Preliminary Study on the Theory of Environmentally Adaptive Changes in Flue-Cured Tobacco during Growth

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Abstract Starting from the foundational static traits underlying the growth and development of flue-cured tobacco, this research conducts a systematic examination of the phenomena and theoretical principles associated with environment-driven adaptive changes during its cultivation. It was found that environmental variables-including temperature, light, and moisture-elicit directional shifts in static traits (*e. g.*, chemical composition, morphological architecture, and leaf tissue structure) toward enhanced environmental adaptation, characterized by graduality, juvenility, similarity, and correlativity. Upon alterations in ambient conditions, flue-cured tobacco modulates its static traits through integrated physical, chemical, and biological-genetic mechanisms, aiming to optimize resource utilization, mitigate environmental constraints, and preserve internal homeostasis alongside metabolic balance. The investigation further reveals that the adaptive scope of flue-cured tobacco to field environments is malleable and can be extended and elevated via adaptive conditioning commencing at the juvenile stage. In addition, the adaptive alignment between static traits and environmental parameters exerts a substantial impact on the plant's growth dynamics, yield performance, and quality attributes. Beyond its relevance to flue-cured tobacco, the proposed theory offers a meaningful framework for elucidating the pervasive adaptive strategies employed by plants and broader biological systems in response to environmental contingencies.

Key words Flue-cured tobacco, Static trait, Environment, Adaptive change

0 Introduction

In addition to advancing the frontiers of science, it is equally important to continuously explore and strengthen its foundational layers. Without this, scientific progress may overlook essential principles and result in an unstable structure at the higher levels. Investigating the origins and underpinnings of science and establishing the fundamental materials that support it, while methodically building a higher-level scientific framework, is a task as intricate as pushing the boundaries at the top. This research represents an effort to analyze the basic static characteristics of flue-cured tobacco growth and examine its developmental patterns.

The static traits of flue-cured tobacco refer to various individual or composite characteristics displayed by the plant at a specific point in time during its growth process. These include individual attributes such as leaf color, shape, and tissue structure; composite attributes such as growth stage and chemical composition; as well as relational characteristics among attributes, such as leaf length-to-width ratio, root-to-shoot ratio, and carbon-to-nitrogen ratio. The difference in the same static trait of the tobacco plant between two adjacent time points constitutes the change in static traits, encompassing both qualitative changes, such as the synthesis and decomposition of sugars and proteins, and quantitative changes, such as increases in leaf length and width. The time required for a tobacco plant to synthesize a macromolecule, or the increase in leaf length or width per unit time, can be defined as the intensity of change in static traits. Some static traits (such as sugar and water content) may appear to change very little or show no obvious change on the surface, but in fact, simultaneous synthesis and decomposition processes in opposite directions may be occurring. Such changes can be regarded as the result of a dynamic equilibrium between changes in different directions. The performance of static traits in tobacco plants over consecutive equal time intervals constitutes their dynamic traits, while the comparison of the intensity of changes in static traits across these intervals reflects the trend of change in dynamic traits. Changes in static traits manifest the outcomes of changes in dynamic traits, whereas changes in dynamic traits reveal the processes underlying changes in static traits. The change in static traits within a given time interval can also be regarded as the cumulative result of multiple consecutive changes in dynamic traits over that period.

The static traits of flue-cured tobacco are rooted in the seed-borne original traits, which evolve under given environmental conditions to form the immediate static traits expressed at a specific growth moment. The plant's immediate static traits (including its genetic traits) and its concurrent growing environment jointly determine the direction and intensity of changes in all static traits. Moreover, within a uniform environment, alterations in certain static traits (such as growth stage, protein and chlorophyll content) may further trigger directional or quantitative shifts in other traits, such as photosynthetic intensity.

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1 Performance and principle of the adaptation of the static traits of flue-cured tobacco to the environment

1.1 Changes in adaptation to climatic environment The field growth climate for flue-cured tobacco primarily consists of two patterns: prolonged sunny weather and prolonged rainy conditions[1]. In environments characterized by sustained low temperatures and rain, tobacco plants exhibit static traits including a decreased root-to-shoot ratio, thinner leaves, loosely organized leaf tissue, as well as elevated levels of leaf moisture, protein, and chlorophyll[2]. Such traits facilitate the expansion of the photosynthetic surface area in flue-cured tobacco and improve light utilization under low-temperature and dim-light conditions. In contrast, during extended sunny periods, tobacco plants often display static traits such as an increased root-to-shoot ratio, leaf thickening, compact leaf tissue structure, and a rise in leaf cell solute concentration. These adaptive modifications contribute to enlarging the root absorption area, reducing leaf water potential to enhance water uptake, minimizing water evaporation, and alleviating photodamage to leaf cells, thus supporting adaptation to high-temperature and high-light environments.

Current explanations for this phenomenon focus primarily on the physiological regulatory mechanisms activated by flue-cured tobacco to adapt to dim-light conditions. However, the complete pathways involved in this process, such as how nitrogen resources are preferentially allocated to protein and chlorophyll synthesis under low light, remain unclear. In reality, any environmental factor can influence the static traits of flue-cured tobacco through multiple pathways. The key lies in identifying the environmental factors that play a decisive role in shaping specific traits, as well as elucidating their precise mechanisms of action. It can be speculated that the reasons for the adaptation of static traits in flue-cured tobacco to the environment, apart from physiological regulation, can largely be attributed to simple physical and chemical factors. For example, under rainy weather conditions, the filling of water expands both the cell volume and intercellular spaces in leaves, resulting in larger and thinner leaves. When soil moisture is sufficient and drainage is good, water-soluble nitrogen fertilizers dissolve, diffuse, and are absorbed more readily, providing a nitrogen source for protein and chlorophyll synthesis. Meanwhile, lower transpiration intensity and higher soil water potential reduce the consumption of carbohydrates for root growth, thereby supplying a carbon source for related synthesis processes. Higher leaf water content also facilitates the synthesis of proteins and chlorophyll.

Tobacco plants grown under sustained low-temperature and rainy conditions, if subsequently exposed to sunny and high-temperature weather, often experience a sharp increase in transpiration and a rapid loss of leaf water, leading to a significant decline in photosynthetic intensity. Leaf cells become vulnerable to high-temperature and strong-light stress, resulting in leaf yellowing, wilting, or even plant death. In contrast, plants grown long-term in sunny and high-temperature environments, if transferred to low-temperature and rainy conditions, tend to suffer from reduced photosynthetic accumulation due to thicker leaves, compact tissue structure, high respiratory consumption, and restricted expansion growth, which can trigger premature senescence.

If rainy weather persists not long or if conditions transition smoothly from rainy to sunny days, tobacco plants respond in the early sunny phase by enhancing transpiration, re-allocating organic assimilates to the below-ground parts, and retarding shoot growth. Concurrently, under higher light intensity, leaf expansion is limited due to water loss, and leaves instead undergo thickening. The palisade tissue, which exhibits greater light tolerance, develops more prominently, whereas the spongy tissue grows relatively less. These modifications diminish light penetration through the leaf blade and elevate both the photosynthetic light saturation point and light compensation point, thus enabling acclimation to a higher-light environment. After static traits—including the root-to-shoot ratio, leaf thickness, and the contents of protein and chlorophyll—have been adjusted to a state that suits the ambient conditions, the tobacco plants grow at a relatively stable pace[3].

1.2 Morphological conformity with environmental conditions The morphological adaptation of flue-cured tobacco to its environment refers to the process by which leaves adjust their orientation during growth to extend into the inter-row space, avoiding shading from upper leaves, and to position the leaf surface at an optimal angle for light reception. This ensures that the most developed and light-efficient part of the palisade tissue receives the strongest illumination. Meanwhile, the root system tends to grow toward areas of the soil that are rich in water and nutrients, loose, and well-aerated, forming thicker roots in regions with larger soil pores and finer roots in areas with smaller pores.

After transplanting, tobacco seedlings require a certain recovery period. In addition to root damage, another important reason is that the previously established conformity between the seedlings and their environment formed during the nursery stage is disrupted. Larger leaves may receive light at suboptimal angles, preventing the most light-efficient parts from facing the light directly, while thinner, less efficient leaves may be oriented at more favorable angles. This mismatch reduces overall photosynthetic efficiency. Besides, existing thicker roots may be located in unsuitable soil zones, while suitable areas lack sufficient root development. It takes time for the root system to readjust and re-establish a certain degree of environmental conformity. The larger the seedling, the longer this re-adaptation takes, and the greater the adverse impact on growth.

From the perspective of environmental conformity, the competition between flue-cured tobacco and weeds involves not only contention for nutrients, water, and light, but also the weeds' occupation of favorable soil positions where water, nutrients, and aeration are well balanced. This reduces the degree of conformity between the tobacco root system and the soil, further inhibiting tobacco growth. Similarly, earlier-emerging tobacco plants are more likely to occupy advantageous positions in both soil and aerial spaces, thereby widening the growth gap with later-emerging plants.

The primary mechanism underlying the morphological conformity of flue-cured tobacco with its environment is physiological regulation, in other words, hormone-mediated directional growth of roots toward water and nutrients and of leaves toward light. In addition, the tendency of roots to grow into loose, well-aerated soil can also be regarded as a result of physical and chemical influences exerted by the soil environment on root morphology and distribution.

2 Patterns of variation in static traits of tobacco plants in adaptation to the environment

2.1 Graduality The gradual adaptation of static traits in flue-cured tobacco to the environment is mainly manifested in three aspects:

(i) Dynamic traits such as photosynthesis and respiration in flue-cured tobacco leaves respond almost instantaneously to environmental changes like temperature and light[4]. In contrast, changes in static traits, such as the root-to-shoot ratio, leaf angle, tissue structure, thickness, and the content of proteins and chlorophyll, are more gradual. These are formed slowly through the accumulation of dynamic processes under specific environmental conditions. The more stable the environment and the longer the growth period, the more pronounced the changes in these static traits become, and the higher their degree of adaptation to the environment. When the environment undergoes significant changes, tobacco plants require a considerable amount of time to gradually adjust their static traits to re-adapt to the new conditions and resume balanced growth[5]. Furthermore, the greater the environmental change, the longer this adaptation period. In terms of graduality, water-restriction hardening promotes early adaptation of tobacco seedlings to field environments, yet excessive hardening demands a recovery phase before normal growth can occur. A trial on water-controlled hardening of pseudo-planted tobacco seedlings in Liuyang, Hunan (March – April 2022) revealed that seedlings subjected to 7 d of water restriction grew markedly faster in the initial field period than those hardened for 20 d. The likely explanation is that 7-d hardened seedlings increased leaf thickness and root-shoot ratio, facilitating rapid post-transplantation growth. However, 20-d hardened seedlings showed limited root-shoot ratio improvement constrained by nutrient pot size, and their tightly packed leaf cell structure restricted leaf expansion. Rapid growth resumed only after newly formed leaves assumed a looser anatomical arrangement.

(ii) Drastic changes in environmental conditions such as temperature, light, and moisture may lead to metabolic imbalance in tobacco plants, damage to cellular and tissue structures, resulting in poor growth or even death; whereas gradual environmental changes can more effectively induce adaptive modifications in static traits[6]. For instance, an experiment conducted in a greenhouse in Liuyang, Hunan, during March – April 2022 showed that tobacco seedlings transplanted on sunny days all died, while those transplanted during continuous cloudy or rainy days mostly survived. However, under subsequent sunny conditions, whether watered or immersed, most of these seedlings still died. In contrast, when seedlings that had survived transplantation on cloudy or rainy days were first placed in a shaded outdoor area to gradually adapt to increasing temperature and light intensity, and then transferred into water, they maintained some growth even under sunny conditions. Analysis suggests that the combination of weak roots, intense light, and high temperature exacerbated water stress, heat damage, and sunscald, leading to seedling death. Through gradual acclimatization, tobacco seedlings can progressively adjust their root-to-shoot ratio, leaf thickness, and tissue structure, thereby enhancing stress tolerance and improving survival rates.

(iii) Lower-temperature environments can reduce the transpiration and metabolic intensity of tobacco plants, thereby enhancing their ability to gradually adapt to environmental changes. Experiments conducted in seedling greenhouses in Liuyang, Hunan, from 2021 to 2022 showed that the survival rate of tobacco seedlings transplanted on sunny days was 70% – 80%, while that of seedlings transplanted during continuous cloudy or rainy days exceeded 98%. This indicates that under low temperature and weak light conditions, the metabolism of tobacco plants slows down. Even if the root system is severely damaged, the low transpiration rate and minimal impact of water stress on photosynthesis allow more photosynthetic products to be allocated to the roots. As a result, tobacco plants can gradually re-establish root-to-shoot balance and resume growth[7].

2.2 Juvenility The adaptability of static traits in flue-cured tobacco to environmental changes partially stems from the graduality during juvenility. If tobacco plants undergo prolonged and profound gradual acclimation to a specific environment at their early tender stage, they ultimately exhibit the strongest adaptability to that environment. For example, when subjected to water stress acclimation from the seedling stage, the thickening of lower leaves promotes even greater thickening in upper leaves, accompanied by a more vertical root growth angle, resulting in the highest drought resistance. Similarly, if exposed to unidirectional light from the seedling stage, leaves orient at the maximum angle toward the light source, achieving optimal chimerism, whereas delayed exposure reduces both the angle and the degree of chimerism.

If tobacco plants are maintained in a stable soil environment from the tender stage, their root systems will grow in the most economical manner. For example, an experiment conducted in Liuyang, Hunan, from 2020 to 2021 showed that after transplanting robust tobacco seedlings, the remaining weaker seedlings were evenly spaced and returned to the seedling-raising pool. These seedlings were then transplanted at the same time as those potted in nutrient bowls. Although both types of seedlings exhibited identical recovery periods and growth vigor after transplantation, the spaced seedlings developed more functional leaves and yielded higher. Analysis suggests that after spacing in the floating seedling system, the seedlings enjoyed sufficient light, water, and nutrients, resulting in stronger photosynthesis, enhanced stress resistance, and faster recovery. In contrast, seedlings potted in nutrient bowls developed dense but finer root systems; after transplantation, only a few roots managed to extend outward, while some roots remained in the shallow, high-temperature soil layer, leading to reduced efficiency, accelerated lignification, and fewer leaves. In contrast, the spaced seedlings grew economically in suitable soil, achieving higher root system chimera efficiency, which contributed to their superior growth.

Tobacco plants' environmental adaptability is not only influenced by genetic traits but is also closely related to juvenility. For instance, under conventional conditions, the east-facing leaves of flue-cured tobacco exhibit stronger photosynthesis and transpiration in the morning, while the west-facing leaves show higher activity in the afternoon. However, if plants are exposed exclusively to eastern light from the seedling stage, the east-facing leaves grow flat and the west-facing leaves become erect, resulting in higher light energy utilization efficiency. In contrast, if unidirectional light exposure begins only at the vigorous growth stage, adaptability decreases significantly.

Although juvenile tobacco plants have a narrow adaptive range to environmental factors such as light and water, they exhibit vigorous respiration, strong cell division capacity, rapid wound healing, and good disease resistance, enabling higher regulatory efficiency in response to environmental changes. During the juvenile stage, leaves display high plasticity in size and thickness, roots can quickly adjust their growth direction to adapt to water and nutrient distribution, and leaves can maximize light utilization through expansion, thickening, or angle adjustment. However, after entering the mature stage, these adaptive capacities decline significantly: when seasonal changes alter the angle of sunlight, leaves fail to adjust their orientation promptly, leading to reduced photosynthetic intensity or susceptibility to photodamage; the roots' ability to adapt to changes in soil water levels weakens, relying only on a limited number of fine roots to adjust their absorption range, which may result in adaptation failure if water level fluctuations are too severe. In comparison, plants with lower maturity retain a degree of adaptability, demonstrating stronger drought and waterlogging tolerance[8].

Although the juvenile stage exhibits the highest plasticity, the biomass of flue-cured tobacco is predominantly formed during the vigorous growth stage. The climatic and soil conditions during this period determine the final static traits of leaves, such as chemical composition, morphology, and tissue structure, as well as the adaptability during the mature stage. After the vigorous growth stage, both cell division capacity and trait plasticity decline significantly[9-10]. Even seedlings cultivated under intense light and drought conditions, if subjected to prolonged overcast and rainy environments during the vigorous growth stage, will develop characteristics such as thin leaves, high water content, and loose tissue structure, making them prone to disease and premature senescence[11].

Furthermore, a certain level of photosynthetic intensity is a prerequisite for tobacco plants to rapidly develop adaptive changes, and higher photosynthetic intensity generally reflects greater fitness between static traits and the environment. Gradual changes in environmental factors help maintain relatively high photosynthetic intensity, thereby supplying more energy and materials for adaptive adjustments[12], primarily by slowing the rate of photosynthetic decline. Meanwhile, adequate water and nutrient availability also enhance photosynthesis, accelerating the adaptive modification process of static traits.

2.3 Similarity andcorrelativity

2.3.1 Similarity. The principle of similarity in tobacco adaptation describes how static traits respond in analogous ways to distinct environmental factors, such that acclimation to one factor often generates cross-tolerance to others. This arises from two main mechanisms. First, multiple stressors may trigger adaptation via a shared pathway—for example, high soil density, drought, heat, intense light, low humidity, and wind all induce water stress. Therefore, traits like enhanced root-to-shoot ratio or thicker leaves that evolve under one stressor also confer resilience to the others. Second, diverse factors can exert congruent directional effects on traits, consistently increasing or decreasing parameters such as root-to-shoot allocation, leaf thickness, and tissue structural compactness.

2.3.2 Correlativity. The correlativity includes three aspects.

(i) Changes in environmental factors often exhibit correlativity and generate compounding effects. For instance, overcast and rainy weather is typically associated with increased soil moisture, lower temperatures, and reduced light intensity, which collectively lead to a decreased root-to-shoot ratio and thinner leaves. In contrast, sunny weather often coincides with reduced soil moisture, rising temperatures, and stronger light, and the compounding effects of water stress, high temperature, and solar scorch increase the difficulty of adaptation for tobacco plants.

(ii) Environmental adaptation in tobacco involves coordinated multisystem adjustments in chemical composition, morphology, and histology, rather than isolated changes in individual static traits. Under water deficiency, for example, plants concurrently enhance root-to-shoot allocation, increase leaf thickness, raise cellular osmotic concentration, and promote tighter tissue packing. Adaptive pathways, however, diverge with soil texture: in sandy loam, adaptation emphasizes greater root-to-shoot investment, expanded root-soil interface, and stomatal regulation to limit transpiration; in clay loam, dependence shifts toward leaf morphological and anatomical modifications (thickening, compactness) coupled with elevated cell sap concentration to sustain hydraulic balance.

(iii) The static traits of tobacco plants exhibit mutual influence among roots, stems, and leaves, as well as between upper and lower leaves. They often show coordinated changes in chemical composition, cell size, and tissue structure. For instance, when lower leaves are thicker, the middle and upper leaves also tend to be thicker. However, senescent leaves are less affected by environmental factors and exert weaker influence on other plant parts.

3 Conclusions

During seed germination and early growth stages, flue-cured tobacco has relatively strict environmental requirements. However, as development proceeds, its static traits continuously adjust through adaptive changes, enabling the plant to achieve water and nutrient balance—and thus complete its growth cycle—under varying conditions by adopting different static traits (such as root-to-shoot ratios and leaf thickness) and distinct photosynthetic and metabolic patterns. Nevertheless, the duration and vigor of the growth period, as well as the resulting yield and quality, depend not only on environmental factors but also closely on the fitness between static traits and the environment, particularly near critical thresholds of temperature, light, moisture, and other conditions. This fitness encompasses both general adaptability to factors like temperature and light, and local adaptability to microenvironmental variables such as soil bulk density, water-nutrient distribution, and light angle—factors that ultimately determine whether the plant survives and how well it grows. Therefore, it is essential to strengthen research on the patterns and mechanisms of environmental adaptation during flue-cured tobacco growth, as well as on strategies to enhance its adaptability.

Based on the theory that flue-cured tobacco growth involves continuous adaptation to the environment, it can be argued that its adaptive range to field conditions is not fixed but can be adjusted through adaptive changes. The adaptation limits to environmental factors such as temperature and light, as well as traits like leaf thickness and growth duration, can be progressively enhanced—or even surpassed—through adaptive training initiated from the juvenile stage. Further speculation suggests that crops need to undergo a period of growth near the critical thresholds of key parameters—such as soil bulk density, water availability, fertility, temperature, and light—in order to maintain strong environmental adaptability in subsequent generations. Currently, crops like flue-cured tobacco are often cultivated generation after generation under controlled nursery conditions and in optimized field environments. This practice may lead to root system degeneration and a narrowing of the adaptive range, which is a significant reason for the decline in crop competitiveness and their difficulty surviving in the wild. In the event of major environmental changes on Earth, this could have disastrous consequences. Therefore, maintaining a certain scale of wild populations or subjecting crops to generational training within critical environmental ranges could help broaden their adaptive capacity to environmental changes.

The principles governing the adaptation of static traits to the environment are not exclusive to flue-cured tobacco but may also apply broadly to plants, animals, and even inorganic systems. The difference lies in the fact that flue-cured tobacco and other living organisms can carry out adaptive regulation through more complex physical, chemical, and physiological activities. A deeper study of these principles and their extension to other fields holds significant importance.

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