CHAPTER 4

Growth and Development of Wild Oat Plants

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This section, which considers all aspects of the growth cycle of wild oats and the influence of various factors upon it, reviews a total of 52 papers on seedling establishment, vegetative development, factors affecting wild oat incidence and development and reproduction.

The main conclusions (they relate mainly to *A. fatua*) are that wild oat seed is capable of germinating over a wide range of temperatures (2°-35° C), that the seedling is at first weak and very susceptible to competition, but that, with an enlarging root system and an initially higher net assimilation rate, it gradually catches up the cereal crop in which it frequently occurs.

Vegetative growth varies with competition. In the absence of competition very large plants can be produced with a considerable reproductive capacity, but in the conditions of a cereal crop the development of the plant is normally very restricted.

Climate has some influence on wild oat populations through severe cold in winter. Seedlings of *A. fatua,* which germinate in the autumn, are vulnerable to frost. This vulnerability decreases with increasing age. Other factors may affect population behaviour indirectly by influencing the incidence of dormancy in seeds.

Nitrogen has a marked effect upon *A. fatua* growth, but P and K appear relatively unimportant. Manganese deficiency affects growth and health of wild oats.

Soil type influences the incidence of certain species, and can affect the growth of *A. fatua* directly and indirectly.

A. fatua seedlings are capable of regeneration, even if cut up, provided there is a node present. Older plants readily re-grow if cut over for silage.

Panicle emergence of *A. fatua* and *A. ludoviciana* in England occurs at a mean of 106 days after planting, but for alien seed grown alongside them the number of days was roughly proportional to the latitude of the country of origin. Daylength plays an important part in flowering, for flowering is normally suppressed by short days. Northern cultivars of *A. sativa* are the most sensitive to photoperiod, diploid species from the Mediterranean are moderately sensitive, while tetraploids of the *A. abyssinica–barbata* group are least sensitive. A short-day vernalisation response has been obtained from two species and a cold vernalisation response from a number of species.

Wild oats are normally self-pollinated, but up to 12% cross-pollination can occur in some species. Crosses between *A. fatua* and *A. sativa* can occur.

Seed production in *A. fatua* ranges from 1 to 500 or more per plant. The amount is regulated by various factors such as the time of emergence, the competitive ability of the crop it infests, the density and spacing of the crop and the soil type.

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SEEDLING ESTABLISHMENT

GERMINATION AND EMERGENCE

Spring germination and emergence of wild oats in the field is mainly dependent upon soil temperature and moisture (Green and Helgeson 1957b). Seedling emergence in Germany occurred 10-14 days after the soil temperature first exceeded 5°C (Kühnel 1965), in England when the soil temperature rose to 6-7°C (Chancellor and Peters 1972), in Russia when the soil reached 10-13°C (Zverev 1966) and in Canada 10-15°C (Friesen and Shebeski 1961). In the laboratory, germination occurred between 2-35°C, with the optimum at 15°C (Koch 1968).

The influence of moisture level was investigated in a sandy loam soil with 3% organic matter in pots kept at 18-20°C in the laboratory. Germination occurred when the soil moisture content lay between 20-100% of the total water capacity of the soil, with optimum germination between 65-90% (Koch 1968). Excessive waterlogging can not only induce secondary dormancy (Hay and Cumming 1957), but also lead to death of the seed within 1-2 months (Lewis 1961, Rademacher and Kiewnick 1964).

A two-year study in Germany of emergence in the field showed that in both years the earliest *A. fatua* seedlings emerged shortly before spring barley (Koch and Rademacher 1966). The germination of wild oats continues of course over several weeks, but the earliest emerging plants are the most important for they are more likely to survive and they also produce most seed (Pfeiffer *et al* 1960, Chancellor and Peters 1974).

Initially in germination, the coleorhiza emerged and was followed by the coleoptile after 3-5 days. Three seminal roots then appeared and penetrated the soil (Green and Helgeson 1957).

A review of other factors that can influence germination and emergence can be found under Seed Behaviour, p. 72.

SEEDLING GROWTH

At emergence the wild oat seedling consists solely of a long narrow leaf. It is puny and weak and at this stage is easily discouraged or even killed by competition (Dadd 1956, Thurston 1956). An assessment of growth showed that vegetative growth occurred slowly at first, the plant reaching about 25 cm by the thirtieth day after planting. During this period all the leaf initials had been formed and panicle initials had begun to differentiate (Green and Helgeson 1957). Although the seedlings were found to be smaller than cereals, they had a higher net assimilation rate enabling them to overhaul the cereal seedlings. However, the higher net assimilation rate did not persist (Thurston 1959a).

ROOTS

The development of the root system is to a large extent responsible for the initial weakness of the wild oat seedling and subsequently for its increasing vigour. Studies in Canada showed that five days after emergence wild oats had a greater length of root than nine other weeds, all dicotyledons, but that 11 varieties of cereals had much longer roots than wild oats. Twenty-one days after emergence, wild oat roots were longer than those of only three of the nine dicotyledonous weeds and all but one cereal had much longer roots (Pavlychenko and Harrington 1934). Pavlychenko (1937, 1940) found that the reason for the initial disparity between wild oats and cereals was due to the numbers of seminal roots produced by each species. Wild oats had three or fewer seminal roots, cultivated oats three or four, wheat four or five, rye five or six and barley six to thirteen. Later the position changes, for the crown roots of wild oat are more vigorous. The development of roots was studied with and without competition. Wild oats grown as separate plants without competition developed about 88.9 kilometres of root. When grown in 15 cm rows with 18-20 plants/30 cm of row they each had about 978 m of root. When grown between 15 cm rows of wheat they had 57 m (the wheat had 158 m) and between 15 cm rows of barley, 36 m (the barley had 195 m) (Pavlychenko 1937).

The initial rate of growth of *A. sterilis* roots, along with three other large-seeded range plants, lay between 2 and 7 cm/day, while roots of smaller-seeded range plants only elongated 0.5-2 cm/day. The elongation of roots was positively correlated with seed weight. The rate of elongation also increased 2-3 fold over the temperature range 10-20°C (Cohen and Tadmor 1969).

The root systems of *A. fatua* and *A. strigosa,* when grown separately or in a mixed stand, were found to have a markedly different distribution down the soil profile. *A. fatua* tended to root at deeper levels than *A. strigosa* (Ellern *et al* 1970).

The roots of *A. fatua* seedlings grown in the laboratory were found to show magnetotropic responses, for they tended to be aligned north and south unless the plants were rotated daily through 90° when the root distribution was more or less completely random (Pittman 1970).

VEGETATIVE DEVELOPMENT

In the field wild oat development was rather slower than that of barley, but after tillering it became much the same (Koch and Rademacher 1966). In a detailed study of vegetative development, Green and Helgeson (1957) found that growth was slow over the first 30 days, but thereafter it increased through activity of the intercalary meristems at the base of each internode. The lowest nodes elongated least. At about 65 days after planting growth ceased somewhat abruptly, when the plant was about 127 cm tall.

The number of functional leaves increased from one at day 5 to around six at day 45, and later declined again to none at about day 75. The flag leaf lived the longest. Factors that contributed to leaf deterioration were: being pierced by adventitious roots, pressure from developing tiller buds, shading, senescence and disease.

They found too that the development of adventitious roots closely followed the growth pattern. When fully developed at about 75 days the number of adventitious roots lay between 20 and 70. The actual number of roots being related to the number of tillers, for the two lowest nodes of each tiller produced whorls of roots from the intercalary meristems.

The first tiller emerged from the prophyllum at about day 20. An average maximum of seven tillers was reached by day 40. As the prophyllum and four nodes of each tiller as well as five nodes on the main stem can produce tiller buds, the potential number of tillers is considerable. However, a maximum of eight reached maturity and the number varied with competition and soil conditions.

Pavlychenko and Harrington (1934) have reported that five days after emergence *A. fatua* had a greater assimilation surface than any of nine dicotyledonous weeds, but less than the four cereal species tested. However, by flowering, the position had been completely reversed, the nine dicotyledonous species having a greater assimilation area than wild oats, which in turn had a greater assimilative area than the four cereals. Thurston (1959a) found that, following a decline in the net assimilation rate of wild oats until it was approximately equal to that of cereals, the subsequent difference in dry matter production between wild oats and cereals was due mainly to differences in leaf areas.

A complicating factor in net assimilation rates and leaf areas is of course shading by other plants. It has been found that *Sinapis alba* when growing with *A. fatua* in barley had a major effect on the leaf canopy by affecting the angular orientation and vertical distribution of wild oat and barley foliage (Haizel 1972).

In the vegetative stages, inter-specific differences of habit occur in *Avena* spp. When grown in pots, fully tillered *A. ludoviciana* plants were procumbent or prostrate and had many tillers, while *A. fatua* (apart from one form) were all upright in habit and had few tillers. *A. barbata* was prostrate in a rosette to start with but, after the panicles began to emerge, growth at lower nodes lifted them erect (Thurston 1963b). The prostrate habit of *A. barbata* has also been commented on by Whalley and Burfitt (1972) who suggest that this could render it very susceptible to crop competition.

Intra-specific variability also occurs. Growth tests made on 83 samples of 4 varieties of *A. fatua* in Western Canada showed that each variety consisted of a number of physiological races or strains differing in life cycle and growth habit. Some races had almost prostrate tillers while others were upright (Lindsay 1956). Similar tests were made with 24 samples also collected in

Western Canada and in Western North America and considerable vegetative variability was found. The plants differed in growth habit and leaf size (Baker and Leighty 1958). Differences in stature of *A. fatua* were also noted when plants from alien seed samples were compared with British plants. Plants from Pakistani seed only grew to 107 cm, plants from Australian seed grew to 137-152 cm, while British plants reached 183 cm (Thurston 1964).

Besides obvious differences in vegetative characteristics, physiological races of *A. fatua,* which were adapted to different day lengths, have been found, but these were morphologically indistinguishable (Odgaard 1972).

FACTORS AFFECTING WILD OAT INCIDENCE AND DEVELOPMENT

CLIMATE

Climate not only regulates flowering by day length and cold weather (p. 96), but also affects incidence and survival in direct and indirect ways. Perhaps the most important of these is the severity of winter cold.

Mortality from cold weather of autumn-germinated *A. fatua* decreased with increasing age (Holroyd 1972c). As soon as the second leaf developed, the chances of survival were markedly increased and those with three leaves by mid-December suffered less than 20% mortality. In contrast those plants with only one leaf by mid-December suffered more than 70% mortality. Schaeffler (1950) has also reported severe winters as limiting the incidence of *A. fatua* along with soil type, other climatic factors, and even land configuration and land tenure systems. Kühnel (1965) has suggested that climate-soil interactions limit wild oat incidence. On heavy loam soils a severe winter followed by a dry spring resulted in an increase of wild oats, while on a sandy loam soil wild oats were decreased. These climatic influences were only effective when temperature and humidity stresses were prolonged. Skorda (1972) suggested that the recent increase of *Avena* spp. as weeds in Greece may be associated with the mild winters over the previous 3-4 years.

Development of *A. ludoviciana* seedlings has been arrested by frozen soil preventing their emergence over varying periods of time between December and March (Thurston 1961). Seedlings of *A. ludoviciana* were slightly more hardy than those of *A. fatua.*

Climatic factors of indirect effect are temperature and moisture. Sexsmith (1969) has reported that a higher level of dormancy occurred in seeds from plants grown at low temperatures and moist soil than from those grown at high temperatures in dryer soil. This could affect development indirectly through date of germination. In Norway, *A. fatua* is reported as commonest in areas with an annual rainfall of less than 600 mm/year (Storhaugen 1961a).

NUTRIENTS

Various tests have been carried out with fertilisers in crops to see the effects on the competitive interaction with wild oats. These interactions are reviewed in Chapter 5. Fertilisers containing nitrogen have also been found to affect dormancy and hence the germination of wild oats and this aspect has been reviewed in Chapter 3, p. 79. The present section is therefore concerned solely with the use made of various fertilisers by wild oats during growth, although where comparisons with other plants have been made these have been included.

Nitrogen has a marked effect upon growth of *A. fatua* (Pawlik 1957, Chancellor 1969a). It increased plant height, straw weight and seed production (Sexsmith and Russell 1963). In a growth chamber experiment, nitrogen significantly increased dry matter production, the number of fertile tillers and hence the number of seed produced by both wild oats and barley, but not of wild oats in a field experiment (McBeath *et al* 1970). In both experiments barley was more responsive than wild oats to nitrogen in vegetative growth and in seed production. This is contrary to results obtained at Rothamsted in the field and also from plants grown in a greenhouse where, by adding nitrogen to the soil, growth of *A. ludoviciana* and *A. fatua* was affected in the same ways as cultivated cereals. They took up the same amount of nitrogen per plant as winter oats and winter wheat, but more than spring barley (Thurston 1959). When winter wheat, barley, *Alopecurus myosuroides, Avena fatua* and *Sinapis arvensis* were grown separately in nutrient solution, they showed no difference in percentage nitrogen content although the weeds took up rather less than the crops (Koch and Köcher 1968). The reason for this variation is not known. In addition, no significant difference was observed in the pattern of nutrient uptake, although *Sinapis arvensis* showed an earlier nutrient requirement than barley or *A. fatua.* The root/shoot ratios of *A. fatua* and *Alopecurus myosuroides* were found to vary according to the level of nitrogen in the nutrient medium.

Phosphate, in contrast to nitrogen, has little (Pawlik 1957) or no effect upon growth of wild oats (Sexsmith and Russell 1963, Chancellor 1969). *A. fatua* plants were as heavy and as tall and contained the same P content when competing with wheat, barley, oats and other *A. fatua* whether grown at low or at high nutrient levels (Halloin and Sudia 1967). *A. fatua* grown in nutrient solution without competition had the same phosphate content as wheat, barley, *Alopecurus myosuroides* and *Sinapis arvensis* grown similarly, although the weeds took up rather less than the crops (Koch and Köcher 1968).

The use of potassium is less certain. *A. fatua* has been reported as being relatively insensitive to potassium (Pawlik 1957), although it has caused a slight weight increase in top growth (Chancellor 1969). When grown separately in nutrient solution, *A. fatua* took up rather less than wheat and barley (Koch and Köcher 1968). When grown in competition with barley and wheat, wild oat plants were the same height and weight and had the same K content when grown at high or low nutrient levels; but when grown with *A. sativa* they contained less K than wild oats growing with other wild oats and this difference was greater with increased nutrient concentration (Halloin and Sudia 1967).

A. fatua and *A. ludoviciana* have been grown in comparison with *A. sativa* in manganese-deficient soils (Thurston 1951). *A. ludoviciana* had different leaf symptoms (interveinal chlorosis) from the other two species (grey speck lesions), but other effects were similar although the severity varied. As assessed by dry weight at harvest *A. ludoviciana* was most affected, *A. sativa* less so and *A. fatua* least. Manganese deficiency resulted in fewer viable seeds and less dormancy in both wild oat species. *A. strigosa* is reported to be virtually unaffected by manganese deficiency (Gallagher and Walsh 1943).

Decreasing the magnesium available had no effect on *A. fatua*; but boron proved essential for growth (Pawlik 1957).

SOIL

Soil type and characteristics have direct and indirect effects on *Avena* incidence and development. *A. fatua* occurs widely on arable soils in temperate climates in the northern hemisphere (Odgaard 1972). Incidence can be modified by an interaction between soil and climate. It is reported that on heavy loam soils a severe winter followed by a dry spring resulted in an increase of *A. fatua* plants, but under these conditions on sandy loam soils there was a decrease (Kühnel 1965).

Soil acidity affected barley more severely than *A. fatua* so that on acid areas wild oats were larger than on areas where the pH was higher. In infested wheat and rye, soil pH had no such effects (Thurston 1962a).

A. fatua was grown without a crop in four soil types, fen, sandy soil, loam and heavy marsh soil. On sandy and loam soils the wild oats developed panicles earlier than on the other two soils. The straw was longest on the fen soil, which may be because it was more fertile. Flowering continued longer on the fen soil (Odgaard 1972).

Other less weedy species of *Avena* may be more restricted by soil type than the widespread important ones. In Israel, *A. clauda* is restricted to marls, chalks and hard limestone areas, and absent from light sandy soils. Conversely, *A. longiglumis* is restricted to sandy loams, consolidated dunes and other sandy places (Ladizinsky 1971b). It may be that lack of adaptability reduces the weed potential of a species.

REPRODUCTION

VEGETATIVE REGENERATION

Wild oat seedlings are capable of regeneration even when cut into pieces, provided that a node is present (Kirk and Pavlychenko 1932). Very young seedlings (just after emergence) regrew from just below ground, but older seedlings (between 1-3 leaf stage) regenerated best from the lowest node above ground. At later stages wild oats can be cut with a suitable crop for silage and because of their regenerative powers can be cut thus several times (Thurston 1956).

FLOWERING

The panicles of *A. ludoviciana* in England appear towards the end of June and the seeds ripen in mid-July. Spring-germinated *A. fatua* is a little later, the ears emerging in July and shedding seed about the beginning of August (Thurston 1956). Panicle emergence in wild oats started at 85 days after sowing at the earliest and continued until the 134th day. The mean number of days to 50% panicle emergence was 106 days for both species collected in England, but there was considerable variation especially in *A. ludoviciana* (Thurston 1957). Considerable variability has been reported from elsewhere. Seed collection from 24 localities in Western Canada and Western North America were grown alongside each other in Montana. There were considerable differences between plants in dates of panicle emergence (Baker and Leighty 1958). Similarly 83 collections in Western Canada of four varieties of *A. fatua* were grown under similar conditions and some lines were found to be as much as 10 days behind others in time of heading and flowering (Lindsay 1956). There were also differences in panicle shape and size and two lines had noticeably larger seeds. At Aberystwyth (Wales) a single strain of *A. fatua* took 76 days from sowing to heading under normal daylength, 103 days under 11-hour days and 120 days under 9-hour days (Griffiths 1961).

Variability of time to panicle emergence has been shown for various species from different countries, but it was greater between countries for a single species than between species. Thus the number of days to 50% panicle emergence for *A. fatua* from Russia was 124 days and for *A. fatua* from Iraq was 97 days. *A. ludoviciana* from Russia was likewise 124 days and from Iraq 94-101 days. *A. sterilis* from Israel needed 93 days, from Crete 119 days and from France 134-140 days. This and other data showed in general that the higher the latitude of origin the greater the number of days to 50% panicle emergence (Thurston 1962b).

In many weeds there is a shortening of life span with increasing lateness of emergence during the growing season, but in Russia late-germinating plants of some species, including *A. fatua,* did not even begin to flower before the winter (Fisyunov 1968).

Daylength, which appears to be the controlling factor in flower initiation, has been investigated by Griffiths (1961). He tested nine species of *Avena.* The hexaploids *A. sativa, A. byzantina, A. fatua* and *A. nuda;* the tetraploids *A. abyssinica* and *A. barbata* and the diploids *A. strigosa, A. brevis* and *A. longiglumis.* These species showed considerable diversity in their response to daylength. All were essentially long-day plants, but varied greatly in flowering ability at 12 hour or shorter days. Panicle emergence was completely suppressed at these daylengths in certain cultivars of *A. sativa* which have been bred for high yields in northerly latitudes. All *A. fatua* plants had emerged inflorescences with 11-hour days, but only 17% had with 9-hour days. There appeared to be a definite relationship between geographic origin and the limits of tolerance to short days. Plants from more southerly latitudes suffered less from short days than those of more northerly origin.

It is of interest that Griffiths dissected plants that had failed to flower and found that floral differentiation had not been inhibited by the shortened photoperiods, but that full elongation of the internodes, especially the uppermost, had been suppressed. Breeding experiments indicated that the daylength effect is under genetic control.

Subsequent investigations by Sampson and Burrows (1972) have explored further the influence of photoperiod and also the effects of short-day vernalisation and cold vernalisation on flowering. They studied the hexaploids *A. sativa, A. sterilis* and *A. byzantina*; the tetraploids *A. abyssinica, A. vaviloviana, A. barbata* and *A. magna* and the diploids *A. strigosa, A. hirtula, A. longiglumis, A. pilosa, A. clauda* and *A. ventricosa.* Their general classification of northern *A. sativa* cultivars as very sensitive to daylength, of Mediterranean diploids as moderately sensitive and of the tetraploids of the *A. abyssinica–barbata* group as least sensitive agrees quite well with Griffiths (1961).

Sampson and Burrows (1972) also showed a short-day vernalisation response in *A. hirtula* and a cultivar of *A. sativa.* A strong cold vernalisation response (after 7.2°C for 39 days) was obtained from *A. hirtula, A. clauda, A. ventricosa, A. abyssinica, A. sterilis* and weaker responses from a cultivar of *A. sativa* and from *A. byzantina* and *A. strigosa.* They postulated that these mechanims prevent floral initiation in the autumn when daylength is the same as that which promotes flowering in the spring. This enables autumn-germinating plants to overwinter in the vegetative stage.

Whalley and Burfitt (1972) report from New South Wales that two samples of *A. barbata* and one of *A. sterilis* exhibited a vernalisation requirement for flowering, but that a sample of *A. fatua* did not.

Other characteristics of flowering which differed with geographical origin when plants were grown under the same conditions in England are the number of culms and seeds per plant (Thurston 1964). British plants of *A. fatua* had five culms and produced 800 seeds, plants of Pakistani origin had 10-12 culms and produced less than 500 seeds and Australian ones had 7-8 culms and produced 400-530 seeds.

Maturation of *A. fatua* panicles occurs basipetally, but the individual spikelets mature acropetally. Florets appeared to be self-pollinated at about the 55th day (Green and Helgeson 1957).

Wild oats are normally self-pollinated and isolated plants will therefore set seed. Cross-fertilisation can also occur and crosses of *A. fatua* can occur with cultivated oats to produce intermediates (Thurston 1956). In *A. sterilis* and *A. fatua* cross-pollination can reach 1-12% (Imam and Allard 1965).

SEEDING

The time from planting to seeding naturally varies with the same factors affecting flowering (Lindsay 1956, Baker and Leighty 1958). In spring-sown cereals in Europe such as barley, first seeds of wild oats mature shortly before harvest (Koch and Rademacher 1966).

As the tillers of *A. fatua* matured rather faster than the main stem, their seeds started to mature at about the same time. The tertiary and secondary seeds started abscissing at about the 70th day reaching 97% seed shed by the

90th day. Primary seeds were slower and began shedding at the 75th day and reached 75% seed shed by the 90th day (Green and Helgeson 1957).

The number of seeds produced per plant depends on many factors and varies for *A. fatua* from 10 (Thurston 1956) to 500 or more (Thurston 1956, Green and Helgeson 1957). The time of emergence of an individual wild oat plant in a cereal crop regulates to some extent the amount of seed it produces, the earliest emerging producing most seed (Holroyd 1972c). Studies of seed production by successively emerging groups of wild oats in a series of twelve natural populations in spring barley have shown that the earliest emerging plants produced up to 200 seeds each while the last to emerge (up to 85 days after drilling) produced between 1 and 11 seeds each. Total seed production for the populations ranged from 944-28,512/m^2 (Chancellor and Peters 1972).

Wild oat seed production in other crops will vary according to the competitive ability of the crop. In an experiment with wild oats planted at 20/0.84 m^2 in four crops, the mean seed produced per 0.84 m^2 by them was 428 in barley cv. Zephyr, 569 in barley cv. Deba Abed, 789 in wheat cv. Rothwell Sprite and 4784 in field beans cv. Maris Bead (Chancellor and Peters 1970). Even in a single crop wild oat seed production varies according to the density and spacing of the crop and position of the weed. In an experiment in which 30 plants of *A. fatua* were planted per 0.84 m^2 within rows of spring barley sown at 188.1 kg/ha in 20.3 cm rows, the wild oat seed production was 35 seeds per plant. On the other hand, *A. fatua* plants growing between rows of the same cultivar sown at 93.9 kg/ha in 20.3 cm rows, each wild oat plant averaged 108 seeds, a three-fold increase (Bate *et al* 1970).

Soil type may also influence seed production of *A. fatua.* When grown without a crop, wild oats in four soil types showed variation in the number of spikelets produced, the 1000 grain weights and in levels of dormancy (Odgaard 1972). On fen soil spikelets produced per m^2 were 28,412, on sandy soil 15,028, on loam soil 20,712 and on heavy marsh soil 18,020. The 1000 grain weights were 11.0 g on fen soil, 13.4 g on sandy soil, 14.7 g on loam soil and 14.0 g on marsh soil. The germination percentage taken after seven days was 35% for seeds produced on fen soil, 17% for seeds from sandy soil, 10% from loam soil and 6% from marsh soil, but the relationship was probably indirect.

All these factors influence the behaviour of wild oat populations: for further information on population dynamics see Chapter 7.