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Push–pull farming systems

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Farming systems for pest control, based on the stimulo-deterrent diversionary strategy or push–pull system, have become an important target for sustainable intensification of food production. A prominent example is push–pull developed in sub-Saharan Africa using a combination of companion plants delivering semiochemicals, as plant secondary metabolites, for smallholder farming cereal production, initially against lepidopterous stem borers. Opportunities are being developed for other regions and farming ecosystems. New semiochemical tools and delivery systems, including GM, are being incorporated to exploit further opportunities for mainstream arable farming systems. By delivering the push and pull effects as secondary metabolites, for example, (*E*)-4,8-dimethyl-1,3,7-nonatriene repelling pests and attracting beneficial insects, problems of high volatility and instability are overcome and compounds are produced when and where required.

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Introduction

All farming systems require crop protection technologies for predictable and economic food production. Pesticides currently serve us well, with no convincing evidence for legally registered pesticides causing problems of human health or environmental impact [1•]. In terms of risk analysis, risks associated with use of pesticides have been extremely low for some time [2]. However, for sustainable pest management, seasonal inputs requiring external production and mechanical application need to be replaced by approaches involving direct association with the crop plants themselves [3]. Current synthetic chemical pesticides have often been designed from natural product lead structures or are themselves natural products and, although they are in no way more benign than synthetic pesticides, there are, in nature, genes for their biosynthesis which could be exploited for delivery to agriculture via crop or companion plants, or via industrial crops. Production by the latter is not sustainable because of the need for extraction and then application to the crop, although on-farm extraction, or at least some processing, could be employed where the necessary quality control and safety can be achieved. Many crop plants incorporate biosynthetic pathways to natural pesticides which could be enhanced by breeding. Alternatively, pathways can be added by genetic engineering, for example, for *Bacillus thuringiensis* endotoxin production or with genes for entire secondary pathways, for example, for toxic saponins such as the avenacins [4••], including from other plants or organisms entirely.

Pheromones and other semiochemicals have long been regarded as presenting opportunities for pest management and many biosynthetic pathways have been elucidated [5]. For semiochemicals, there is a further advantage in that beneficial organisms can also be advantageously manipulated [6]. Thus, semiochemicals that recruit predators and parasitoids (parasites that kill their hosts), or in other ways manage beneficial organisms, can be released by crop or companion plants, thereby providing new approaches to exploiting biological control of pests. Although biological control is sustainable in the example of exotic release of control agents, registration may not be granted because of potential environmental impact, and inundative release requires production and delivery. Therefore, managing the process of conservation biological control, which exploits natural populations of beneficial organisms, expands the potential value of releasing semiochemicals from crops or companion plants [7•]. Many semiochemicals are volatile, for example those acting at a distance as attractants or repellents. Also, in order that the signal does not remain in the environment after use, these compounds are often highly unstable chemically, which again promotes the concept of release from plants.

From the attributes of a natural product pest control agents, as described above, follows the concept of stimulo-deterrent or push–pull [8] farming systems (Figure 1). The main food crop is protected by negative

Figure 1

Push-pull: the concept

Natural product pest control agents are, by definition, biosynthesised naturally. The genes for semiochemical biosynthesis expressed in companion plants, or in the crop plants themselves, give a "push" to pests and attract predators and parasitic insects (e.g. parasitoids). At the same time, companion plant genes associated with semiochemicals attractive to pests provide a "pull". Genes for toxicant biosynthesis can be expressed in the latter in order to reduce pest populations.

"Push"

Produce repellent semiochemicals against the pest, for example (1) from non-host taxa, e.g. organic isothiocyanates, typical of brassicaceous crops, against non-brassicaceous plant feeding pests; (2) feeding stress related semiochemicals that denote pest infestation and also recruit predators and parasitoids.

Crop

Provided with attributes of "push" plants via advanced breeding technologies or GM.

"Pull"

Produce attractant semiochemicals, e.g. associated with host plants and effects heightened by maximising these signals.

Produce toxicants enhanced from levels produced in host plants, e.g. benzoxazinoids in certain cereals or from non-host plants, e.g. glucosinolates from brassicaceous plants.

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cues that reduce pest colonisation and development, that is, the ''push'' effect. This is achieved either directly, by modifying the crop, or by companion crops grown between the main crop rows. Ideally, the modified crop, or the companion crop, also creates a means of exploiting natural populations of beneficial organisms by releasing semiochemicals that attract parasitoids or increase their foraging. The ''pull'' involves trap plants grown, for example, as a perimeter to the main crop and which are attractive to the pest, for example by promoting egg laying. Ideally, a population-reducing effect will be generated by trap plants, such as incorporating a natural pesticide, or some innate plant defence. Push–pull may use processes, largely semiochemical based, each of which, alone, will exert relatively weak pest control. However, the integrated effect must be robust and effective. The combination of weaker effects also mitigates against resistance to the overall system of pest control because of its multi-genic nature and lack of strong selection pressure by any single push–pull component.

Push–pull for smallholder cereal farming in sub-Saharan Africa

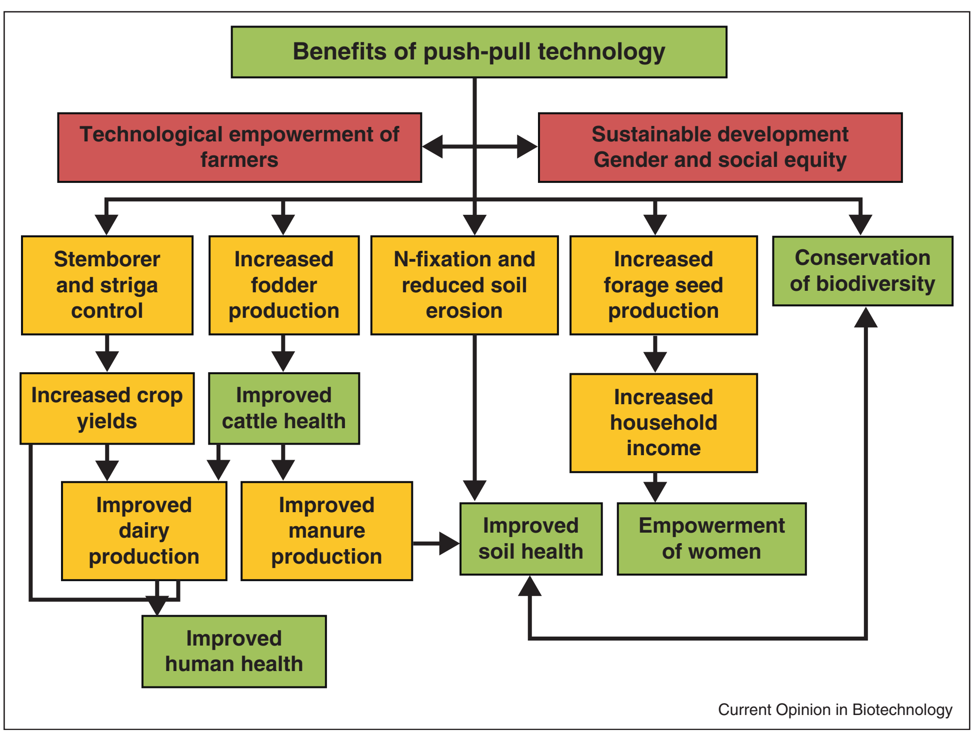
Smallholder farmers in developing countries traditionally use companion crops to augment staple crops such as cereals. Development of the push–pull farming system for these farmers employed the companion cropping tradition in establishing an entry point for the new technology. ''Push'' and ''pull'' plants were identified initially by empirical behavioural testing with lepidopteran (moth) stem borer adults. Having begun experimental farm trials in 1994 and moving on-farm in 1995, farmers very swiftly adopted the most effective companion crops [9,10] (Figure 2) and the benefits soon became apparent (Figure 3). The semiochemistry underpinning the roles of the companion plants in this push–pull system was then investigated by taking samples of volatiles released from companion plants and analysing by gas chromatography, coupled with electrophysiological recordings from the moth antennae [11••]. In addition to well-known attractants from the trap plants (''pull''), including isoprenoidal compounds such as linalool [9] and green leaf alcohols from the oxidation of long chain unsaturated fatty acids, other semiochemicals arising through the oxidative burst caused by insect feeding offered negative cues for incoming herbivores. These are isoprenoid hydrocarbons, for example, (*E*)-ocimene and (1*R*,4*E*,9*S*)-caryophyllene, and some more powerful negative cues, the homoterpenes, that is, homo-isoprenoid, or more correctly, tetranor-isoprenoid hydrocarbons [11••] (Figure 4). Most importantly, these latter compounds also act as foraging recruitment cues for predators and parasitoids of the pests [11••], and molecular tools for investigating other activities are being developed [12••]. Technology transfer for this push–pull system requires new approaches, and although such transfer benefits by a tradition of companion cropping, training is required for extension services and farmers, and availability of seed or other planting material, although, being perennial, these companion plants are one-off inputs. All the companion plants are valuable forage for dairy (cow and goat) husbandry and potentiate zero grazing, which is advantageous in the high population density rural areas in which most of the population live in sub-Saharan Africa. The legume intercrop plants, *Desmodium* spp., also fix nitrogen, with *D. uncinatum* being able to add approximately 110 kgN/ha/yr and contributing approximately 160 kg/ha/yr equivalent of nitrogen fertilizer [13•]. *Desmodium* spp. intercrops also

Figure 2

Conventional push–pull field showing maize intercropped with silverleaf desmodium (*Desmodium uncinatum*) and with Napier grass (*Pennisetum purpureum*) planted as a border crop (left); climate-adapted push–pull field showing sorghum intercropped with drought tolerant greenleaf desmodium (*D. intortum*) and *Brachiaria* cv *mulato* II as a border crop (right).

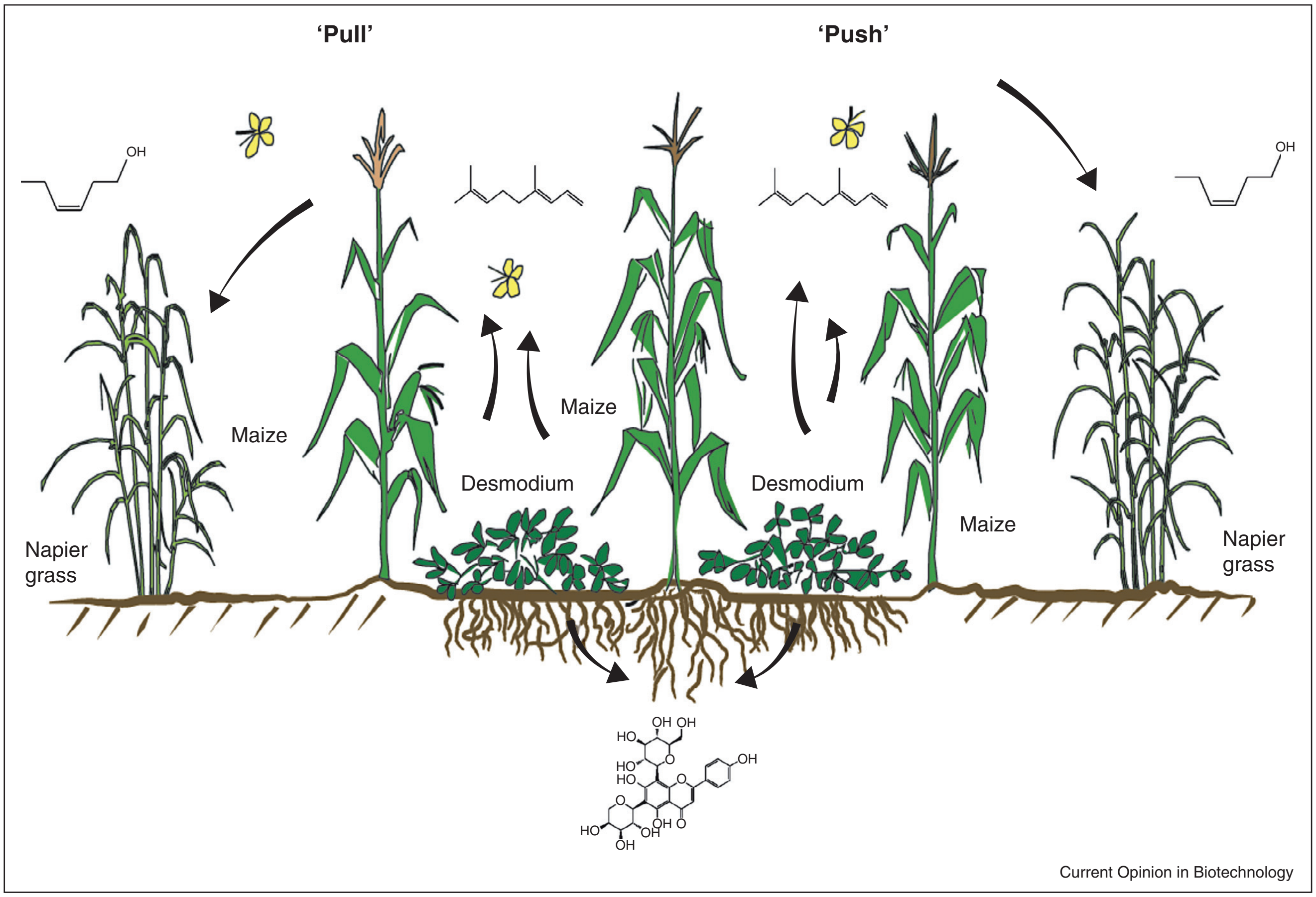
control parasitic striga weeds, for example, *Striga hermonthica* [13•], via release of allelopathic *C*-glycosylated flavonoids [14••], which represents another facet of push–pull in providing weed control [15]. Overall, there is a high take-up and retention in regions where the technology is transferred; for example, in western Kenya in 2013, nearly 60,000 farmers are using these techniques [16•]. Although this represents a very small percentage of the millions of people who could benefit, so far there have been very few resources for technology transfer. A recent

Figure 3



Benefits of push–pull technology, now and under future climate change [10,16•].

Figure 4



Potentially universal ''push'' semiochemicals, that is homoterpenes such as (*E*)-4,8-dimethyl-1,3,7-nonatriene, biosynthesised via cytochromes P450 from the higher homologue isoprenoid α-unsaturated secondary alcohols, for example, nerolidol, repel herbivorous insects and attract their parasitoids [36••]. Attractants from ''pull'' plants include unsaturated fatty acid products such as (*Z*)-3-hexen-1-ol. Allelopathic compounds, for example, the di-*C*-glycosylflavone isoschaftoside, protect the crop from antagonistic organisms such as parasitic weeds [14••].

EU-funded research initiative, ADOPT (''Adaptation and Dissemination Of the 'Push–pull' Technology''), has sought companion plants that can deal with drought, a rapidly growing problem in sub-Saharan Africa as a consequence of climate change, and new companion crops have already been identified and taken up by farmers [16•] (Figure 2).

The ''push'' plants imitate damaged crop plants, particularly maize and sorghum which produce the homoterpenes, and although normally too late to be of real value in economic pest management, production of these compounds is induced by the pest. Recently, we found that this can also be caused by egg-laying, specifically on the open pollinated varieties of maize normally grown by the smallholder farmers [17•], but not on hybrids [11••]. An egg-related elicitor enters the undamaged plant and the signal travels systemically, thereby inducing defence and causing release of the homoterpenes. Exploitation of this phenomenon (see later) will offer new approaches to push–pull farming systems.

Biotechnological development of push–pull for industrialised farming

New approaches to breeding by alien introgression of genes from wide crosses, including from the wild ancestors of modern crops [18•], as well as incorporation of heterologous gene incorporation by GM [19,20], genome engineering [21–23] and creation of synthetic crop plants by combining approaches including new crop genomic information [24], can contribute to push–pull farming systems. Mixed seed beds are now in use for cereals, even in industrial agriculture, and push–pull could be created without separated ''push'' and ''pull'' plants, including regulated stature facilitating selective harvesting. The new generation of GM and other biotechnologically derived crops [3] could revolutionise the prospects for push–pull in industrialised farming systems by offering crop plants that could themselves embody the ''push'' trait, thereby obviating the need for labour to manage the intercrop.

Toxicants for population reduction

The expression of *B. thuringiensis* derived genes against certain insect pests has been highly successful [25], but we are now able to manipulate secondary metabolite pathways to produce pesticides, related to the synthetic versions, with a much greater range of activities, for example, cyanogenic glycosides [26], glucosinolates [27,28,29••] and avenacins [30]. The latter, and also the benzoxazinoids (hydroxamic acids) [31–35], are biosynthesised by pathways involving a series of genes co-located on plant genomes, potentially facilitating enhancement or transfer to crop plants by GM [4••]. These pathways could be expressed in ''pull'' plants for population control. They could also enhance the ''push'' effect. However, for both, attention must be directed towards obviating interference with the ''push'' and ''pull'' mechanisms.

Repellents for pests and attractants for beneficials

Already, in sub-Saharan African push–pull, the value of the homoterpenes can be seen [11••,17•]. Laboratory studies have demonstrated the principle, more widely, of enhancing production by GM [12••]. Biosynthesis of both the alcohol precursors [36••] and the homoterpenes has been demonstrated with, for the latter, *Cyp82G1* being the enzyme in the model plant *Arabidopsis thaliana* [37]. This is now being explored for insect control in rice (BBSRC International Partnering Award BB/J02028/1 and the BBSRC China UK Programme in Global Priorities BB/L001683/1).

Pheromones also offer opportunities and, after demonstrating the principle in *A. thaliana* [38], the heterologous expression of genes for the biosynthesis of (*E*)-β-farnesene, the alarm pheromone of many pest aphid species, after success in the laboratory, is being field tested (BBSRC grant BB/G004781/1, ''A new generation of insect resistant GM crops: transgenic wheat synthesising the aphid alarm signal'') as a means of repelling aphids and attracting parasitoids to the crop. Nonetheless, as well as overcoming the demanding issues of GM, these sophisticated signals will need to be presented in the same way that the insects themselves do, which, for the aphid alarm pheromone, is as a pulse of increased concentration. Indeed, as well as demands of behavioural ecology, complicated mixtures may also be necessary to provide the complete semiochemical cue. However, it is already proving possible to make relatively simple targeted changes in individual components of mixtures [39], which could allow an economic GM approach. The latter is likely to become even more appealing with the development of new technologies arising from genome editing [21–23]. Genes for biosynthesis of the aphid sex pheromone could be used to establish a powerful ''pull'' for the highly vulnerable overwintering population, but would need to be isolated from the insects themselves so as to avoid the presence of other plant-related compounds that inhibit the activity of the pheromone. Recent discoveries in plant biosynthesis of compounds related to aphid sex pheromones [40] will facilitate this quest. Attractant pheromones of moth (Lepidoptera) pests may also become available as a consequence of attempts to use GM plants as ''factories'' for biosynthesis (Christer Löfstedt, Lund University, personal communication).

Induction of push–pull

A number of biosynthetic pathways to plant toxicants and semiochemicals are subject to induction or priming [41,42]. Elicitors can be generated by pest, disease or weed development. Volicitin (*N*-(17-hydroxylinolenoyl-L-glutamine)) [43–45] and related compounds produced in the saliva of chewing insects induce both direct and indirect defence, often involving the homoterpenes, but require damage to transfer the signal to the plant. The egg-derived elicitor (see above) [11••] should overcome the problem. Plant-to-plant interactions mediated by volatile compounds, for example, methyl jasmonate and methyl salicylate, related to plant hormone stress signalling, are associated with these effects and can induce defence. However, there can be deleterious or erratic effects in attempting to use such general pathways [46]. *cis*-Jasmone signals differentially to jasmonate [47] and, without phytotoxic effects, regulates defence, often by induction of homoterpenes [48] in crops even without genetic enhancement, for example, in wheat [49], soy bean [50], cotton [51] and sweet peppers [52]. In addition to aerially transmitted signals that could be used to induce ''push'' or ''pull'' effects, signalling within the rhizosphere directly [53,54••], or via the mycelial network of arbuscular mycorrhizal fungi [55••], is now showing exciting promise. The ''pull'' effect can be enhanced by raising the levels of inducible attractants, provided there is no interference with the population controlling components of the push–pull system. However, attractive plants, without population control or with a late expressed control, could be valuable as sentinel plants. Thus, highly susceptible plants, either engineered or naturally susceptible, could, on initial pest damage, release signals via the air or rhizosphere that could, in turn, switch on defence in the recipient main crop plants, creating elements of the push–pull farming system as a fully inducible phenomenon activated without external intervention.

Conclusions

Push-pull is not only a sustainable farming system, but can also protect the new generation of GM crops against development of resistance by pests. Although considerable work still needs to be done for all the new tools of biotechnology to be exploited in push–pull, agriculture must sustainably produce more food on less land as it is lost through diversion to other uses and climate change, and so presents an extremely important target for new biotechnological studies.

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