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# Investigations on the Endogenous Levels of Abscisic Acid in a Range of Parasitic Phanerogams

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**Abstract.** The endogenous levels of abscisic acid in the parasitic phanerogams *Arceuthobium oxycedri* (DC) Bieb., *Cassytha filiformis* L., *Lathraea squamaria* L., *Melampyrum pratense* L., *Orobanche hederae* Duby., and *Viscum album* L. were investigated. In general, the content of abscisic acid was high in parasites which deprive their hosts of both phloem- and xylem-transported substances and much lower in those that deprive their hosts of sap from the xylem only. Within the parasites studied in more depth (e.g., *Orobanche hederae, Lathraea squamaria,* and *Melampyrum pratense*) the highest abscisic acid levels were found in their sink regions, especially in their inflorescences. It is suggested that a high concentration of abscisic acid is associated with plant tissues showing a high demand for phloem-transported substances. The possible role of abscisic acid in such tissues is discussed.

The phanerogamic parasite *Cuscuta*, parasitizing a flowering host plant, may completely inhibit the subsequent development of the fruit, a process normally representing a very strong sink (Wolswinkel 1974). Most of the assimilates produced by the host plant will then be accumulated in the parasite. Such an intensive transfer of $^{14}C$-labeled assimilates from host to parasites has also been reported by many other authors. Several explanations for the ability of parasites to accumulate host-produced assimilates are possible, one explanation is that these processes might be under hormonal control. Information about the level of plant hormones in phanerogamic parasites and their hosts is limited. Gustavson (1946) reported on a slightly increased content of auxinlike substances in the haustorial region of *Cuscuta polygonorum* compared with

the bordering tissues of their hosts, *Impatiens balsamea* and *Helianthus annuus*.

Drennan and El Hiweris (1979) investigated changes in growth-regulating substances in the xylem exudate of *Sorghum vulgare* after infection by *Striga hermonthica* and found a decrease in cytokinins of 90–95% and in gibberellins of 30–80%, whereas the amount of inhibitors was slightly increased. Jacob et al. (1975), studying the level of cytokinins in *Cuscuta reflexa* and its host, recognized a high cytokinin content in the host tissue compared with the bordering tissue of the parasite twining round the host stem. Ihl et al. (1984) investigated the endogenous auxins, gibberellins, cytokinins, and abscisic acid in the parasite *Cuscuta reflexa* and in the host, *Vicia faba*. Because the content of auxins, gibberellins, and cytokinins was somewhat higher in the host than in the parasite, these phytohormones are not expected to be involved in the absorption of nutrients by *Cuscuta*. However, the content of growth inhibitors, especially free abscisic acid (ABA), was much higher in *Cuscuta* than in the host. Therefore ABA seems to be connected with the special type of parasitic nutrition. On the other hand, it cannot be excluded that the high content of ABA detectable in *Cuscuta* may be related to the continuous aging and dying of the basal region, typical of the growth behavior of this rootless parasite. Kimura et al. (1982) showed that the level of ABA also increased dramatically in *Cuscuta pentagona* during the senescent stage.

In this article a number of investigations on the endogenous level of ABA in several phanerogamic parasites are described. Some of them deprive the host phloem of food substances; others are satisfied with the withdrawal of xylem sap by the haustoria. In all cases the mode of growth is different from that of *Cuscuta*.

## Materials and Methods

### *Plant Material*

A range of parasitic plants was collected from several localities (Table 1).

### *Extraction and Purification*

The homogenized plant material was repeatedly extracted with 80% (v/v) methanol, and the extract evaporated. The aqueous phase was cleaned by freezing and subsequently partitioned at pH 7.5 with light petroleum (30–50°C) and at pH 2.5 with ethyl acetate (EtOAc). Light petroleum extracts have been checked for inhibitory activity without further purification by bioassaying varying dilution steps. The EtOAc extracts were separated on columns (25 × 1.2 cm) of DEAE-Sephadex A-25 according to Gräbner et al. (1975). Figure 2 shows the scheme of fractionation. Aliquots of the fraction obtained were bioassayed for inhibitor activity. The ABA-like fractions (5 and 6) were further purified by analytical thin-layer chromatography with silica gel (Merck $GF_{254}$) using the benzene:EtOAc:acetone:acetic acid (80:20:10:1) system. Inhibitor

**Table 1.** Parasites investigated.

| Parasite species | Organs investigated | Origin | Host plant |
|---|---|---|---|
| *Arceuthobium oxycedri* (DC) Bieb. | Whole parasite without endophytic parts | Mediterranean coastal region, France | *Juniperus* sp. |
| *Cassytha filiformis* L. | Whole parasite | Botanical Garden of Halle University, GDR (greenhouse) | *Pavonia spinifex* (L.) Willd. |
| *Lathraea squamaria* L. | Subterranean organs (=rootstock, scaly leaves) | Corylus-Fagus forest near Schkölen, GDR | *Corylus avellana* L. |
| | Aerial organs (=inflorescence) | | |
| *Melampyrum pratense* L. | Roots | Town forest near Halle, GDR | Unknown |
| | Stem and leaves | | |
| | Inflorescence | | |
| *Orobanche hederae* Duby. | Stem (basal bulbous part bearing haustoria) | Botanical Garden of Halle University, GDR | *Hedera helix* L. |
| | Stem (middle part) | | |
| | Inflorescence | | |
| *Viscum album* L. | Whole parasite without endophytic parts | Botanical Garden of Halle University, GDR | *Acer carpinifolium* Sieb. et Zucc. |
| | Leaves | | |
| | Stem | | |

substances at $R_f$ 0.27–0.30, corresponding to authentic ABA, were eluted with methanol and separated on DEAE-Sephadex A-25 again. The ABA-like fractions (5 and 6) were methylated with diazomethane, and the inhibitors were identified by gas chromatography (GC) and GC-MS analysis.

### *Hydrolysis*

To characterize the inhibitor in neutral fractions, hydrolysis was performed in 1 N HCl (30 min, 70°C) followed by partition with EtOAc at pH 2.5, rechromatography on DEAE-Sephadex A-25, and bioassay of aliquots of the fractions obtained.

### *Bioassay*

In all chromatographic fractions inhibitor activity was determined using the wheat seedling bioassay (*Triticum aestivum* L. cv. "Hatri") according to Dathe et al. (1978).

### *Physical Methods for Identification*

GC-ECD was carried out on a chromatron GC-HT 18.3 according to Dathe et al. (1982) using the following conditions: glass column (2 m × 4 mm), 3% QF1 on Gaschrom Q (100–120 mesh), isothermal column temperature 180°C, carrier gas $N_2$ at 45 ml/min. ABA-Me was identified by comparing the retention times of the samples with that of authentic ABA-Me ($R_t$ = 5.8 min) and its 2-*trans*-isomer ($R_t$ = 8.5 min). The latter was produced by UV irradiation (Lenton et al. 1971). GC-MS was performed on a Varian MAT 111 with 80-eV mass spectrometer using a glass column (1.80 m × 2 mm), with 3% QF1 on Gaschrom Q (125–160 mesh), column temperature 210°C, carrier gas He at 12 ml/min. MS fragmentation pattern of the methylated inhibitors have been compared with that of authentic (±)ABA-Me, corresponding to data given in the literature (Gray et al. 1974).

## Results

### *Orobanche hederae* Duby.

*Orobanche* was investigated in two experiments. The first was performed with plant material harvested in July 1981, the second with material obtained in July 1982. All organs of the parasite contained two inhibitor compounds—the first in fractions 1–3 and in neutral fractions V1 and V2 from the subterranean organs, and the second in fractions 5–7, corresponding to ABA (Fig. 1). The inhibitor compound in fractions 5–7 was identified by GC-ECD to be ABA. The nature of the inhibitor substance(s) localized in fractions 1–3 and partially

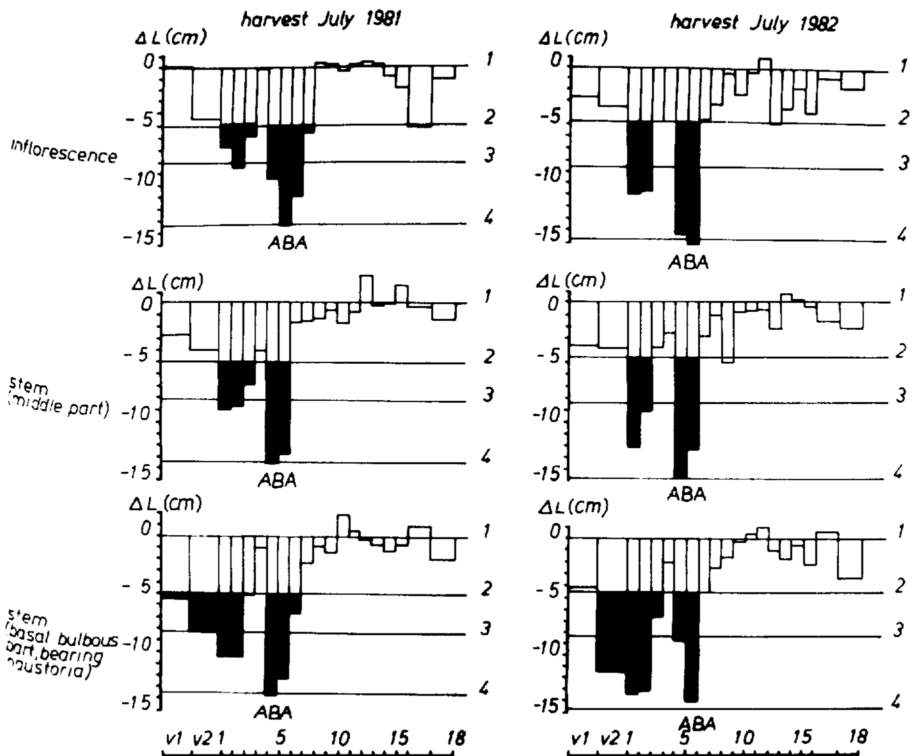


Fig. 1. Histograms of EtOAc-soluble inhibitors in different regions of *Orobanche hederae* Duby. Separation of EtOAc extracts by column chromatography on DEAE-Sephadex A-25. Determination of inhibitor activity in each fraction by wheat seedling bioassay. 1, water control; 2, $10^{-6}$ M ABA; 3, $10^{-5}$ M ABA; 4, $10^{-4}$ M ABA; ΔL(cm), length of seedlings:difference (cm) to water control.

in V1 and V2 remains unknown. Apparently it does not represent an ABA conjugate, because it could not be hydrolyzed. After acidic hydrolysis of this compound, subsequent participation with EtOAc at pH 2.5, and repeated separation on DEAE-Sephadex A-25, one inhibitor compound was eluted in fraction V2, as before hydrolysis.

Quantification of endogenous inhibitors in *Orobanche* was done in inflorescences, the middle part of the stem without flowers, and the subterranean bulbous part of the stem, bearing haustoria, too. The highest content of ABA was detected in the inflorescence (Table 2). A high content of ABA was found in the subterranean part too, where haustoria are localized. This corresponds to the high ABA level in the haustoria-bearing stem region of *Cuscuta reflexa* (Ihl et al. 1984). The middle part of the *Orobanche* stem showed an intermediate content of inhibitors.

In contrast to ABA, the amount of inhibitors in fraction 1–3 (V1/V2) does not differ clearly in the different regions of the parasite investigated.

**Table 2.** Content of EtOAc-soluble inhibitors in different organs of *Orobanche hederae* Duby. Inhibitor contents (ng ABA Eq./g fresh wt.) were determined by wheat seedling bioassay.

Fractions after chromatography on DEAE-Sephadex A-25: V1, V2 (Neutral inhibitor), 1, 2, 3, 4, 5, 6 (ABA), 7, 8, 9, 10. Bars in the printed table show the fraction range of each activity (given here in parentheses).

| Organ | Harvest | Inhibitor (fractions V1–4) | Inhibitor (fractions 5–10) |
|---|---|---|---|
| Inflorescence | July 1981 | 419 (1–3) | 1427 (5–8) |
| | July 1982 | 670 (1–3) | 1403 (5–6) |
| Stem, middle part | July 1981 | 388 (1–3) | 930 (5–6) |
| | July 1982 | 630 (1–2) | 1118 (5–6) |
| Stem, basal bulbous part bearing haustoria | July 1981 | 466 (V1–3) | 853 (5–7) |
| | July 1982 | 1355 (V2–3) | 788 (5–6) |

*Cassytha filiformis* L.

The plant material harvested in May 1984 was not separated into the different parts of the parasite. The light petroleum extract contained only negligible inhibitor activity. EtOAc extracts after chromatographic separation on DEAE-Sephadex A-25 gave a high inhibitor activity in fractions 5 and 6 (Fig. 2), corresponding to 1468 ng ABA Eq./g fresh wt. The inhibitor compound of these fractions was identified by GC-ECD as ABA. Small additional inhibitor activities found in neutral fractions V1 and V2 and in fraction 3 remained unidentified.

*Arceuthobium oxycedri* (DC) Bieb.

The inhibitor activities detectable by wheat seedling bioassay have been investigated in two samples. One sample was harvested at the beginning of September 1982, and the other one in the middle of October 1983. Only aerial organs of the parasite, including stem, reduced scaly leaves, buds, and flowers were investigated. After chromatographic separation on DEAE-Sephadex A-25, at least four inhibitor substances were detected in the following fractions (Table 3): V1 + V2; fractions 4–6 (corresponding to ABA); fractions 11–14; and fractions 17 and 18. The inhibitor compounds in fractions 4–6 have been further characterized; the others remain unknown. One compound in fractions 4–6 representing about 30% of the total inhibitory activity could be identified as ABA by means of thin-layer cochromatography with ABA, GC-ECD, and

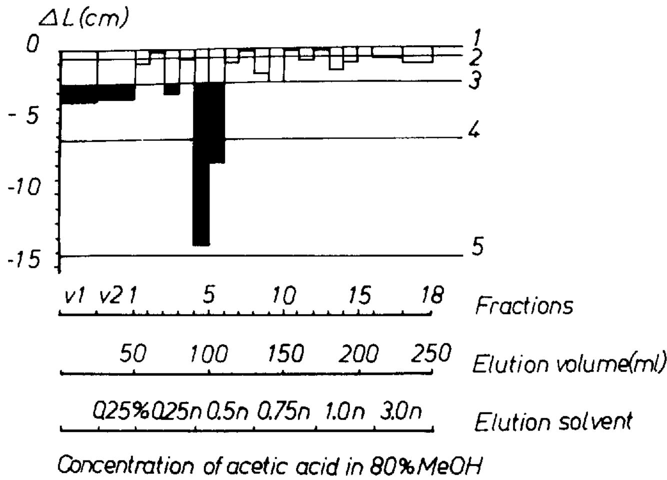


Fig. 2. Histogram of EtOAc-soluble inhibitors in *Cassytha filiformis* L. Separation of EtOAc extract by column chromatography on DEAE-Sephadex A-25. Determination of inhibitor activity in each fraction by wheat seedling bioassay. 1, water control; 2, $5 \times 10^{-7}$ M ABA; 3, $10^{-6}$ M ABA; 4, $5 \times 10^{-6}$ M ABA; 5, $5 \times 10^{-5}$ M ABA; ΔL(cm), length of seedlings:difference (cm) to water control.

Table 3. Content of EtOAc-soluble inhibitors in the aerial organs of *Arceuthobium oxycedri* (DC) Bieb. Inhibitor contents (ng ABA Eq./g fresh wt.) were determined by wheat seedling bioassay.

| Harvest | Fractions after chromatography on DEAE-Sephadex A-25 | | | |
|---|---|---|---|---|
| | V1 V2 1 2 3 | 4 5 6 7 8 9 | 10 11 12 13 14 15 16 | 17 18 |
| | Neutral inhibitor (V1–V2) | ABA (4–6) | | Polar inhibitor (17–18) |
| 1982 | 681 | 563 | 119 | 269 |
| 1983 | 347 | 660 | 274 | 541 |

GC-MS. The fragmentation pattern in MS of the methylated inhibitor was similar to authentic ABA-Me (Gray et al. 1974). The remaining 70% of the total inhibitory activity of fractions 4–6 was different from ABA, showing, by means of thin-layer chromatography, $R_f$ values of 0–0.15 (about 50%) and 0.43–0.57 (~20%), respectively.

## *Viscum album* L.

The contents of ABA-like substances in *Viscum* were investigated in three different samples. For the first one the plant material was harvested in February 1984, and for the second one in April 1984. On both dates the host, *Acer*

*carpinifolium,* was leafless, but in April, sap streaming had started. For the third preparation, parasitic material was harvested in July 1984, when the host was in full leaf. In the first and third preparations, the whole shoot of *Viscum* was extracted; in the second one, the parasite material was separated into leaves and stem. In the EtOAc extracts of all tissues, inhibitor activity was detected corresponding to ABA (fractions 5 and 6; Table 4). After further purification the inhibitor compound in these fractions was identified by GC-ECD as ABA. The endogenous ABA level in *Viscum* was high in the material harvested in winter but low in July, when the host was in full leaf. The light petroleum extracts contained only low inhibitor activities.

### *Lathraea squamaria* L.

Two different samples harvested in April 1981 and April 1982 were investigated for ABA-like substances. The plant material was separated into aerial organs (inflorescence) and subterranean organs, including rhizome, scaly leaves, and haustoria. The light petroleum extracts contained only negligible inhibitor activity. After chromatographic separation on DEAE-Sephadex A-25 columns in the EtOAc extracts of the aerial organs, three inhibitor compounds were detected: in the neutral fractions V1 and V2; in fractions 4–6, corresponding to ABA; and in fractions 9 and 10 (Table 5). In fractions 4–6, the inhibitor substance could be identified by GC-ECD as ABA. Its amount was rather low (Table 5). The highest inhibitor activity detectable in the bioassay was located in fractions 9 and 10. The chemical identity of this inhibitor remains unknown. It might be of a phenolic nature, because amino antipyrin gave a strong positive reaction.

In the subterranean organs, the main inhibitor activity occurred in neutral fractions V1 and V2 (Table 5). In plant material harvested in 1982, this inhibitor activity was extremely high and caused injuries in the bioassay plants. Thus quantitative interpretation seemed to be inaccurate. The chemical identity of this inhibitor remains unknown. It does not seem to be a neutral ABA conjugate, because acidic hydrolysis was not able to release an ABA-like compound. Rather, after hydrolysis, subsequent partition with EtOAc at pH 2.5 and repeated separation on DEAE-Sephadex A-25, the inhibitor activity was again found in the neutral fraction V1. Less pronounced inhibitor activity occurred in a wide range of fractions (4–11). In those fractions corresponding to ABA (4–6), only limited inhibitor activity could be measured (Table 5), and efforts in further characterization of this inhibitor (thin-layer cochromatography with authentic ABA) failed to detect ABA.

### *Melampyrum pratense* L.

Plant material was harvested in July 1984 and separated into root, shoot, and inflorescence. In the EtOAc extracts of all tissues investigated, inhibitor activities were found in fraction 5 and, less remarkably, in fraction 6 (Table 6), the active compound of which has been identified by GC-ECD as ABA. The

**Table 4.** Content of EtOAc-soluble inhibitors on *Viscum album* L. on *Acer carpinifolium* as host. Inhibitor contents (ng ABA Eq./g fresh wt.) were determined by wheat seedling bioassay.

| Parasitic material | V1 | V2 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Neutral inhibitor (V1–V2) | | | | | | ABA (5–6) | | | | | | | | | | | | | |
| Aerial organs, harvest February 1984 | 513 (V1–V2) | | | | | | 3113 (5–7) | | | | | | 101 (11–13) | | | | | | | |
| Leaves, harvest April 1984 | | | | | | 1035 (4–6) | | | | | | | | | | | 300 (15–16) | | | |
| Stem, harvest April 1984 | 548 (V1) | | | | | | 735 (5–6) | | | | | | | | | | | 548 (16–17) | | |
| Aerial organs, harvest July 1984 | | | | | | | 113 (5) | | 135 (7–8) | | | | | | | | 128 (15–16) | | | |

highest content of ABA was found in the inflorescence of *Melampyrum*. The stem and leaves contained another inhibitor compound eluted in fraction 8 of DEAE-Sephadex A-25 column.

Another preparation was performed using plant material (whole parasite without inflorescences) harvested in July 1983. In addition to ABA-like inhibitor activity (251 ng ABA Eq./g fresh wt., fractions 5 and 6), a strong inhibitor activity that had not been found in the parasite material harvested in 1984 was detected in neutral fractions V1 and V2 (344 ng ABA Eq./g fresh wt.). The light petroleum extracts of all parasite materials did not contain inhibitor activity.

## Discussion

According to Tsivion (1978), parasitic phanerogams can be classified into three groups: (1) Autotrophic facultative parasites characterized by the formation of functional roots, being able to supply the parasites to some extent with water and minerals and possessing a photosynthetic capacity sufficient for the development of the parasite. Such parasites, like *Rhinanthus*, are able to grow on mineral solution without being connected to a host. However, under these conditions plants are much reduced in growth and produce fewer flowers than parasitizing individuals (Klaren 1975). (2) Autotrophic obligate parasites like *Viscum* and *Phoradendron*, having no functional roots but not withdrawing assimilates from their hosts. (3) Obligate heterotroph parasites having no functional roots and being dependent on some supply of carbohydrates from their hosts. Members of all three groups were investigated in this paper.

*Melampyrum pratense* L. can be attributed to the first group (Cantlon et al. 1963, Weber 1981). *Viscum album* L. belongs to the second group, tapping only the host xylem and deriving no nutritive benefit from its hosts other than

**Table 5.** Content of EtOAc-soluble inhibitors in different organs of *Lathraea squamaria* L. Inhibitor contents (ng ABA Eq./g fresh wt.) were determined by wheat seedling bioassay.

| Parasitic material | Harvest | Fractions after chromatography on DEAE-Sephadex A-25: V1–V2 (Neutral inhibitor) | 4–7 (ABA-like inhibitor) | 8–12 |
| --- | --- | --- | --- | --- |
| Aerial organs | April 1981 | 94 | 360 | 980 |
| | April 1982 | 49 | 143 | 859 |
| Subterranean organs | April 1981 | (Test plants injured) | 53 | 102 |
| | April 1982 | 310 | 66 | 82 |

Table 6. Content of EtOAc-soluble inhibitors in different organs of *Melampyrum pratense* L. Inhibitor contents (ng ABA Eq./g fresh wt.) were determined by wheat seedling bioassay.

<table>
<tr><th></th><th colspan="12">Fractions after chromatography on DEAE-Sephadex A-25</th></tr>
<tr><th></th><th>V1</th><th>V2</th><th>1</th><th>2</th><th>3</th><th>4</th><th>5</th><th>6</th><th>7</th><th>8</th><th>9</th><th>10</th></tr>
<tr><th></th><th></th><th></th><th></th><th></th><th></th><th></th><th colspan="2">ABA</th><th></th><th></th><th></th><th></th></tr>
<tr><td>Stem and leaves</td><td></td><td></td><td></td><td></td><td></td><td></td><td>52</td><td></td><td></td><td>62</td><td></td><td></td></tr>
<tr><td>Inflorescence</td><td></td><td></td><td></td><td></td><td></td><td></td><td colspan="2">417</td><td></td><td></td><td></td><td></td></tr>
<tr><td>Root system</td><td></td><td></td><td></td><td></td><td></td><td></td><td>247</td><td></td><td></td><td></td><td></td><td></td></tr>
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small amounts of organic carbon and nutrients, especially nitrogen, carried in the transpiration stream (Ehleringer et al. 1985).

In contrast, the dwarf mistletoe *Arceuthobium* accumulates rather large amounts of photosynthates from the host in its endophytic system and aerial shoots (Hull and Leonard 1964). Thus it can be regarded as a representative of obligate heterotrophic parasites. Also *Orobanche*, *Lathraea*, and *Cassytha* belong to this third group. An intensive transfer of organic substances from host plants to *Orobanche* species has been described by several authors (Whitney 1972, Singh et al. 1972, Aber et al. 1983), but little information is available about the physiology of the parasitic Lauraceae *Cassytha filiformis* L. (De la Harpe et al. 1981). The transfer of organic substances from the host *Alnus glutinosa* to *Lathraea clandestina* was described by Renaudin and Larher (1981).

Concerning the withdrawal of organic substances from host plants, there are big differences between the obligate heterotrophic parasite *Lathraea* and obligate heterotrophic parasites like *Orobanche* and *Cuscuta*. The latter withdraw assimilates from the phloem of the host plants. Specialized phloemlike cells within the haustoria of these parasites form a bridge between host and parasite, however, obviously without any symplastic connection (Dörr and Kollmann 1975, Israel et al. 1980). In contrast, *Lathraea* is believed to withdraw all metabolites directly from the host xylem via a lignified bridge which branches out from the host vessels (Renaudin 1974). Thus the parasite may obtain sucrose too, previously recycled from the phloem. The content of sucrose in the xylem of the woody host plant species is especially high in spring, the time in which *Lathraea* forms its flowers and seeds. Therefore the term "bleeding sap parasite" has been introduced for *Lathraea* (Ziegler 1955).

Our results concerning the endogenous level of ABA in the different parasitic phanerogams clearly show that a high level of this hormone was only detectable in obligate heterotrophic parasites, which deprive their hosts of both xylem- and phloem-transported substances. The content of ABA, especially in *Orobanche hederae*, is very similar to the high ABA level in *Cuscuta reflexa* (Ihl et al. 1984). As already mentioned, the two obligate heterotrophic

parasites seem to be quite similar with respect to the haustorial connection to their host plants (Dörr and Kollmann 1975, Israel et al. 1980) and the manner of nutrient withdrawal from their hosts (Wolswinkel 1979). However, *Orobanche* does not show such abnormal growth behaviour as *Cuscuta*, with continuous aging and dying in the basal region. The basal, bulbous stem of *Orobanche*, bearing the haustoria, remains functional during the whole vegetation period. Thus it seems unlikely that the high content of ABA detectable in *Cuscuta*, including their inflorescences (unpublished), and *Orobanche* can be related to senescense processes.

On the contrary, the contents of ABA were much lower in parasites that deprive their hosts of xylem-transported substances only. This applies independently of the stage of parasitism, for facultative autotrophic parasites like *Melampyrum pratense*, for *Viscum album* (in summertime) as a member of obligate autotrophic parasites, and for *Lathraea squamaria*, an obligate heterotroph (xylem) parasite. The exception of a high ABA content in *Viscum album* during the leafless stage of the host *Acer carpinifolium* in February and April might be related to a limited water supply to the parasite from the host during this season and therefore can be put forward as a result of water stress. Evidence for increased water deficiency and osmotic values in *Viscum album* during the leafless stage of its host *Betula* sp. are given by results of Härtel (1937).

Within the parasites studied in more detail, like *Orobanche hederae*, *Lathraea squamaria*, and *Melampyrum pratense*, we found the highest ABA levels in the sink regions of the parasites—i.e., in their inflorescences. Thus it seems to be a general situation to find high ABA concentrations associated with tissues having a high demand for phloem-transported substances. This phenomenon is not restricted to parasitic plants, as parasitism does not seem to be a quality confined to specific plants but a widespread phenomenon, if achlorophyllous cells in green plants are considered to be parasitic (Tsivion 1978). High levels of ABA have often been described as occurring in the sink regions of nonparasitic phanerogams, like apices of castor oil plants (Hoad 1973) and sugar beet storage tissue (Elliott et al. 1986), as well as the growing fruits and seeds of soybeans (Quebedeaux et al. 1976), broad beans (Gräbner et al. 1980), wheat (Radley 1976, King 1976, Dewdney and McWha 1979), and grapes (Coombe and Hale 1973, Düring and Alleweldt 1980, 1984). Some further results concerning the possible role of ABA in assimilate transport and accumulation were given by Dörffling et al. (1984).

The reason for the high ABA concentration in the sink regions of different types remains uncertain. ABA can be either a result of or the reason for enhanced phloem unloading and/or accumulation processes in sink regions.

Like some xenobiotic substances and nonproteinogenic amino acids transported by the phloem, ABA might be accumulated passively in sink regions. However, in contrast to these substances, plants have a well-defined ABA metabolic system.

Furthermore, it has to be considered that the increase of ABA in sink regions might be the result of an increased osmotic potential due to sugar accumulation (Düring and Alleweldt 1980). Also, the potency of parasites for intensive starch accumulation (Singh et al. 1968) and the phenomenon of sucrose

secretion via extrafloral nectaries by *Cuscuta* (Schaffner 1979) could be considered as a mechanism in these plants to decrease the content of (imported) osmotic active substances under the conditions of a limited water supply.

On the other hand, some results are known that suggest a special, active role of ABA in loading or unloading processes (Malek and Baker 1978, Saftner and Wyse 1984, Clifford et al. 1986). In this respect, ABA, it has been claimed, influences proton or K fluxes in sieve tube membranes, a theory supported by the fact that ABA obviously affects the membrane transport of these ions in the guard cells of stomata, too (Walton 1980, Van Steveninck and Van Steveninck 1983). However, other authors failed to detect this type of ABA potency (Vreugdenhil 1983, Dörffling et al. 1984). These authors assume that ABA might have some direct effects on membrane integrity. Last but not least, a possible influence of ABA on invertase activity is discussed (Düring and Alleweldt 1984). The enzyme is known to induce hydrolysis of sucrose in the free space, which is possibly a prerequisite for phloem-unloading processes (Eschrich 1980).

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