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THE DYNAMICS OF ENDEGENOUS HORMONE ACTIVITY IN PLANT LEAVES DEPENDING ON THE ALTITUDE OF THEIR GROWING

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ABSTRACT

The hormonal response of cultivated and wild plants to high intensity UV-radiation and other stress factors of the highlands was studied. The activity of auxins and growth inhibiting substances in wheat (*Triticum aestivum L*), barley (*Hordium vulgare L*), horse bean (*Vicia faba L*), and eurotia (*Ceratoides papposa*) leaves that grew in a field condition, were analyzed at different stages of development, using thin-layer chromatography and bioassay. The leaves of cultivated plants (2320 m and 2700 m above sea level) and wild plants (2320 and 4000 m above sea level) were collected at two elevations in Pamir highland (Tajikistan). The level of auxin activity at the beginning of ontogenesis in plant leaves that grew at both elevations was relatively higher in comparison with the activity of growth inhibitors. However, at the end of the vegetation period an increase in growth inhibitor activity was observed in plant leaves at both elevations. An increase in the total auxin activity in plants was observed at low altitude compared to higher altitude. Conversely, the activity of growth inhibiting substances increased in plants that grow at higher elevations.

UDC & KEYWORDS

■ UDC: 581.1 ■ TRITICUM AESTIVUM L ■ VICIA FABA L ■ AUXINS ■ HORDIUM VULGARE L ■ CERATOIDES PAPPOSA ■ GROWTH INHIBITORS ■ HIGHLAND ■ UV-RADIATION

INTRODUCTION

Depletion of stratospheric ozone as a result of industrial activities has exposed organisms to higher levels of ultraviolet radiation, especially in the UV-B 280-315 nm region (McKenzie et al., 2007). Indeed, strong absorption of UV-B photons by proteins and nucleic acids results in a range of adverse impacts on plants (Caldwell et al., 2003; Jenkins, 2009).

Plants are exposed to various abiotic and biotic stress factors throughout their life and are able to adapt to changing environmental, natural and agricultural conditions by different morphological, physiological and biochemical means as reported by Walling, (2000) and Diaz et al. (2007). Rozema et al. (1997) and Jansen (2002) conclude that UV-B reduces the level of indoleacetic acid that leads to an inhibition of cell expansion and changing in plant morphology. Plants have developed various ways to cope with UV-B radiation, mainly by incorporating UV absorbing flavonoids and phenolic compounds in the epidermis (Kolb et al., 2001), changing endogenous growth hormones content (Stratmann, 2003) and decreasing growth stimulators activity (Aknazarov, 1991).

However, apart from UV-B, production of UV-B absorbing compounds and changing hormone activity in plants can be induced by other abiotic stresses like nutritional stress (nitrogen and phosphorus), low temperatures and water stress that was shown by several studies (Bongue-Bartelsman & Phillips, 1995; Shomansurov & Aknazarov, 2005; Huyuan et al. 2007) and considered as adaptive response to the impact of these unfavorable conditions.

A wide range of biochemical, physiological, morphological, and growth responses of plants to elevated UV-B radiation have been reported by Feng et al. (2003), Zhang et al. (2003), Tegelberg and Julkunen-Tiitto (2001). One-third to two-thirds of all tested plants were susceptible to UV-B radiation (Lavola et al., 1998; Hofmann et al., 2003; Wang et al., 2007). Much of our knowledge about impacts of increasing UV-B is drawn from observations on crop plants in laboratory conditions differing from the natural conditions in terms of background ultraviolet-A (UV-A; 315-400 nm) and photosynthetically active radiation (PAR; 400-700 nm) that can lead to unrealistic conclusions (Fiscus & Booker, 1995; Rozema et al., 1997; Veteli et al., 2003). Thus, there is a need of assessing the impacts of UV-radiation on both domesticated and wild species in natural conditions.

One of the internal factors that control plant growth is the balance between growth stimulators and inhibitors, the activity of which changes under the influence of stress factors of the highland like high intensity of UV-radiation, drought and low temperatures (Aknazarov, 1991). Since the UV-B intensity, increases with elevation 14% per 1000 m that was demonstrated by Dehne (1989), comparison of hormonal responses of different plant species at two elevations may provide insight about the impacts of increase in UV-B radiation on plants.

The objective of the present study was to investigate the influence of natural UV-radiation in interaction with other climatic factors on auxins and the activity of growth inhibiting substances in various plant species' leaves that grow at different altitudes in the highlands of the Pamirs.

Materials and Methods

Plant material and study area

Three crops viz. wheat, barley and horse bean and one wild species of eurotia growing at two elevations differing in UV-B intensity and other climatic factors were compared in respect of hormonal activity in leaves. The experiments were carried out at two elevations above the sea level in Pamir highland area in Tajikistan. Leaves of *Triticum aestivum L*, *Hordium vulgare L* and *Vicia faba L* plants were collected for lab analysis in 2014-2015 at the altitude of 2320 m above sea level in the experimental plots of the Pamir Biological Institute, near Khorog, the administrative center of the mountain province of the republic (Figure 1). Another altitude of study was 2700 m: at this elevation plant leaves were collected at the Ishkashim research base station (Eastern Pamir). In addition, leaves of the wild growing plant, *Ceratoides papposa* were gathered at the elevations of 2320 m and 4000 m above sea level in Murgab district (Western Pamir). All elevations differ in climatic characteristics (Table 1).

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Figure 1: The map of study areas

Source: Authors

Table 1: Climatic characteristics of the study areas

Index	Western Pamir; 2320 m amsl	Eastern Pamir; 4000 m amsl
Name of the location	Khorog	Chechekdeh
UV-light percentage from total solar radiation (%)	5	7
Average annual temperature (ºC)	6.6	-1.6
Maximum temperature s (ºC)	33	24
Minimum temperature s (ºC)	-20	-42
Annual Precipitation (mm)	220	65
Relative humidity (%)	46.7	28.5
Frost free period (day)	182	60

Source: Shomansurov & Aknazarov (2005)

Leaves sampling

Leaf samples of all studied plants for determination of auxins and plant growth inhibitor activity like abscisic acid were collected in field through random sampling. Afterwards in lab condition the obtained leaf mass, after careful mixing, was prepared for further fixation. Leaves of wheat and barley plants were collected at tillering and earing periods, horse bean plant's leaves at the stage of 2-4 leaf and flowering and eurotia leaves at foliation and flowering periods.

Leaf fixation and hormones extraction

Leaf fixation was conducted in ethanol stream within 5 minutes, after that the material was extracted immediately or kept at 3-5ºC temperature for some time.

Extraction and determination of endogenous growth hormones was performed as described by Kefeli et al. (1973). To extract auxins and plant inhibiting substances we used 80% ethanol. Flasks with samples were placed in a shaker and jolted for 2 hours. Then the ethanol was poured into other flask and a new ration of ethyl alcohol was added to the residuary sample. The process was repeated three times. Extracts were combined and ethanol was evaporated to hydroxyl, whereupon it was acidulated by 2% hydrochloric acid to a pH of 3 and further utilized for the next extraction. As a leach for natural endogenous growth regulators from hydroxyl we used ethyl ether. Before using it, ether was purified from peroxides by metabisulfite sodium solution and then was acidulated by 2% of hydrochloric acid (10 ml to 11 ml ether). For extraction, hydroxyl was saturated by ether and shaken in separating funnel for 2-3 minutes. After 5-6 minutes infusion ether was poured out into evaporation bowl. The process was repeated three times till absolute ether discoloration. Ethereal extract was evaporated by cold air. Solid residue was solved with 90% ethanol. In one spot on the chromatogram 0.5 ml extract that ejected from 5g raw sample in terms of sensitivity of wheat coleoptiles was marked.

The chromatographic division of extracted substances

For chromatographic separation of extracts we utilized "Sulivol UV 254" thin plates. Before using, plates were cleaned by ethanol to avoid contamination. For separation of auxins and growth inhibitors at the chromatogram we used the isopropanol-ammonia-water (10:1:1) solvent system. In order to determine the activity of auxins and growth inhibitors, the eluates from chromatogram zones were tested using bioassay on the growth of wheat coleoptiles section that are characterized by high sensitivity to the auxins and growth inhibitors impact. Concurrently with extracts the standards of the IAA (Indoleacetic acid) and ABA (Abscisic acid) were applied on the chromatogram in order to compare extracted substances location on the chromatogram with the location of these hormones.

Bioassay of hormonal activity on wheat coleoptiles growth

For identification of hormonal activity in extracts from studied plant leaves using bioassay we used the wheat cultivar of Safedak ishkashimskiy that had good germinating ability and was applicable for this test. Seeds of this wheat cultivar were soaked within 18-24 hours in distilled water, after that it was put into cuvette with filter paper that was abundantly saturated by water. Cuvette was covered by glass and placed in thermostat at 25ºC for 2 days. The three days old coleoptiles of wheat seedlings were sampled with optimal length (18-20 mm). From selected coleoptiles the midsection was cut (5 mm length) by special machine with stenciled division (Boyarkin, 1984). After removing the first leaf by glass needle, in tens, cut pieces of coleoptile were placed into small porcelain cuvette with eluates obtained from different zones of chromatogram. The incubation period of coleoptiles in eluates was 18-20 hours at 25ºC in thermostat. Each coleoptile from eluates of the test and control (coleoptiles incubated in 2% of sucrose) was measured separately on cross-section paper for calculation of average length.

Statistical analysis

The statistics were carried out using one-way analysis of variance (ANOVA, Excel Data Analysis). The significance of differences among treatments is presented as comparison between eluates of the test from different zones of chromatogram and control (2% sucrose) ($P \leq 0.05$).

Result & Discussion

Result

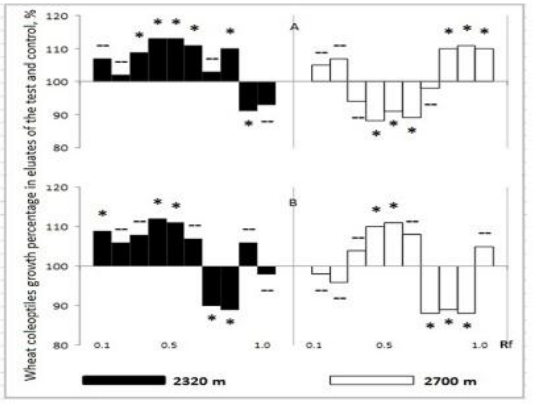
The dynamics of auxins and growth inhibitors activity in wheat and barley plant leaves

For determination of hormonal activity within vegetation period and between two altitudes, leaf of studied plants for analysis were sampled at early and later stages of development at both elevations. Comparison of obtained histograms showed that in wheat plant leaves grown at an altitude of 2320 m amsl, in tillering period, revealed five zones with Rf (Retention factor) values of 0.3, 0.4-0.5, 0.6 and 0.8 that had significant stimulative influence on growth of coleoptiles at ($p \leq 0.05$) compared to control coleoptiles that incubated at 2% sucrose. Only a zone with significant inhibitory activity in Rf value of 0.9 was detected on this chromatogram. Stimulation of coleoptile growth relatively declined in eluates from wheat plant leaves that in tillering

period grew at elevation of 2700 m (Figure 2). In this case the histogram suggests along with growth stimulator activity the existence of zones with inhibitory effect on coleoptiles growth. The Rf values of these zones were 0.4, 0.5 and 0.6 that had statistically proven inhibitory activity on coleoptiles growth.

Dynamics of auxins and growth inhibitors activity in wheat plant leaves (*Bobillo cultivar*) in different growth period at two elevations. A-tillering period, B-earing period. The average growth of coleoptiles from eluates of the test is evaluated in percentage to the growth of coleoptiles in control option that incubated in 2% sucrose, were taken as 100% on histogram. In this figure, each point of each parameter was the mean of ten replicated measurements (n = 10). The asterisks above the columns indicate significant differences at ($p \leq 0.05$) values between coleoptiles growth in eluates of the test and control option by ANOVA. The minuses are indicating not significant differences (Figure 2).

Figure 2: Dynamics of auxins and growth inhibitors activity in wheat plants leaves (Bobillo cultivar) in different growth period at two elevations



Source: Authors

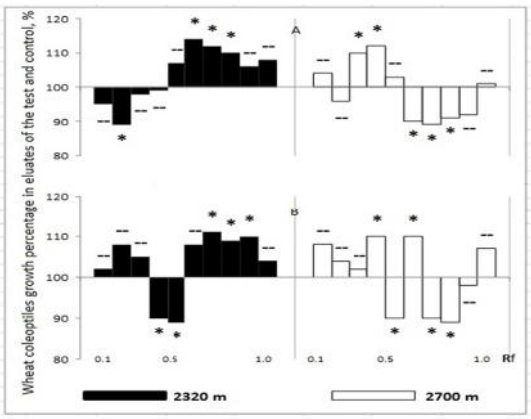
In the earing period (Figure 2) it was found comparative decreasing in activity of auxins in plant leaves at both elevations. Moreover in this case on the chromatograms were revealed two-three zones that significantly inhibited the coleoptiles growth at bioassay. However, it should be mentioned that the inhibitory activity of revealed zones at upper elevation was relatively higher compared to lower elevation. Comparison of these zones with standards of ABA showed their closeness on the chromatogram in Rf location (ABA Rf values 0.89-0.96, Kefeli et al., 1973) and color reactions that were displayed in the day and artificial UV-light. This situation is giving us the right to consider them as the ABA activity.

The analogous trend in growth stimulators and inhibitors activity was observed in barley plants. The results showed that auxin activity in barley plant leaves that grew at 2320 m elevation in tillering period were comparatively higher in zones with Rf value of 0.6, 0.7 and 0.8 (Figure 3) that had statistically significant stimulatory activity at ($p \leq 0.05$) compared to control coleoptiles. In this chromatogram a zone with Rf value of 0.2 was also found that had inhibitory influence on coleoptiles growth. In plant leaves that grew at higher elevation (2700 m) in this growth period on the chromatogram three zones were revealed that inhibited coleoptiles growth. However, the histogram suggests the existence of substances with stimulative influence on coleoptile growth in the zones with Rf values of 0.3 and 0.4 that had the same location on the chromatogram as the standard of IAA that has Rf value of 0.34-0.41 (Kefeli et al., 1973), thus giving us the right to consider them as the auxins.

No significant change was observed in quantity of zones with stimulatory activity in the earing stage in barley plants at both elevations compared to tillering period (Figure 3). However, the zones with inhibitory activity are increased at this stage. The results show that the coleoptiles growth was significantly decreased in the zones with Rf values of 0.4 and 0.5 by substances extracted from plant leaves at 2320 m. Analogous situation was observed in plants grew at 2700 m elevation.

Dynamics of auxins and growth inhibitors activity in barley plants leaves (Jaw-kabutak cultivar) in different vegetation period depending on altitude of its growing. A-tillering period, B-earing period. The average growth of coleoptiles from eluates of the test is evaluated in percentage to the growth of coleoptiles in control option that incubated in 2% of sucrose, were taken as 100% on histogram. In this figure, each point of each parameters was the mean of ten replicated measurements (n = 10). The asterisks above the columns indicate significant differences at ($p \leq 0.05$) values between coleoptiles growth in eluates of the test and control option by ANOVA. The minuses are indicating not significant differences (Figure 3).

Figure 3: Dynamics of auxins and growth inhibitors activity in barley plants leaves (Jaw-kabutak cultivar) in different vegetation period depending on altitude of its growing



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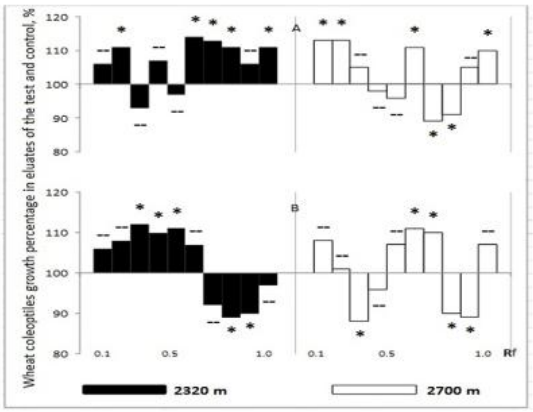
The dynamics of auxins and growth inhibitors activity in horse bean plants leaves

Dynamics of auxins and growth inhibitors activity in horse bean plants leaves in different vegetation period depending on altitude of its growing. A-2-4 leaf, B-flowering period. The average growth of coleoptiles from eluates of the test is evaluated in percentage to the growth of coleoptiles in control option that incubated in 2% sucrose, were taken as 100% on histogram. In figure 4, each point of each parameters was the mean of ten replicated measurements (n = 10). The asterisks above the columns indicate significant differences at ($p \leq 0.05$) values between coleoptiles growth in eluates of the test and control option by ANOVA. The minuses are indicating not significant differences.

Figure 4: Dynamics of auxins and growth inhibitors activity in horse bean plants leaves in different vegetation period depending on altitude of its growing



Source: Authors

High stimulatory activity of substances was detected in horse bean plants leaves at the 2-4 leaf stage at 2320 m elevation. Analysis showed that (Figure 4) on the chromatogram were revealed five zones with eluates that stimulated coleoptiles growth at bioassay. The Rf values of these zones were 0.2, 0.6, 0.7, 0.8 and 1.0 that had statistically significant differences compared to control coleoptiles. The similar trend was observed in horse bean plants that grew on upper elevation. However, here the coleoptiles growth was inhibited in eluates from the zone with Rf value 0.7 and 0.8.

Conversely, the quantity of zones with stimulatory activity on the chromatograms was declined at both elevations in flowering period. Moreover, it was observed comparative increase in inhibitors substances activity in plants leaves. The histograms suggest inhibition of coleoptiles growth by eluates from the zones of the chromatogram with Rf value 0.8 and 0.9 at both 2320 m and 2700 m elevation that had significant inhibitory influence on coleoptiles growth at ($p \leq 0.05$) compared to control coleoptiles. The Rf location and the color reactions of these zones were similar with the standard of ABA on the chromatogram and were consider as the ABA activity. It should be mentioned that the activity of growth inhibitors was higher at upper elevation (Figure 4).

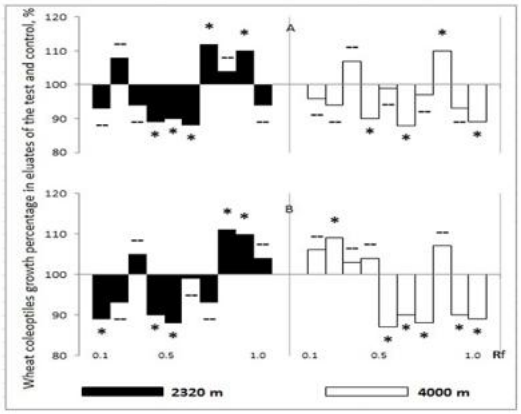
The dynamics of auxins and growth inhibitor activity in eurotia plants leaves

The auxin activity in wild plant leaves of eurotia were significantly decreased compared to cultivated plants at both elevations. At foliation period of this plants that grow at 2320 m elevation on chromatogram two zones that stimulated coleoptiles growth at bioassay were identified (Figure 5). At the same time on this chromatogram zones with Rf value of 0.4, 0.5, 0.6 were revealed that inhibited coleoptiles growth compared to control option. Analogous trend was observed in plants that grew at 4000 m elevation, at the stage where we detected three zones that had significant inhibitory influence on coleoptiles growth, ($p \leq 0.05$) that were compared to control coleoptiles. However, on this chromatogram a zone with stimulative activity was detected with Rf value of 0.8.

The minor variation in auxins and the activity of growth inhibitors in eurotia plant leaves between foliation period and flowering period that grew at 2320 m elevation was observed. Conversely, the activity of growth inhibiting substances like ABA in flowering period at 4000 m elevation significantly increased in zones with Rf values of 0.5. 0.6, 0.7, 0.9, and 1.0 that had statistically significant inhibitory influence on coleoptiles growth at ($p \leq 0.05$) compared to control coleoptiles, whereas, a zone with Rf value of 0.2 was detected with stimulatory activity in leaves was observed in this growth period (Figure 5).

Dynamics of auxins and growth inhibitors activity in eurotia plants leaves in different vegetation period depending on altitude of its growing. A-foliation period. B-flowering period. The average growth of coleoptiles from eluates of the test is evaluated in percentage to the growth of coleoptiles in control option that incubated in 2% sucrose, were taken as 100% on histogram. In this figure, each point of each parameters was the mean of ten replicated measurements (n = 10). The asterisks above the columns indicate significant differences at ($p \leq 0.05$) values between coleoptiles growth in eluates of the test and control option by ANOVA. The minuses are indicating not significant differences.

Figure 5: Dynamics of auxins and growth inhibitors activity in eurotia plant leaves in different vegetation period depending on altitude of its growing



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Discussion

Endogenous hormones play important roles in many plant processes, including growth, development, morphology, stress tolerance and adaptation to stress. Yang et al. (2004) reported that enhanced UV-B radiation, as well as other environmental stresses can induce hormonal changes in vegetative tissues. UV radiation had obvious effects on ABA content of most wheat cultivars under field conditions that leads to its significant increasing and decreasing the IAA content of six from ten studied wheat cultivars, thus affecting its growth, morphology and biomass that was concluded by (Li et al., 2000; Yuan et al., 2010). The effects of UV radiation in interaction with other stress factors in the highlands on hormone-inhibitor balance in plants leaves were studied in this work (Figure 5).

Hormonal-inhibitor balance in plant leaves within growth period at different elevations

The results showed that at the beginning of plants development in cultivated plants of wheat and barley (tillering period) and horse bean (2-4 leaf period) at both 2320 m and 2700 m elevation significant increasing in auxin activity and minor inhibitory activity in leaves was detected (Figure 2, 3, 4). By the end of the grow that both elevations

we found relative increase in the ABA and other growth inhibitors activity in all cultivated plants and decrease in auxin activity in both wheat (earing period) and horse bean (flowering period) and no change was observed in barley (earing period) plants. This variation in hormonal activity within plant growth period could be explained by having the common precursor as tryptophan for IAA and phenolic compounds (Millborrow & Robinson, 1973) and mevalonic acid for gibberellins and ABA (Kefeli et al., 1989) within the growth period depending on different internal and external factors the biosynthesis of stimulators is declining that leads to the increasing of inhibitors or vice-versa. Aknazarov (1991) reported that at the stage of heavy growth at the cost of active transforming of tryptophan into the IAA their content is increasing whereas the biosynthesis of the ABA from the mevalonic acid increased to end of vegetation period. Alteration in hormone metabolism (such as gibberellin) under UV-B radiation might associate with the changing of developmental stages that was reported by Caldwell et al. (1998). Conversely, in wild plants of eurotia at the beginning of growth (foliation period) minor growth stimulators activity in leaves at 2320 m elevation was found where as activity of growth inhibitors in this period was relatively higher. No appreciable change was observed in growth stimulators and inhibitors balance in eurotia leaves in later stage (flowering period) of growth (Figure 5). Significant increasing in growth inhibitors substances and ABA activity in leaves was detected in plants grow at 4000 m at both foliation and flowering period compared to auxin activity. However, the inhibitory activity in eurotia leaves was significantly higher at flowering period.

Hormonal-inhibitor balance in plant leaves between two elevations

Obtained results showed that the total activity of ABA and other unidentified growth inhibiting substances in leaves of all studied cultivated plants at both growth periods was higher at upper elevation while the auxin activity was significantly increased at lower elevation. Decline in auxin activity at higher elevation could be related to damaging influence of enhanced UV-B radiation in interaction with other stress factors that lead to the IAA decomposition in plants (Borman, 1989; Jansen et al., 2001) directly or by an activation of peroxidases that dismantle IAA and its photo-oxidation (Ros and Tevini, 1995) or else by auxin photolysis and its further transformation into the anthranilic acid under impact of UV-radiation that does not have stimulatory function in plants (Melchior,1958).

The reaction of wild plants of eurotia was different compared to cultivated plants. In this case, we observed increase in growth inhibitor activity at both elevations whereas the auxin activity significantly decreased. Moreover at upper altitude significant increase in the ABA activity in plant leaves was observed that might be related to plant's adaptation response to harsh condition of the highland as described by Shomansurov and Aknazarov (2005), who found that displacement of plant from lower elevation to higher during growth period the ABA activity increased while the gibberellin activity significantly declined in plants leave that was induced by enhanced UV radiation in interaction with low temperatures.

CONCLUSION

The above experimental information has shown that hormonal response of cultivated and wild plants to influence of UV-radiation and other stress factors of highland climate were different. Using thin-layer chromatography and bioassay, it was observed the negative impact of unfavorable environmental condition on endogenous auxins activity in leaves of all studied plants. As it was shown in this study, the relative severe climatic condition at upper elevation comparatively decreased the auxin activity and increased the activity of stress hormones such as abscisic acid and other growth inhibiting compounds in leaves of cultivated plants. While the auxin activity was higher at lower elevation. Conversely, in wild plants leaves we observed significant increase in growth inhibitors and abscisic acid activity at both elevations that indicate their adaptability to the influence of stress factors compared to cultivated plants.

In conclusion, endogenous hormones can be used as indicators of the sensitivity of plants species to enhanced UV-radiation and other stress factors under field condition especially in the highland where due to severity of climate the plant growth and productivity is strongly depressed.

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