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SIMULATION OF INTEGRATED CONTROL STRATEGIES FOR *OROBANCHE* SPP. BASED ON A LIFE CYCLE MODEL

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SUMMARY

A computer simulation model was developed to investigate strategies for control of the parasitic weed species of *Orobanche*. The model makes use of data from published literature and predicts infestation levels in a dynamic and deterministic way. It is predicted that sustainable control of the parasite can only be achieved by reducing the soil seed bank to levels of 1000–2000 seeds m^{-2} and maintaining it at that level in subsequent years. When cultural control methods such as hand weeding, trap/catch cropping, delayed planting, resistant cultivars and solarization were considered individually, a relatively high level of effectiveness was required to contain the soil seed bank. An integrated approach with a selection of appropriate cultural methods is therefore recommended for further testing and validation in the field. The simulations demonstrate the importance of preventing new seeds entering the soil seed bank and that although reducing the soil seed bank may not increase yield for the first few years, it will ultimately increase production.

INTRODUCTION

Orobanche spp. are obligate holo-parasitic weeds which cause major crop losses especially in Mediterranean and sub-tropical climates. *Orobanche* parasitizes important crop species such as tomato (*Lycopersicon esculentum*), faba bean (*Vicia faba*), lentil (*Lens culinaris*) and chickpea (*Cicer arietinum*).

A mature *Orobanche* plant produces on average more than a quarter of a million seeds (Parker and Riches, 1993). Before they emerge successfully from the ground to flower and bear seeds for the next generation, the seeds must go through the various processes of conditioning, stimulation, germination, host penetration and attachment. Research has been carried out on the different aspects of the life-cycle of *Orobanche* but has largely excluded the advances made in seed technology. According to Teryokhin (1997), however, the germination process in *Orobanche* has great significance because the dispersal of these plants occurs exclusively by seed and he attributed the adaptation of *Orobanche* spp. to high fecundity, a germination stimulant requirement and the preservation of viability for long periods.

Orobanche seeds are persistent in soil largely due to the dual germination requirements of a moist period (conditioning) and a chemical stimulus from a

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nearby host root (stimulation). This means that weed seeds only germinate when a suitable host is present. The longevity of its seeds, which could exceed 20 years in dry storage (Kebreab and Murdoch, 1999a), together with its fecundity (Parker and Riches, 1993), makes *Orobanche* extremely difficult to control, especially for smallholder farmers in developing countries.

Saxena *et al.* (1994) emphasized that keeping the seed bank of *Orobanche* below a certain threshold is an important consideration in integrated management of *Orobanche*. They considered weeding, delayed sowing, solarization, biological control, crop rotation particularly with trap or catch crops, host resistance and chemical control to be important tools in integrated weed management strategies for *Orobanche* control. Based on results of research on germination biology by the authors and other published material, a life-cycle model of *Orobanche* is developed in this paper in order to simulate the impact of various control measures on the *Orobanche* infestation as reflected in the size of the soil seed bank.

Specific aims of the simulations were to estimate (a) consequences of reducing or preventing seed production of *Orobanche* plants, (b) the amount of depletion by trap or catch cropping necessary to prevent an increase in the soil seed bank, (c) the level of control which must be achieved for solarization to be used as an effective tool in depleting the soil seed bank, (d) the effects of delayed sowing, (e) the effect of resistant plants in reducing the soil seed bank and (f) the advantages of using an integrated approach for *Orobanche* control.

MODEL DEVELOPMENT

The life-cycle of *Orobanche* spp. as it would apply in a Mediterranean or semi-arid climate with a prolonged dry season each year was used for simulation modelling and is shown in Fig. 1. Simulations of control strategies including hand weeding, trap/catch cropping, delayed planting, using resistant cultivars and solarization were carried out using STELLA modelling software (STELLA Technical Documentation, 1996). The probabilities of transition from one stage of the *Orobanche* life-cycle to the next were entered either as constants or density-dependent variables (Fig. 1). Except where stated otherwise, the probabilities of transition were incorporated in the simulation model as fixed variables in a deterministic way and their derivation is now described.

Seed production

Estimates of seed productivity are variable ranging from 31 000 (Teryokhin, 1997) to 500 000 (Cubero *et al.*, 1979) seeds per plant. According to López-Granados and García-Torres (1991), seed production is density dependent and there is a negative linear relationship between the number of fertile capsules per plant and the number of *Orobanche* shoots per host plant. Unfortunately their model predicts negative seed production for densities above 25 plants. The results of López-Granados and García-Torres (1991) have been re-analysed and an

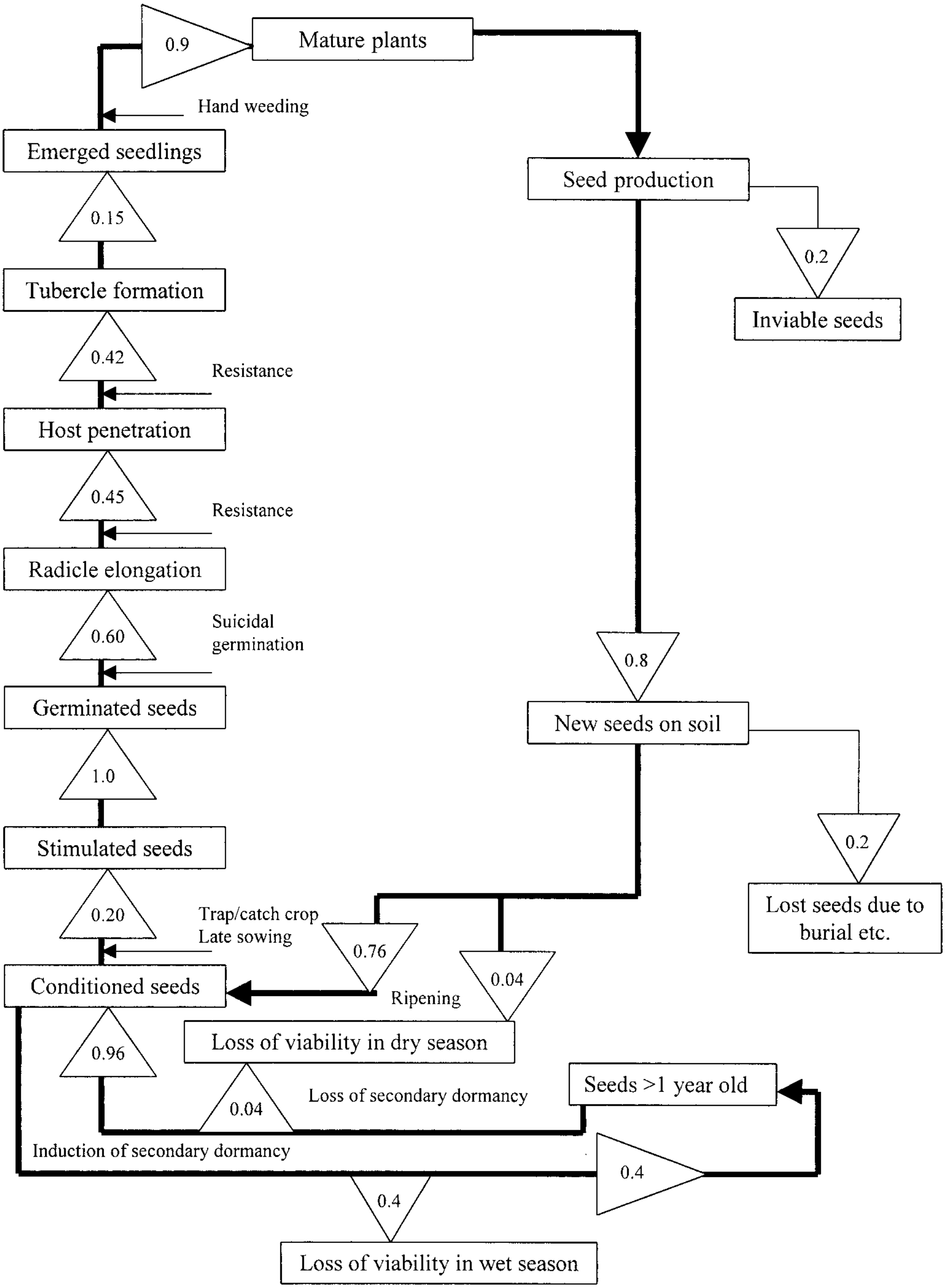

Fig. 1. Life cycle of *Orobanche*. Thick lines represent the major route of the life cycle and the numbers surrounded by a triangle indicate the probability of transition from one stage of the life-cycle to the next. Annotations describe stages where integrated control measures may act.

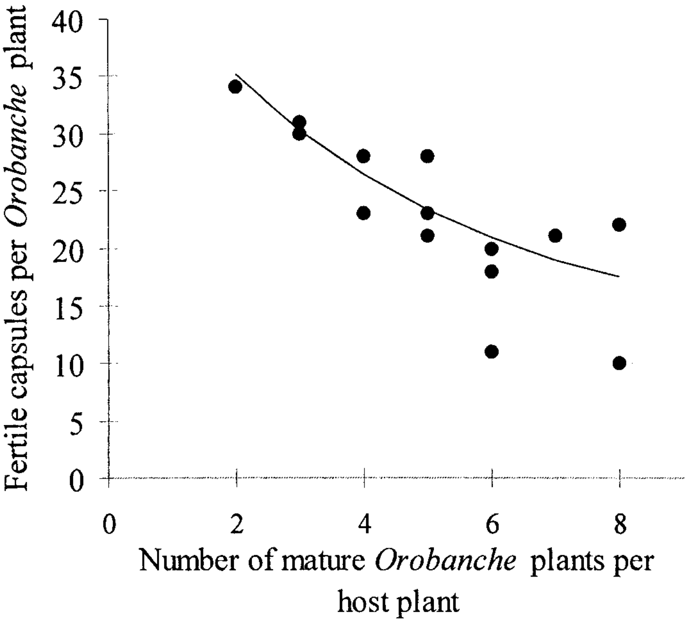

Fig. 2. The relationship between the number of fertile capsules per *Orobanche crenata* plant and the number of mature *O. crenata* plants per host plant. Original data (symbols) taken from López-Granados and García-Torres (1991). The fitted line is, Fertile capsules $= 11.5 + 37.42(0.795)^{\text{Mature plants}}$. The standard errors were 11.00, 5.94 and 0.16 for the parameter estimates in the order in which they appear in the equation.

exponential relationship was fitted which increased the goodness of fit (R^2) from 47.5% to 86.3% (Fig. 2).

The average number of seeds per capsule varied from 1000 to 4400 (Teryokhin, 1997; López-Granados and García-Torres, 1991). An average number of 2500 seeds per fertile capsule is assumed in the model and the number of fertile capsules per plant was density-dependent (Fig. 2). An extensive study of *Orobanche* capsules revealed that, with rare exceptions, 10–25% of seeds in each capsule were not developed enough to germinate and were therefore non-viable (Teryokhin, 1997). It is assumed here that 20% of new seeds produced are not viable.

A study on the vertical distribution of *Orobanche* seeds in the soil profile revealed that 78% of the seeds were found in the top 30 cm (Sauerborn *et al.*, 1991). Very few seeds are capable of emerging from such a depth (Mohammed-Ahmed, 1995). It is assumed in the model that 20% of the seeds become deeply buried and are therefore unable to emerge.

Loss of viability

Survival curves for *Orobanche* seed populations stored between 11 and 88% equilibrium relative humidity (e.r.h.) follow negative cumulative normal distributions and have been quantified by the viability equation for *O. aegyptiaca*, *O. crenata* and *O. minor* (Kebreab and Murdoch, 1999a). In conditions of imbibition,

Table 1. Prediction of loss of viability of *Orobanche aegyptiaca* under rainfed farm conditions in the highlands of Eritrea in a full year. Meteorological data from FAO (1994). After Kebreab and Murdoch (1999a).

Season	Mean temperature (°C)	Relative humidity (%)	Period (months)	Predicted loss of viability (%)†
Early dry season	20	53	5	3.0
Late dry season	26	40	5	2.5
Rainy season	25	imbibed	2	33.0
Cumulative total loss			12	38.5

† Assumes initial viability of seeds to be 98% in early dry season.

however, loss of viability of *Orobanche* seeds is more rapid than predicted by the viability equation although the survival curve again follows a negative cumulative normal distribution curve (Kebreab and Murdoch, 1999b). In contrast with the predictability of seed survival in dry storage the effects of temperature and of high relative humidity (88 – 100% e.r.h.) need to be established for accurate estimation of loss of viability in the soil. A 38.5% annual loss of viability has, however, been predicted for seeds of *O. aegyptiaca* infesting rainfed crops of tomato in Eritrea (Table 1).

Conditioning

Orobanche seeds need a moist pre-treatment period known as ‘conditioning’ before they can germinate (Joel *et al.*, 1995). However, prolonged conditioning can induce secondary dormancy and the rate at which induction occurs varies among species (Kebreab and Murdoch, 1999b).

Stimulation

The number of stimulated seeds depends on the root length density of the host species. Linke and Vogt (1987) showed that only seeds within 1.5 mm of the roots are stimulated by the root exudates, although others have argued that successful attack could be achieved from as far as 2.5 mm (Kadry and Tewfic, 1956). The probability of stimulation of seeds in the soil was calculated to range from 2.5% to 16.4% in legumes and, due to a higher density of roots in soil, 20% is arbitrarily assumed here for tomato.

Germination

Germination of stimulated seeds depends on temperature and moisture availability. Assuming moisture is not limiting, no seeds are expected to germinate below 4.9 °C as this is the calculated base temperature for rate of germination which is common to *Orobanche* spp. (Kebreab and Murdoch, 1998). Percentage germination is expected to increase as the temperature increases up to 20 °C (Kebreab and Murdoch, 1999c). A further increase in temperature was deleterious to seeds and the proportion of seeds failing to germinate was largely a function of the maximum temperature and therefore the extent of diurnal temperature fluctuation (Kebreab and Murdoch, 1999d).

Orobanche spp. can be conditioned in water potentials of less than -10 MPa and can germinate with water potentials as low as -1.2 MPa (Kebreab, 1997). An equation which estimates germination at any water potential and temperature has been developed for *O. aegyptiaca* (Kebreab, 1997). For this simulation, it is assumed, however, that during germination moisture is available and the temperature ranges between 10 and 20 °C. Under these conditions, germination of viable seeds is predicted to approach 100% and a constant probability of germination of 1 was used in the model.

Penetration, attachment and emergence

In *O. crenata*, only half of the germinated seeds elongated their radicles sufficiently to penetrate the host (Linke and Vogt, 1987) compared with 60–80% in *O. cumana* (Dorr *et al.*, 1994). In the model, the probability that a radicle would elongate sufficiently was assumed to be 0.6.

The probabilities of germinated seeds penetrating host root and forming a tubercle were reported to be 0.3 and 0.125 respectively by Dorr *et al.* (1994) for *O. cumana* in sunflower (*Helianthus annuus*), while the probabilities of forming a tubercle supported by Schnell *et al.* (1996) were 0.048 for *O. crenata* in *Vicia villosa* subsp. *dasycarpa* and 0.175 for *O. crenata* in *Cicer arietinum*. Probabilities of penetration and tubercle formation of germinated seeds were assumed to be 0.27 and 0.11 respectively, where applicable.

An emergence probability of 0.15 was assumed based on 10–30% emergence of attached parasites in the field (Sauerborn, 1994). Schnell *et al.* (1996) reported that about 90% of emerged plants produced seeds and this value has been used as the maturity index.

Model initialization and evaluation

The initial number of *Orobanche* seeds in the soil seed bank varies widely between fields. Sauerborn *et al.* (1991) considered 13 000 seeds m^{-2} to be a field with medium infestation and that figure is used as a starting point in the simulations.

Effectiveness of control measures is assessed either in terms of percentage annual change in the soil seed bank or in the ability of a strategy to reduce or contain the soil seed bank at about 2000 seeds m^{-2}. According to Linke *et al.* (1991), this seed density resulted in no significant yield loss in faba bean and there were only a few *O. crenata* shoots at that level of infestation.

RESULTS

Simulation of the effect of weeding on the Orobanche seed bank

A ten-year simulation was run to determine the effect of the degree of weed control on seed bank size assuming relatively low, average or high seed production (Fig. 3).

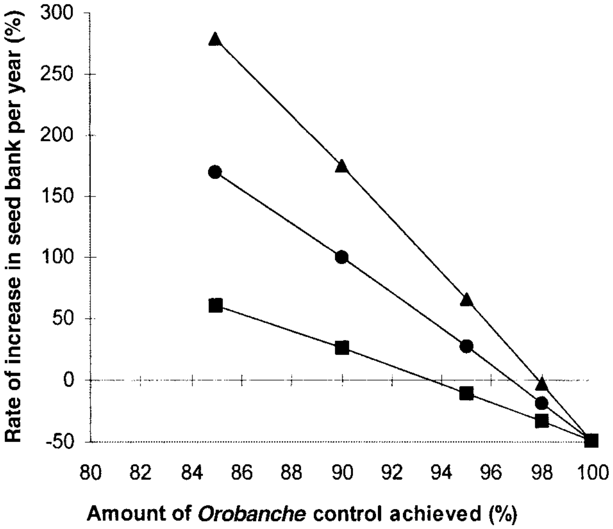

Fig. 3. Predicted annual rate of change in the *Orobanche* soil seed bank at various levels of weed control. The average number of viable seeds per capsule was assumed to be 4000 (▲), 2500 (●) and 1000 (■).

To maintain an equilibrium between seed depletion and seed influx, 94–98% control of *Orobanche* seed population has to be achieved (Fig. 3). Seeding must be prevented in order to avoid massive accumulations of seeds in the soil seed bank. Nevertheless, the advantage of preventing seeding may not be obvious to the farmer. There will be little or no gain in yield of the infected crop as the parasites would already have reduced its potential yield at the time of weeding. Seed production is, however, crucial in determining subsequent infestations.

Simulation of the effect of crop rotation with trap/catch crop

Depending on the density of the catch/trap crop, it is predicted to take 3–4 years to reduce the infestation from 13 000 to 2000 seeds m^{-2} (Fig. 4). However, just one year's cropping with an unweeded susceptible host can undo the benefits of 3–4 trap crops and the soil seed bank increased to about 25 000 seeds m^{-2} (Fig. 4a). A further 3–5 years of trap/catch cropping would then be needed for seed reserves to drop to a safe level again (Fig. 4a). Schnell *et al.* (1996) predicted that after growing a lentil crop infested with 1800 *Orobanche* seeds m^{-2}, it would be necessary to grow a non-host crop for at least six years to reduce the soil seed bank back down to about 1000 seeds m^{-2}. A practical example of the use of trap crops which roughly confirms the need for 3–5 years of trap/catch cropping was provided by Al-Menoufi (1991) in an experiment carried out in Egypt. He reported a 3% and a 1% *O. crenata* infestation in faba bean following three and four crops of berseem (*Trifolium alexandrinum* L.) respectively compared with 67% when faba bean was grown continuously.

If, however, the mature *Orobanche* plants were largely prevented from seeding then the soil seed bank could be maintained at a low level (Fig. 4b). Farmers will

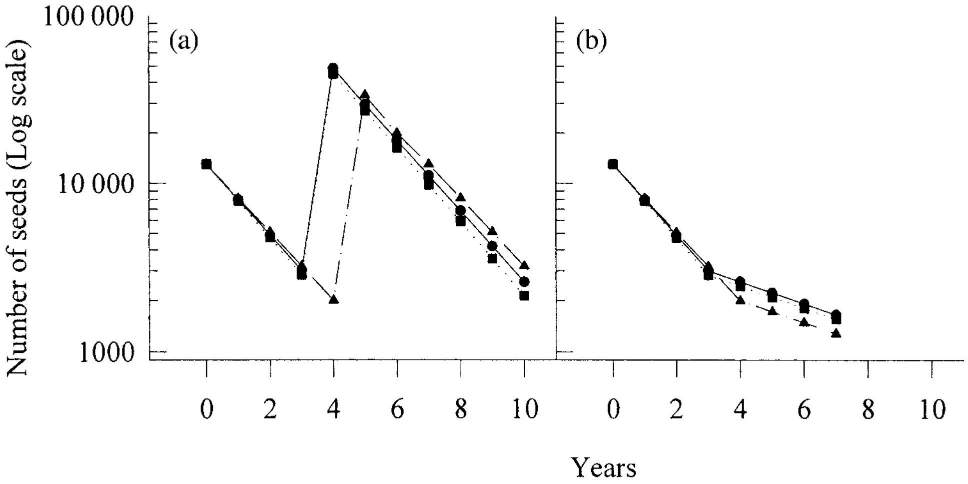

Fig. 4. Predicted changes in the *Orobanche* soil seed bank as a result of crop rotation with trap crops. Three densities of trap crops were tested with probabilities of stimulation of 10% (■), 20% (●) or 30% (▲) of seeds in the soil. After the soil seed bank declined to $\leqslant 2000$ seeds m^{-2}, (a) an unweeded susceptible crop was grown for one season followed by further trap crops or (b) susceptible crops were grown each year with 95% weed control achieved.

not grow non-host crops for long periods, but trap crops may help to reduce the seed bank in highly infested soils after which susceptible crops could be grown and weeded as required.

Simulation of the effect of planting date

Although the underlying processes were previously not well understood, several authors including Mesa-García and García-Torres (1986) and van Hezewijk (1994) have recorded the effect of delayed sowing in the field. Van Hezewijk (1994) suggested that early planted susceptible legumes in Mediterranean climates would be more severely infested than later planted crops because low soil temperature in later planted crops reduces *O. crenata* germination. Kebreab and Murdoch (1999b; d) showed that this lower infestation would result partly because the rate of induction of secondary dormancy in *Orobanche* seed increases with decrease in temperature from 20 to 10 °C, and partly because the lower temperature is sub-optimal for germination whether or not the seeds are dormant. Fewer seeds would therefore germinate. For example, assuming a mean temperature of around 15 °C is maintained for two months, delaying sowing from October to December would be predicted to induce secondary dormancy in about 20%, 40% and 4% of *O. aegyptiaca, O. crenata* and *O. cernua* seeds respectively (Fig. 5). Any attempt to limit the infestation in the field by induction of secondary dormancy is however subject to the crucial proviso that moisture would need to be continuously available.

In addition to the induction of secondary dormancy during prolonged conditioning, there is also a reduction in germination due to the effect of temperature

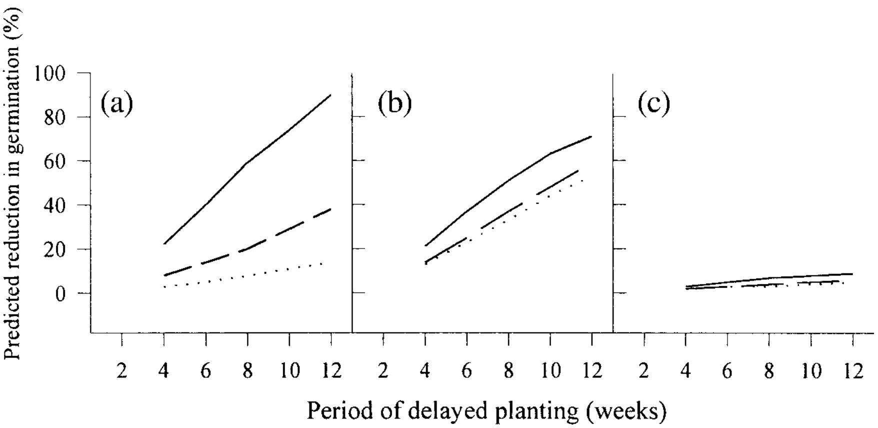

Fig. 5. Effect of delayed sowing on the predicted reduction of germination of (a) *Orobanche aegyptiaca*, (b) *Orobanche crenata* and (c) *Orobanche cernua* due to induction of secondary dormancy. The mean soil temperature was assumed to be 10 °C (solid line), 15 °C (broken line) and 20 °C (dotted line). Predictions based on models described in Kebreab and Murdoch (1999b).

on the germination stage. Therefore, germination is the result of two independent processes the estimates of which are given in Table 2. Final predicted germination percentages are taken from Kebreab (1997).

The simulation demonstrates that delayed planting of susceptible (weeded) crops could reverse the trend of the soil seed bank from a net increase to a net depletion (Fig. 6).

Farmers will not want to plant late every year due to the likely yield penalty. Delayed planting must, however, be used along with other control methods. For example, the soil seed bank is stabilized with a combination of delayed sowing and at least 89% effective weed control (Fig. 6).

Simulation of the effect of solarization

Solarization can effectively reduce the *Orobanche* soil seed bank (Sauerborn and Saxena, 1987). However, the temperature and moisture requirements for loss of viability during solarization are less clear. In imbibed storage at 40 °C, re-analysis

Table 2. Predicted net germination of three *Orobanche* spp. assuming a mean soil temperature of 10 °C and delaying planting for 10 weeks. Predicted net germination was calculated as the proportion of seeds without secondary dormancy multiplied by 1 minus the reduction in germination due to low temperature.

	Reduction in germination due to		
Species	secondary dormancy (%)	low temperature (%)	Predicted net germination (%)
O. aegyptiaca	70	12	26.4
O. crenata	60	49	20.4
O. cernua	5	24	72.2

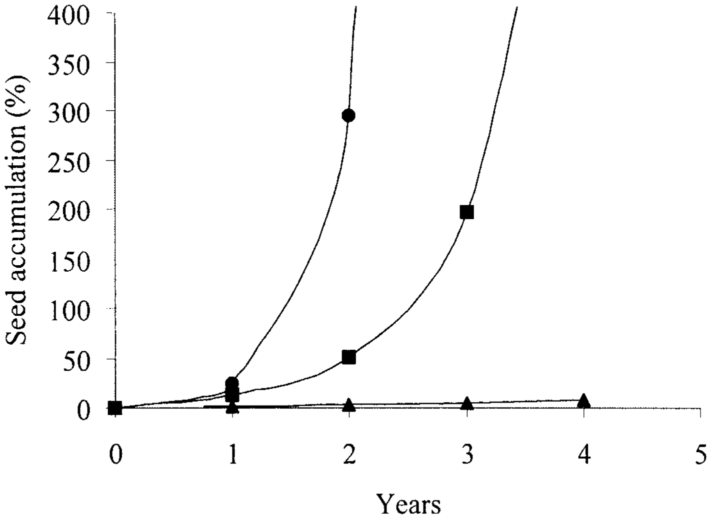

Fig. 6. The effect of early (●) or late (six weeks later assuming a mean of 10 °C achieved during the delaying period) (■) planted crops on percentage accumulation of *Orobanche aegyptiaca* seeds in the soil seed bank. The effect of delayed planting with 89% effective weed control (▲) is also shown for comparison.

of data published by Dawoud (1995) indicates that the slope of the survival curve could lead to a 75% loss of viability (from 87.5% to 12.5%) in about 12 d. A similar depletion at 30 °C is predicted to take about 75 d in *O. crenata* and over 160 d in *O. cernua* (cf. Kebreab and Murdoch, 1999a).

The ability to achieve high temperatures through the ploughed horizon is therefore crucial for the success of solarization. Indeed, more than 95% of seeds have to lose their viability if no other method of control is used to start reversing the trend of soil seed bank accumulation (Fig. 7). However, if only 75% of seeds were to lose their viability due to solarization, then approximately 80% of plants would need to be prevented from seeding to contain the soil seed bank (Fig. 7).

Simulation of the effect of resistant plants on seed bank

Breeding for resistance could be achieved either by blockage of haustorial penetration or tubercle formation or by breeding for resistance based on the action of germination stimulants.

According to Fig. 1, only 11% of non-resistant plants that germinated formed tubercles. For a net depletion of the seed bank to occur, it is predicted that 99.6% of germinated seeds must fail to attach to the host plant without any other weed control (Fig. 8). Dorr *et al.* (1994) reported that only 1% of germinated seeds formed turbercles on resistant *Helianthus* varieties. If 80% of plants were prevented from seeding, the resistance mechanism would need to be 98% effective for a stable seed bank (Fig. 8).

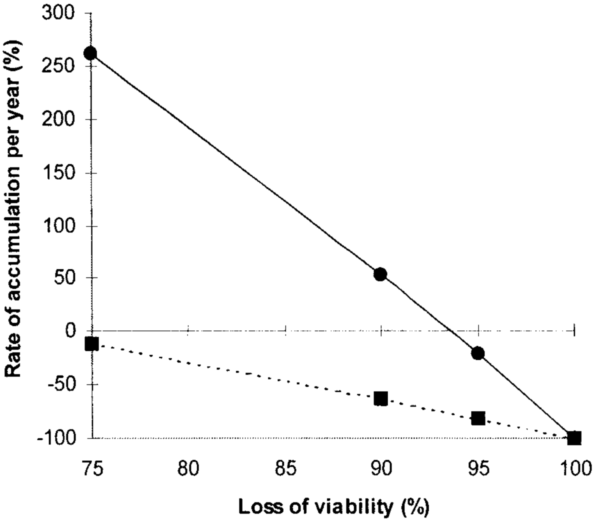

Fig. 7. Predicted *Orobanche* seed bank accumulation as a function of loss of viability due to solarization. Solid line represents simulation with no weeding and broken line shows 80% of mature plants prevented from seeding.

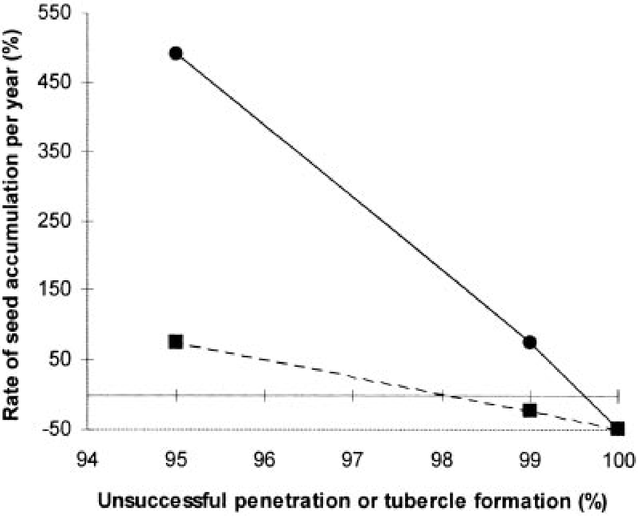

Fig. 8. Prediction of the annual rate of *Orobanche* seed accumulation in the soil seed bank depending on the percentage of unsuccessful attachments to resistant host plants. The simulation assumed either no other control method (solid line) or that 80% of mature plants were prevented from seeding (broken line).

Integrating methods of Orobanche *control*

A further simulation was carried out to show the effect of using a combination of control measures for several years on depletion of the seed bank. The cropping system proposed here includes solarization and trap cropping in the first year, followed by two year's host cropping with about 90% effective weed control by hand weeding. In the fourth year, solarization followed by trap cropping and

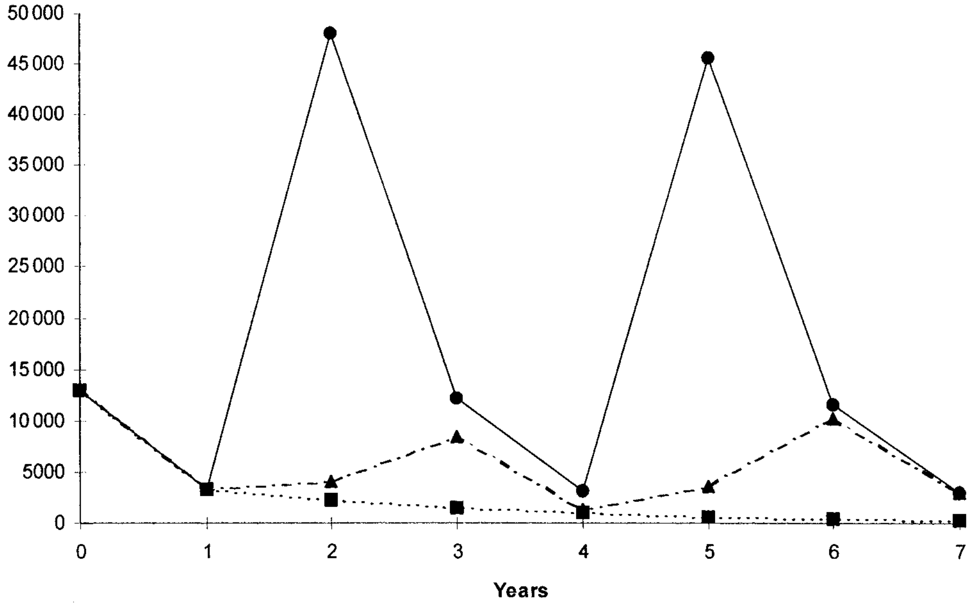

Fig. 9. Simulation of the effect of solarization and trap cropping for the first year followed by a weeded (a level of weeding that would stabilize the seed bank (in this case, 90%) (■) or unweeded (●) host crop for one season. In the third and fourth seasons trap crops are introduced in the unweeded field to reduce the number of *Orobanche aegyptiaca* seeds to a safe level (2000 seeds per m^2) before sowing a susceptible crop and then the cycle continues. In the weeded field, host crops are planted each year. The third option was a rotation involving one year's trap cropping followed by host crops sown 10 weeks late for two years (▲).

delayed sowing would make it possible to keep the infestation level down for the next two years' host crops with an 80% level of weed control (Fig. 9).

The simulation shows that once a sufficiently small soil seed bank has been achieved through, in this case, solarization and trap cropping, all that is required to keep the weeds in control is prevention of seeding by any means the farmer can afford (Fig. 9). On the other hand, if left to produce seeds, most of the control measures are unlikely to be effective.

DISCUSSION

The simulation model developed considers only the basic life cycle of *Orobanche* and the assumptions made require verification for different host and trap crops in the field, and variability due to edaphic and weather variables needs more study to validate the simulations and recommendations. Furthermore, detailed field and laboratory experiments are required to develop a mechanistic, dynamic and deterministic model.

There is no one way of integrating the control methods discussed above for all conditions. The selection of control measures depends on the intensity of the problem, accessibility to resources, type of host plants, *Orobanche* species involved, weather conditions and other factors. For example, a combination of three weeks delay in sowing with glyphosate application has been quite effective in studies made at ICARDA in faba bean (Saxena *et al.*, 1994). In dry pea production, a combination of delayed sowing, post-emergence imazaquin application and use of a resistant cultivar resulted in high seed yield and complete control of *Orobanche* (Saxena *et al.*, 1994). Therefore, a combination of the various means of control can be successful depending on the farm conditions.

Planting resistant cultivars will certainly reduce the build up of the *Orobanche* seed bank and can be used as part of an integrated control system. Although some spontaneous germination has been known to occur, breeding plants to stop releasing stimulants would have a big impact on the number of germinating seeds. Increasing the amount of stimulant produced by trap/catch crops could be a promising means of depleting the soil seed bank as it may induce a large number of seeds to germinate. The role of biological control methods and herbicides cannot be under-estimated.

Since the dispersal of the parasite occurs exclusively by seeds, prevention of seeding is one of the most important ways of reducing the size of infestations. The importance of hand weeding to prevent seed influx is, therefore, obvious. It should however be carried out just before the seeds begin to ripen as removing shoots earlier could result in the emergence of additional *Orobanche* shoots (Sauerborn, 1991). For farmers who can afford to use herbicides, Jurado-Exposito *et al.* (1997) have shown that soaking broad beans with imazethapyr resulted in 60–80% *Orobanche* control and, if coupled with a post-emergence herbicide, almost complete control was achieved and yields were more than tripled.

Where possible and depending on availability of water, farmers should consider solarization as an effective tool to reduce the existing *Orobanche* seed bank. However, the process involves using a relatively expensive polythene mulch which puts it out of the reach of poor farmers (Sauerborn and Kroschel, 1996).

An advantage of understanding the underlying mechanisms of dormancy induction and breakage and prediction of germination is that it helps to make a decision on when to plant crops. Late planted host crops may substantially reduce infestations whereas trap/catch crops must be planted at the optimum time for maximum stimulation to make it worthwhile for the farmer.

In developing countries, *Orobanche* can cause devastating crop losses to the farmer (Abu-Irmaileh, 1998). At present, until resistant crops or other means of control are available cheaply to the poorer farmers, an integrated approach based on cultural control methods has to be adopted by the farmer to prevent the fate of countries like Egypt which according to Gressel (1995), has in the last decade alone, gone from being an exporter to an importer of grain legumes due to *Orobanche*. Before adopting such integrated weed management strategies, the predicted effects on both seed production and depletion of the soil seed bank clearly need to be validated in the field for different *Orobanche* species. The appropriateness of such strategies for resource-poor farmers must also be assessed.

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