

their own recommendations following consultations. As our industry progresses and becomes more specialized this communication and understanding becomes more and more important and we make a point of regularly meeting with our customers for this purpose. It is in this last respect in the creation of better knowledge and understanding in the spirit of true cooperation that the role of I.P.P.S. features in the progress of the nursery industry.

LITERATURE CITED

1. Aldhous, J.R. 1972. Nursery Practice. Forestry Commission Bulletin 43, London.
2. Fordham, D.N. 1976. Production of plants from seed. *Proc. Inter. Plant Prop. Soc.* 26:139-145.
3. McMillan, Browse P.D.A. 1979. Hardy Woody plants from Seed. Grower Books, London.
4. Wood, A.T. 1977. Efficiency and Quality in Seedling Production. The proceedings of the twelfth refresher course for Nurseryman held at the Pershore College of Horticulture, Worcs. England.

SEXUAL FLEXIBILITY IN PLANTS

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Finding and producing non-fruiting trees is an important way of providing buyers with improved selections of landscape trees, but unexpected sex expression of trees can thwart such aspirations. Notwithstanding a possible mixup of budwood, an ephemeral change in the sex of a tree or any other plant can occur. Typically non-fruiting individuals occasionally may shift towards femaleness and bear fruit. In other cases, plants that normally have female sex expression, may shift in some years towards maleness and have only male flowers and, of course, no fruit.

From an ecological viewpoint, there seems good reason for expression of sexual flexibility in plants. Because of immobility, plant survival depends on the ability to cope in place, whatever the environmental stresses may be. Charnov and Bull (3) proposed that "labile sex determination (not fixed at conception) is favored by natural selection when an individual's fitness (as a male or female) is strongly influenced by environmental condi-

tions and where the individual has little control over which environment it will experience.”

Despite the probability of a plant's inherent traits to shift sex according to environmental constraints, sexual stability is critical in producing non-fruiting clones of trees. Incidents of sex shift and possible physiological bases for this shift are presented here to support the use of genetically uniform rootstocks to control sex expression of trees producing for landscape purposes.

SHIFT TOWARD INCREASED FEMALENESS

Several commercially produced tree clones are unique for their fruitlessness because they have exclusively male or asexual flowers. But occasionally some trees of these typically non-fruiting clones also will have female flowers that develop into fruit (Table 1). Noteworthy are clones of silver maple (*Acer saccharinum* L.), green ash (*Fraxinus pennsylvanica* var. *lanceolata* (Borkh.) Sarg.), thornless honeylocust (*Gleditsia triacanthos* forma *inermis* (L.) Zabel.), and prairie crabapple (*Malus ioensis* (Wood) Britt.). Without exception, these examples of fruiting or increased femaleness of typically non-fruiting clones were associated with severe drought or unusually low winter temperatures.

Table 1. Fruiting of typically non-fruiting tree clones.

Clone	Sex of typical flowers	Age of trees (estimated years)	Location (U.S.A.)	References*
<i>Acer saccharinum</i> 'Silver Queen'	Male	12	Michigan	2
		15	Iowa	5
		4	Nebraska	1
<i>Fraxinus pennsylvanica</i> var. <i>lanceolata</i> 'Marshall'	Male	4	Illinois	3
		4	New Jersey	4
<i>Gleditsia triacanthos</i> forma <i>inermis</i> ; variously named clones	Male	4	Illinois	3
		4	New Jersey	4
<i>Malus ioensis</i> 'Plena' (Bechtel crab apple)	Asexual, flowers double	10	Utah	6

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Clones that characteristically bear only a moderate amount of fruit also may exhibit erratic sex expression. For example, the original tree, or ortet, of the Moraine ash (*Fraxinus* 'Moraine'), located in Dayton, Ohio, bears only meager amounts of fruit (pers. communication, John Siebenthaler, Siebenthaler Nursery, Dayton, Ohio). A group of 47 trees, or ramets, of this clone are located in Berkeley, California. They were planted in 1963 as 8- to 9-foot budded stock on green ash seedlings grown from seed collected in Kansas and Oregon. Apparently the degree of femaleness, as suggested by fruit yield, was markedly different among these trees in both 1978 and 1979. The most pronounced difference was in 1978, following two years of severe drought, at which time 8 of the trees had abundant fruit, 7 had no fruit, and the others had amounts varying between these two extremes (Figure 1). The variable degree of fruiting might be linked to site differences, but there was no significant correlation between fruit yield and tree size for either year.

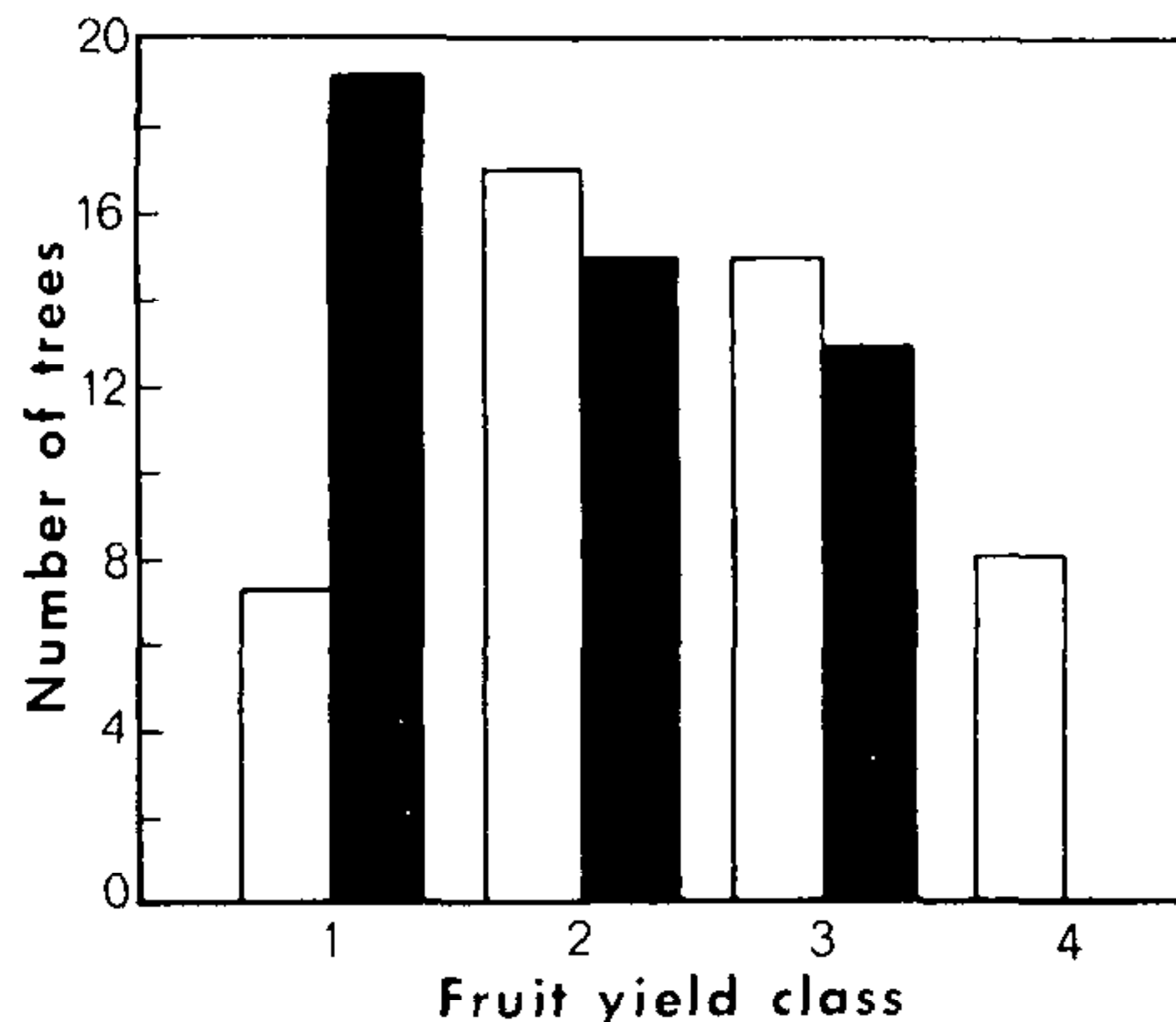


Figure 1. Frequency of fruit yield classes in 1978 (open bars) and 1979 (closed bars) of 47 *Fraxinus* 'Moraine' trees in Berkeley, California. Fruit yield classes: 1, none; 2, meager, 3, moderate; 4, abundant.

A shift towards increased femaleness has also been reported in conifers. At Wooster, Ohio, male plants of three dioecious species of yew (*Taxus*) have occasionally had a branch that produced fruit (14). At Philadelphia, Pennsylvania, following a drought year, conelets of several species of the monocious spruce (*Picea* spp.) appeared to be basically male but had female tissue of varying amounts. That is, instead of being typically male, some conelets were bisexual (22).

SHIFT TOWARD INCREASED MALENESS

Ephemeral or periodic shift of either an individual plant or a plant species towards increased maleness is also evident. We

monitored the sex expression of 46 trees of canyon maple (*Acer grandidentatum* Nutt.) in native stands in northeastern Utah in two consecutive flowering years, 1977 and 1979. The 1977 flowering coincided with a severe drought that had lasted for several months. Precipitation was more normal in 1979. During each of the two years 8 of the 46 trees had only male flowers and 26 had both female and male flowers (Figure 2). Sex expression differed from year to year in the remaining 12 trees. In 9 of them there were only male flowers in 1977 and both female and male flowers in 1979. The reverse was true of the other 3 trees; they had female and male flowers in 1977 and only male flowers in 1979. A male-flowering tree selected in 1977 from these 46 trees would thus have had over a 50-percent chance of fruiting in 1979.

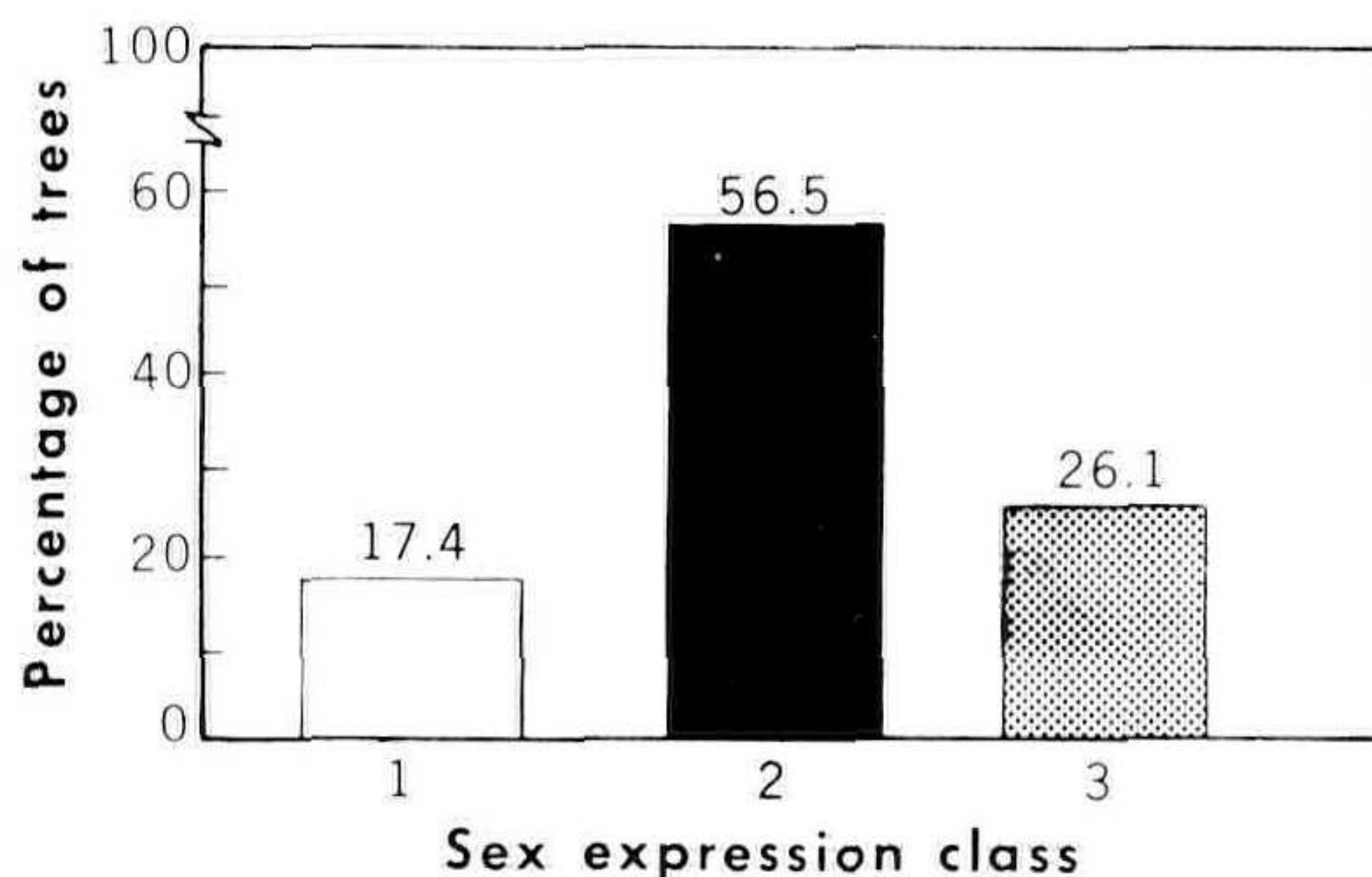


Figure 2. Frequency of 46 *Acer grandidentatum* trees by sex expression class: 1, only male flowers, 1977 and 1979; 2, both female and male flowers, 1977 and 1979; 3, sex conversion; only male flowers one of the years and both female and male flowers the other year.

These findings are supported by numerous reports of increased maleness in various plant species when grown under arid versus more favorable soil moisture conditions. Male plants of five dioecious species in natural stands in Utah were most abundant on sites considered to be under intense water stress (5). Among a group of Norway maples (*Acer platanoides* L.) planted in Stockholm, Sweden, exclusive maleness was higher on poor, dry soil than on more moist sites (25). In the generally dioecious bog myrtle (*Myrica gale* L.) proportionately more male plants have been found in dry areas than in wet areas of peat moors in the United Kingdom (4).

Ordinarily, the earliest flowers on young cucumber (*Cucumis* spp.) plants are male; then with advancing age of the plant, female flowers are also produced. Again, the expression of exclusive maleness in cucumbers was stronger and of longer duration in plants grown in dry, versus wet, soil (18).

Some plants provide evidence that stressful temperatures

promote maleness corresponding to the effect of drought stress. McArthur (17) observed significantly fewer female plants in a plantation of the dioecious shrub *Atriplex canescens* (Pursh) Nutt. following a mild fall and then a winter of unusually low temperatures as opposed to previous years of more normal temperatures.

PHYSIOLOGICAL BASES FOR SEXUAL FLEXIBILITY

Several deductions can be made from these reports of apparent sexual flexibility in plants. First, the phenomenon is evidently not unusual. As reasonably large populations of plants are observed over successive years and under a wide range of climatic conditions, certain plants within many species will undoubtedly be found to vacillate in their sex expression from year to year. That the sex of plants is genetically fixed is not always valid.

But if sex expression in plants is not genetically fixed, then how is it regulated? Evidence suggests that a delicate balance in critical hormones influences sex expression. A shift in this hormonal balance mediates a corresponding shift in sex expression (2,16). An increase of one hormone (from endogenous or exogenous sources), or a decrease of another, may alter the sex expression of a plant.

Cytokinins may be the most important group of hormones regulating sex expression of plants. These plant hormones are essential in the meiotic cell division of pistillate tissue of undifferentiated flower buds in grape (*Vitis*) (20) and spider flower (*Cleome*) (13), species of two widely separated genera. The ratio of cytokinins to gibberellins was recently reported to determine the sex of individuals of spinach (*Spinacia oleraca* L.) and hemp (*Cannabis sativa* L.) (2). In these two species, female plants resulted from a proportionate abundance of cytokinins.

Roots are considered a major site of biosynthesis of cytokinins (2,15). Apparently the rate of cytokinin synthesis or transport is strongly influenced by root environment (24). For example, root systems subjected to water stress (drought) export lowered amounts of cytokinins via the xylem sap to the shoot system (11,12,19). Similarly, the cytokinin supply becomes depressed when roots are subjected to other stresses such as salinity (9,10), flooding (1,21), and heat (8,9). The similarity of response to diverse environmental stresses suggests that plants have a common regulatory mechanism which responds to environmental stresses, and this mechanism involves rapid change in hormonal balance within a plant (24).

Hypothetically, then, an ephemeral shift in sex expression in plants is the result of an unusually stressful environment that

affects biosynthesis of cytokinin and possibly other hormones in the roots which in turn affects the balance of hormones in the shoot tips when flowers are sexually differentiating.

This hypothesis could account for the apparent shift towards increased maleness in the canyon maple, discussed above. That is, the drought preceding the 1977 flowering season inhibited cytokinin biosynthesis in the roots and export to the shoots. Consequently pistil development was inhibited, resulting in repressed femaleness. In the case of all male-flowering plants that year, the cytokinins possibly dropped to a threshold level that precluded pistil development in any of the flowers.

But how does this hypothesis explain those instances cited where typically male and asexual plants fruited? It is possible that cytokinins normally are near a threshold level and that environmental stress lowers that level even further; auxins (6,7), or other feminizing hormones, respond to this hormonal change by accumulating to a proportional level that affects sex expression.

In the case of each of the tree clones and the canyon maple, shift in sex expression has been observed in only a portion of extensive populations from virtually the same environment. This phenomenon can perhaps be attributed to the root system of each plant which was of seed origin and therefore genetically different from the others. As such, each root system probably had a varying influence on hormone balance in the roots and, therefore, on sex expression of the plant. Some root systems may have been genetically more capable than others of affecting sex expression of the top, as shown in grape plants (23). When the same clone of a Sultana grape (*Vitis vinifera* L.) was grown on three different rootstocks, the plants on one rootstock had the highest concentration of cytokinin in the sap, the most grapes per bunch (probably due to the most female flowers per inflorescence), and the highest yield by weight. Further evidence demonstrates that cytokinin affects sex expression: the gene for femaleness in the herbaceous annual *Mercuriales annua* L. was discovered to be the gene that controls cytokinin biosynthesis in the plant (16).

Indeed, if sex expression in plants is influenced by the amount of biosynthesis in the roots of cytokinins or other hormones, then stabilizing sex expression in typically non-fruiting clones that occasionally fruit may be achieved by homogeneous or genetically uniform rootstocks or by propagating clones on their own roots.

In summary, because of the plant hormone-environment interactions that apparently influence sex expression in plants, sexual flexibility in naturally occurring plants may be quite

common. But a shift in sex expression in commercially produced clonal plants in which sexual stability is desired is a breakdown in quality control. The problem may be prevented by clonal rootstocks or by "own root" production of clones, but the effectiveness of either practice needs to be determined.

LITERATURE CITED

1. Burrows, W.J. and D.J. Carr. 1969. Effects of flooding the root system of sunflower plants on the cytokinin content in xylem sap. *Physiol. Plant.* 22:1105-1112.
2. Chailakhyan, M. Kh. 1979. Genetic and hormonal regulation of growth, flowering and sex expression in plants. *Amer. J. Bot.* 66:717-736.
3. Charnov, E.L., and J.L. Bull, 1977. When is sex environmentally determined? *Nature* 266:828-830.
4. Davey, A.J. and C.M. Gibson. 1917. Note on the distribution of the sexes in *Myrica gale*. *New Phytol.* 16:147-151.
5. Freeman, D.C., L.G. Klikoff, and K.T. Harper. 1976. Differential resource utilization by the sexes of dioecious plants. *Science* 193:597-599.
6. Friedlander, M., D. Atsmon, and E. Galun. 1977. Sexual differentiation in cucumber: Abscisic acid and gibberellic acid contents of various sex genotypes. *Plant Cell Physiol.* 18:681-692.
7. Galun, E., S. Izhar, and D. Atsmon. 1965. Determination of relative auxin content in hermaphrodite and andromonoecious *Cucumis sativus* L. *Plant Physiol.* 40:321-325.
8. Itai, C., and A. Benzoini. 1974. Regulation of plant response to high temperatures. In *Mechanisms of regulation of plant growth* (Papers presented at the International Plant Physiology Symposium, Palmerston North, N.Z., Aug. 1973). *Royal Soc. N.Z. Bull. No.* 12:477-482.
9. Itai, C., A. Benzoini, and L. Ordin. 1973. Correlative changes in endogenous hormone levels and shoot growth induced by short heat treatments to the root. *Physiol. Plant.* 29:355-360.
10. Itai, C., A.E. Richmond, and Y. Vaadia. 1968. The role of root cytokinins during water and salinity stress. *Isr. J. Bot.* 17:187-193.
11. Itai, C., and Y. Vaadia. 1965. Kinetin-like activity in root exudate of water-stressed sunflower plants. *Physiol. Plant.* 18:941-944.
12. Itai, C., and Y. Vaadia. 1971. Cytokinin activity in water-stressed shoots. *Plant Physiol.* 47:87-90.
13. Jong, A.W. de, and J. Bruinsma. 1974. Pistil development in *Cleome* flowers. III. Effects of growth-regulating substances on flower buds of *Cleome iberidella* Welw. ex Oliv. grown in vitro. *Jacq. A. Pflanzenphysiol.* 72:227-236.
14. Keen, R.A., and L.C. Chadwick. 1954. Warn propagators to watch for sex reversal in *Taxus*. *Amer. Nurseryman* 100(6):13-14.
15. Kende, H., and D. Sitton. 1967. The physiological significance of kinetin and gibberellin-like root hormones. *Ann. N.Y. Acad. Sci.* 144:235-243.
16. Louis, J.P., and B. Durand. 1978. Studies with the dioecious angiosperm *Mercurialis annual* L. ($2n = 16$). *Molec. Gen. Genet.* 165:309-322.
17. McArthur, E.D. 1977. Environmentally induced changes of sex expression in *Atriplex canescens*. *Heredity* 38:97-103.
18. Minina, E.G., and P.P. Matskevich. 1944. *Izmenenie seksualnosti rastenii*

- v raznykh usloviyakh vlazhrosti sredy (Changes in sex of plants under various environmental moisture conditions). *Doklady Akademii Nauk* 12:323-326.
19. Mizrahi, Y., and A.E. Richmond. 1972. Hormonal modification of plant response to water stress. *Aust. J. Biol. Sci.* 25:437-442.
 20. Negi, S.S., and H.P. Olmo. 1966. Sex conversion in a male *Vitis vinifera* L. by a kinin. *Science* 152:1624-1625.
 21. Reid, D.M., and I.D. Railton. 1974. Effect of flooding on the growth of tomato plants: Involvement of cytokinins and gibberellins. *R. Soc. N.Z. Bull.* 12:789-792.
 22. Santamour, Frank S. 1959. Bisexual conelets in spruce. *Morris Arbor. Bull.* 10(1):10-11, Univ. Pa., Phila.
 23. Skene, K.G.M. 1972. Cytokinins in bleeding sap of the grape vine. p. 476-483. In D.J. Carr (ed.), *Plant growth substances*. Springer-Verlag, New York.
 24. Torrey, J.G. 1975. Root hormones and plant growth. *Ann. Rev. Plant Physiol.* 27:435-459.
 25. Wittrock, V.B. 1886. Uber die Geschlechterverteilung bei *Acer platanoides* L. und einige anderen *Acer*. Arten *Bot. Centralblatt.* 25(2):55-68.

MAXIMIZING SEEDLING GROWTH UNDER MIDWEST CONDITIONS

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