Gibberellin-Induced Inhibition of Bud Development in Some Species of Prunus

Abstract. Development of both floral and vegetative buds was inhibited by application of gibberellin to branches of *Prunus* species. The development of the lateral meristem was blocked, in general, through inhibition of mitosis, while, concurrently, the growth of certain other plant organs was stimulated in some cases. That higher dosages were required to block vegetative than floral bud growth suggests that gibberellin also exerts the more specific effect of inhibiting floral initiation.

The literature contains various references to stimulation of flowering of certain types of plants after gibberellin application. But only two reports of inhibition of flowering or floral initiation by treatment with gibberellin have come to our attention. When plants of *Kalanchoë blossfeldiana*, a short-day plant, were treated during noninductive conditions, buds appeared at about the same time as on controls in which budding was induced through short days; but few buds developed, and reversal to a vegetative phase ensued (*1*). In *Weigela* (*2*), flowering was induced in control plants exposed to the appropriate short-day photoperiod, but plants treated with gibberellin after exposure to that photoperiod failed to flower.

The following report deals with inhibition by gibberellin of both floral and vegetative bud development in certain species of *Prunus*. In photoperiod requirements, *Prunus* is not comparable to the other two genera, for its species are generally considered day-neutral. In one sense, however, the situations in *Prunus* and in *Weigela* were alike, for in both cases gibberellin was applied at times when conditions were otherwise suitable for floral initiation.

The first observations were made in 1957. Branches of apricot (*P. armeniaca* cv. Royal) were sprayed at the initiation of pit-hardening (10 April) with 100, 500, or 1000-mg/lit. concentrations of Gibrel (Merck and Co.), and some of the branches received a second application on 24 April. Branches of sweet cherry (*P. avium* cv. Bing) were treated at a similar phase of development with one application of a 500-mg/lit. concentration. As the season progressed, retardation of bud development on treated branches of both cherry and apricot became apparent. Approximately 15 buds in positions on control spurs normally occupied by floral buds were collected on 24 August from each species, and the same number were collected from spurs which had received an application of 500-mg/lit. concentration. Vegetative buds from long shoots were also collected. All buds were fixed in Newcomer's solution, embedded, sectioned, and stained with hematoxylin-fast green.

In the apricot, flower buds from controls contained well-defined primordia of sepals, petals, and stamens (Fig. 1*a*). In buds from treated branches, however, the rounded, rather than flattened, growing points showed that the buds had not attained the initial phase of floral differentiation (Fig. 1*b*). Bud scales were still being cut off from the growing points, indicating considerable retardation in development; the completion of bud scale formation normally occurs some time before signs of floral differentiation appear. At the time of bloom the following spring practically no flowers developed on any treated branches except on the tips of some long shoots, where the nodes involved probably developed after gibberellin treatment.

In sections of vegetative buds from treated apricot branches, the buds were found to be generally as inhibited in development as the flower buds. Cell division must have been slowed or blocked early, as indicated by size of the bud in camera-lucida outline in Fig. 1*d* when compared to the control in Fig. 1*c*. This is shown more strikingly when the extent of zones of cells considered by staining quality and other cytological features to be capable of division is compared in those figures. Also, in treated buds, fully differentiated parenchyma cells with thick walls, prominent intercellular spaces, and enlarged and presumably endopolyploid nuclei were separated from the zones of cell division by only one or two cell layers. In the control buds, by contrast, many layers of differentiating cells intervened between the cell division zones and the regions where the cells were completely differentiated. The following spring the lethal effects of the gibberellin dosages at and above 500-mg/lit. concentration became apparent in the general failure of vegetative buds to develop.

In the cherry, sections of the compound flower buds from control branches showed the usual one to five individual flower buds among a number of bracts; developing sepals, petals,

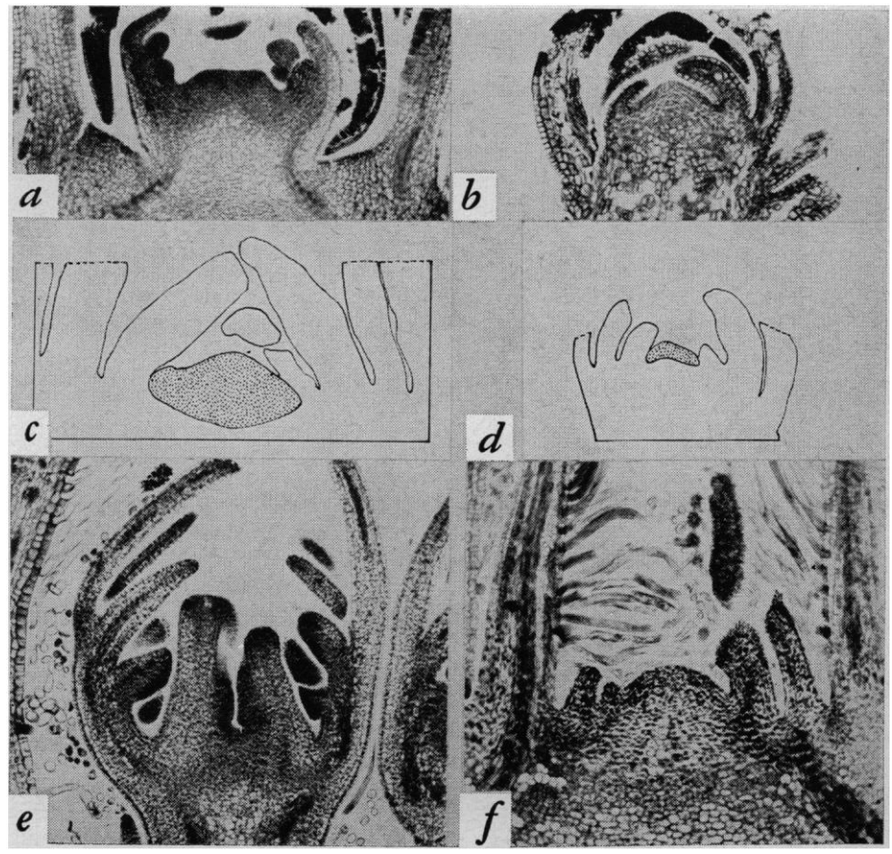

Fig. 1. Median longisections of buds. (*a* and *b*) Flower buds of apricot, from control and treated branches, respectively (× 96). (*c* and *d*) Camera-lucida outlines of sections of vegetative buds of apricot, the stippled areas representing the extent of the zones of cells capable of division from a control (*c*) and from a treated (*d*) branch (× 72). (*e* and *f*) Flower buds of cherry, from control and treated branches, respectively (× 96).

Table 1. Lowest gibberellin dosages causing complete inhibition of bud development in *Prunus* species.

Species	Floral buds		Vegetative buds	
	Mg/lit.	No. of applications	Mg/lit.	No. of applications
Peach	>500	2	>500	2
Apricot	50	2	250	2
Cherry	250	1	>500	2
Almond	50	2	250	2
Plum	50	2	250	2

stamens, and pistils were clearly distinguishable (Fig. 1*e*). However, none of the buds from treated branches showed signs of even the first phase of floral differentiation. The central regions were occupied by growing points of the vegetative, rather than the floral, form (Fig. 1*f*). Bracts were still being cut off from the growing points. No primordia of flower buds appeared in the axils of any bracts. The following spring a few flowers were formed, showing that floral differentiation and development had occurred in the exceptional bud. In vegetative buds from treated branches, microscopic structure was indistinguishable from that of control buds. In the spring there was no evidence of any previous damage to these buds.

In 1959, the effects of gibberellin were investigated in almond (*P. amygdalus* cv. Jordanola), plum (*P. domestica* cv. President), and peach (*P. persica* cv. Fay Elberta) as well as apricot and cherry. Treatments included 50, 250, and 500-mg/lit. concentrations; some branches of each species received a single application at full bloom, and other branches were sprayed a second time approximately one week later. [For details of treatment procedures and other types of gibberellin effects, see Crane *et al.* (3)].

The effects of the treatments on bud development were studied in the latter part of September. In all the species floral development in the controls had advanced to stages comparable to those illustrated for the apricot and cherry in the 1957 experiments. More than a dozen buds of treated and control branches were dissected under a stereoscope (×20) to determine whether flower buds had formed and whether vegetative buds appeared capable of survival and future development. Criteria used in the latter evaluation were color (whether a healthy green, or yellowish or brown) and texture (succulent versus granular and partially desiccated). The lowest dosages which inhibited bud development so severely that continuing development was considered unlikely are given in Table 1.

As expected, the five forms of *Prunus* studied here exhibited variation in response to gibberellin dosage. In the peach, two applications of gibberellin, of 500-mg/lit. concentration, were not sufficient to influence floral or vegetative bud development. In the apricot, almond, and plum, however, two applications, of 50-mg/lit. concentration, completely inhibited flower bud development. The cherry was intermediate in its response to dosage.

The inhibition of lateral bud development by gibberellin was not an aspect of general growth restriction. Excessive growth was stimulated in other plant regions; the higher the dosages the more extensive such growth and the greater the bud inhibition. Internodes lengthened in some spurs and long shoots. Stem diameter increased in certain species; in the apricot this was found to result from stimulated cambial activity (*4*). Petiole length, or diameter, or both, were increased in some cases. In the cherry (the only one of these species in which terminal buds remain viable from year to year), length growth of spurs was stimulated by some gibberellin doses, resulting in about twice the number of nodes as in control spurs. Similarly in some other species, the vegetative bud immediately below the dead terminal bud of a spur developed into a short branch.

Inhibition of cell division was an immediate effect of gibberellin, leading to restriction of lateral bud development. This was apparent from the greatly reduced zones of cells capable of dividing in treated buds, and also from retarded formation of leaf and bud scale primordia. The failure of inhibited vegetative buds to survive and develop the following year suggests either a toxic effect or one of prolonged starvation, either of which could have blocked cell division. The situation in lateral buds of *Prunus* is in sharp contrast to that in terminal buds of the rosette plants *Hyoscyamus niger* and *Samolus parviflorus*, in which gibberellin greatly stimulated mitosis in subapical regions (*5*). It contrasts also with the stimulated cell division implicit in excessive growth of terminal buds in the cherry after gibberellin treatment. Apparently physiological or anatomical differences, or both, between terminal and lateral buds may influence the effects of gibberellin. In *Prunus*, lateral bud inhibition can scarcely be considered a matter of intensified apical dominance, as indicated by the following evidence. When excessive terminal growth of cherry shoots was stimulated, development of lateral vegetative buds was not blocked. Also, in other species, when the first subterminal vegetative bud on a spur failed to develop, even after high gibberellin doses, the other lateral buds were nevertheless inhibited.

That gibberellin may have blocked floral initiation by affecting other processes than those concerned with cell division alone is suggested by the inhibition of floral bud development by considerably lower dosages than those required to suppress vegetative bud development. Reasons for considering floral initiation, rather than floral differentiation, as the blocked phase are as follows. Gibberellin was applied during the floral initiation period in both years. The interval between floral initiation and differentiation is 3 months in cherry, 4 in peach and plum, and 6 months in apricot and almond (*6*). An all-or-none effect in flower bud formation was noted; all treated floral buds examined were either as advanced in development as controls, or showed no evidence that floral differentiation had begun. It appears, therefore, that gibberellin may have interfered in some manner with processes concerned in floral initiation.

MURIEL V. BRADLEY
JULIAN C. CRANE
Department of Pomology, University of California, Davis

References

1. R. Harder and R. Bünsow, *Naturwissenschaften* **43**, 544 (1956).
2. H. Davidson and M. J. Bukovac, *Am. Soc. Hort. Sci., 56th Ann. Meeting, Abstr.* No. 361, 61 (1959).
3. J. C. Crane, P. E. Primer, R. C. Campbell, *Proc. Am. Soc. Hort. Sci.*, in press.
4. M. V. Bradley and J. C. Crane, *Science* **126**, 972 (1957).
5. R. M. Sachs and A. Lang, *Science* **125**, 1144 (1957); R. M. Sachs, C. Bretz, A. Lang, *Exptl. Cell Research* **18**, 230 (1959).
6. W. P. Tufts and E. B. Morrow, *Hilgardia* **1**, 1 (1925).

2 November 1959

The Sun Azimuth Compass: One Factor in the Orientation of Homing Pigeons

Abstract. In accordance with the theory of the sun azimuth compass (*1*), displaced homing pigeons are misled in a predictable way if their "internal clock" has been reset by exposure to a time-shifted sequence of day-night cycles.

Several species of birds have been trained to respond to particular compass directions in stationary training cages (*2*). By resetting the birds' chronometers, or "internal clocks," predictable deviations from the training direction were obtained (*3, 4*). The question as to whether homing by free flying pigeons could be influenced in a similar manner has not previously been clearly answered, the relevant experiments (*5*) having been inconclusive.