Shade avoidance and Zahavi’s handicap principle in dense plant populations

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I propose that tall plants ‘show off’ and that the shade avoidance syndrome is a case of spectral communication among plants in dense populations, enabling the operation of Zahavi’s handicap principle in plants. The costly signal triggering shade avoidance is composed of: (1) the far-red (FR) irradiation that plants emit as a by-product of photosynthesis, and (2) the phytochromes and the down-stream factors that respond to phytochrome signalling that evolved to analyse the FR emission and respond. This is a special case of a complex system serving as a signal. Because various types and levels of shade avoidance are common in most, if not all, dense plant populations, it seems that the operation of Zahavi’s handicap principle in plants is a common phenomenon. Although plants do not see, they can use light for interplant communication about their relative strength. Unlike the many types of species-specific operations of Zahavi’s handicap principle in animals, the handicap signal in plants is not species-specific, like prey–predator interactions. This difference probably stems from the fact that plants are sessile, have no animal-like vision, and compete with individuals of many other species. © 2005 The Linnean Society of London, Biological Journal of the Linnean Society, 2005, 84, 313–319.


INTRODUCTION

THE HANDICAP PRINCIPLE

The handicap principle (Zahavi, 1975) states that animal signalling is costly and therefore reliable. It has been proposed that the characteristics exhibiting the handicap principle (Zahavi, 1975, 1977, 1987; Grafen, 1990; Zahavi & Zahavi, 1997) evolved in the animal kingdom as a measure of the quality of males in systems of female mate choice. This principle is also applicable, however, to several other signalling systems: (i) offspring–parent need signalling, (ii) male–male or female–female signalling in competition for status that might later influence sexual selection, and (iii) prey–predator signalling (Zahavi & Zahavi, 1997). Organisms that operate under the handicap principle send honest (and usually, but not always, costly) signals (see Lachmann, Számadó & Bergstrom, 2001), which the receiver can evaluate in the process of deciding whether to respond. The value of the honest signal, however, is not always absolute but can depend on the temporal and spatial combination of signalers and receivers. If, when a certain individual sends a signal according to his ability, he happens to be among stronger individuals, then his signal appears relatively weak, and he will be considered weak in this particular situation and might lose. If, however, the same individual happens to be among weaker individuals, the same signal appears relatively strong, and he may be considered to be relatively strong. The importance of signal relativity is that it shows that the operation of the system is influenced by temporal and spatial conditions, or in other words, there is no constant value of the signal and no guaranteed gain or loss to the signaler.

Recently, there have been several attempts to apply the handicap principle to cellular and microbial systems. Honest signalling has been proposed to exist among gametes (Pagel, 1993), among cells within a multicellular body (Jablonska, 1996; Krakauer & Pagel, 1996), and in yeast, in which large proteins
with post-translational modifications are involved in mating and, as they are more costly signals than are short peptides, they enable evaluation of an individual's quality (Nahon et al., 1995).

WHAT IS A SIGNAL?
Zahavi & Zahavi (1997) define a signal as a trait whose value to the signaler is that it conveys information to those who receive it. According to their formal definition, signals evolve solely to convey information, although other traits that should not be regarded as signals according to this definition might also convey information. Zahavi & Zahavi (1997) emphasize that the fundamental difference between signals and other traits that might convey information is the relationship between the signal and its cost. In spite of their formal definition, in reality it is difficult to judge whether a specific trait is purely a signal or whether it has some other function, and it is difficult to demonstrate or dispute these other functions. For instance, certain coloured organs that serve as intraspecific or interspecific signals (e.g. black, white, red, yellow) may influence heat balance and resistance to pathogens or abiotic factors. Therefore, there is no theoretical reason to dismiss the operation of the handicap principle when a certain signal also fulfils another function. There is probably a functional gradient between signals that serve solely as handicap signals and those that do not. There is also no reason to ignore the possibility that a signal evolved primarily as a handicap signal and then lost its value or gained an additional function, or that a non-handicap signal became so because of a biotic or an abiotic change in the habitat. Assuming that all signals act only as costly signals and serve no other function, as proposed by Zahavi & Zahavi (1997), implies that their evolution either ended or that such a trait evolved at once, in a single step. This view seems to be an idealization and simplification of a much more complicated evolutionary and functional situation. I think that we are quite far from a full or even a good understanding of signal evolution according to any type of definition. Like Grubb (1992), in his distrust of simple hypotheses, I propose using modest, flexible definitions for the time being and being less dogmatic.

APPLICATION OF THE HANDICAP PRINCIPLE TO PLANTS
It has been proposed recently that the handicap principle operates in plant–herbivore interactions. Archetti (2000), Hamilton & Brown (2001) and Hagen, Folstad & Jakobsen (2003) proposed that the various bright colours of autumn leaves in many deciduous trees signal the tree’s vigour to parasitic insects, especially aphids. However, not all have accepted this view (Wilkinson et al., 2002). If aposematic coloration is considered a handicap signal (Grafen, 1990; Zahavi, 1991; Zahavi & Zahavi, 1997) a view that has not been accepted by all (e.g. Guilford & Dawkins, 1993), then it follows that because aposematic coloration is common in plants (Lev-Yadun, 2001, 2003a,b; Lev-Yadun & Inbar, 2002; Lev-Yadun & Ne’eman, 2004), Zahavi’s handicap principle probably operates commonly in plants. Unlike other signals, most of the cost of the aposematic coloration might be not the coloration itself, but the consequences of being conspicuous. Plants sense many biotic and abiotic components of the environment and respond to them (Simons, 1992; Buchanan, Gruissem & Jones, 2000), a basic requirement for the operation of Zahavi’s handicap principle among plants. It is an intriguing question as to whether the handicap principle also applies to plants not only in terms of plant–animal interaction, but also in plant–plant interactions.

Here, I discuss interactions among plants in dense populations (annuals, trees or shrubs as well as mixed populations) and propose that a certain signal (far-red (FR) emission and its perception) in the context of relationships within these populations operates according to Zahavi’s handicap principle.

DISCUSSION
THE SHADE AVOIDANCE SYNDROME
Plants have a well-known, reliable system that enables them to determine whether there are other plants in their vicinity and whether they are taller. Sensing of neighbours is based mostly on the fact that green tissues emit and reflect FR (λ = 700–800 nm) light, because the visible light used for photosynthesis is emitted in longer wavelengths after plants capture some of the photon’s energy. In addition, the gaseous hormone ethylene seems to have some role in the shade avoidance syndrome (Pierik et al., 2003, 2004a, b), although the data concerning this role is still fragmentary. The ratio of FR/red light is measured by a family of specific proteins (phytochromes) that activate a chain of signal transduction and thus regulate a cascade of physiological and developmental processes, known generally as the ‘shade avoidance syndrome’, including triggering of height growth and branch bending (Schmitt, 1997; Smith & Whitelam, 1997; Smith, 2000; Gilbert, Jarvis & Smith, 2001; Maddonni et al., 2002; Morelli & Ruberti, 2002; Schäfer & Bowler, 2002). A higher ratio of FR/red illumination is positively correlated with height growth rate (Gilbert et al., 2001) and avoidance of neighbours (Ballaré et al., 1987; Maddonni et al., 2002). The importance of height growth for the competitive ability of individuals and the role of shade avoidance in triggering it are well documented and have been care-
fully analysed (Horn, 1971; Iwasa, Cohen & Leon, 1984; Ballaré, Scopel & Sánchez, 1990; Schmitt, 1997; Henriksson, 2001). The fundamental biological aspects of shade avoidance in plants are well understood not only at the physiological but also at the molecular level (Smith, 2000; Gilbert et al., 2001; Morelli & Ruberti, 2002; Schäfer & Bowler, 2002; Devlin, Yanovsky & Kay, 2003).

There are plants that have a strong genetic tendency to grow tall (trees) and there are plants that have a strong genetic tendency to remain short (herbaceous plants). However, members of both groups can be quite flexible in their final height, within their genetic potential. In spite of the considerable contribution of the genetic component in determining plant height and architecture, plants do not grow in height or determine their architecture only according to an inflexible pre-existing genetic program. They make decisions according to the light regime, wind and neighbouring plants, all of which influence both height and overall branching and architecture.

**Dense and Sparse Plant Populations**

Plant populations may be dense or sparse. In dense populations interplant interactions dominate, and in sparse populations plant–environment interactions dominate (Fritts, 1976). There are several known interplant communication methods. Many woody plants have root grafts and they transfer hormonal signals among themselves (Graham & Bormann, 1966). Plants may use chemical signalling to reduce germination or growth of their neighbours, a phenomenon known as allelopathy (Rice, 1974). Plants attacked by herbivores send volatile signals, such as methyl jasmonate, that may induce defensive responses by other parts of the individual or even by neighbours (Karban & Baldwin, 1997). All these types of communication usually operate in dense plant populations.

**Definition of the Plant far-red (FR) Signal**

A major question that should be addressed here is whether the FR irradiation emitted by plants is indeed a signal according to the limited definition of Zahavi & Zahavi (1997). At first glance, FR irradiation does not seem to fulfil the requirements for a classic signal, because plants emit it as a by-product of photosynthesis. I argue that the FR emission should not be considered by itself, but rather that the FR signalling system should be considered as a whole, i.e. as composed of two components: (1) the FR component, and (2) the phytochromes and downstream response component. The phytochromes and downstream response factors are not a by-product; they evolved and are produced (with a cost) to be complementary to the emission of FR. I therefore propose considering the whole coupled entity, FR/phytochrome complex, as a signal. The fact that plants may use the FR signal for other purposes is in accordance with what we know about other handicap signals that do so, as described earlier.

**Do Plants Show Off?**

Jablonska (1996) asked the question, ‘Do cells show off?’ when discussing the application of Zahavi’s handicap principle for intercellular signalling. I find this point of view stimulating. To the best of my knowledge, the question, ‘Do plants show off?’ has never been asked concerning the shade avoidance syndrome. In other words, do plants grow in height just as much as they need for photosynthesis, reproduction (pollen and seed dispersal), defence or other physiological functions, or are they in many cases taller than they need to be for these regular functions? The answer is that we do not know enough about this issue. There are indications that at least concerning reproduction, as a measure of fitness, there are no 1:1 relationships between height or even biomass and the number of seeds and their potential for dispersal. Salisbury (1942) stated that, like height, seed production is subject to a considerable range of variation. It seems clear that there are unexplained reasons for the actual height of many plants. Many trees, for instance, have a tendency to grow tall even if they do not sense neighbours via the phytochrome system. They grow taller than required for defence against large herbivores or fires, or than required for light capture or reproduction, and they allocate resources to height growth that could be allocated instead for reproduction. It seems as if they are partly trapped in an automatic system shaped by their evolutionary history, like a peacock that grows a huge tail even when there are no other males around. This partly automatic response is limited and does not seem to be the whole picture. Here I propose a reasoning that might at least help in explaining this tendency of plants to be taller than is apparently necessary. I conclude that plants do in fact show off by growing taller than the minimum required for regular functions, and that, by so doing, they impose parallel action on their neighbours.

**Shade Avoidance as a Handicap**

I thus propose that certain shade avoidance responses fulfil the requirements of the handicap principle because shade-avoiding plants sense their relative condition within a dense population and change their behaviour in ways that benefit both themselves and the signallers. Before I describe several cases in which the FR signal from certain plant individuals influences the behaviour of other plants in ways that may...
benefit both signaler and receiver, I wish to specify the facts related to the operation of the handicap principle in the process of shade avoidance: (i) the signalers and receivers are all green land plants; (ii) the signal is composed of FR photons emitted and reflected from photosynthetic tissues and the phytochrome system, including the interactions of the phytochromes with the FR photons and all downstream factors that respond to phytochromes; (iii) the FR emission is received and processed by other plants or other plant parts of the same individual via phytochromes; (iv) the signal is honest and costly in that it comes mostly from above (as will be discussed later); (v) the receiver can respond to the signal by growth or other physiological responses (all are costly) that are in many cases beneficial for both signaler and receiver, and in some cases only for the signaler.

Taller plants can ‘show off’ and signal to lower ones with FR from above much more easily than can shorter plants to taller ones by reflection. The high cost of the signal is not only the combined cost of the emission of FR, phytochromes and downstream factors, but also the cost of the ability to send it from above. To be a taller plant is a handicap, because such a plant must have more resources and be able to allocate them for maintenance and construction of larger canopies, must be able to transport water against increased hydraulic stress, be able to withstand more wind action or snow load, and be able to support a larger self-load (see King, 1981; Batista & Platt, 2003; Falster & Westoby, 2003; Midgley, 2003; Koch et al., 2004). A shorter plant in the open can have a wider canopy and produce more seeds (Smith, 1981). The enhanced height growth in dense populations, with its consequences, is imposed on plants by the shade avoidance syndrome and is not an endogenous independent character (McMahon, 1975). Thus, being tall is a reliable indication of competitive ability for light in dense plant populations. Similarly, larger plants can better signal (emit or reflect FR) to the side. FR photons can also be reflected upwards from shorter plants below taller ones and probably cause elongation in the taller plants in order to escape, and stronger plants can elongate and escape from the FR-rich zone beneath them better than can weaker ones. Moreover, taller plants that continue to grow even taller can better shade the shorter ones, thus further reducing the light absorbed by the photosynthetic tissues of the shorter ones and the subsequent emitted and reflected FR from below. Therefore, it is risky for shorter (weaker) plants to stimulate height growth competition with taller plants by FR signalling from below. Although taller plants within a dense population will reproduce less compared with shorter and wider ones in a sparse population (Kozlowski, Kramer & Pallardy, 1991), they will still reproduce more than their shorter shaded neighbours, thus gaining an advantage. Of course, there is no linear relationship between height and the amount of shade. Plant crowns (and thus their shade) may reach a finite size but continue height growth. In any case, because there is general allometry, covering a considerable range between height and canopy size (Niklas, 1994), height is usually predictive of the amount of shade.

**RELATED BENEFITS**

There are several well-known responses of plants that perceive the FR signal from a taller or an adjacent plant, which benefit both signaler and receiver. (i) Seeds of many species do not germinate when exposed to high levels of FR in the shade of other plants (Fenner, 1985). The gain to the signaler is that there is less competition with other plants; the benefit to the receivers is that they can germinate only under better conditions. In addition, for large perennial plants, there will be less sibling competition among their offspring or with other competitors, an effect of direct value for any genotype. (ii) In many forests, there are suppressed dwarfs that do not even try to compete with the taller individuals, but sit and wait, even for decades, until the taller trees are damaged by hurricanes or other types of catastrophe (Harper, 1977). Again, the signaler enjoys a lower rate of competition and thereceiver does not waste its limited resources on deadly or otherwise risky competition, but rather waits for an opportunity. (iii) The third type of response is turning away from neighbours. Whole trees or just individual branches bend away from a neighbouring tree or a branch if there is a non-shaded space to the side (Büsgen & Münch, 1929; Timell, 1986). This phenomenon benefits the individual who shades because it reduces competition and wounding by abrasion of branches that sway in the wind (i.e. Putz, Parker & Archibald, 1984). The same benefits are valid for the individual that bends away. (iv) Frequently, weaker plants, triggered by a high FR/red light ratio, grow towards the light using all their available resources, and thus have very thin stems and can become exhausted and die or at least reproduce less effectively because of this forced response (Harper, 1977). This type of response benefits only the strong signalers. The gain for strong signalers is weakening or even elimination of at least some of their neighbours, and thus they reproduce more successfully, or in other words, have a better fitness.

**THE HANDICAP PRINCIPLE AND HORN’S VIEWS ON THE ADAPTIVE GEOMETRY OF TREES**

Horn (1971), while studying forest succession, distinguished between two basic tree types. (i) Monolayers

are trees characterized by uniformly distributed large leaves, low growth rate in open areas, low drought resistance, considerable shade tolerance and the ability to cast deep shade. When young, monolayer trees are flat and spreading. They change their height to width ratio slowly and they are tall at maturity. They form the understory and become common in late successional stages. (ii) Multilayers are trees characterized by randomly distributed small or lobed leaves, high growth rate in open areas, high drought resistance, shade intolerance, and they cast light shade. When young, the trees are tall and thin. They quickly change the ratio of canopy height to width and they have a cone shape at maturity. They are common and form the canopy in early successional stages. Early successional trees should be multilayered since at that stage there is a race to form the canopy. Height growth is important as multilayered trees are shade intolerant. Late successional trees should be monolayered since they invade the shaded understory (Horn, 1971). Measurements of growth and FR signalling in early and late successional trees planted at various densities showed that early successional ones generate small proximity signals and respond strongly to them, while late successional ones generate strong signals and respond weakly (Gilbert et al., 2001). These results fit the hypothesis presented here: multilayered early successional trees should have a weaker tendency to ‘show off’ – a weaker ability to operate Zahavi’s handicap principle – compared with the late successional monolayered trees that exist in shadier habitats. Early successional trees respond strongly to the FR signal and are thus forced to allocate resources to extension growth, probably to a greater extent than do late successional trees, which respond in a more modest manner. Thus, late successional trees may cause early successional ones to exploit their resources to a point where the early successional ones will be damaged and leave the territory to the late successional ones.

CONCLUSIONS

The interactions among plants in dense populations that operate through the perception of the FR signal via the phytochrome system are cases in which the conditions for the operation of Zahavi’s handicap principle in plants are fulfilled. Plants are not stuck in the position where they have germinated, but grow in height and change their architecture according to the biotic and abiotic environment to which they are exposed. An important factor of the flexible plant response is the proximity to neighbours, mediated mostly by FR irradiation. There are differences between groups of plants according to their successional state in FR signalling and response. The fact that the various types of shade avoidance are common in most if not all dense plant populations implies that Zahavi’s handicap principle operates commonly in plants. Although plants do not see, they may use light for interplant communication about their relative strength. The shade avoidance syndrome (Ballaré et al., 1990; Schmitt, 1997; Ballaré, 1999; Gilbert et al., 2001; Henriksson, 2001) is thus a case of spectral communication among plants, enabling the operation of Zahavi’s handicap principle via a show off. Unlike the many types of species-specific operations of Zahavi’s handicap principle in animals, the handicap signal in plants is not species-specific, like prey–predator interactions. This difference probably stems from the fact that plants are sessile, have no animal-like vision, and compete with individuals of many other species.

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