

# Rising from the shadows: Selective foraging in model shoot parasitic plants

Thomas Bawin  | Kirsten Krause 

Department of Arctic and Marine Biology, UiT  
The Arctic University of Norway, Tromsø,  
Norway

## Correspondence

Thomas Bawin and Kirsten Krause,  
Department of Arctic and Marine Biology, UiT  
The Arctic University of Norway, Tromsø,  
Norway.

Email: [thomas.bawin@uit.no](mailto:thomas.bawin@uit.no) and  
[kirsten.krause@uit.no](mailto:kirsten.krause@uit.no)

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## Abstract

Despite being sessile, plants nonetheless forage for resources by modulating their growth. Adaptative foraging in response to changes in resource availability and presence of neighbours has strong implications for performance and fitness. It is an even more pressing issue for parasitic plants, which draw resources directly from other plants. Indeed, parasitic plants were demonstrated over the years to direct their growth towards preferred hosts and invest resources in parasitism relative to host quality. In contrast to root parasites that rely mostly on chemical cues, some shoot parasites seem to profit from the ability to integrate different types of abiotic and biotic cues. While significant progress in this field has been made recently, there are still many open questions regarding the molecular perception and the integration of diverse signalling pathways under different ecological contexts. Addressing how different cues are integrated in parasitic plants will be important when unravelling variations in plant interaction pathways, and essential to predict the spread of parasites in natural and agricultural environments. In this review, we discuss this with a focus on *Cuscuta* species as an emerging parasitic model, and provide research perspectives based on the recent advances in the topic and plant–plant interactions in general.

## KEYWORDS

dodders, foraging, host selection, plant–plant interaction

## 1 | INTRODUCTION

Plants gain access to resources including light, nutrients and water by modulating their growth (De Kroon et al., 2009). Just like animals, plants can indeed perceive, integrate and actively respond to physical, chemical and biological cues from their surrounding environment such as light, odours, sounds and touch, a process being crucial for their survival, growth and reproduction (Bilas et al., 2021). These environmental cues bear, for instance, the signature of neighbours, and their interpretation can lead to behavioural alterations that benefit either

the individual plant's fitness or that of conspecifics (Anten & Chen, 2021; Bilas et al., 2021). Resource acquisition can, for example, be secured by selective root placement in nutrient patches or by shoot elongation to evade canopy shade, both of which requiring energy investment in morphological modulations, but are nonetheless adaptative foraging behaviours in response to variations in resource availability over space and time (Bilas et al., 2021; De Kroon et al., 2009). Important questions not only include how different types of cues are perceived at the molecular level and lead to a response, but also encompass their relative significance in a given environmental

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context, their ecological functions and consequences, and ultimately their influence on community structures and ecosystem dynamics (Bilas et al., 2021; Huber et al., 2021; Kessler et al., 2023). Especially, the considerable knowledge of the perception of (changes in) light quality, which identified the phytochrome receptors as central organisers of resource allocation, together with the growing interest in the molecular detection and ecological significance of volatile emissions, pave the way for integrative studies on the interaction of these two important types of above-ground cues (Ballaré, 2009; Cheng et al., 2021; Huber et al., 2021; Kessler et al., 2023; Ninkovic et al., 2021).

Interpreting environmental cues is an even more pressing issue for parasitic plants, which draw resources directly from other plants by developing infective structures (haustoria) upon their contact. Parasitism in angiosperms evolved independently at least 12 times, and parasite species vary considerably in their lifestyle (Nickrent, 2020). Among them, root parasites such as the widely spread *Striga* and *Orobanch*e are largely dependent on host-derived chemicals contained in the soil that drive the progress of many crucial steps of parasitism including seed germination, active foraging by the radicle and initiation of haustorium development (Kokla & Melnyk, 2018; Mutuku et al., 2021). By contrast, *Cuscuta* (dodder) members differ from other parasitic groups in that they are not known to depend on special stimulants for germination and rather depend on foraging by the seedlings to find a host (Figure 1a). Seedlings, however, face the challenge to succeed within a few days before their nutritional reserves are exhausted, or else they die. Indeed, dodders appear as thread-like shoots with no leaves or roots, exhibiting at best a residual photosynthetic activity and being entirely dependent on a host for their survival (Hartenstein et al., 2023; Shimizu & Aoki, 2019). Foraging occurs by circumnutation, both in seedlings and older shoots. The negative gravitropic growth is in both cases accompanied by a rotation in a counter-clockwise motion until the shoots or seedlings find a host to attach to in tight coils. Among parasitic plants, many *Cuscuta* species are known for their broad host range, strengthening their ability to find a suitable host in a timely fashion in their immediate surroundings (Shimizu & Aoki, 2019).

Parasitic plants may have major impacts by shaping plant community structures and damaging economically important crops (Grewell, 2008; Parker, 2012; Pennings & Callaway, 1996, 2002; Press & Phoenix, 2005; Vurro et al., 2017). Their intimate physiological connection with their often closely related host and, in some cases, resilient seed banks, make it challenging to manage infestations (Benvenuti et al., 2005; Parker, 2012; Vurro et al., 2017). Increased concerns in a context of global change foster the need of refining predictive models to guide conservation of endangered species and pest control (Cai et al., 2022; Masanga et al., 2021; Ren et al., 2020). While successful parasitism critically depends on efficient host location, evidence has accumulated that parasitic plants can evaluate the quality of available hosts and 'choose' which ones they parasitise (Li et al., 2023; Marquardt & Pennings, 2010; Sandner & Matthies, 2018). Searching for and selectively exploiting resources from different host plants via nonrandom placement of parasitic

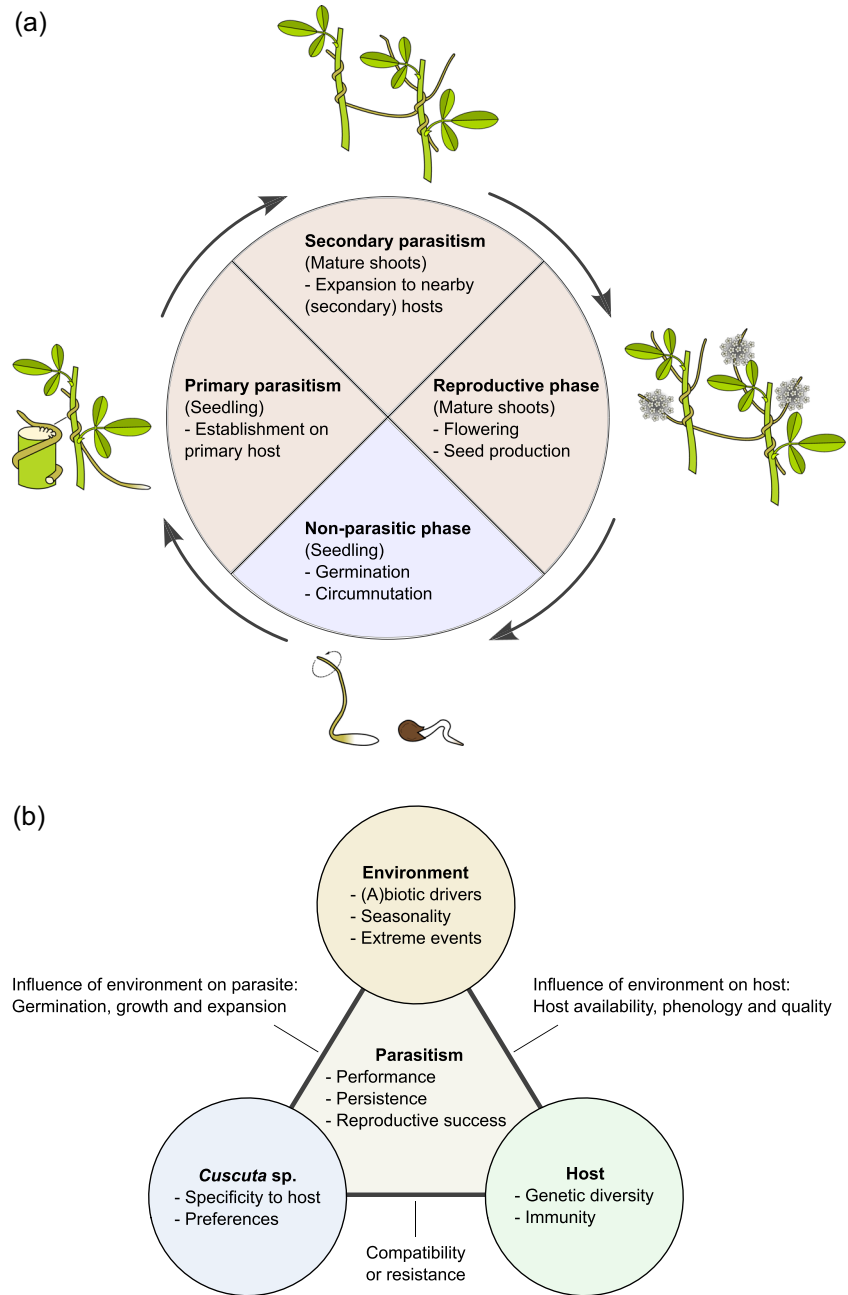
structures is described in the literature as involving host-derived cues including soil chemicals (root parasites), as well as transmitted light and airborne volatiles (dodders) as main drivers (Hartenstein et al., 2023; Li et al., 2023). A general consensus is that a parasite is likely to target hosts of higher nutritional quality, with the parasite performance increasing as it attaches to them, possibly benefitting from mixed diets via simultaneous interactions with hosts of different nature (Marquardt & Pennings, 2010; Sandner & Matthies, 2018). As environmental constraints may shape parasite–host interactions (Figure 1b) (Zagorchev et al., 2021), understanding the interpretation of cues leading to selective foraging and its context-dependency will help addressing the adaptative value of such behaviour in parasitic plants, its ecological relevance and consequences. Such knowledge will further be valuable to predict the distribution of parasites and to design sustainable strategies for infection mitigation or prevention.

Studies of the interactions between parasitic plants and their hosts can lead to discoveries of mechanisms or molecules that are more concealed in other plants. This can be exemplified with strigolactones which were originally identified as hormone cues that trigger seed germination in a root parasitic plant (Yoneyama et al., 2010). In the recent years, *Cuscuta* arose as an important parasitic model with the emergence of tools that open new avenues to investigate parasitism in greater details (Jhu & Sinha, 2022). Addressing how different cues are perceived and integrated by *Cuscuta* species, leading to 'decision making' and directed growth, promises novel, outstanding findings due to their specificities, including unique genomic and morphological features, and atypical responses to light. In this review, we describe the current knowledge of the factors influencing the selection of hosts by *Cuscuta* parasites and the underlying mechanisms, from directed growth of foraging individuals to coiling response and haustorium initiation. We then discuss the characteristics of this unique behaviour and provide research perspectives in light of the recent advances in the topic and plant–plant interactions in general.

## 2 | CUSCUTA SELECTIVELY FORAGES FOR POTENTIAL HOSTS

Evidence has accumulated over the years that, when presented with options, *Cuscuta* parasites seem to go for what is best for them. Kelly (1990) demonstrated that *Cuscuta* discriminates among host species and invests resources in stem coiling and haustorium initiation depending on the perceived host quality. The coiling response positively correlated to fitness in terms of survival and seed abundance. In another experiment, Kelly (1992) showed that *Cuscuta* was more likely to accept hosts of high nutritional quality and grow away from poor quality ones. The hypothesis that *Cuscuta* selectively forages was further supported by Koch et al. (2004), who showed that the most rewarding hosts were parasitised the fastest. More recently, Touchette et al. (2022) suggested a positive influence of the host nutritional status on *Cuscuta* preferences, although this was solely based on biomass and nutrient measurements in plants

**FIGURE 1** Life cycle and key factors that influence parasitism in *Cuscuta* parasites. (a) Dodders rely on foraging by the seedlings (which solely live on nutritional reserves) to find a suitable host. Primary parasitism occurs when a germinated seedling coils around and infect the basal parts of a host. Once parasitism is established by the seedling, shoot elongation resumes and side shoots spread onto other, higher parts of the host, as well as other host individuals including species that may not be good providers. Seedlings and mature shoots may differ in their infective behaviour during primary and secondary parasitism. Mature shoots eventually flower and produce seeds that are dispersed in the environment. (b) The interaction between a *Cuscuta* parasite, its host and the surrounding environment determines the success of parasitism in a given location. The environment likely influences parasite germination dynamics, growth and expansion onto various hosts, as well as host availability, phenology and quality. Beyond the compatibility of an interaction with a host, factors such as local adaptation and variations in host nutritional status may further shape dodder preferences and influence the performance and fitness of the parasite and its offspring. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



harvested from the field. Variation in size within host species is another factor that may influence host selection, as it was found that *Cuscuta* preferentially parasitises tall plants over short ones (Marquardt & Pennings, 2010). It was also observed that prior dodder parasitism and herbivory events can, depending on the host species, reduce subsequent attachment, suggesting that *Cuscuta* preferences may be influenced by the identity and the outcome of the initial attack, and that induced physiological changes in potential hosts may have a repellent effect on *Cuscuta* (Tjuriutue et al., 2016, 2017). It should be pointed out that parasitism varies in intensity for a given host species between different environments, shaping its preferred status in a given location (Baráth, 2021). While dodder preferences were mostly measured in the above-mentioned reports based on their attachment rate and performance, it has

recently been confirmed via electrophysiological recordings that *Cuscuta* discriminates from a distance between different host species (Parise et al., 2021). Although the mechanisms of perception of these remote host-derived cues and their effect on the foraging strategy were not directly investigated, the authors suggested that the interaction from a distance with other plants may cause changes in the physiology of *Cuscuta* parasites as, when they detected a host, they refrained from synthesising chlorophylls, indicating a switch in their survival strategy. A follow-up study revealed that the processing of host-derived cues might be related to low-band electrophysiological frequencies and supports the hypothesis of selective attention in dodders (Parise et al., 2023). Together, these findings substantiate that *Cuscuta* evolved pre- and postcontact mechanisms driving the selection of potential hosts.

### 3 | LIGHT CUES MEDIATE HOST PERCEPTION AND HAUSTORIUM INITIATION

Over the years, light has emerged as a crucial determinant of parasitism in *Cuscuta* species. Orr et al. (1996) reported that seedlings grow in the direction of far-red light and suggested a role of phototropism towards regions of lowered red:far-red (R:FR) ratio in locating and attaching to potential hosts. Accordingly, circumnutation accelerates as red light increases, while host location and subsequent attachment is dramatically reduced (Johnson et al., 2016). It should be highlighted that *Cuscuta* parasites do not only direct their growth towards specific light cues, but also use them to distinguish potential hosts based on attributes that may indicate their compatibility or nutritional quality. It was indeed shown that seedlings use lower R:FR ratios to search for the most potentially rewarding hosts, being attracted towards leaves with darker shades, which is indicative of a higher chlorophyll content (Benvenuti et al., 2005). Seedlings can further discriminate amongst potential hosts using differences in R:FR signatures as a function of their relative proximity and architecture, the later differing, for instance, between host species and growth stages (Smith et al., 2021). The role of light in driving host preference was suggested to be preponderant over differences in nutrient concentration between potential hosts (Wu et al., 2019). Light cues have also been abundantly demonstrated to influence coiling around the host and haustorium initiation. Lane and Kasperbauer (1965) showed that far-red and blue lights were effective in potentiating coiling in *Cuscuta* seedlings, and that effect could be reversed by red light. K. Furuhashi et al. (1995) reported that blue and far-red lights also induced haustorium formation, and pointed towards a crosstalk between them as they had an increased effect when applied together. Tada et al. (1996) stressed that both light and physical contact were required to induce haustoria. Subsequent reports further supported to various degrees the role of those wavelengths, their ratio and intensity as important factors for parasitisation (Bawin et al., 2022; K. Furuhashi et al., 1997, 2021; Haidar, 2003; Haidar & Orr, 1999; Haidar et al., 1997, 1998; Kaga et al., 2020; Pan et al., 2022). In an environmental context, all of these are dependent on the surrounding host tissues, their morphology and phenological stage. The perception in *Cuscuta* of red and far-red lights on the one hand, and blue light on the other hand, was attributed to phytochromes and cryptochromes, respectively, as a change in R:FR ratio was correlated with the ratio of active phytochromes, and as phytochrome inhibition did not influence the effect of blue light (Haidar, 2003; Lane & Kasperbauer, 1965). It is important to stress, though, that light appears to have different effects on *Cuscuta* parasites depending on their development stage. Yokoyama et al. (2023) recently showed that seedlings were unable to recognise a host under red light of low intensity despite coming into contact with it, while mature shoots elongating from infection sites were able to

initiate parasitism. The authors further observed that, similarly, while red light inhibited coiling in seedlings, mature shoots coiled and produced haustoria to some extent, although the effect was lower than that of blue and far-red light, possibly challenging the widely accepted idea that red light does not contribute to parasitism in *Cuscuta*.

### 4 | VOLATILES MAY PROVIDE ADDITIONAL INFORMATION ON THE HOST QUALITY

A different cue that affirmatively mediates plant–plant interactions are volatile substances, and host-derived volatiles were suggested to be a driver of foraging behaviour in *Cuscuta* parasites. Runyon et al. (2006) first showed that seedlings of the five-angled dodder (*Cuscuta pentagona*) detect and use volatiles to discriminate hosts of different qualities and grow towards their preferred ones. The seedlings responded positively to three terpene volatiles (viz.,  $\beta$ -phellandrene,  $\beta$ -myrcene and  $\alpha$ -pinene) emitted by tomato (*Solanum lycopersicum*) plants, which can sustain the growth of the parasites, while they were repelled by (Z)-3-hexenyl acetate emitted by wheat (*Triticum aestivum*) plants, which are not suitable hosts. The R:FR ratio was later found to influence the terpene volatiles emitted by tomato plants with high ratios inducing fewer quantities (Johnson et al., 2016), suggesting a close relationship between lighting conditions and volatile emissions in directing the growth of *Cuscuta* parasites. In another study, Tjiurutue et al. (2017) suggested that *Cuscuta* seedlings can also distinguish between damaged and undamaged hosts using herbivore-induced plant volatiles. This assumption was, however, solely based on infection trials and volatile profiling, and still awaits a proper, conclusive demonstration. While the findings from Runyon et al. (2006) were largely echoed in the literature, this report surprisingly remains, to our knowledge, the only after more than 15 years to provide strong evidence of a role of volatiles in foraging by *Cuscuta* parasites. In a follow-up study, flax dodder (*Cuscuta epilinum*) seedlings preferentially grew towards tomato plants, which are of poor quality to the parasites, instead of flax (*Linum usitatissimum*) plants, which are necessary hosts (Smith, 2014). No evidence of a role of plant volatiles in this behaviour could be detected, and light cues were suggested as more central cues triggering foraging responses. T. Furuhashi et al. (2011) contested the importance of volatile cues, as the need to detect specific volatiles to search for a suitable host hardly corroborates the generalist profile of many *Cuscuta* species, which are known to parasitise a broad range of hosts. The authors also stressed that *Cuscuta* can initiate parasitic behaviour in absence of a living host, either coiling around artificial rods and producing haustoria, or growing in vitro, pointing as well to a subordinate role of volatiles relative to light. The extent of the role of host-derived volatiles in foraging by *Cuscuta* and its significance for the parasite remains poorly understood and requires further investigation.

## 5 | FUTURE PERSPECTIVES

### 5.1 | *Cuscuta* parasites as plant brain teasers

It is now clear that *Cuscuta* species possess intricate sensorial abilities to locate and parasitise particular hosts, and one could be tempted to interpret this as a conscious, deliberate choice. The concept of plant cognition arose from the suggestion that some plant species learn from environmental cues to make informed decisions that may increase their chances of survival (Calvo Garzón & Keijzer, 2011; Parise & Marder, 2023; Segundo-Ortín & Calvo, 2022). That *Cuscuta* parasites can engage in such a complex process by integrating and weighting cues of different nature against each other to guide their development in an adaptive manner is an enticing thought. In that respect, dodders could indeed be qualified as conscious organisms that are endowed with cognition, allowing for the anticipation of rewards and for sensory-driven decision-making, as opposed to simpler, purely reactive and mechanical objects. Such phenomenon, however, cannot be fully understood as individual responses to single cues (Segundo-Ortín & Calvo, 2022). Many reports on cue perception by dodders and subsequent behaviour are narrowly focused, not to mention that a minor but nonnegligible proportion of dodder individuals sometimes respond differently from the test bulk and can be obliterated in concluding statements. There is limited to no evidence on the capability of dodders to associate different types of cues with one another and learn from these. While some species were shown to discriminate between hosts, there is to our knowledge no study demonstrating adaptive learning and memory of past events. Because dodders have a strong tendency to vegetatively propagate and could thus potentially accumulate 'experience' on the nature of their surroundings, their interactions with different hosts or nonhost surfaces would be expected to lead to either a reinforcement or a deterrent effect and ultimately change their foraging behaviour. This, however, remains to be explored. As modern investigations in plant cognition largely rely on ecological, behavioural and electrophysiological approaches (Segundo-Ortín & Calvo, 2022), to which dodders are particularly amenable, research on *Cuscuta* parasites may reveal important aspects regarding the question of plant consciousness and cognition, and contribute to the debate on these matters.

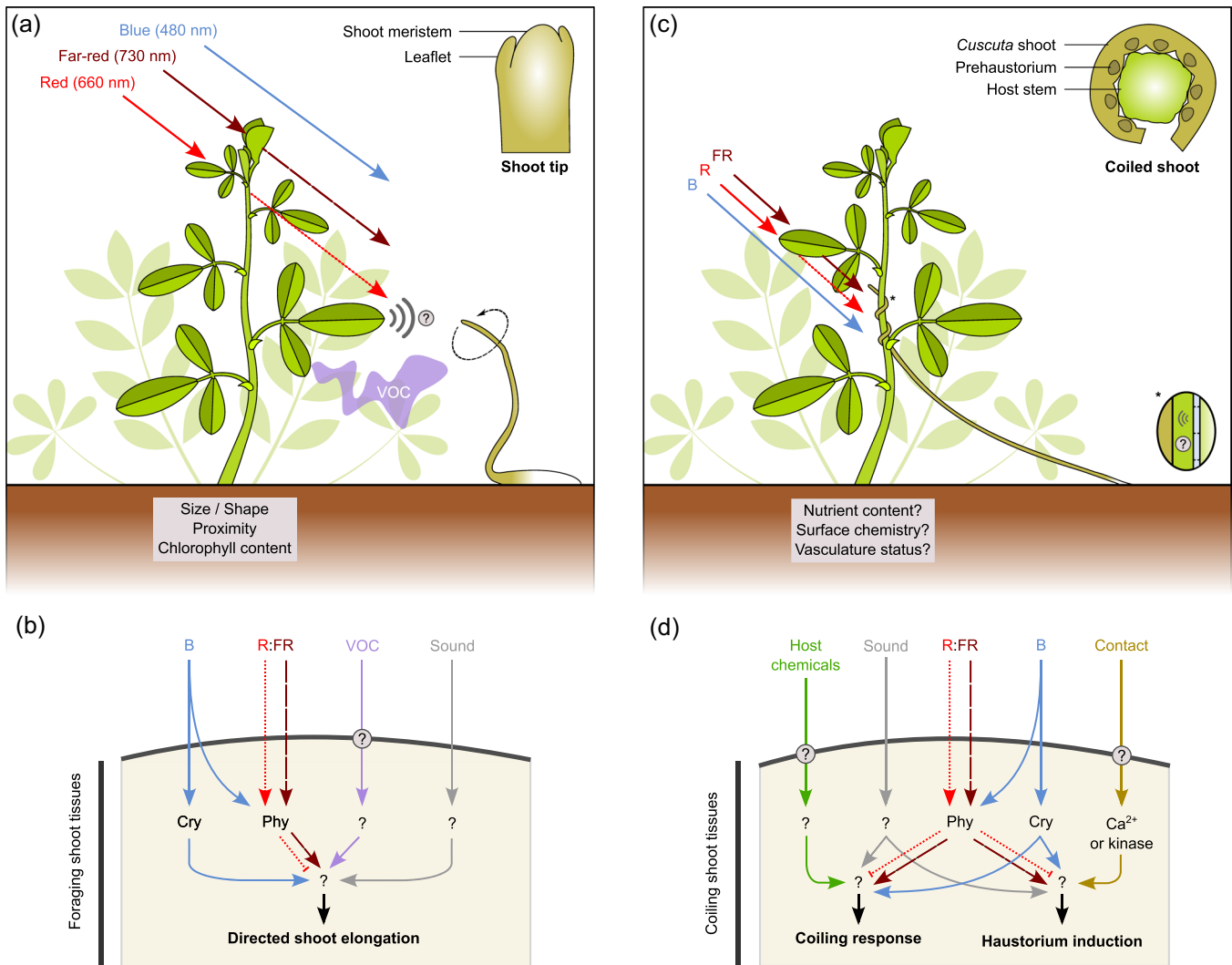
### 5.2 | Taking in the big picture: The parasite, the host and the environment

A general, widely accepted idea is that selective foraging in *Cuscuta* species ensures their survival and optimises their success. There may, however, be additional factors that were not yet identified and that can interfere with the integration of perceived cues, leading to unexpected behaviour as exemplified above with the flax dodder (Smith, 2014). Understanding why *Cuscuta* parasites are tuned towards certain hosts in relation to their performance requires a deeper knowledge of the host traits that matter to them, and should

be put in broader ecological contexts (Figure 1b). Different evolutionary trends were highlighted within the *Cuscuta* genus, with significant genomic and phenotypic variations across more than 200 species, and possibly high genetic variation across locations (García et al., 2014; Hartenstein et al., 2023; Masanga et al., 2022). Current studies so far investigated a limited number of parasite and host species, while factors such as previous selection of a host species, local adaptation and genetic variation were also shown to influence the outcome of an interaction (Koskela et al., 2000, 2001, 2002) but were not tested for their influence on foraging. Many of these studies further addressed the factors that influence the foraging behaviour of an individual using attachment rate and number of haustorial initials as main estimates of its preferences while dodder metabolism, growth and reproductive success as a result of selective foraging have been somewhat neglected. Dodder preferences could for instance result in different ecological niches under competition with co-occurring species, altering their life traits, or confer increased resistance to environmental stresses such as herbivory, making them more resilient (Cai et al., 2022; Smith et al., 2016). Thus, the impact of the 'choices' of a *Cuscuta* parent on the abundance and performance of its offspring is one of the areas that should be given future attention to provide full insights on the benefits of an interaction.

### 5.3 | Rewired circuits: Light perception and parasitism

As *Cuscuta* parasites live in nature within plant communities, another interesting question remains how different cues are perceived and integrated in both seedlings and mature shoots, leading to a possible 'decision making' and directed growth (Figure 2a,b). Plants escape shading and competition for light via phototropic growth towards red and blue lights (Ballaré & Pierik, 2017). While blue light triggers the same type of response in *Cuscuta* species, their response to red and far-red lights (or to R:FR ratios) is opposite with an observed growth in the direction of far-red light and an inhibition of haustorial emergence in elevated quantities of red light. Interestingly, morning glories (*Ipomoea* sp.), which are phylogenetically close to *Cuscuta* and believed to share a common climbing ancestor, were shown to preferentially climb to coloured stakes, suggesting that they possibly use reflectance information to search for structures on which to grow (T. Furuhashi et al., 2011; Price & Wilcut, 2007). Although there was no correlation between R:FR ratio and climbing frequency, these adaptations to a growth on support surfaces could have facilitated the evolution of *Cuscuta* into a parasite by refining and moderating the perception of light quality (or other cues). How these light cues are perceived and translated at the molecular level into an infective behaviour, and how the set of molecules playing a role in shade avoidance has been modified to allow for a different response remains a long-standing, yet unanswered intriguing matter (K. Furuhashi et al., 1997; T. Furuhashi et al., 2011; Hartenstein et al., 2023; Jhu & Sinha, 2022).



**FIGURE 2** Selective foraging in *Cuscuta* parasites. (a) Circumnutating seedlings and mature shoots direct their growth towards preferred hosts based on light and volatile cues. Lower red:far-red (R:FR) ratios of leaf-transmitted light provide information on the proximity, architecture and energetic state of a host plant. Apical tips may act as sensory organs and have a central role in determining growth direction upon light and volatile perception. Whether sound vibrations released from the host xylem influence the selection of hosts by dodders at one or another stage of parasitism remains to be determined. (b) Blue and (far-)red lights are likely perceived by crypto- and phytochromes. Host-derived volatiles possibly enter the parasite tissues through stomata if present and/or diffuse through the cuticle. Volatiles may be perceived, depending on their nature, via (yet undetermined) receptors, transporters, or ions channels. Sound vibrations may be perceived by mechanoreceptors. How and where these different cues are integrated within foraging shoot tissues downstream of their perception, resulting in directed shoot elongation, remains unknown. (c) Seedlings and mature shoots wind in tight coils around the aerial parts of potential hosts and initiate haustoria upon their contact. Blue and (far-)red lights, their ratio, and density, which are dependent on the surrounding host tissues and their characteristics, were attributed a critical role in inducing coiling response and (together with mechanical sensing supposedly via a Ca<sup>2+</sup> or kinase dependent signal pathway) haustoriogenesis. (d) Besides light sensing by crypto- and phytochromes, coiling response and acceptance of a host may also be influenced by nonvolatile metabolites including core and defensive compounds that can act as nourishing nutrients as well as chemical messengers. How and where these cues are integrated, resulting in this case in coiling response and haustorium induction, remains unknown as well. Cry, cryptochrome; Phy, phytochrome; VOC, volatile organic compounds. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

#### 5.4 | Keeping senses alert: The scent of a host

The sensing of volatiles was suggested to be exploited by plants when changes in light quality may be difficult to detect (Pierik et al., 2014). The mechanisms by which plant volatiles are taken up and interpreted are barely known for nonparasites (Ninkovic

et al., 2021; Rosenkranz et al., 2021) and studies on *Cuscuta* are lagging even further behind. Owing to the simple morphology of *Cuscuta* seedlings and shoots, and their low number of stomata (if any are present at all) (Clayson et al., 2014), it is possible to speculate that volatiles are perceived in rotating individuals at their apical region, perhaps entering through the cuticle,

converging to the hypothesis that spatiotemporal variation in volatile perception shapes a 'nose' in plants (Wang & Erb, 2022). Especially, while stomata may not develop until the parasitic stage is reached, the apex of seedlings was showed in some species to contain both chloroplasts and large intercellular spaces, the latter of which were suggested to aid the supply of CO<sub>2</sub> during photosynthesis and facilitate apical growth until a host is encountered (Lee et al., 2000; Lysheide, 1985). This could help the spread of volatiles as well within tissues. Sequestration in cuticular waxes and diffusion across the more permeable wall towards the cells is nonetheless expected to have a strong influence on the range of volatiles that can be detected. How the different abiotically and biotically induced signalling cascades at the different points of the life cycle of a parasite are integrated, possibly as part of a learning process, is a further aspect that requires attention.

## 5.5 | Senses that make sense

Recent advances in plant–plant interactions make it feasible to investigate additional cues that may influence the foraging behaviour of *Cuscuta* parasites. Especially, sounds can be released from the xylem depending on the transpiration rate – this from different organs and growth stages, and under different stressful situations – and can be perceived by plants via mechanoreceptors and lead to an adaptative response (Demey et al., 2023; Jung et al., 2018). Although no study investigated yet the response of dodders to sound, both mechanical sensing and host vasculature status are highly relevant aspects for these parasites, and one can speculate that such a mechanism also influences the selection of hosts at one or another stage of parasitism.

As *Cuscuta* parasites entwine a host, they further encounter host-derived cues that possibly influence their preferences (Figure 2c,d). Nonvolatile metabolites include core and defensive compounds that can act as nourishing nutrients as well as chemical messengers during plant interactions (Luo et al., 2023). It is a provocative thought that dodder species possess molecular mechanisms that allow them to perceive and 'taste' a host plant to assess its quality, before committing to its infection, as haustorium initiation can occur independently of the presence of a host. Preliminary evidence, however, suggests that the coiling response could be influenced by the surface chemistry of a host, and that *Cuscuta* parasites can reject it by bending away as an initial response (Kelly, 1990, 1992; Tjiurutue et al., 2017). Recently, it was showed that dodders adapt gene expression to their host during invasion and that host-derived molecules are further required to promote haustorial growth and vascular connection (Bawin et al., 2023; González-Fuente, 2023; Kaga et al., 2020; Narukawa et al., 2021). Much is still to be discovered on the influence of the host on the coiling response and development of haustoria in dodders, and the outcome of parasitism. This also calls for experimental systems that can be easily controlled, quantified and reproduced.

## 5.6 | In technology we trust

Future investigations, which are facilitated by the emergence of tools including, among others, the genomes of the field dodder (*Cuscuta campestris*) and the Australian dodder (*Cuscuta australis*) (Sun et al., 2018; Vogel et al., 2018), the possibility to study fluorescent proteins (Lachner et al., 2020; Švubová & Blehová, 2013) and transiently knock-down specific genes (Alakonya et al., 2012; Jhu & Sinha, 2022) and the development of an advanced artificial host system (Bernal-Galeano et al., 2022), promise outstanding discoveries. The recent demonstration that the bioelectric activity in foraging *Cuscuta* individuals can be recorded and interpreted (Parise et al., 2021), and the possibility to monitor the propagation through *Cuscuta* tissues of systemic signals such as reactive oxygen species (Fichman et al., 2023), open new avenues to screen for host-derived cues that might influence the parasites. Both changes in light availability and exposure to a variety of volatiles participate within seconds or minutes to the generation of (electrical) signals in plants (Asai et al., 2009; de Toledo et al., 2019; Fichman et al., 2023; Zebelo et al., 2012). Those cues that are detected at the tissue level can then be tested for their potential and interaction in triggering a behavioural effect, and assessed for their ecological consequences at both the individual and community levels. Such findings are essential to understand how *Cuscuta* parasites behave in both natural and agricultural environments (Cai et al., 2022; Masanga et al., 2021; Ren et al., 2020), and could feed into an integrated approach including the use of modelling and geographic information systems together with novel/improved management strategies (via e.g., manipulation of light spectra and/or use of companion plants) to decrease the persistent seed bank and mitigate dodder infestations at early steps.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

## ORCID

Thomas Bawin  <http://orcid.org/0000-0002-1042-0725>

Kirsten Krause  <http://orcid.org/0000-0001-9739-2466>

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