Resource competition: are plants involved in a tragedy of the commons?

Bachelor’s thesis

Supervisors: Marina Semchenko (Msc)
Prof. Kristjan Zobel

Tartu 2008
Contents

Introduction ............................................................................................................................................. 3
Hardin’s tragedy of the commons and its application to different areas of science ........ 5
    Hardin’s theory ................................................................................................................................. 5
    Donald’s ideotype and “growth redundancy” .................................................................................. 6
    Types of tragedy of the commons .................................................................................................... 7
    Areas of science where the tragedy of the commons has been applied ....................................... 9
Tragedy of the commons in plant competition ................................................................................. 11
    Competition for light ......................................................................................................................... 11
    Competition for belowground resources .......................................................................................... 12
Self/non-self discrimination in plants and avoidance of belowground competition .............. 17
Cooperation in related plants: sibling competition and kin selection ........................................ 24
Resolving the tragedy of the commons ............................................................................................ 28
Challenging the results of the studies on the tragedy of the commons ...................................... 30
Conclusions .......................................................................................................................................... 32
Summary .............................................................................................................................................. 34
Kokkuvõte .............................................................................................................................................. Error! Bookmark not defined.
Acknowledgements ............................................................................................................................. 38
References ............................................................................................................................................... 39
Introduction

Competition is an important process that plays a significant role in determination of plant performance. Closely located plants often compete with each other for above- and belowground resources that are necessary for plant growth, survival and reproduction. Thus, plant performance directly depends from individual’s competitive ability. Successful competitors are those who manage to capture the greatest proportion of shared resources. For example, plants need to invest more resources in root proliferation to obtain more nutrients and in elongation of stems and into production of leaf area to gain more light (Schieving & Poorter 1999; Gersani et al. 2001; Falster & Westoby 2003). However, competition can lead to overproduction of resource-acquiring organs at the expense of reproductive yield. Such a situation represents a tragedy of the commons (after Hardin 1968).

The tragedy of the commons occurs in conditions when the same common resource is limiting and shared by many individuals. Although selfish use of a common resource by individuals can lead to decreased fitness at the population level or even extinction of the whole population, it is more advantageous for an individual to be selfish and to maximize its own fitness at the cost to the populations a whole. Evolutionary theory predicts that this is the only evolutionary stable strategy in competition for resources with unrelated neighbours (a strategy or strategy mixture that cannot be invaded by mutants within the same population or by a stranger species from elsewhere; Futuyma 1998). Plant’s failure to cooperate follows the predictions of the Prisoner’s Dilemma: if one plant proliferates its roots in just one part of the available space (i.e. cooperates), it will lose, as other plants will enjoy their exclusive space and will proliferate into the space of the cooperator (reviewed in Gersani et al. 2001).

The flipside of a tragedy of the commons is that natural selection should favour the evolution of mechanisms that minimize competition between parts of the same plant and between individuals that belong to the same genotype or closely related genotypes (Falik et al. 2003; Gruntman & Novoplansky 2004). Plant self-competition results in increased biomass allocation to competitive organs, lowered reproductive yield and has no benefit for an individual. Therefore, plants would benefit from being able to discriminate between self and non-self, and to avoid competition with self but to steal resources from genetically unrelated competitors. However, the ability of plants to discriminate between self and non-self and to minimise wasteful self-competition has been considered limited in plants (reviewed in Wilson 1987). Recent studies demonstrated that such abilities can be more spread than it was previously thought. It has been shown that plants of some species can
cooperate with closely related or physically connected individuals (Tonsor 1989; Holzapfel & Alpert 2002; Gruntman & Novoplansky 2004; Dudley & File 2007).

In addition to the wide application of the theory of the tragedy of the commons in human sciences and animal ecology, the tragedy of the commons has been used to explain plant competition for light, nutrients and water. The possibility of a tragedy of the commons in competition for light was rarely considered in experimental studies but has got strong support from modelling studies (reviewed in Falster & Westoby 2003). The involvement of plants in a tragedy of the commons belowground (root competition) has received considerable attention and support in both experimental and theoretical studies (Gersani et al. 2001; Maina et al. 2002). However, recent advances in studies on root interactions suggest that some clonal species can exhibit cooperation and avoidance of belowground competition through root spatial segregation (Mahall & Callaway 1991, 1992, 1996; Schenk et al. 1999; Holzapfel & Alpert 2002). Also, the correctness of the experiments that investigated the presence of a tragedy of the commons in plants has been called into question (Semchenko et al. 2007a).

The purpose of this work was to review scientific literature on the topic of the tragedy of the commons in plants and associated phenomena in plant science, and to provide necessary background from other disciplines. Specifically, the aims were:

(i) to investigate the origin of the term “tragedy of the commons” in the human sciences;

(ii) to describe different types of tragedy and application of the theory of tragedy of the commons to plants and other organisms;

(iii) to review studies that demonstrate tragedy of the commons in plant competition for above- and belowground resources;

(iv) to investigate examples of self/non-self discrimination, sibling competition and cooperation in plants;

(v) to describe possible ways of resolving the tragedy;

(vi) to discuss the challenges in designing experiments to demonstrate the tragedy of the commons.
Hardin’s tragedy of the commons and its application to different areas of science

Hardin’s theory

In 1968, Garrett Hardin wrote an article about the problems of human society, including those of pollution, overpopulation and overexploitation of natural resources. The author believed that the occurrence of these problems was promoted by selfish behaviour of members of a society where every person is led by their selfish interests and do not care about impact on society as a whole. A classic example of a tragedy of the commons is herdsmen on a pasture. It is in the interests of every herdsman to maximize their own gain, which is to keep as many cattle as possible. The addition of one more animal to the herd has two consequences. The first is positive to the owner of the animal: the herdsman receives all the profit from the sale of that animal. The second is negative to the community: one more animal creates additional overgrazing and this time all of the herdsmen share the cost of the overgrazing. Hence, the benefit of the addition of one more animal for the owner of that animal is higher than its cost. Consequently, a rational herdsman concludes that the most advantageous strategy for him is to continually add further animals to his herd. This conclusion is reached by every herdsman sharing a common pasture, resulting in a tragedy of the commons. Each man increased his herd without limit till the pasture becomes so overgrazed that it can no longer support any animals. The main idea of Hardin’s theory is that selfish use of common resources that are limited and shared by many individuals leads to a tragedy. Hence, the term “tragedy of the commons” was coined to reflect the inevitable consequence of unrestricted use of common resources.

The tragedy of the commons can also be observed in overpopulation (Hardin 1968). Overpopulation is one of the major modern problems of human society and it leads to other complications such as overexploitation of natural resources. Members of a society consume energy and resources in an unsustainable way and do not recognise that resources are limited. Each person maximises their fitness by increasing the number of descendants, which leads to unlimited birth rates and to growing costs to the human population as a whole. However, a rational person understands that it is unprofitable for them to restrict their reproduction because the place of their descendants will be occupied by descendants of other people who adopt selfish behaviour, while their own genes will stop to exist. In some countries with particularly fast population growth, special governmental policies have been introduced that
encourage or force the population to limit birth rates. Some people consider it an infringement of the human rights. However, Hardin was convinced that freedom to breed will bring a tragedy to all people in the world, and that the only solution for this type of problems is the restriction and regulation by the state of activities that can cause damage to the common benefit of the population. The main conclusion of Hardin’s work was that common resources would be always overexploited when utilized by self-interested individuals. Only the input of strict social arrangements and increase of moral standards could rescue human society from a future tragedy (Hardin 1968).

Donald’s ideotype and “growth redundancy”

However, Hardin did not connect his theory with the problems of evolutionary biology. Donald was the first scientist who applied the principle of a tragedy of the commons to plants (Donald 1968). Interestingly, Donald’s essay was published the same year (1968) as Hardin’s theory and has much in common with the idea of the tragedy of the commons. Donald considered the same phenomenon in agricultural plants and referred to it as “growth redundancy” in plants. It is known that the maximization of offspring production is the primary goal of each individual plant that can be achieved by intense resource acquisition at the expense of neighbouring plants. However, the performance of the population as a whole may not benefit from the presence of such prolific plants. On the contrary, the total crop will decrease as the frequency of prolific genotypes increases.

Donald was the first to pay attention to the impact of above- and belowground competition among cultivated plants on crop yield. He introduced the concept of “growth redundancy” to describe excessive investment of biomass in growth of resource-acquiring organs in plants. A new breeding approach called “ideotype breeding” was suggested. Donald suggested developing a “communal ideotype” in plants that would secure high yields in a crop monoculture by means of minimising competition between neighbouring plants. Such communal plants should show low fitness when grown in isolation but result in higher total yield when grown in dense monoculture where normally intense competition would take place. Such plants should be weak competitors and invest more to reproductive yield at the expense of growth of competitive organs than plants with strong competitive ability. Donald considered “growth redundancy” in height in competition for light and redundant growth of roots in competition for nutrients.

Despite receiving considerable attention, Donald’s ideotype has not gained wide acceptance among breeders, partly because there was no scientific proof to his theory.
However, Donald’s ideas have gained support from a game-theoretical model of competition for water (Zhang et al. 1999). The study showed that the optimal distribution of resources in plants that would result in maximum crop yield is not evolutionarily stable. The proof to it is the frequent presence of “growth redundancy” in modern cultural plants. Population in which all plants are weak competitors and maximise population benefit will be quickly superseded by mutant genotypes with greater competitive ability and individual reproductive potential. Thus, only breeders can limit competitive ability of cultivated plants by means of interfering with such genetic changes.

Types of tragedy of the commons

The theory of the tragedy of the commons has been successfully applied to many areas of science. The analogy to the tragedy of the commons helped to explain why selfish individuals in animal and plant populations do or do not destroy collective resources completely (Rankin et al. 2007). The definition of the tragedy of the commons has some distinctions in different areas of evolutionary biology, but it has one major principle: selfish use of resources by the individual leads to reduction of a resource and consequently reduction of the fitness of whole group.

Three types of resources over which a tragedy of the commons might occur can be distinguished (Rankin et al. 2007). Firstly, individuals can compete and overexploit an extrinsic pre-existing resource. Competition for a pre-existing resource results in a lower average fitness of the population. An example of a pre-existing resource could be lizard females in the context of male-male competition. As a result of male harassment, the mortality rates of females increase and female fecundity decreases leading to population decline. Another example is competition within the host that leads to virulence of some virus phages being so high that they destroy the bacteria on which they exist (reviewed in Rankin et al. 2007).

The second type of resources is social goods formed by cooperation. This kind of tragedy is connected with a common resource that is shared by all members of a population or group and is created by cooperating individuals. The tragedy appears when cheaters can gain common goods, which were provided by cooperating individuals, without contributing to the cooperation themselves. In this case, selfish use of a resource can drive the whole population extinct. For example, plant-microorganism mutualism can break down due to cheating by one of the participants, or cheating by some microbe individuals leads to the
breakdown of intraspecific cooperation because of individual interests (reviewed in Rankin et al. 2007).

Social goods formed by restraining from conflict are the third type of resources prone to a tragedy of the commons (Rankin et al. 2007). Engaging in competition brings cost to all members of the group and individuals involved in competition are forced to invest more in the conflict at the expense of reproduction. Thus, it would be advantageous for the individuals to restrain from resource competition. A good example of this type of a tragedy of the commons is plants competing for light (Schieving & Poorter 1999; Falster & Westoby 2003). Theoretically it is better for the population as a whole to produce short stems. However, there are selfish individuals investing in height more than their neighbours. Taller plants have an advantage in gaining light in competition with shorter neighbours, but they invest a lot of resources in vertical growth that compromises their reproductive success. Despite restricting their height and investing more in reproduction shorter plants will lose as a result of shading by taller neighbours. Thus, taller plants will always have a higher relative fitness than shorter competitors within the same stand. Individual competition over common resources reduces the amount of these resources and, consequently, fitness of the whole group (population, species). In other words, individuals are maximizing own fitness at the expense of collective productivity. The same principle can be applied competition for water and nutrients (Zhang et al. 1999; Gersani et al. 2001; Maina et al. 2002; reviewed in Rankin et al. 2007).

There are also collapsing and component tragedies. “Collapsing” tragedy is a situation where selfish individual behaviour leads to entire resource vanishing. If resource is essential for the survival of the whole group, its complete loss drives the population extinct. An example of “collapsing” tragedy is reproduction of workers in honey bees (reviewed in Rankin et al. 2007). When workers stop to help the colony and begin to invest in their own reproduction, the number of individuals becoming workers decreases that leads to colony collapse. In the case of a “component” tragedy, common resource does not disappear completely. Thus, population can survive with reduced amount of resource or persist on alternative resources. Despite lower average fitness of the population, it is still able to survive. This type of tragedy should be very common as it only needs the existence of conflict between individual and common interests. Examples of a “component” tragedy are male-male competition for females in population of lizards and plant competition for light, water or nutrients (reviewed in Rankin et al. 2007).
Originally, the tragedy of the commons has been applied to the problems of human society such as overpopulation, pollution, climate change and others (Hardin 1968). For example, tragedy of the commons has been applied to explain pollution problems such as water pollution with sewage to the commons is less than the cost of purifying own wastes. Each man has temptation to cheat by refusing to purify his own waste and discharging it to the common water resources. Cheating happens because it brings economical advantages to an individual whereas costs are distributed among all members of the community. Considering that everyone thinks this way, we are faced water pollution that affects the whole society. Likewise, world’s oceans continue to suffer from the logic of the commons: maritime nations still believe that resources are “inexhaustible”, and it brings species of fish and whales closer to extinction.

Numerous studies have demonstrated that the similar problems are inherent not only to people but also to other organisms, including bacteria, viruses, plants and animals (reviewed in Rankin et al. 2007), which are all involved in competition for shared resources (e.g. food, territory, mates). This theory has been applied in competition for social goods that are formed by restraining from competition. For example, a tragedy of the commons can be observed in plants competing for light (Schieving & Poorter 1999; reviewed in Falster & Westoby 2003), nutrients (Gersani et al. 2001; Maina et al. 2002) and water (Zhang et al. 1999). Also the tragedy of the commons can involve social goods that are formed by cooperating individuals. In populations of bacteria and social insects, selfish behaviour of individuals that increases their own fitness at the expense of population fitness leads to “collapse” or “component” tragedies by breaking down cooperation between members of the population (reviewed in Rankin et al. 2007). Examples of a tragedy of the commons can be observed in the context of virulence, intraspecific mutualism, social cooperation and conflict, intra-organismal conflict, parent-offspring conflict, sexual conflict and resource competition (reviewed in Rankin et al. 2007).

Examples of the absence of a tragedy of the commons under competitive conditions have also been recorded (reviewed in Rankin et al. 2007). The closer inspection of such situations allows predicting mechanisms that could prevent the tragedy. Coercion and punishment are widely investigated as mechanisms for avoiding a tragedy of the commons in human sociobiology and evolutionary biology studies (reviewed in Rankin et al. 2007). Policing and punishment prevent the cooperation from breaking down in populations of social insects. The benefit gained from a good reputation could prevent the breakdown of
cooperation between animals. Conflict between sex chromosomes over sex ratio is suppressed by autosomes. Thus, competition does not always result in a tragedy of the commons, and this evidence gives the basis for future research into ways to resolve the tragedy of the commons in different biological systems.
Tragedy of the commons in plant competition

Competition for light

Plants can potentially compete for several common goods such as light, water, nutrients and oxygen. Competition for light is most evident and extensively investigated. To capture more light at the expense of surrounding competitors, it is necessary for plants to be taller than their neighbours. Empirical and theoretical evidence suggests that the evolutionarily stable strategy that would displace any other strategy is to be taller and mature later and at larger size (i.e. to have greater shading capacity) than would be required for maximum whole-canopy productivity (reviewed in Falster & Westoby 2003). However, it is obvious that not all plants aspire to the infinite height. It happens because increment in height entails high costs such as energy expenses on stem support and maintenance, inconvenience in water transport and the increased risk of stem breakage (reviewed in Falster & Westoby 2003). Thus, optimal plant height directly depends on the received benefit (light acquisition) and on costs for height achievement.

Tragedy of the commons is considered to be a widespread phenomenon in competition for light (Falster & Westoby 2003). In conditions of unrestricted access to limiting resources, the most competitive strategy is to maximize own benefit at the expense of competitors. However, this evolutionarily stable strategy leads to overexploitation of the resource and hence lowered fitness of the whole plant population. Short plants would be most efficient in maximizing collective profit from intercepting light. If plant communities consisted of completely non-competitive individuals, vegetation would be a thin skin of green near the ground with minimum investments in stem production (Falster & Westoby 2003). However, each individual is under selection to produce a taller stem or trunk to intercept more light and shade competitors. Once all plants respond in kind, the benefit of additional height is lost and the population has to pay a larger cost by supporting the additional stems and trunks (Falster & Westoby 2003). As a result, plant populations have a significantly lowered productivity. Thus, present-day terrestrial vegetation is often characterized by tall stems and represents the inevitable outcome of a wasteful arms race between plants competing for light rather than the achievement of maximum productivity.

The influence of specific leaf area and photosynthetic nitrogen-use efficiency on plant competition for light has been investigated in a model using principles of game theory (Schieving & Poorter 1999). This model was formulated for monospecific stands in which
canopy total photosynthesis is influenced by distribution of light, leaf area and nitrogen. In this model, resident plants had an opportunity to maximize canopy photosynthesis by allocating high nitrogen contents per unit leaf area to the top of the canopy and low contents to the bottom of the canopy. For better investigation of leaf area influence on the canopy photosynthesis, other species were allowed to invade the community. Invader species were the same as resident plants (had the same vertical distribution of nitrogen and biomass) but were able to change their specific leaf area (SLA-leaf area per unit leaf mass). The rule of the model was that invaders would replace the residents if they had higher carbon gain per individual than resident plants. The model showed that, in these conditions, invaders with higher SLA had a greater carbon gain and finally replaced the resident plants completely. This situation can happen repeatedly until the formation of a monostand that cannot be invaded by any other species; it will be reached if no further SLA mutations could be produced. However, the resultant monostand does not maximise canopy-level photosynthesis. Compared with the stand that had maximised canopy photosynthesis, the stand invaded by a species with high SLA showed also an increase in leaf area index and changes in the vertical distribution of nitrogen that collectively leads to a decrease in total canopy photosynthesis. Therefore, the outcome of the model was a classic tragedy of the commons: strategy that maximises canopy photosynthesis becomes outcompeted by the strategy that maximises individual carbon gain which in turn leads to inefficient resource use.

**Competition for belowground resources**

Plants require a certain volume of soil containing resources for successful germination, growth and reproduction. Therefore, a plant would benefit from the ability to defend its belowground territory by limiting neighbours’ access to its soil space (Schenk et al. 1999). It has been demonstrated that restricted soil volumes can significantly reduce plant growth and photosynthesis, even when other resources are abundant (reviewed in Hess & de Kroon 2007). Hence, plants prefer to occupy soil volumes free of roots of other plants. However, plants often share soil with their competitors and are faced with the choice of proliferating their roots in either space already occupied by their own roots or space occupied by the roots of a competitor. Root growth in the presence of neighbours can be analysed using game theory according to which the optimal root allocation of an individual is strongly influenced by the root proliferation of other plants. Three models of habitat selection for how a plant could allocate roots between two habitat patches have been proposed: inter-plant avoidance, resource matching, and intra-plant avoidance (Maina et al. 2002).
The first model, inter-plant avoidance, considers plants as competitive populations of redundant organs. It predicts that a plant prefers soil volumes free from other roots and proliferates its roots away from neighbouring plants. Plants could avoid inter-plant competition because of resource depletion or because of plants exhibiting some form of territoriality (i.e. spatial segregation of roots). Territoriality can be a result of allelopathy (toxic root exudates) or non-toxic signals. Plants may be able to detect the presence of neighbours and restrict growth towards them. In the case of inter-plant avoidance, there would be no difference between fence-sitters and owners in total yield and root production (Fig. 1).

The second model, resource matching, predicts root growth allocation in plants in accordance with density-dependent habitat selection and ideal free distribution (the number of individuals in this environment depends from amount of resources containing in this environment). Being based on the theory of ideal free distribution, this model assumes that plants tend to equalise average rates of nutrient uptake per unit investment in roots, regardless of the degree of neighbouring root’s relationship. Individuals will proliferate their roots within a habitat in response to availability of resources. In this case, plant’s root proliferation will depend on the total amount of roots that the plant has already produced and the nutrient uptake opportunities in each habitat. Also it is obvious that habitat selection will be dependent on the number of competitors within each habitat patch as the competitors will change the availability of nutrients in the soil. According to this model, the yield and root production per individual would have no differences between owners (Fig. 1A) or fence-sitters (Fig. 1B).

The model of resource matching has been experimentally confirmed in a study on density-dependent habitat selection in pea plants (Gersani et al. 1998). The experiment focused on the reactions of a fence-sitter plant to the presence of competitors in a habitat patch (a plant that has roots in two adjacent pots, Fig. 2A). In one of the adjacent pots, there were only roots of a fence-sitter; no, one, two, three or five competitors were planted in addition to the roots of a fence-sitter in the other pot (Fig. 2). Strong density-dependence was observed in the given example: the fence-sitter preferred to invest resources in root growth in an empty pot than in a pot with competitors and the shift of root growth from the pot with competitors to the pot free of competition was proportional to the number of competitors. In the presence of a considerable number of competitors, plant preferred to place roots in a pot without competitors even if there was smaller concentration of nutrients than in a pot with several competitors.
In the third model of habitat selection, *intra-plant avoidance*, habitat selection by roots is considered to present a behavioral game. It predicts that a plant allocates resources to root growth in a way that maximises the fitness of the whole plant. According to this model, individuals should avoid intra-plant competition rather than inter-plant competition. The winning strategy would be to proliferate roots preferentially in volumes of soil free of roots and, given choice between a habitat already occupied by its own roots and by roots of competitors, to prefer inter-plant competition to the intra-plant competition. Considering the fitness of an individual, intra-plant competition is wasteful and should be discouraged whereas stealing nutrients from a competitor can be advantageous. These predictions are based on the comparison of marginal benefits of producing additional roots in different situations. The marginal benefit of root production includes both uptake of new resources and uptake of resources that would be otherwise acquired by neighbouring roots. Marginal benefit of stealing nutrients from a different plant is always higher than the marginal benefit of uptaking nutrients that would otherwise be acquired by the roots of the same plant (i.e. stealing from oneself). However, as the neighbours respond in kind, the benefit of producing additional roots in the presence of a competitor is negated, and plants get involved in a tragedy of the commons (Gersani *et al.* 2001; Maina *et al.* 2002). Therefore, according to this model, owners (Fig. 1A) should allocate resources to root production optimally and achieve maximum net nutrient gain and reproductive yield. The fence-sitters (Fig. 1B) should, on the contrary, over-produce roots due to the higher marginal benefit of additional roots compared to owners. As the competitors would also over-produce roots, the reproductive performance of fence-sitters is expected to be lower than that of owners.
Figure 1. Experimental design of studies on the tragedy of the commons in root competition (Gersani et al. 2001; Maina et al. 2002; Falik et al. 2003): A (owners) – one player game in which all roots of each plant are allocated in its habitat (pot); B (fence-sitters) – two player game in which each plant has roots in both habitat (pots).

Figure 2. Experimental design of the study on habitat selection by Gersani et al. (1998): A (single fence sitter) – one plant straddling two adjacent pots; B (fence sitters) - in one of the adjacent pots, there were only roots of a fence-sitter; in the other pot, two (or one, or three, or five) competitors were planted in addition to the roots of a fence-sitter.
Several studies provided support to the game-theoretic model of intra-plant avoidance (Gersani et al. 2001; Maina et al. 2002; Falik et al. 2003). All of these studies employed different variations of “owners and fence-sitters” design to test their predictions (Fig. 1). Owners were planted in two adjacent pots but with both roots of a split root system placed in a single pot (no competition treatment; Fig. 1A). Fence-sitters were planted in two adjacent pots so that each bean had one root of a split root system in each pot (root competition treatment; Fig. 1B).

Results have shown that individuals sharing their soil volume (fence-sitters) and owners differed significantly in their allocation of biomass to shoots, roots and reproductive yield (Gersani et al. 2001; Maina et al. 2002; Falik et al. 2003). Owners outperformed fence-sitters in all measures of reproductive yield, such as the number of pods, the number of seeds per pot and individual mass of each seed. Owners allocated a great amount of total biomass to reproductive yield and shoots, Fence-sitters, on the other hand, allocated a higher percentage of total biomass to roots. Fence-sitters produced significantly more root mass than owners and, consequently, exhibited redundant root growth at the price of lowered reproduction. These results clearly showed that root competition between individuals sharing soil space resulted in a tragedy of the commons: in competitive conditions, fence-sitters prefer to steal the nutrients from neighbours by over-proliferating roots at the expense of reproduction (Gersani et al. 2001). Also, the results can be viewed in the context of the avoidance of intra-plant competition: plants curtailed root production in conditions of intra-plant competition but exaggerated their root production in the presence of competitor’s roots (Maina et al. 2002).

The timing of the effects of inter-plant competition for resource had been also investigated (Maina et al. 2002). When plants were harvested several times during the experiments, the response of plants to the presence of competitors was already manifested by the 10th day of growth. Therefore, stimulated root production in response to neighbours occurred even before there was a significant overlap between root systems of competitors.
Self/non-self discrimination in plants and avoidance of belowground competition

It is widely recognised that the ability to discriminate between genetically closely related (including self) and unrelated competitors would be highly advantageous to many organisms, including plants. Moreover, a tragedy of the commons in root competition may be directly related to and depend on the ability of plants to distinguish their own roots from the roots of other individuals. It is always advantageous for a plant to avoid intra-plant root competition and rather engage in inter-plant root competition (usually the tragedy of the commons appears between roots of different individuals). Until recently, only animals were considered to possess mechanisms that would enable self/non-self discrimination. However, recent evidences indicate that roots of plants can detect and avoid competition with neighbouring roots (reviewed in Schenk et al. 1999). Self/non-self discrimination could allow plants to increase competition for resources with non-self neighbours and decrease wasteful competition with itself. As animals, plants were also shown to have internal chemical signals that can be used to coordinate the form and functions of different parts of the same individual (reviewed in Falik et al. 2003).

One of the best known examples of root interactions between plants of different identities has been provided by studies of desert shrubs (Mahall & Callaway 1991, 1992, 1996). The involvement of different signals had been shown on the example of interactions between roots of Ambrosia dumosa and Larrea tridentata (Mahall & Callaway 1991). Scientists used root observation chambers to measure root elongation rates in response to contact with neighbouring roots. The results showed that Larrea roots inhibited elongation of either Larrea or Ambrosia roots at distances up to 1 cm, irrespective of the presence or absence of contact between roots. The Ambrosia roots, on the contrary, inhibited only elongation of roots of other Ambrosia plants and the inhibition occurred only after actual contact between roots. It was suggested that Larrea roots released diffusible inhibitory substance into the soil that affected all roots independent of their identity. Roots of Ambrosia, on the other hand, released signals that had short range of action and only affected intra-specific neighbours. These results confirmed the presence of different self/non-self recognition mechanisms in different plant species and suggested that interactions between plants were not entirely based on a simple depletion of resources.

Self/non-self discrimination abilities of Ambrosia and Larrea and possible exudation of inhibitory substances by these plants were further investigated using activated carbon
Mahall & Callaway 1992). The authors tested the hypothesis that inhibitory chemicals were involved in root interactions by removing such substances with activated carbon (activated carbon is known as a strong adsorbent of organic compounds). The responses of Larrea and Ambrosia to the presence of activated carbon were totally different: in the presence of activated carbon in the soil, Larrea roots did no longer inhibit elongation of neighbouring roots, whereas Ambrosia roots showed no responses to carbon. The inhibitory effect of Larrea exudates extended even to the sister roots of the same Larrea individual. This experiment fully supported the results of the previous experiment. The mechanisms of self/non-self discrimination of Ambrosia and Larrea were fundamentally different: Larrea roots responded to the presence of activated carbon – Ambrosia did not; Larrea roots inhibited elongation of other roots in their vicinity even before contacting them – Ambrosia roots had an inhibitory effect on other roots only after actual contact between the roots; Larrea inhibited elongation of all neighbouring roots – Ambrosia inhibited elongation of the roots of the same species only.

In the third experiment, the effects of regional origin and genotype on intra-specific root interactions in Ambrosia were investigated (Mahall & Callaway 1996). Different clones from the same population and clones originating from different populations were used. A significant reduction in root elongation occurred after contact between plants of the same origin. When roots of plants from different populations touched each other, no changes in root elongation rates were observed. The elongation rates were reduced to a similar extent upon contact between roots belonging to two plants of the same clone (same genotype) and between roots belonging to different genotypes from the same population.

However, the fact that genetically identical roots on separate plants did inhibit each other, whereas roots of the same plant did not, demonstrates that genetic relatedness did not guarantee contact inhibition. Roots that contacted only sister roots connected to the same plant showed no significant change in elongation rates, and their growth rates were almost identical to the roots of the same plant that did not contact any roots at all. It was concluded that, while non-self recognition required a degree of genetic relatedness (origin from the same population), self recognition and associated release from growth inhibition was likely to be physiological rather than genetic in nature. The authors also suggested that the lack of intra-specific inhibition between plants from different populations could be explained by possible differences in chromosome numbers between these populations. These results demonstrated a specific recognition system that can allow the avoidance of belowground competition between plants from the same population, which are likely to be genetically related.
Even though the existence of self/non-self discrimination in roots has been repeatedly demonstrated (Mahall & Callaway 1991, 1992, 1996; Falik et al. 2003; Gruntman & Novoplansky 2004), the mechanisms of self/non-self discrimination are still largely unknown. These mechanisms can involve allelopathy (inhibition of root growth due to release of toxic substances into the soil), allogenetic recognition or physiological coordination between roots of the same plant (Mahall & Callaway 1992, 1996; Gruntman & Novoplansky 2004). Recently, the role of physiological coordination has received considerable attention in studies on self/non-self discrimination in roots (Falik et al. 2003; Gruntman & Novoplansky, 2004).

Physiologically mediated self/non-self discrimination was most evidently demonstrated in a clonal grass *Buchloe dactyloides* (Gruntman & Novoplansky 2004). Two-branched cuttings were used in the experiment that were either left intact or were severed longitudinally to produce two genetically identical but physiologically independent individuals (Fig. 3). Severed plants were separated from each other for variable periods of time before being planted back together in the same pot (immediately put back together – TWINS, separated for 7 days - SEMI-ALIENATED and separated for 60 days – ALIENATED; Fig. 3). Also cuttings from genetically different clones (ALIEN) were planted together (Fig. 3). In addition, the effect of spatial distance between nodes of the same clone was tested. Root growth was compared between plants grown in the vicinity of adjacent shoots of the same clone (TWINS) and in the vicinity of shoots that originated from distant nodes of the same clone (REMOTE TWINS; Fig. 3). It was predicted that root growth should be limited in the presence of roots of the same plant (INTACT; Fig. 3) and increase in the presence of the roots of other plants irrespective of their genetic identity (i.e. in all other treatments). Also, root proliferation should be greater in treatments where plants have been separated longer or originated from distant nodes.
Figure 3. Experimental design of the study by Gruntman & Novoplansky (2004) on self/non-self discrimination: plant cuttings with two equal halves planted as INTACT, TWINS (no separation), SEMI-ALIENATED TWINS, ALIENATED TWINS, ALIEN (different genotypes) and REMOTE TWINS (spatial distance experiment).
The results showed that ALIENATED TWINS and ALIENS had the same rates of root growth and that ALIENATED and SEMI-ALIENATED TWINS increased root growth compared with INTACT plants. This indicates that self/non-self discrimination was physiologically mediated rather than mediated by allogenetic recognition. However, the similarity of root growth in ALIENATED TWINS and ALIENS and in INTACT and TWINS plants showed that self/non-self discrimination is mediated by signals that have an ability to keep their efficiency even some time after plant separation. It is only after a period of independent growth when plants become eventually so alienated that they begin to interact with each other like true ALIEN plants. Physiological coordination among parts of the same plant is also limited spatially: when plants originated from three nodes apart (REMOTE TWINS), increased root growth was observed compared with plants from adjacent nodes. These results demonstrated that self/non-self discrimination can enable plants to avoid wasteful competition with self by restricting root proliferation and improve their competitive ability by increased allocation to root growth when grown with non-self (Gruntman & Novoplansky 2004).

In addition to the ability to increase root proliferation in the presence of competitors, plants can also regulate the spatial arrangement of roots in the soil in relation to the position of competitor’s roots (Falik et al. 2003; Semchenko et al. 2007b). In a study on a vectorial component in self/non-self discrimination in roots, the initial growth of two equal roots of a pea plant (*Pisum sativum*) was restricted using Plexiglas spacers which allowed roots to grow without interference from other roots (Fig. 4). At the distance of five centimetres from the rooting point, the roots were released from the tubes and allowed to grow freely in every direction. In case of INTACT plants, each target root had a choice of growing towards a self root on one side or a non-self root on the other side. The target roots of TWIN plants had choice of growing towards non-self roots or roots that were genetically identical but physiologically independent. The roots of ALIEN plants had non-self roots on both sides (Figs. 4 and 5).
**Figure 4.** Experimental design of the study by Falik *et al.* (2003) on self/non-self discrimination: INTACT- two plant halves remained physiologically integrated; TWINS – two plant halves belonged to the same individual but were physically separate; ALIEN – two plant halves belonged to two different genotypes and.

**Figure 5.** Vectorial root responses in INTACT or TWINS or ALIEN plants described in Fig. 4. Roots directed by 4-mm Plexiglas spacers in the length 50 mm, thereafter plant roots could develop freely. In the INTACT and TWINS treatments, each of the target roots had a self root on one side and non-self root on another side. In the ALIEN treatment, both neighbouring roots belonged to non-self roots. To avoid the edge effect, more plants were planted on both sides of the target plant (Falik *et al.* 2003).
The results showed that INTACT plants produced more and longer lateral roots towards non-self than towards self neighbours. The severed pairs produce equal amounts of roots in both directions independent of the identity of neighbouring roots (TWINS or ALIEN). Thus, self/non-self discrimination in roots of *Pisum sativum* had a vectorial component and it was physiologically mediated rather than relied on allogenetic recognition (Falik *et al.* 2003).

It is known that physiological coordination among organs of an individual can be controlled by hormones such as auxin and cytokinins (Sachs 1991; Gersani *et al.* 1998; Gersani *et al.* 2001; Falik *et al.* 2003; Gruntman & Novoplansky 2004). Hormones can regulate root formation and growth and the root-tip can send signals to other parts of a plant and regulate the flow of hormones when the presence of competitor’s roots is perceived. It has also been suggested that physiological coordination could be dependent on the electrical oscillations created by roots in the soil, which might be perceived without direct contact between roots (Gruntman & Novoplansky 2004).
Cooperation in related plants: sibling competition and kin selection

The evolution of cooperation in animals has always been one of the most important areas of research in evolutionary biology. The most common explanation for the evolution of cooperation is the theory of inclusive fitness (Hamilton 1964). According to this theory, an increase or decrease in allele frequency is affected by the allele’s effect on the fitness of the individual bearing it and by the effect of that allele on neighbouring individuals that carry copies of the same allele. These neighbouring individuals are usually the bearer’s relatives, which is why this process is often referred to as kin selection (this term was firstly used by Maynard Smith 1964). The simplest example of altruism that evolved by kin selection is parental care. The theory of inclusive fitness predicts that altruism will spread in a population if the benefit received by donor’s relatives, weighted by their genetic relatedness to the donor, exceeds the cost of the altruistic action to the donor’s fitness. Consequently, many animals behave differently towards presumably related individuals than towards others.

Evolutionary theory also predicts that natural selection should favour mechanisms that minimise wasteful competition among parts of the same individual, clonemates and kin, because competition leads to resources allocation to non-reproductive organs and functions resulting to a tragedy of the commons. Several studies have shown that plants can exhibit different reactions to related versus unrelated individuals and can, therefore, be subject to kin selection (Tonsor 1989; Cheplick 1992; Holzapfel & Alpert 2002; Dudley & File 2007). It was demonstrated that the avoidance of competitive interactions can occur between closely spaced members of the same clone (Holzapfel & Alpert 2002; Gruntman & Novoplansky 2004) as well as between genetically different but closely related individuals (Tonsor 1989; Dudley & File 2007).

Kin recognition was recently described in an annual plant species Cakile edentula that can often experience kin competition in its natural habitat (Dudley & File 2007). Three types of planting scenarios were used. In the first, four kin individuals were planted together in a pot. In the second, a pot had been shared by strangers (unrelated individuals) and, in the third, plants were grown without competitors but each plant had access to only a quarter of space in a pot. The experiment indicated that the allocation of roots increased when a group of strangers shared a common pot and decreased when a group of closely related neighbours shared a pot compared with plants grown without competitors. However, the total biomass and allocation to reproductive functions depended on the presence of competitors but did not depend on relatedness between competitors. These results showed that plants may have an ability to recognise kin in competitive interactions and behave towards them in a special way.
However, competition with unrelated competitors did not result in a tragedy of the commons that would be indicated by lower reproductive performance of the group of strangers.

Different predictions have been proposed in relation to the outcome of sibling competition. For example, delayed seed germination and dormancy in species with poor dispersal ability were explained as an adaptation to avoid sibling competition (reviewed in Cheplick 1992). Another popular hypothesis is that competition between unrelated seedlings should be less severe than competition between genetically identical or closely related siblings because related individuals should have more similar environmental preferences (niches) than unrelated plants. This hypothesis was tested in several studies involving a variety of plant species. A review of these studies showed that relatedness between competitors often had no effect on the intensity of competition and, in some cases, competition between siblings was less severe than between unrelated individuals, which is opposite to the prediction (Cheplick 1992). Thus, the hypothesis of a more severe competition between siblings had very little empirical support and the necessity of further research is obvious.

One of the results which confirm that sibs have an advantages in competition in comparison with less related individuals was observed using Plantago lanceolata (Tonsor 1989). This experience indicated that the number of plants flowering per pot increased with an increase of genetic relatedness in experimental plants, whereas vegetative mass and total dry weights did not depend on relatedness between competitors. Due to asymmetric competition for light and limitation of resources, only one plant from three had the threshold size for flowering in the pots of unrelated individuals. On the other hand, sibling plants had similar growth rates and, consequently, experienced less asymmetric competition. The resources were shared between siblings more evenly and, as a result, more plants per pot reached flowering stage. These results allow concluding that sibling plants had a less-severe competition than unrelated individuals. However, it was noted that, if the nutrient availability in experimental pots was slightly higher or lower, the results could have been different.

The theory of reduced competition for resources between related plants was also tested using a clonal plant species Fragaria chiloensis (Holzapfel & Alpert 2002). The results clearly showed the presence of root cooperation between physically connected members of a clone. Plants that were connected by runners minimised overlap between their root systems that reduced wasteful belowground competition between identical competitors. Such behaviour resulted in increased clone performance and can, therefore, be considered an example of cooperation in plants. Connected plants apparently exchanged signals through runners that allowed plants to reduce root growth towards related competitors.
The effects of physical connection and genetic relatedness between plants on root-placement patterns was investigated in more details using two clonal species, *Glechoma hederacea* and *Fragaria vesca* (Semchenko et al. 2007b). The two species were characterised by different frequencies of within-clone competition in their natural habitats and were, therefore, predicted to exhibit different types of root interactions and patterns of root placement. Three patterns of root placement were tested: the avoidance pattern in which root growth decreases in the presence of competitor’s roots; the intrusive pattern in which root growth increases in the presence of neighbouring roots; and the unresponsive pattern in which the presence of competitor’s roots has no effect on root growth. The experiment was designed to investigate root responses to the presence of neighbouring roots that belonged to a connected or disconnected individual of the same clone, an individual of different genotypes and individuals of a different species (Fig. 6).

The results showed that *Fragaria vesca* was unresponsive to all types of neighbours, irrespective of connection between plants or neighbour’s genetic identity. Equal root masses were allocated towards a neighbouring plant and away from it (i.e. space free of neighbour’s roots). Thus, the presence of a physical connection between plants had no effect on root allocation and there were no evidences of root segregation or cooperation between plants. However, the second tested species, *Glechoma hederacea*, showed a totally different behaviour from that of *Fragaria vesca*. *Glechoma* exhibited strong avoidance of competition with all types of neighbours and the presence of root segregation in both connected and unconnected plants. Plants of *Glechoma* allocated significantly less root mass in the substrate volume towards the neighbour than in the substrate volume away from the neighbour. Obviously, *Fragaria vesca* plants used the unresponsive pattern of root placement, whereas plants of *Glechoma hederacea* used the avoidance pattern of root placement. These results indicated that investigated species had significant differences in patterns of root allocation in response to the presence of neighbouring roots.

In conclusion, the results of studies on clonal plants have shown that the extent of cooperation between related plants, root-placement patterns in response to the presence of neighbours, and the mechanisms involved in these responses, can vary considerably between species. However, it is clear that sibling competition and kin selection are processes that should be considered when making generalisations about the importance of the phenomenon of the tragedy of the commons in plant competition. Also, field experiments are urgently needed to test the ecological and evolutionary importance of kin selection in natural plant populations.
Figure 6. Experimental design of the study by Semchenko et al. (2007b): A – connected members of the same clone, B – disconnected members of the same clone, C – individuals of different genotypes, D – individuals of different species.
Resolving the tragedy of the commons

Theoretical work and some experimental studies predict that the tragedy of the commons should be a widespread phenomenon in nature. However, many component tragedies never develop into collapsing tragedies and there are instances where no tragedy takes place at all (Rankin et al. 2007). As discussed above, several studies have demonstrated that plants are able to segregate roots in the soil and to avoid harmful competition for resources that lead to a tragedy of the commons (Mahall & Callaway 1991, 1992, 1996; Schenk et al. 1999; Holzapfel & Alpert 2002). It is known that it is more advantageous and less costly for plants to defend their soil space and resources contained within it than to compete directly for the same resources in the shared soil volume where root systems spatially overlap (Schenk et al. 1999). Spatial root segregation could be achieved through responses to nutrients, water, and oxygen, as well as a response to allelopathic (toxic) root exudates or non-toxic signals (Schenk 2006).

The most evident example of the effect of allelopathic exudates on the roots of neighbouring plants is provided by the study of root interactions in a desert shrub Larrea tridentata (Mahall & Callaway 1991, 1992). Larrea plants inhibited elongation of either Ambrosia or Larrea roots in their vicinity, not even having an actual contact with neighbouring plant’s roots. The Larrea’s allelopathy is so effective that even sister roots on the same individual have an ability to inhibit each other. At the first sight, it seems that root-mediated allelopathy of Larrea individuals simply harms neighbours. However, Larrea’s allelopathy leads to a regular distribution of plants in space that can be viewed as a mechanism of avoidance of direct competition for resources. The exclusion of neighbours’ roots from the soil space means that plants can utilise resources more. Consequently, territoriality in plants can be viewed as an example of resolving the tragedy of the commons and escaping wasteful inter-plant root competition and allocation of resources to competitive organs.

Other examples of apparent escape from the tragedy of the commons are provided by studies on clonal plants and sibling competition. For example, cooperation though avoidance of competition between roots of connected members of a clone was demonstrated in Fragaria chiloensis (Holzapfel & Alpert 2002). Reduced intensity of competition was shown in groups of siblings compared with groups of unrelated plants in Plantago lanceolata (Tonsor 1989). Numerous other examples of reduced root growth towards neighbours were recorded (reviewed in Schenk et al. 1999). This evidence collectively suggests that many
plant species are able to resolve the tragedy of the commons. Since many examples of avoidance of competition were recorded for groups of closely related individuals, kin selection can be proposed as one of the most likely processes that can lead to escape from the wasteful allocation of resources to competitive organs at expense of reproduction.
Challenging the results of the studies on the tragedy of the commons

The experimental design used in most studies on the tragedy of the commons in root competition has recently been criticised for having confounding effects (Schenk 2006; Hess & de Kroon 2007; Semchenko et al. 2007a). Specifically, previous experiment of the tragedy of the commons did not consider the possibility that, in addition to reactions to the presence of neighbours, plants may also be affected by the availability of space (soil volume). In these experiments, constant volume of substrate and amount of nutrients per plant were provided in all treatments (Gersani et al. 2001; Maina et al. 2002; Falik et al. 2003). However, this resulted in plants that share rooting space with a neighbour (fence-sitters in Fig. 1B) potentially having access to twice as much substrate as plants grown without a neighbour (owners in Fig. 1A). It is widely recognised that the volume of substrate that is available for each plant can significantly influence plant performance and a variety of morphological and physiological traits (reviewed in Semchenko et al. 2007a). Thus, it is possible that responses to the presence of neighbours were confounded with plant responses to the change of rooting volume that was available for each competitor. The reduced root growth in the treatment with owners compared with the treatment with fence sitters (Fig. 1) could be caused by the sensitivity of roots to the accumulation of own toxic exudates in the vicinity of pot walls in small substrate volumes rather than by responses of to neighbours (Falik et al. 2005). Also, as fence-sitters will have to explore twice as large substrate volume to obtain the same amount of nutrients as owners, fence-sitters may exhibit lower performance than owners due to lower resource acquisition efficiency.

It has also been noted that that the occurrence of the tragedy of the commons can depend on the ability of plants to discriminate between self and non-self (Semchenko et al. 2007a). Interestingly, root allelopathy, which plays a significant role in the detection of neighbours, usually caused the inhibition of root growth rather than root overproduction (Mahall & Callaway 1992, 1996). In addition, it is extremely difficult to distinguish true neighbour recognition from plant response to neighbours mediated by simple resource depletion (Schenk et al 1999).

The experimental test of confounding effects in studies on the tragedy of the commons confirmed that restricted soil volume causes self-inhibition of root growth due to concentration of root exudates in the vicinity of pot walls (Semchenko et al. 2007a). The fragmentation of substrate and dispersal of nutrients throughout larger substrate volumes reduced plant growth, suggesting that reductions in performance of plants that share a large
substrate volume with competitors (fence-sitters) can be caused by inefficient resource uptake instead of neighbour recognition.

In conclusion, it was demonstrated that two general processes could have a significant influence on the results of experiments that observed a tragedy of the commons in root competition. The first is the evidence of increased self-inhibition in more limited substrate volumes of the treatment without competition (owners in Fig. 1). The second is inefficient root placement in larger space which is shared with roots of competitors (fence-sitters in Fig. 1). Together with clear examples of cooperation between plants, these results suggest that biotic interactions between plants are probably more complex than has previously been thought and further investigation is required to determine how widespread the tragedy of the commons actually is in plant kingdom.
Conclusions

The theory of the tragedy of the commons has found application in a wide range of disciplines in science. It was originally presented as an inevitable consequence of freedom to use common resources. In theoretical and empirical work on plant interactions, the tragedy of the commons was also often presented as the only evolutionarily stable strategy in plant competition for light, nutrients and water. However, it was soon realised that the tragedy of the commons can often be at least partially resolved, and organisms can restrain themselves from wasteful competition and prevent the collapse of the population due to the overexploitation of resources. Numerous studies have shown that the tragedy of the commons can also be prevented in plants. However, many processes in plant interactions such as self/non-self discrimination, kin recognition and cooperation are still poorly understood and impede our ability to draw a full picture of interactions occurring between plants. Also, the experimental design of studies on plant interactions needs to be improved to exclude possible confounding effects. The challenge remains to determine the relative frequency at which the tragedy of the commons or cooperation occur in plant communities and what processes determine this frequency. Given the contradictory results of the previous studies and the criticism they received (summarised in Table 1), no generalisations can be made at present.
Table 1. Summary of the studies that demonstrated either tragedy of the commons or avoidance of competition for different resources in plants. This table does not cover all of the studies on this subject but is a representative sample of it.

<table>
<thead>
<tr>
<th>Phenomenon</th>
<th>References in support</th>
<th>Criticism</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tragedy of the commons:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>a) Competition for light</td>
<td>Schieving &amp; Poorter 1999; reviewed in Falster &amp; Westoby 2003</td>
<td></td>
</tr>
<tr>
<td>b) Competition for nutrients and water</td>
<td>Zhang et al. 1999; Gersani et al. 2001; Maina et al. 2002</td>
<td>Schenk 2006; Hess &amp; de Kroon 2007; Semchenko et al. 2007a</td>
</tr>
<tr>
<td>Avoidance of inter-plant root competition between:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b) unrelated individuals</td>
<td>Mahall &amp; Callaway 1991, 1992; reviewed in Schenk et al. 1999; Semchenko et al. 2007b</td>
<td></td>
</tr>
</tbody>
</table>
Summary

Theoretical studies predict that selfish use of common resources that are limited and shared by many individuals will inevitably lead to a “tragedy of the commons”, a situation in which competition leads to wasteful use of resources and to lower overall fitness of all members of a population. This theory has also been applied to interactions between plants and has recently triggered intense empirical work that produced rather equivocal results. The aim of this study was to provide general information on the origin of the term “tragedy of the commons” and its applications in different areas of science, and to review the scientific literature on the topic of the tragedy of the commons in plant competition studies. Examples of avoidance of competition and escape from the tragedy were also discussed.

The tragedy of the commons has been originally proposed as an explanation to the problems of human society, such as pollution, overexploitation of natural resources and overpopulation. These problems apparently occurred because of selfish behaviour of members of a society where every person is lead by their selfish interests and does not care about the impact on the society as a whole. This theory was subsequently applied to a wide range of biological phenomena extending from viruses and bacteria to animals with sophisticated social behaviour. If originally the tragedy of the commons considered only competition over extrinsic pre-existing resources, recent studies have shown that social goods formed by cooperation or restraining from conflict can also be prone to a tragedy of the commons.

There is accumulating evidence that plants may also exhibit a tragedy of the commons in competition for light, nutrients and water. Plant competition for above- and belowground resources can lead to overproduction of resource-acquiring organs at the expense of reproductive yield. The overproliferation of shoots and roots in the presence of competitors can be predicted from higher marginal benefits of stealing resources from a different individual than from self (i.e. from other parts of the same individual). Therefore, the outcome of competition may strongly depend on the ability of plants to discriminate between “self” and “non-self”. This ability would allow plants to avoid wasteful self-competition and to preferentially steal resources from unrelated neighbours. Also plants would benefit from the ability to reduce competition with closely related individuals or members of the same clone. Self/non-self discrimination has now been demonstrated in a variety of plant species. The perception of self seems to rely on physiological coordination between parts of the same individual but the exact mechanism remains largely unknown.
Despite theoretical predictions, it has repeatedly been demonstrated that some plant species can exhibit cooperation and avoidance of belowground competition through root spatial segregation between individuals that are not necessarily closely related. The correctness of the experiments that investigated the presence of a tragedy of the commons in plants has also been called into question. Also, the great lack of field experiments inevitably leads to the conclusion that more research is needed before generalizations can be drawn. Consequently, the question of whether plants are involved in the tragedy of the commons remains open.
Ressursikonkurents: kas taimeriigis esineb ühisomanditragöödiat?

Kokkuvõte

Teoreetilised uuringud ennustavad, et ühiste ja piiratud ressursside egoistlik kasutamine viib vältimatult „ühisomanditragöödiani“, s.t. olukorrani, kus konkurents põhjustab ressursside raiskavat kasutamist ja seeläbi kogu populatsiooni madalamat keskmist kohasust.

Ühisomanditragöödia teooriat on korduvalt rakendatud taimedevaheliste interaktsioonide seletamiseks, saades tihti vastakaid tulemusi. Selle tõo eesmärgiks oli hankida informatsiooni „ühisomanditragöödia“ termini sisu ja rakenduste kohta erinevatel valdkondadel ning teha ülevaade teaduslike publikatsioonidest, mille teemaks on ühisomanditragöödia taimekooslustes.


mitmel taimeliigil. Enese tunnetamine näib põhinevat taimte erinevate moodulite füsioloogilisel koordineeritusele kuid täpseid mehhanisme tänapäeval veel ei teata.

Acknowledgements

I thank my supervisors Kristjan Zobel and especially Marina Semchenko for helpful comments on earlier version of this study and great help in preparation of this work.
References


