

Selection on apomictic lineages of *Taraxacum* at establishment in a mixed sexual–apomictic population

C. G. F. DE KOVEL & G. DE JONG

Evolutionary Population Biology, Faculty of Biology, Utrecht University, Padualaan 8, NL-3584 CH Utrecht, The Netherlands

Keywords:

apomixis;
asexuality;
evolution;
polyploidy;
selection;
Taraxacum.

Abstract

A species' mode of reproduction, sexual or asexual, will affect its ecology and evolution. In many species, asexuality is related to polyploidy. In *Taraxacum*, apomicts are triploid, and sexuals are diploid. To disentangle the effects of ploidy level and reproductive mode on life-history traits, we compared established apomictic *Taraxacum* genotypes with newly synthesized apomictic genotypes, obtained from diploid–triploid crosses. Diploid–triploid crossing is probably the way that most apomictic lineages originate. New genotypes had on average a much lower seed set than established genotypes. Established genotypes differed on average from new genotypes, in particular under shaded conditions: the established genotypes had longer leaves and flowered later. The differences between new and established triploids resembled the differences that have been found between sexual diploids and established apomictic triploids. We conclude that ploidy differences alone are not directly responsible for observed differences between sexual diploid and apomictic triploid dandelions.

Introduction

Sexual and asexual reproduction

The disparate consequences of sexual vs. asexual reproduction for a species' evolution have been discussed many times over the past decades (Williams, 1975; Bell, 1982; Crow, 1994; Barton & Charlesworth, 1998). Evolutionary paths of sexual and asexual species are likely to diverge when environmental conditions are heterogeneous in time or space. Theoretically, the faithful reproduction of the genotype in an asexual lineage will allow such a lineage to dominate in its favoured niche, if this niche is constantly available over time (Vrijenhoek, 1984). Such conditions are favourable for specialized asexual genotypes. Sexual types will not be able to compete successfully with such asexual lineages, as recombination will break up their genotypes every

generation (Case & Taper, 1986). In this way, a combination of asexual lineages outcompetes a population of sexual conspecifics in a spatially heterogeneous, but constant environment (Weeks, 1993). The breaking-up of genotypic combinations by recombination may also hinder sexual species in extending into new niches (García-Ramos & Kirkpatrick, 1997; Kirkpatrick & Barton, 1997). Asexuals do not have this limitation (Roughgarden, 1972). When conditions vary over time at an intermediate time scale, a combination of recombination and changes in allele frequencies can create new genotypes in sexual species so that the majority of the population consists of adapted specialists (Crow, 1994; Bürger, 1999), provided the genetic variation is large enough. Asexual lineages are unable to do so. Selection between asexual lineages, of course, can alter the genetic composition of an asexual community, but new, better-adapted genotypes do not arise by mutation alone at a sufficient rate (Bürger, 1999). Under these conditions, selection will favour generalist asexual genotypes over specialist genotypes. Such genotypes have been called general-purpose genotypes (Lynch, 1984).

Two reproductively isolated species, occupying the same niches, can diverge during evolution (Abrams,

Correspondence: Ms C. G. F. de Kovel, Faculty of Biology, Utrecht University, Padualaan 8, NL-3584 CH Utrecht, The Netherlands.
Tel.: +31 30 2532266; fax: +31 30 2542219;
e-mail: C.G.F.deKovel@bio.uu.nl

1986). Such displacement will reduce competition. Competing sexual and asexual types of species are reproductively isolated and competition between them may lead to niche divergence. As they experience different constraints on evolution, the sexual and asexual types might therefore well diverge in directions that are not random. Sexuality, or the lack of it, may also 'pre-adapt' species for certain conditions, affecting further evolution. So, for several reasons sexual and asexual forms of a species may diverge with time.

Theoretical concepts about sex are well developed, but empirical data are still scarce (West *et al.*, 1999). In laboratory experiments, directional selection on geotaxis caused an increase in recombination (Korol & Iliadi, 1994). The expectation of faster adaptation of sexuals to changing conditions was confirmed in an experiment with yeast (Greig *et al.*, 1998), but was not borne out in some other experiments (Da Silva & Bell, 1996; Turner & Chao, 1998). Field experiments also have shown mixed results (Antonovics & Ellstrand, 1984; Ellstrand & Antonovics, 1985; Kelley *et al.*, 1988). The type and extent of environmental heterogeneity that species encounter in the field, however, cannot easily be quantified and compared to theoretical models. One approach to study the significance of sexual reproduction is to compare sexually and asexually reproducing types of the same species. We would like to understand the niche relationships of sexuals and asexuals. If no different opportunities or constraints apply to the different types, asexual phenotypes can be a random subset of those present in the sexual population, so-called 'frozen niches' (*sensu* Vrijenhoek, 1984). Non-random subsets could be wide-niched clones, i.e. 'general-purpose genotypes' (Lynch, 1984). Alternatively, asexuals could have niches that are shifted away from the sexuals by competition (Weeks, 1993) or because their mode of reproduction makes them better suited to certain niches. In this study, we investigate for what traits asexual clones are selected on establishment in a mixed sexual–asexual population.

Taraxacum as a model system

In many species, asexuality is related to polyploidy (Bierzychudek, 1985); this is also the case with *Taraxacum*. *Taraxacum* forms an agamic complex comprising sexually reproducing diploids and apomictic polyploids. The most common polyploid is triploid. The species shows geographical parthenogenesis over Europe. Diploid sexual genotypes are common in France, but their relative frequency declines towards the north. In the northern parts of Europe, diploids are virtually absent (Den Nijs & Sterk, 1984a,b). Another area of diploid occurrence is in Central Europe with its focus in Slovakia (Den Nijs *et al.*, 1990).

The origin of the triploid apomictic genotypes is largely unknown (Richards, 1973). They may result from ancient hybridizations. However, triploids are able to

backcross with diploids in mixed populations. Female meiosis in apomicts is usually restitutional and produces unreduced, parthenogenetically developing seeds. Male meiosis is irregular, producing pollen containing from only a few chromosomes up to a complete triploid set of chromosomes (Jenniskens *et al.*, 1985). Unreduced pollen or pollen accidentally containing one or two viable set of chromosomes can fertilize reduced ovules in sexual diploids. Crosses with diploids acting as mothers and triploids as fathers have low success. Such crosses usually result in triploid and tetraploid offspring (Morita *et al.*, 1990). The frequency of such hybridizations in nature is likely to be low. From an extensive study on allozyme variation in mixed diploid/triploids *Taraxacum* populations, Menken *et al.* (1995) concluded that gene flow between the two ploidy levels is common. This conclusion was based on the facts that allozyme polymorphisms were shared within mixed populations, and that population-unique alleles occurred at both ploidy levels. It is therefore possible that most extant triploid lineages are of recent origin.

If most extant triploid lineages have been created through backcrossing, comparing established and newly formed triploid apomicts allows us to identify the traits for which apomictic triploids are selected. Triploids formed by backcrossing under controlled conditions have experienced little selection. Established lineages are expected to be a subset of those genotypes that are formed.

In addition, such backcrosses that produce new apomicts can give insight in the nature of the observed differences between sexuals and apomicts. Some differences found so far between diploid sexuals and triploid apomicts (Elzinga *et al.*, 1987; De Kovel & De Jong, 1999) may be solely the result of the higher ploidy level in apomicts, whereas other differences potentially reflect different responses to selection pressures. If newly formed triploids are on average more similar to diploids than established triploids are, this indicates that differences between established triploids and the sexual diploids could be the result of selection. We studied growth, morphological and life-history traits that have been shown to differ between diploid sexuals and triploid apomicts.

Materials and methods

Seeds

New triploids. Diploid plants were collected in a mixed diploid/triploid population, called Bovenste Polder in Wageningen, the Netherlands (52°N, 5°E). Diploidy of the collected plants was established by flow cytometry (Ulrich & Ulrich, 1991), which measures the amount of DNA per nucleus. Seeds from these plants were grown at the Nederlands Instituut voor Oecologisch Onderzoek (NIOO-CTO, Heteren) and mature diploid plants were

put into a field containing only triploid dandelions. This field was a moist meadow used for haymaking. Seeds recovered from these diploid mother plants were grown in the greenhouse at the Institute and screened for ploidy level. Triploid offspring plants that produced triploid seeds apomictically were selected for the current experiment. Seed set percentage varied hugely among these new genotypes. For practical reasons we selected 12 plants with seed set above 50% for this experiment.

Established triploids. In the same all-triploids field that had provided the fathers for the new triploids, a number of plants were screened with the intergenic spacer of ribosomal DNA as a marker (Van Dijk, 1997). Eleven plants with different genotypes were selected and seeds from these plants were used in this experiment. One capitulum per mother was randomly selected to provide the seeds for the experiment.

Pilot experiment

From each mother 10 mature-looking seeds were weighed. Per mother 20 seeds were put in a Petri dish and stored in an incubator with 16 h of light per 24 h and temperature of 17 °C during daytime and 14 °C during night hours. After 21 days, the number of germinated seeds was counted.

Treatments

The experiment was carried out on benches in an open greenhouse. On 29 June 1998, seeds were sown in 12 × 12 cm pots, filled with a 1:1 mixture of sieved black soil and sand. Per pot, three mature-looking seeds were sown. On 1 September, plants were removed until one per pot was left. Two treatments were applied and each genotype was replicated within the treatment, so a total number of 96 pots were employed. Treatments were either shaded or unshaded. Shade was provided by a cage covered by green foil, whereas the unshaded treatments were carried out in cages covered with transparent foil. The treatments received enough water to saturate the soil. Water application was decreased when temperatures dropped and was stopped altogether when frost set in. In spring, water application was resumed.

Measurements

Germination was recorded regularly. The length of the longest leaf per plant was recorded on 25 August, 17 September, and 12 October 1998 and on 27 May 1999; the number of leaves per plant was recorded on the same dates as well as on 31 July 1998 and 17 March 1999. Flowers were counted when fully open, every other day during the flowering period. Seeds were collected in paper bags. From the first capitulum of each plant, 10

seeds were weighed collectively. Twenty seeds from each of the first three capitula per plant were placed on a wet filter paper in a Petri-dish right after harvesting under conditions as mentioned above and the number of germinated seeds was counted after 14 days.

Harvest

All plants were harvested on 7 and 8 June 1999, when flowering appeared to have ended. Plants were separated into leaves, tap root and fine roots. All plant parts were dried at 70 °C for at least 48 h and subsequently weighed.

Data analysis

Pilot experiment. Weights of the seeds were compared between the new and established genotypes with ANOVA. To test whether germination ability of the seeds used for the experiment differed between new and established genotypes, a nonparametric Mann-Whitney *U*-test (MWU) was used.

Growth. Data from the same genotypes were pooled before further analysis. The effects of origin and treatment on leaf length and leaf number were analysed with ANOVA with treatment and origin (established vs. newly synthesized) as fixed factors and date as a covariate.

Plasticity was calculated per genotype, after averaging over duplicates, as the leaf length or leaf number in the shaded treatment minus that value in the unshaded treatment. Effect of origin on plasticity was analysed using ANOVA with origin as fixed factor and date as covariate.

Flowering. The number of capitula per plant was analysed with the MWU-test, as this value was not normally distributed. The analysis was carried out, either with origin as the grouping factor or with treatment as the grouping factor. The number of days until flowering was also tested with the MWU-test. The effect of origin was tested separately for the different treatments. The effects of origin and treatment on the number of seeds per capitulum were tested with ANOVA, as were the effects on weight of mature-looking seeds. The proportion of seeds that germinated was compared between plants from different origin with an MWU-test. The same test was used for the proportion of seeds per capitulum that had not developed. A Spearman rank correlation was used to analyse the relation between parental and offspring seed weight, as well as for the relation between seed weight and germination proportion. Plasticity in seed weight was analysed as plasticity in morphological traits.

Harvest. Dry weights were analysed with ANOVA with origin and treatment as fixed effects.

Results

Seed weight and germination in pilot experiment

Mature-looking seeds from established triploids were on average 0.716 ± 0.169 mg, whereas those from the new genotypes weighed only 0.568 ± 0.154 mg ($P = 0.039$). Germination ability differed also between the two sets: significantly more seeds from the established genotypes germinated than from the new genotypes: 13.7 ± 5.2 and 9.8 ± 4.1 out of 20, respectively ($P = 0.032$).

Germination

In the unshaded treatment, 19 out of 22 established and 14 out of 24 new plants survived until census, whereas 20 established and 13 new plants, out of 22 and 24, respectively, were counted in the shaded treatment. In both treatments, this made 11 established genotypes and nine new genotypes.

Growth

Leaf length increased during the summer. In winter, most plants had few leaves. During flowering in spring few new leaves emerged. The leaves measured on 27 May 1999 were the new leaves that sprouted after flowering and these were smaller than the earlier leaves. Treatment had a significant effect on leaf length on all four measurement dates: shaded leaves were longer ($P < 0.05$ for all dates). In addition, leaf number was lower in the shaded than in the unshaded treatment on all dates except 27 May 1999 ($P < 0.05$, 27 May $P = 0.525$). In the shaded treatment, the leaves of the new genotypes were shorter than those of established genotypes ($P < 0.05$), but in the unshaded treatment, no difference was found ($P = 0.355$) (Fig. 1). Origin of the genotypes did not affect the number of leaves ($P = 0.549$).

With respect to leaf length, the established genotypes were more plastic than the new genotypes ($P < 0.05$). Leaves of established triploids were, on average, 8.3 cm longer under shade conditions, whereas the new triploids were 4.6 cm longer. Plasticity in leaf number did not differ between plants from different origins ($P = 0.327$).

Flowering and seed set

The plants in the experiment flowered some days before the wild populations. The average number of capitula per plant over two treatments was $3.9 (\pm 1.9)$. Shading decreased the number of capitula significantly from 5.1 to 2.8 ($P < 0.05$, MWU). New and established genotypes produced the same number of capitula on average ($P = 0.261$ MWU). Flowering was delayed by shading. New genotypes flowered on average almost 2 days earlier

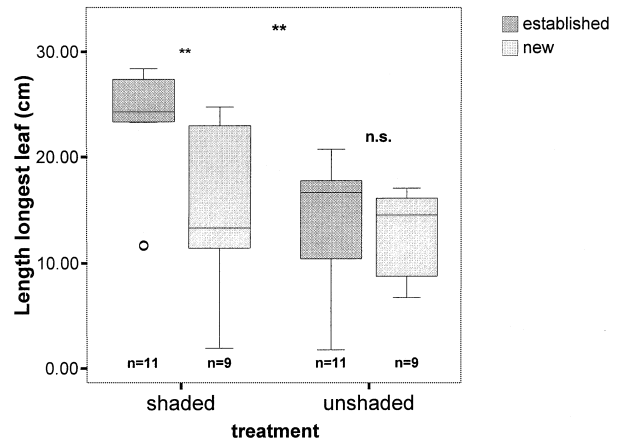


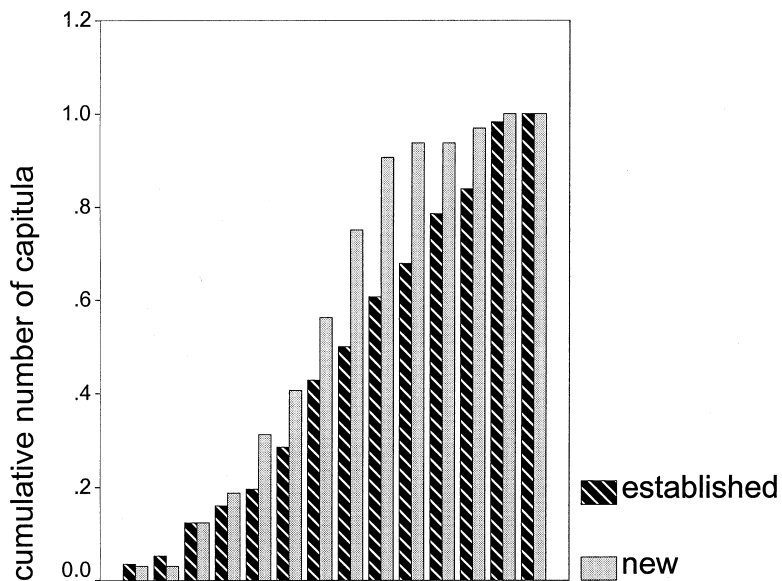
Fig. 1 Lengths (cm) of the longest leaf per genotype of established and new *Taraxacum* genotypes under shaded and unshaded conditions on 17 September 1998. The box contains 50% of the data; the whiskers extend from lowest to highest values, excluding outliers (○).

($P = 0.03$, MWU). This effect was only due to the shaded treatment (Fig. 2). The number of ovules produced per capitulum was on average 187 ± 35 . This was not affected by shading ($P = 0.788$), nor by origin of the genotypes ($P = 0.560$). Some seeds in each capitulum were small and white instead of brown. We considered them undeveloped. The fraction of seeds that looked mature was lower in the new genotypes than in the established ($P < 0.05$): 71% and 88%, respectively. A lower fraction of the mature-looking seeds germinated in the new genotypes ($P < 0.05$), also after correction for seed weight ($P < 0.05$). The average probability that an ovule of a new genotype would produce a viable seed was therefore 46%, while in the established genotypes the average was 71% ($P < 0.05$). Germination probability ranged from 12 to 73% in the new genotypes and 20 to 89% in the established genotypes. A treatment effect on germination of mature-looking seeds was not found ($P = 0.242$) (Fig. 3). The weight of apparently mature seeds was on average 29% lower in the shaded treatment than in the unshaded treatment ($P < 0.05$) (Fig. 4). Plasticity in seed weight did not differ significantly between genotypes from different origins ($P = 0.605$). Origin of the genotypes did not affect the weight of these seeds significantly ($P = 0.056$). Seed weight of the mature seeds was positively correlated with germination percentage ($r = 0.346$, $P < 0.01$).

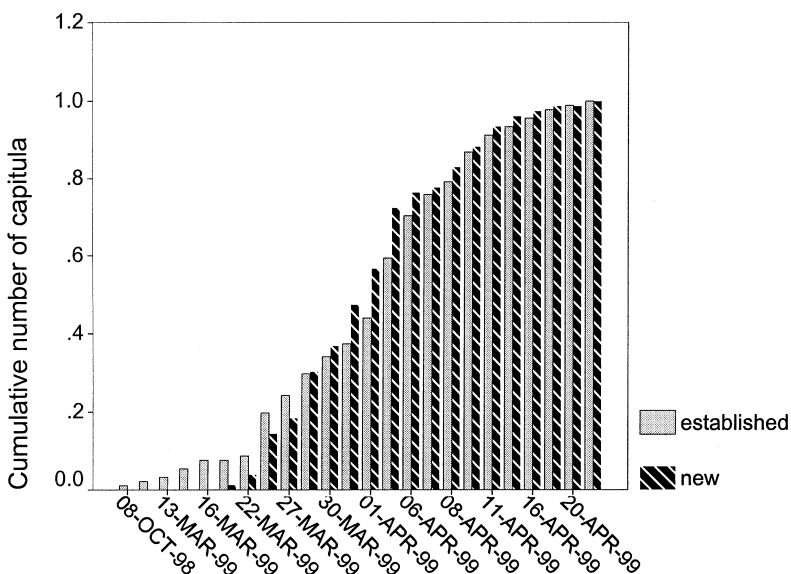
The weight of the seeds produced by the plants in the experiment did not correlate with the weight of the original seeds ($r = -0.088$, $P = 0.554$).

Harvest

Total dry weights were 2.62 g (± 1.12) in the shaded and 4.44 g (± 1.66) in the unshaded treatment ($P < 0.05$), and



(a) Date



(b) Date

Fig. 2 Cumulative proportion of flowering capitula on established and new genotypes of *Taraxacum*: (a) shaded treatment; (b) unshaded treatment.

a smaller proportion of biomass was present in the leaves in the unshaded treatment ($P < 0.05$). Between new and established genotypes, no differences were found in total dry weight ($P = 0.861$), nor in the ratio of leaf weight to total weight ($P = 0.182$).

Correlation coefficients between leaf length and germination probability in the newly synthesized triploids were positive for some dates and negative for others, but not significant for any date ($P = 0.084$, $P = 0.210$, $P = 0.143$, $P = 0.146$).

The seeds used for the experiment of the new genotypes were lighter than those of the established genotypes. The origin of the seeds differed: seeds from new genotypes had been collected in the greenhouse, whereas seeds from established genotypes were collected in the field. As seed weight is plastic with respect to environmental conditions, this difference may have been environmental rather than genetic. These differences may conceivably have affected subsequent growth as a maternal effect (Andalo *et al.*, 1999). Against this, it can

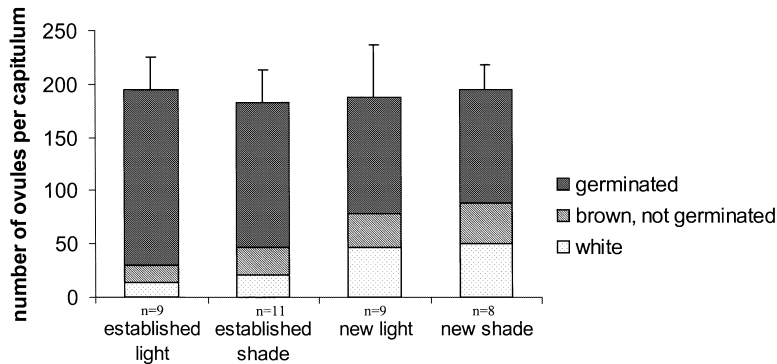


Fig. 3 Total number of ovules per capitulum of established and new *Taraxacum* genotypes under shaded and unshaded conditions. Data are shown for the first capitulum per plant. Error bars represent one standard deviation. Patterns show the fractions that looked undeveloped and that looked mature. The fractions of mature-looking seeds that germinated are extrapolated from the germination experiment.

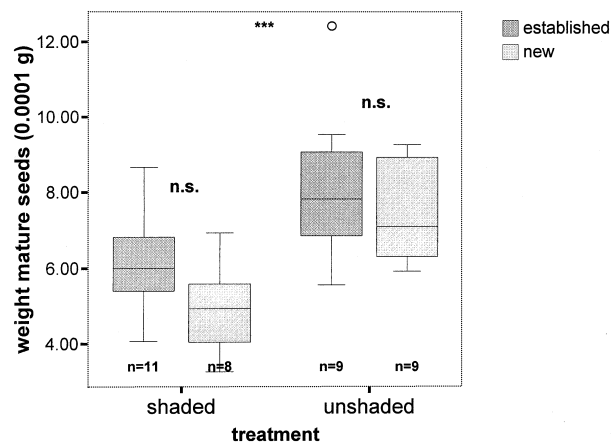


Fig. 4 Weight of 10 apparently mature seeds (mg) of new and established *Taraxacum* genotypes under shaded and unshaded conditions. The box contains 50% of the data; the whiskers extend from lowest to highest values, excluding outliers.

be argued that dry weight at harvest did not differ between plants from different origin.

Discussion

Differences between sexual diploid and apomictic triploid *Taraxacum* have been found previously; diploids had shorter leaves than triploids, in particular in shaded conditions (De Kovel & De Jong, 1999). In another study, diploids had lighter seeds than triploids; shifts in flowering time between diploids and triploids have been found in both directions, depending on the conditions (De Kovel & De Jong, 1999; unpublished). In these observations the effects of ploidy level and mode of reproduction were confounded. To study the consequences of reproductive mode, it is necessary to distinguish between any effects of asexuality and ploidy level. We therefore compared newly synthesized triploids with established triploids. If ploidy level by itself leads to a difference with diploids, it should be visible in the new triploids. If ploidy is the only cause of any difference, new

and established triploids should be identical. On the other hand, if the new triploids differ from established triploids, a range of alternative hypotheses about the ecological relation between sexuals and asexuals comes into view.

In this study, we found that established triploids were not a random selection from the new triploids. New triploids had shorter leaves on average than established triploids, especially under shaded conditions, and they seemed to be less plastic in leaf size response to shading. In addition, new triploids flowered slightly earlier, again mainly under shaded conditions. Mature seeds of new triploids tended to be lighter in shade than those of established triploids. The longest leaves and the heaviest seeds belonged to the established triploids; shortest leaves and lightest seeds belonged to the new triploids. So, an explanation beyond the effects of polyploidy is needed.

The most obvious difference between new and established triploids was in the production of germinating seeds. Though the number of capitula and the number of ovules per capitulum were the same in both types of dandelions, the number of germinating seeds was much lower in the new triploids. For this experiment, we used only those new genotypes that had above average seed set in the previous generation (see Materials and methods). If seed set characteristics in these genotypes are heritable, the difference in production of germinating seeds between new and established triploids will be much larger than shown in this experiment. The same low fecundity of new asexuals was found in a comparable experiment with *Poeciliopsis* fish (Wetherington *et al.*, 1987).

In a weedy species like dandelion, selection for high fecundity will be strong. If other traits are correlated with fecundity, they will hitchhike along with it. In our study, no correlation between morphological traits and fecundity was found in the new triploids, which means that a response to selection on those traits will be independent from selection on fecundity.

If conditions have not changed directionally over time, the new triploids could represent the pool of genotypes from which established triploids have been recruited. The differences in trait values between new and established

triploids then correspond to selection for those traits. The conclusion would be that asexuals are selected for longer and more plastic leaves than sexuals. If this interpretation is correct, the question is: why would the two reproductive types have different optima? It is curious that the differences seem larger under shaded conditions. A first explanation is that ploidy level causes differences in physiology that define different optimal values. It has been shown that for a number of species, polyploidization changes photosynthetic rates, because it affects cell size (Warner & Edwards, 1993). This in turn may influence the optimal shape and positioning of leaves and possibly other traits. There are other possibilities, though.

The difference between new and established triploids could be a case of niche shift and character displacement through competition with the sexuals (Abrams, 1986). Because of this competition between sexuals and apomicts, apomictic genotypes that have less niche overlap with the sexual population are more likely to establish (Weeks, 1993). This view assumes that asexual genotypes are specialized to some subniche that is available at all times. Many different asexual lineages can establish as long as they have limited overlap with niches of other asexual lineages or with the sexual population. This corresponds to the frozen niche variation hypothesis (Vrijenhoek, 1979). In the above hypothesis, new triploids will be similar to diploids, but established lineages will show traits that enable them to exploit niches that are not fully exploited by the sexuals. In the current study, established triploids had longer leaves than the average of the new genotypes: a trait that probably enables them to grow in high vegetation (Van Hinsberg, 1997). In a field survey in the Netherlands, diploids had a more xerothermic distribution than triploids (Roetman *et al.*, 1988). This supports the idea of a niche shift between the reproductive modes, though its cause is not clear.

It is also possible that the new triploids do not resemble the pool from which the majority of the established triploids have been recruited. The diploid mothers had been collected in a field at about 5 km distance from the field where the established triploids and the triploid fathers had been collected. It is therefore possible that the diploid mothers were adapted to some local conditions and for that reason had alleles for, e.g. shorter, less plastic leaves than the established triploids. They would have transmitted these alleles to the hybrid offspring. It is intriguing, though, that the differences observed between new and established triploids were in the same direction as those observed between sexual diploids and apomictic triploids from the same field (De Kovel & De Jong, 1999). For this last study, diploids and triploids had been collected in the same field from where the diploids had been collected for the current study. This suggests that the pattern goes beyond local adaptation. A replicate experiment using plants from different localities may be able to make this more clear.

In summary, the data show that established apomictic triploids differ in a number of traits from triploids created by backcrosses between sexual diploids and apomictic triploids. New triploids have shorter leaves under shaded conditions as well as delayed flowering, and their leaf morphology responds less plastic to shading. In these respects, they are more similar to sexual diploids than are the established triploids. This suggests that differences found in previous experiments between sexual diploids and apomictic triploids are not solely the direct consequence of polyploidization, but that selection also plays a role.

The majority of the triploids created by backcrossing produced fewer viable seeds than the established triploids. Establishment chances of backcross offspring created under natural conditions are considered to be very low, but existing.

Acknowledgments

This work was supported by the Life Sciences Foundation (SLW), which is subsidized by the Netherlands Organization for Scientific Research (NWO). We thank P. van Dijk from the NIOO for providing the new triploids, and Z. Bochdanovits and two anonymous reviewers for comments on the manuscript.

References

- Abrams, P.A. 1986. Character displacement and niche shift analyzed using consumer-resource models of competition. *Theor. Popul. Biol.* **29**: 107–160.
- Andalo, C., Mazer, S.J., Godelle, B. & Machon, N. 1999. Parental environmental effects on life history traits in *Arabidopsis thaliana* (Brassicaceae). *New Phytol.* **142**: 173–184.
- Antonovics, J. & Ellstrand, L.C. 1984. Experimental studies of the evolutionary significance of sexual reproduction. I. a test of the frequency-dependent selection hypothesis. *Evolution* **38**: 103–115.
- Barton, N.H. & Charlesworth, B. 1998. Why sex and recombination? *Science* **281**: 1986–1990.
- Bell, G. 1982. *The Masterpiece of Nature: The Evolution and Genetics of Sexuality*, 1st edn. Croom-Helm, London.
- Bierzzychudek, P. 1985. Patterns in plant parthenogenesis. *Experientia* **41**: 1255–1264.
- Bürger, R. 1999. Evolution of genetic variability and the advantage of sex and recombination in changing environments. *Genetics* **153**: 1055–1069.
- Case, T.J. & Taper, M.L. 1986. On the coexistence and coevolution of asexual and sexual competitors. *Evolution* **40**: 366–387.
- Crow, J.F. 1994. Advantages of sexual reproduction. *Dev. Gen.* **15**: 205–213.
- Da Silva, J. & Bell, G. 1996. The ecology and genetics of fitness in *Chlamydomonas* VII. The effect of sex on the variance in fitness and mean fitness. *Evolution* **50**: 1705–1713.
- De Kovel, C.G.F. & De Jong, G. 1999. Responses of sexual and apomictic genotypes of *Taraxacum officinale* to variation in light. *Plant Biol.* **1**: 541–546.

- Den Nijs, J.C.M., Kirschner, J., Štěpánek, J. & Van der Hulst, A. 1990. Distribution of diploid sexual plants of *Taraxacum* sect. *Ruderalia* in east-Central Europe, with special reference to Czechoslovakia. *Pl. Syst. Evol.* **170**: 71–84.
- Den Nijs, J.C.M. & Sterk, A.A. 1984a. Cytogeography of *Taraxacum* sectio *Taraxacum* and sectio *Alpestris* in France and adjacent parts of Italy and Switzerland, including some taxonomic remarks. *Acta Bot. Neerl.* **33**: 1–24.
- Den Nijs, J.C.M. & Sterk, A.A. 1984b. Cytogeography and cytotaxonomy of some *Taraxacum* sections in Belgium and northern France. *Acta Bot. Neerl.* **33**: 431–455.
- Ellstrand, L.C. & Antonovics, J. 1985. Experimental study of the evolutionary significance of sexual reproduction. II. a test of the density-dependent selection hypothesis. *Evolution* **39**: 657–666.
- Elzinga, D., Van der Kamp, J., Den Nijs, J.C.M. & Sterk, A.A. 1987. Cytogeography and ecology of diploids and triploids of *Taraxacum* section *Taraxacum* in South Limburg, Netherlands. *Proc. K. N. A. W.* **90**: 431–442.
- García-Ramos, G. & Kirkpatrick, M. 1997. Genetic models of adaptation and gene flow in peripheral populations. *Evolution* **51**: 21–28.
- Greig, D., Borts, R.H. & Louis, E.J. 1998. The effect of sex on the adaptation to high temperatures in heterozygous and homozygous yeast. *Proc. R. Soc. Lond. B.* **265**: 1017–1023.
- Jenniskens, M.-J.P.J., Den Nijs, J.C.M. & Sterk, A.A. 1985. Crossability and hybridization of taxa of *Taraxacum* section *Taraxacum* from central and western Europe. *Proc. K. N. A. W.* **88**: 297–338.
- Kelley, S.E., Antonovics, J. & Schmitt, J. 1988. A test of short-term advantage of sexual reproduction. *Nature* **331**: 714–716.
- Kirkpatrick, M. & Barton, N.H. 1997. Evolution of a species' range. *Am. Natur.* **150**: 1–23.
- Korol, A.B. & Iliadi, K.G. 1994. Increased recombination frequencies resulting from directional selection for geotaxis in *Drosophila*. *Heredity* **72**: 64–68.
- Lynch, M. 1984. Destabilizing hybridization, general-purpose genotypes and geographic parthenogenesis. *Q. Rev. Biol.* **59**: 257–290.
- Menken, S.B., Smit, E. & Den Nijs, J.C.M. 1995. Genetical population structure in plants: gene flow between diploid sexual and triploid asexual dandelions (*Taraxacum* section *Ruderalia*). *Evolution* **49**: 1108–1118.
- Morita, T., Sterk, A.A. & Den Nijs, J.C.M. 1990. The significance of agamospermous triploid pollen donors in the sexual relationships between diploids and triploids in *Taraxacum* (Compositae). *Pl. Species Biol.* **5**: 167–176.
- Richards, A.J. 1973. The origin of *Taraxacum* agamospecies. *Bot. J. Linn. Soc.* **66**: 89–111.
- Roetman, E., Den Nijs, J.C.M. & Sterk, A.A. 1988. Distribution and habitat range of diploid sexual dandelions (*Taraxacum* section *Vulgaria*), a Central European flora element in the Netherlands. *Acta Bot. Neerl.* **37**: 1–4.
- Roughgarden, J. 1972. Evolution of niche width. *Am. Natur.* **106**: 683–718.
- Turner, P.E. & Chao, L. 1998. Sex and the evolution of intrahost competition in RNA virus phi 6. *Genetics* **150**: 523–532.
- Ulrich, L. & Ulrich, W. 1991. High-resolution flow cytometry of nuclear DNA in higher plants. *Protoplasma* **165**: 212–215.
- Van Dijk, P. 1997. Molecular markers for clone identification in *Taraxacum officinale* in the field. *Belgian J. Bot.* **129**: 156.
- Van Hinsberg, A. 1997. Morphological variation in *Plantago lanceolata* L. effects of light quality and growth regulators on sun and shade populations. *J. Evol. Biol.* **10**: 687–701.
- Vrijenhoek, R.C. 1979. Factors affecting clonal diversity and coexistence. *Am. Zool.* **19**: 787–797.
- Vrijenhoek, R.C. 1984. Ecological differentiation among clones: the frozen niche variation model. In: *Population Biology and Evolution* (K. Wöhrmann & V. Loeschcke, eds), pp. 217–231. Springer-Verlag, Berlin.
- Warner, D.A. & Edwards, G.E. 1993. Effects of polyploidy on photosynthesis. *Photosynthesis Res.* **35**: 135–148.
- Weeks, S.C. 1993. The effects of recurrent clonal formation on clonal invasion patterns and sexual persistence: a Monte Carlo simulation of the frozen niche-variation model. *Am. Natur.* **141**: 409–427.
- West, S.A., Lively, C.M. & Read, A.F. 1999. A pluralist approach to sex and recombination. *J. Evol. Biol.* **12**: 1003–1012.
- Wetherington, J.D., Kotora, K.E. & Vrijenhoek, R.C. 1987. A test for the spontaneous heterosis hypothesis for unisexual vertebrates. *Evolution* **41**: 721–731.
- Williams, G.C. 1975. *Sex and Evolution*. Princeton University Press, New Jersey.

Received 13 March 2000; accepted 2 May 2000