

SRI VENKATESWARA INTERNSHIP PROGRAM FOR RESEARCH IN ACADEMICS (SRI-VIPRA)

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"A crosstalk between strigolactone and mycorrhization for the amelioration of biotic and abiotic stress"

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Signature of Mentor

Certificate of Originality

This is to certify that the aforementioned students from Sri Venkateswara College have participated in the summer project SVP-2437 titled " **A crosstalk between strigolactone and mycorrhization for the amelioration of biotic and abiotic stress"**. The participants have carried out the research project work under my guidance and supervision from $1st$ July, 2024, to 30th September, 2024. The work carried out is original and carried out in an online/offline/hybrid mode.

Showtony Mandal **Signature of Mentor**

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A crosstalk between strigolactone and mycorrhization for the amelioration of biotic and abiotic stress

Introduction

In the past few decades with the increase in population a greater demand for food security by an increase in global food production has come to the forefront. However, with the ever increasing prices of the fertilizers , pesticides , and weedicides accompanied by the consequences of using such chemicals regularly on soil has made it necessary to look for alternatives which are not only eco-friendly but also not too heavy on the farmers pockets. Keeping such ordeals in view usage of Arbuscular mycorrhizal symbiosis provides a much needed opportunity to bridge the gap between the much needed nutrient supply and the healthy growth of plants in the changing climatic conditions (Mitra et al., 2021)

This AMF is capable of establishing a mutually beneficial relationship with more than 100,000 plant species, in a typical set up the mycelial fungal network of the fungal partner spreads along the host plant roots supplying it with the suitable nutrients such as phosphorus and nitrogen in return for the carbohydrates and starch.

During the pre-symbiotic process the host plant releases certain root exudates in order to attract the nearby fungal partners to facilitate root colonization and subsequent formation of internal edifices for easy transport of material. One of the most important of these root exudates is a newly found class of phytohormones known as strigolactone which act as the main modulators in the face of nutrient deficit conditions to ensure the proper and coordinated growth of the plant species. Strigolactone are secreted by the roots of the host plants in very small amounts into the rhizosphere as a means of communication between the plant and its environment. They are carotenoid derivatives produced by a conversion mediated by βcarotene isomerase (D27) where *trans*-β-carotene is transformed to 9-*cis*-β-carotene by a series of reactions. (Mitra et al., 2021)

Strigolactone once released helps detect the nearby fungal partner arbuscular mycorrhiza along with some root parasitic weeds such as *Orobronche* and *striga spp.*(Wang et al., 2022).

Once detected the symbiosis relationship formed helps the plants not only in better acquisition of nonmobile nutrients specially phosphorus but also imparts additional benefits such as better tolerance towards both biotic and abiotic stresses for example water scarcity , salinization , drought conditions and weed removal (Andreo-Jimenez et al., 2015).

Apart from this the studies have showcased the enhanced root development in plants and change in the architecture of plants above ground with respect to nutrient deficit conditions due to this association hence helping the plant to optimise its resources and undergo complete growth. Strigolactone promotes the growth of adventitious roots and seminal roots while repressing the growth of lateral roots and tiller buds in case of rice. This is done simultaneously with the promotion of AMF symbioses to activate hyphal branching to better reach the nutrient. The benefits associated with this relationship to mitigate the consequences of various biotic and abiotic stresses are summarized in the present chapter.

Strigolactone, a key regulator of nutrient allocation in plants

Strigolactones (SLs) are a novel class of plant hormones that have undergone extensive study in recent years. The broad range of SLs actions, which include the regulation of shoot/root architecture, the stimulation of interactions between roots and fungi or bacteria, the stimulation of the germination of parasitic plants, and others, suggest that this group of hormones may be crucial in the mechanisms that regulate soil exploration and the root-mediated uptake of nutrients.

The amount of macronutrients in the soil is a significant regulator of the production and exudation of SLs, according to studies on several plant species. The first studies examining the relationship between nutritional insufficiency and increased SL secretion were published in Matusova. (Matusova et al.,2007) *Trifolium pretence* L., which is known to be a host for the parasitic plants and AMF, was used to study the effects of nutritional deficiencies on the biosynthesis and exudation of SLs.

The understanding that SLs function as the branching factor for arbuscular mycorrhizal (AM) fungus was a significant development (Akiyama et al., 2005; Parniske 2008). According to Akiyama and Hayashi (2006), mycorrhizae are symbiotic relationships between soil, fungi, and plant roots. According to Brachmann and Parniske (2006), this relationship is likely the most significant and pervasive symbiosis in all of nature. A suitable host is required for AM fungus to complete their life cycle, making them obligate symbionts. The importance of endogenous SLs in the regulation of plant architecture was then shown. Examples of typical examples include preventing bud development and preventing shoot branching (Gomez-Roldan et al*.* 2008; Umehara et al*.* 2008).

It has long been understood that auxin and cytokinines, two other groups of plant hormones, play a role in regulating shoot branching. SLs are now acknowledged as a third class of novel plant hormones.

Inorganic nutrient deficiencies, such as those in nitrogen and Pi (Lopez-Raez et al., 2008; Umehara et al., 2008; Yoneyama et al., 2007a; Yoneyama et al., 2007b), cause an increase in SL levels. The host plant can receive both Pi and nitrogen from AMF (Govindarajulu et al., 2005). SL is exclusively produced by some leguminous plants in response to Pi deficit, such as red clover and Lotus japonicus, which can interact symbiotically with root nodule bacteria.

In times of a shortage, plants rely on AMF to acquire both nitrogen and Pi. However, many plants commonly increase their SL levels in response to Pi shortage. High endogenous SL levels under Pi deprivation suggest that SLs may be crucial for the effective uptake of Pi by plants.Additionally, shoot branching is typically reduced by nitrogen deficiency in addition to endogenous SL levels enhanced by Pi deficiency in roots. It is currently unknown, nevertheless, whether SL synthesis in response to nitrogen deficit impacts shoot branching. Both root and shoot branching are regulated by SLs. Contrary to Arabidopsis, white lupin does not experience an increase in SL levels in response to Pi shortage (Yoneyama et al., 2008). Auxins are crucial for the development of lateral roots and cluster roots in both Arabidopsis and white lupin, although SL production under Pi deprivation differs significantly between the two species, both of which are not AMF hosts. Figure 1 showcases the phosphorus utilisation and acquisition in case of its deficiency.

The relationship between SL production and AMF Colonization

Many plant species' roots manufacture SLs in large quantities when Pi is insufficient (Lopez-Raez et al., 2008; Umehara et al., 2008; Yoneyama et al., 2007a; Yoneyama et al., 2007b). AMF's hyphal branching, which provides the host with vital inorganic nutrients, particularly Pi, is induced by SLs (Akiyama et al., 2005). Therefore, lowering SL levels lowers the rate of AMF colonisation.

Both root parts exhibit low levels of SL and AMF colonisation comparable to roots under high-Pi conditions when the pea root system is divided into two parts, with one part placed in low-Pi solution and the other in high-Pi solution but both still connected to the same shoot (Balzergue et al., 2011). This suggests that by systemic signalling, the higher Pi side of these split-root plants negatively restricted SL production on the lower Pi side. It's interesting to note that the Pi concentration of these split-root plants is higher in the leaves than in the roots. These findings imply that plants react to Pi levels in the shoot.

The physiological roles of SLs are thought to be crucial for effective nutrient allocation in plants, especially Pi acquisition. In low nutrient conditions, the limited supply of mineral nutrients is needed for new leaf development or plants like growing seeds and leaves when leaves begin to senescence of their delayed leaf senescence.

The axillary buds can develop using the Pi that was translocated from the roots when SL levels are still low. Contrarily, when Pi is deficient, which prevents tiller bud formation in shoots, SL levels in roots are dramatically increased.

By promoting hyphal branching, SLs released into the soil improve symbiotic interactions with AMF. Pi is given to the host plants by AMF, which also gets carbon from them. Additionally, root-parasitic plants extract carbon from the host plants by recognising the SL signals. Thus, a process that at first glance seemed to be harmful actually serves the plant in many ways.

SLs will work in conjunction with other plant hormones rather than independently. . The action and production of SL are controlled by other hormones. For example, in the regulation of axillary bud outgrowth (Dun et al., 2012) and in the regulation of mesocotyl elongation in darkness (Hu et al., 2014), cytokinins function as SLs' antagonists. In addition to being one of the primary regulators of SL production, auxins may function as antagonists since SLs may improve auxin transport (Hayward et al., 2009; Al- Babili and Bouwmeester 2015). Abscisic acid, one of the fundamental regulators of plant response to abiotic stress, plays a role in SL biosynthesis, as Lopez-Raez et al., (2010) shown, but SLs can also have an impact on abscisic acid biosynthesis (Al-Babili and Bouwmeester 2015). In addition to phytohormones, it is known that phosphate influences SL biosynthesis, which means that a phosphate deficit enhances the production of SL (Koltai 2015 and references therein).

Table 1. A set of the gene encoding proteins involved in the biosynthesis and signaling of SLs

Strigolactone and its role in biotic stress

Strigolactones (SLs) are plant secondary metabolites generated from carotenoids that are crucial for different aspects of plant growth and development as well as for communication with symbiotic microorganisms and root parasitic weeds in the rhizosphere. The symbiosis of beneficial bacteria, such as arbuscular mycorrhizal (AM) fungi, is therefore anticipated to be promoted by sophisticated control of SL biosynthesis, perception, and functions. It is also anticipated that this will delay parasitism by destructive root parasitic weeds. Weak but significantly increased plant resistance to diseases was the consequence of the AM colonisation. SL mimics can be employed to encourage AM symbiosis and lower the pace at which systemic inducers of acquired resistance, which are often phytotoxic to horticulture crops, are applied.

Striga and *Orobanche* species of root parasitic weeds were initially shown to respond favourably to Strigolactones (SLs) as germination stimulants. However, it has been demonstrated that SLs are produced and released into the rhizosphere by both their hosts and non-hosts. This is due to the fact that SLs serve as crucial cues for the colonisation of arbuscular mycorrhizal (AM) fungi (Akiyama et al., 2005). Plants develop and release SLs for AM fungus rather than root parasites. .(Xie et al.,2010; Al-Babili S and Bouwmeester HJ et al.,2015). In addition to serving as rhizosphere signalling agents, SLs or their subsequent metabolites are a group of plant hormones that control things like shoot and root structures, secondary growth, and leaf senescence.(Xie et al.,2010; Al-Babili S and Bouwmeester HJ et al.,2015).

Communication between the AM fungus and the plant host begins in the rhizosphere with the generation and exudation by the host plant of signalling molecules that are recognised and encourage hyphal development by the AM fungus. While other substances, including flavonoids and hydroxy fatty acids, have also been reported to stimulate hyphal growth (Scervino et al., 2005; Nagahashi and Douds 2011), Strigolactones have emerged as crucial cues among these signalling molecules (Akiyama et al., 2005; Bouwmeester et al., 2007) . By operating alone or in concert with other related microbes inhabiting in areas that are directly influenced by the plant, AM defends host plants against a variety of biotic stressors. Plants that have been colonised by AM have improved growth and tolerance to plant diseases. . According to the research results, host defence induction, rhizosphere modification, and competition for resources, space, and photosynthates are the most common conceivable processes.

To obtain the photosynthates generated by their host, pathogens also infect a plant. In the case of soil-borne diseases, they first infiltrate the roots, which is a vital location for the virus to travel further throughout the body. The presence of photosynthates at this location is also significant (Wheatley and Poole 2018). Higher carbon demand may have a deleterious impact on pathogens when AMF have main access to photosynthates (Poveda et al., 2020). As a generalised method for pathogen biocontrol through AMF symbiosis, competition for photosynthate is not supported by any evidence. Actually, under nutrient-limited circumstances, ectomycorrhizal hyphae are known to be important in the quick transfer of plant-derived carbon to maintain bacterial populations in root- distant locations (Gorka et al., 2019).

Under the conditions of our experiment, AM colonisation increased the pathogen resistance of tomato and rice (Kusajima et al., unpublished). Because it fills the SL binding pocket and blocks SL signalling, it is likely that the SL-signalling inhibitor KK094 upregulated SL production to further increase pathogen

resistance brought on by AM colonisation. Additionally, pathogen resistance brought on by AM colonisation had no impact on SAR, indicating that both promoting AM colonisation and bringing on SAR can help plants become more resistant to infections. However, neither the generation of phytoalexins nor the induction of SAR was impacted by AM symbiosis, which increased plant resistance to infections (Kusajima M et al., unpublished). Instead, AM symbiosis would prepare plants for pathogen assault such that mycorrhizal plants respond to pathogen infections far more promptly and effectively. (Pozo et al.,2007 \mathcal{L}

In the mycorrhizal symbiosis between plants and Glomeromycota fungus, SLs have been found to benefit plants. With the roots of terrestrial plants, the fungi in these associations produce arbuscular mycorrhizas. Arbuscular mycorrhizal fungus (AMF) symbiosis, which originated around 460 million years ago and is attributed with the development of terrestrial plants and making them more resilient to abiotic and biotic stressors, is regulated by SLs, which control hyphal branching. (Harrison, 1999; Liu et al., 2007)

Abiotic and biotic stressors are brought on by the constantly shifting and frequently adverse environmental circumstances that plants must contend with. As a result, plants have developed complex systems to quickly adjust to changing environmental circumstances. Significant progress has been made in recent years in identifying the essential elements of plant responses to biotic stress. The phytohormones salicylic acid (SA), jasmonic acid (JA) and derivatives—known as jasmonates (JAs)-and ABA are the major players in the signalling networks regulating plant defence responses against pathogens and pests, although others, such as ET, brassinosteroids, gibberellins and auxins, are now known to contribute to modulate the response (Robert-Seilaniantz et al., 2011; Tonne et al., 2009).

Arbuscular mycorrhizal and strigolactone biosynthesis in abiotic stress conditions

Plants especially agricultural crops unremittingly encounter changing environmental conditions which quite often results in both biotic and abiotic stresses. These stresses may include pathogen, waterlogging, nutrient deficiency, soil salinity and drought. Such conditions hamper the proper development of the plant and its productivity thus adversely affecting the global crop production. (Ruiz‐Lozano et al., 2016) Among the abiotic stresses the most dangerous ones are the drought and salt stresses. Water scarcity increases the risk of many other water stresses while salinity of the lands can affect the 20% of the land which needs to be irrigated for agriculture and produces over 40% of the world's food. Reduced rainfall is high temperatures and over exploitation of the natural water resources only adds to the problem further. (López-Ráez and Juan, 2016)

Owing the two above ordeals a paradigm shift in the new agriculture is required which is based on the environment resilience and sustainability. Eco Friendly alternatives promoting both plant and soil fitness by decreased use of chemical fertilizers and insecticides is the need of the hour. One of the greenest ways of doing this is by using the mutually beneficial plant symbiotic interactions taking place in the rhizosphere. AM symbiosis is one of such plant – microbe interactions which not only helps in the plant growth and fitness but also acts as bioprotective agents that helps alleviate the stress symptoms including the slat and draught stresses by stimulating the production of certain plant hormones which positively impacts the ability of the plant to overcome the these stresses .These obligate biotrophs facilitate the plants in its nutrient and water acquisition via the arbuscules hence acting like biofertilizers used for increasing the biomass production and plant growth. (Saxena et al., 2022)

To begin this plant fungus interaction, the host plant produces and exudes a type of phytohormone known as strigolactone into the rhizosphere. These are detected by the uncharacterized receptor of AM fungi encouraging hyphal growth and branching to come in contact with the host plants. Strigolactone thus play and important role in establishing this symbiosis arrangement and in its subsequent functioning which is beneficial to the host plant especially in conditions of stress. Figure 2 demonstrates the elevation of multiple abiotic stress by the biosynthesis and release of Strigolactones which helps form a symbioses relationship with the Arbuscular mycorrhizal fungi. As previously mentioned, water related stresses presents with a dangerous hurdle that the plants face owing to the increased scarcity of water. So, elevations of these stresses for the proper growth of the crops becomes the primary concern. In such a time the symbiosis relationship which can be established by almost 80% of the terrestrial plants becomes an important alternative way for crop and plant sustainability as opposed to the increasing use of potentially destructive insecticides and pesticides which are not only expensive but also do a lot of harm to the soil health in the long run. (López-Ráez and Juan A., 2016)

Drought stress

Water scarcity has an enormous impact on crop productivity as a result of which improving yield under these antagonistic conditions becomes the top priority. AM symbiosis works to mitigate such effects by regulating various response mechanisms such as morphological adaptations, growth reduction, stomatal closure, photosynthetic reduction and induction of stress responsive genes and proteins such as ABA (abscisic acid) whose increased production helps in the elevation of stress symptoms and in return also further enhance the AM symbiosis. (López-Ráez and Juan A., 2016) Fungal hyphae provided by the mycorrhiza partner increases the accessibility to the water usually inaccessible to the roots as it thinner than roots and hence increases the capacity of soil exploration by plants significantly. (López-Ráez and Juan 2016). This highly expansive AM hyphal network can contribute up to 20% of the plant water uptake further indicating the importance of this rhizosphere interaction. AM symbiosis also helps in the absorption of water via the aquaporins through the passive movement of water thereby regulating the root hydraulic conductivity. (López-Ráez and Juan, 2016).

Finally arbuscular mycorrhizal interaction with plants also induces the production of the phytohormone strigolactone which helps mitigate the draught stress symptoms. Recent experiments performed with tomato and lettuce have shown increased root colonization by mycorrhiza when plants when subjected to draught stress treatments with an increment of 17% in case of lettuce and 8% for tomatoes after the completion of 4 weeks. These values only increased over time establishing the significance of this symbiosis. Further even though the draught stresses conditions significantly reduced the harvest for both plants, the AM tomato and lettuce still exhibited better growth and photosystem efficiency as compared to the non-AM tomato and lettuce with the difference being more evident for the tomato. (Ruiz‐Lozano et al., 2016). AM plants also displayed an upregulation of SICCD7 and SICCD8 which are the two tomato genes involves in the biosynthetic pathway of strigolactone which suggests the induction of SLs to possibly improve the root colonization and carry out its others functions like nutrient uptake in case of nutrient deficiency.

Lastly, AM tomato and lettuce upregulate the encoding of LSNCED2 which is an ABA synthesis gene that is a stress hormone that promotes symbiosis establishment and stress tolerance. The AM plants steadily increased their ABA accumulation by 400 and 760% under moderate and severe stress treatments respectively (Ruiz‐Lozano et al., 2016). Advantageous effects have also been observed in a no. of other species of plants such as rice, barley, maize and pistachio. The AM symbiosis helps the pants grow better in stressful environments and adjust to the changing outside environment sustainably with encourages strategies to optimize the water consumption of the plant.

Salt Stress

Salinization of soils has been on a gradual increase since the past decade and is expected to result in 30% land loss within the next two decades increasing up to 50% by the middle of the 21st century. This makes salt stress on plants one of the major threats towards a food security of the world (Saxena et al.,2022). The accumulation in high concentration of these dissolved salts hinders the plant growth and eventually its survival by its ionic osmotic and cell water homoeostasis. It also affects other physicochemical properties of soil which creates a toxic environment for the plants thereby decreasing their nutrients and water uptake sodium and chlorine are the two ions which when enter into the plant cell disturb the proper function of the plant membranes and prevent the plant from developing properly (Saxena et al.,2022). Under such stressful conditions the symbiotic association between the plant and the AM fungi helps in enhancing the plants phenotypic, biochemical and physiological response thereby promoting salinity tolerance and the production of growth hormones the also boosting the conditions of the rhizosphere the help the plant. Signaling pathways involved in detoxification and ion homeostasis get activated in response to the salt stress in order to counter its ill effects such as increased ROS generation, stomatal closure, increased photorespiration, membrane rupturing, decreased photosynthesis and lower water potential. Associated mycorrhizal partner further reduces these damaging effects by up regulating the jeans for the synthesis of LEA and Osmolytes like proline having the capability of ROS scavenging, cell's osmoprotection and maintenance of the membrane integrity. Cellular hydration and Na+ influx used for maintaining the osmotic potential of the cell is also regulated by mycorrhizal partner by the activation of SOS and AQP genes of the plant. Lastly the AM symbiosis could also help in the activation of various ion channels and carriers specially the Ca2+ channel which increases the concentration of $Ca²$ ion in the cell further activating the kinases responsible for regulating the stress control gene of the plant (Saxena et al., 2022).

AM symbiosis also regulates the expression of multiple aquaporin genes which play an important role in restoring the plant osmotic balance in salt stress conditions. AMF colonized plants instigate the production of the phytohormones such as salicylic acid (SA), abscisic acid (ABA) and strigolactone (SL) which upon accumulation facilitate certain mechanisms in the plant that modulate stomatal conductance and improve the plant's responses to salt stress (Saxena et al., 2022)

Experiments conducted using Triticum Durum (wheat) further shed light on the involvement of arbuscular mycorrhiza in bettering the plants health when subjected to salt stress. The results obtained concluded that while salt stress significantly reduced the wheat growth the plant having AMF partners had significantly improved growth parameters like an increment in the shoot dry weight by 67 grams and that of root by 36 grams. Salt stress inflicted on plants showed a substantial increase in the root colonization. An improved stomatal conductance was also observed along with an increased soluble protein and sugar content in the shoots and the production of antioxidant enzymes for excess ROS removal. It also boosts the uptake of essential minerals like P which enhances the plant growth. (Ikan et al., 2023). AMF as a biofertilizer imparts many advantages to plants under adverse conditions thereby ensuring their survival and sustainable growth in the future. It also opens the gate to many possible green alternatives with the potential to significantly reducing the use of artificial fertilizers which are major contributors of soil degradation.

 Fig. 2. Elevation of various abiotic stresses by strigolactone biosynthesis under stress conditions.

Arbuscular Mycorrhizal fungi as ecosystem engineers

Symbiotic interactions shared between two species can be both mutualistic and antagonistic and can promote a paradigm shift in the structure and function of host plant communities. For example, it has been known for quite some time that the parasitic plants have the ability to cause such shifts in the floristic diversity by suppressing the competitive dominants in order to free the sub dominant species from competitive exclusion. This suppression further causes the competitive hierarchies of the given community to reorder and restore the degraded plant communities thus showcasing the potential of the parasitic plants to act as 'ecosystem agroengineers' (Cameron, 2010). Consequently, AM fungi can also very well fit under this category of ecosystem agroengineers as it can also induce such shifts in the plant communities. AM fungi upon interacting with its host plant forms a mutually beneficial symbiotic relationship with its host plant by increasing its nutrient uptake and providing it protection against various kinds of biotic and abiotic stresses whereas it also showcases antagonistic behavior towards less compatible species and reduce their biomass in the vicinity drastically. (Cameron, 2010)

Such antagonistic interactions can be used to harness the potential of AM fungi as a biocontrol for weed suppression in agriculture by either the inhibiting the growth of a variety of non-mycorrhizal weed families or by increasing the competitive ability of the given crop species against both the mycorrhizal and nonmycorrhizal weeds. Considering that weed poses a serious problem towards the crop production and could reduce the global yield by 34% it has become quite important to explore this arena further. Many experiments have been conducted along these lines to check the efficiency of AM fungi as a weed control one of which was to judge the impact of AM fungi on weed biomass and crop productivity were *Helianthus annuus*—sunflower was grown alongside six different weed species of temperate zone some on which were quite aggressive in nature and the effect of the AM fungi on these microcosms was observed. The results showed high levels of root colonization by AMF in the sunflower ranging from 56.5% to 88% in presence of different weed species whereas for weed themselves these levels ranged from 0.7% to 55% indicating their low compatible with weeds. (Rinaudo et al., 2009)

Although no significant increase was seen in the biomass of sunflower in the presence of AMF the weed biomass however was negatively affected with its average dropping by 47%. This reinforced the antagonistic interactions shared between the two species. Lastly it was also seen that the amount of phosphorus obtained by the AMF sunflower was increased by 48% whereas for 3 weed species this phosphorus uptake was significantly reduced in the presence of AMF. This could possibly be the result of AMF using indirect mechanisms to allocate the nutrients to the host species and depriving the non-host competitors of the same (Rinaudo et al., 2009).

Apart from such indirect methods some direct methods have also been suggested that could be used by the AMF to supress the weed by inducing the plant defence systems and releasing of the toxic allopathic compounds by the AMF having detrimental effects on the weeds.

Over the years many such experiments have been conducted which further prove the potential of the AM fungi to be used as a possible replacement for the chemical herbicides which have degrading effects on both crops and the soil. A substantial change in the modern agricultural practices is required to enhance the populations of AMF and integrate the benefits associated with them into domestic agricultural gains.

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