was further overexpressed, indole-3-acetic acid (IAA) content increased by 71.77%-98.31%, while storage-root yield decreased by as much as 77.91%-80.52% (Xue et al., 2024). These results indicate that auxin needs to be maintained within an appropriate range for normal storage-root development.

Cytokinins, abscisic acid, and gibberellins are also involved in this process. Exogenous application of GA_3 enhances lignification of root vascular tissues and reduces the capacity for storage-root formation. Singh et al. (2019) reported that exogenous GA_3 markedly altered the developmental fate of sweet potato adventitious roots. Following GA_3 treatment, the number of storage roots decreased by approximately 3.3-fold, mean storage-root diameter decreased by about 2.1-fold, and fresh storage-root weight declined by approximately 2.1-fold. At the same time, xylem development and lignin deposition in the roots increased, whereas starch accumulation decreased. At the molecular level, GA_3 upregulated genes associated with vascular differentiation and lignin biosynthesis, including *IbVND7*, *IbSND2*, *IbPAL*, *IbC4H*, *Ib4CL*, *IbCCoAOMT*, and *IbCAD*, while downregulating the starch-synthesis-related genes *IbAGPase* and *IbGBSS*. These findings suggest that high GA levels tend to direct potential storage roots toward the development of lignified conducting roots rather than starch-rich storage organs.

On the other hand, experiments in which low nitrogen supply promoted storage-root formation showed increased levels of zeatin riboside (ZR) and abscisic acid (ABA), together with reduced lignin biosynthesis and enhanced expression of starch-synthesis-related genes. The effects of nitrogen are therefore often intertwined with changes in hormonal signaling and cannot be explained simply by the amount of nitrogen present in the soil.

3 Effects of Nitrogen Management on Sweet Potato Storage Root Development

3.1 Nitrogen supply and storage root initiation

Storage-root initiation is highly sensitive to nitrogen supply, and this sensitivity appears very early in development. In a sand-culture experiment using the cultivar Orleans, four nitrogen levels of 0, 50, 100, and 200 mg/L were evaluated. The 100 mg/L treatment promoted the development of primary and secondary cambia and maintained a relatively high storage-root formation rate from 21 to 56 days after transplanting. Although the 200 mg/L treatment showed faster growth and greater nitrogen uptake after 35 days, its storage-root formation rate and